A new albanerpetontid amphibian from the Barremian (Early Cretaceous) Wessex Formation of the Isle of Wight, southern England

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A new albanerpetontid, *Wesserpeton evansae* gen. et sp. nov., from the Early Cretaceous (Barremian) Wessex Formation of the Isle of Wight, southern England, is described. *Wesserpeton* is established on the basis of a unique combination of primitive and derived characters relating to the frontals and jaws which render it distinct from currently recognized albanerpetontid genera: *Albanerpeton* (Late Cretaceous to Pliocene of Europe, Early Cretaceous to Paleocene of North America and Late Cretaceous of Asia); *Celtedens* (Late Jurassic to Early Cretaceous of Europe); and *Anoualerpeton* (Middle Jurassic of Europe and Early Cretaceous of North Africa). Although *Wesserpeton* exhibits considerable intraspecific variation in characters pertaining to the jaws and, to a lesser extent, frontals, the new taxon differs from *Celtedens* in the shape of the internasal process and gross morphology of the frontals in dorsal or ventral view. It differs from *Anoualerpeton* in the lack of pronounced heterodonty of dentary and maxillary teeth; and in the more medial location and direction of opening of the suprapalatal pit. The new taxon cannot be referred to *Albanerpeton* on the basis of the morphology of the frontals. *Wesserpeton* currently represents the youngest record of Albanerpetontidae in Britain.

Key words: Lissamphibia, Albanerpetontidae, microvertebrates, Cretaceous, Britain.

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Introduction

The Barremian (Lower Cretaceous) Wessex Formation of the Isle of Wight, which is situated off the south coast of mainland Britain (Fig. 1), yields a highly significant vertebrate assemblage. This assemblage is unique in two important respects: it comprises a high diversity of both terrestrial and freshwater aquatic forms; and the co-occurrence of taxa of all sizes in the same deposits indicates they inhabited a plethora of palaeoenvironments (Sweetman and Insole 2010). The macrofauna includes the most diverse Early Cretaceous non-avian dinosaur assemblage yet recorded (e.g., Insole and Hutt 1994; Benton and Spencer 1995; Martill and Naish 2001 and references therein; Naish 2002; Naish and Martill 2002; Naish et al. 2004; Mannion 2009; Sweetman and Insole 2010; Mannion et al. 2011; Sweetman 2011; SCS unpublished data), abundant crocodyliforms belonging to a number of families (reviewed by Salisbury and Naish 2011) and a small vertebrate assemblage containing many genera. The latter includes chondrichthyan and osteichthyan fishes, lissamphibians, the most speciose Early Cretaceous lepidosaur assemblage yet recorded, archosaurs and mammals (Sweetman 2004, 2006a, b, 2008, 2009, 2011; Sweetman and Underwood 2006; Witton et al. 2009; Sweetman and Insole 2010; Sweetman and Martill 2010; Duffin and Sweetman 2011; Forey and Sweetman 2011; Sweetman and Evans 2011a, b; Sweetman and Hooker 2011). Among the lissamphibians (Sweetman and Evans 2011a) are at least three crown-group salamanders, five frogs of "discoglossid grade" (i.e., relatively unspecialised, non-neobatrachian frogs with an iliac morphology similar to that of living Discoglossidae but of uncertain phylogenetic position) and the albanerpetontid reported here.

The lissamphibian clade Albanerpetontidae Fox and Naylor, 1982, is a highly derived group of small, superficially salamander-like amphibians characterised by numer-

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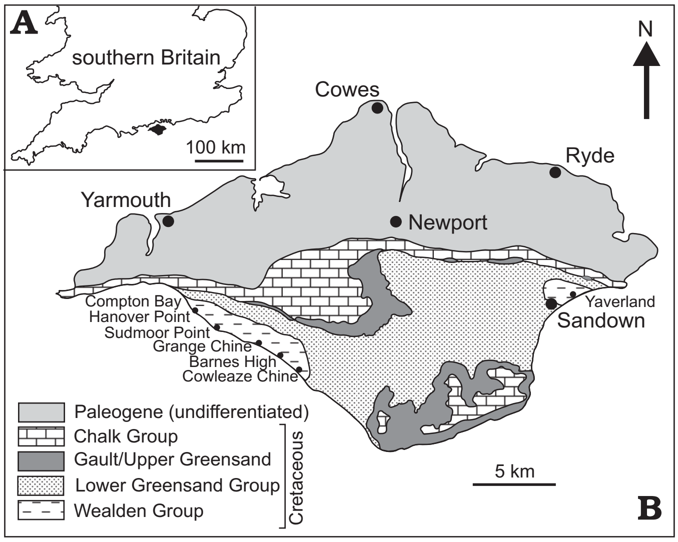

Fig. 1. **A**. Outline map of southern Britain showing the location of the Isle of Wight. **B**. Outline geological map of the Isle of Wight showing localities mentioned in the text.

ous synapomorphies including fused frontals with polygonal dorsal ornamentation, a unique craniocervical joint that convergently resembles the atlas-axis complex of amniotes, strongly pleurodont and non-pedicellate teeth bearing labiolingually compressed, usually tricuspid, chisel-like crowns, and an interdigitating mandibular symphysis (Estes 1969; Estes and Hoffstetter 1976; Fox and Naylor 1982; Milner 1988; McGowan 1994, 1998a, b, 2002; McGowan and Evans 1995; Gardner 2000b, 2001, 2002). An exceptionally preserved specimen from Spain (McGowan and Evans 1995) displaying soft tissue impressions shows that albanerpetontids had scaly skin and eyelids, indicating a primarily or wholly terrestrial habitat preference. Throughout the clade's known temporal range, extending for ca. 165 My from their first reliably documented occurrence in the early Bathonian (Middle Jurassic) (e.g., Evans and Milner 1994) to the late Pliocene (Delfino and Sala 2007), albanerpetontids maintained a conservative body plan. Until 1995 all known species were accommodated within a single genus, *Albanerpeton* Estes and Hoffstetter, 1976. Subsequently, the recognition of taxonomically significant differences in the morphology of the jaws and frontals permitted the identification of three genera accommodating eleven species (see Gardner and Böhme 2008 for a review). The type genus, *Albanerpeton* Estes and Hoffstetter, 1976 includes one species, *A. pannonicum*, from the early Pliocene of Hungary (Venczel and Gardner 2005) and the late Pliocene of Italy (Delfino and Sala 2007), the type species, *A. inexpectatum,* from the Miocene of southern France (Estes and Hoffstetter 1976; Estes 1981; Gardner 1999c; Rage and Hossini 2000), Austria (Sanchíz 1998) and Germany (Böhme 1999; Wiechmann 2003), five species from the Cretaceous (Aptian to Maastrichtian) of North America, and an as yet un-named species (the "Paskapoo species" referred to below) from the late Paleocene of Canada (Estes 1981; Fox and Naylor 1982; Gardner 1999a–d, 2000a, b, 2002). Frontals and other bones referable to *Albanerpeton* sp. have also been reported from the lower Cenomanian Khodzhakul local fauna of Uzbekistan (Skutschas 2007) and the Maastrichtian of the Haţeg Basin, Romania (Grigorescu et al. 1999; Folie and Codrea 2005). Wiechmann (2003) also reported an additional species of *Albanerpeton* from the Barremian of Spain but as further discussed here we do not believe this assignment to be correct. *Celtedens* McGowan and Evans, 1995, from the Late Jurassic and Early Cretaceous of Europe contains two named species, *C. megacephalus* and *C. ibericus* (McGowan and Evans 1995; McGowan 2002). However, re-examination of the type specimen of *Celtedens ibericus* (LH 6020a, b) and of another specimen from Las Hoyas referred to the same taxon (LH 15710a, b), in which the internasal process is completely preserved, indicates that these specimens may not be referable to *Celtedens* (Evans in press; SCS and JDG personal observations 2003). Additional species of *Celtedens* may be present in the substantial collections of albanerpetontid material from the Upper Jurassic (Kimmeridgian) at Guimarota, Portugal and the Lower Cretaceous (Barremian) of Spain (Wiechmann 2000a, b, 2003), and from the Lower Cretaceous (Berriasian) Purbeck Limestone Group of southern Britain (McGowan and Ensom 1997; Evans and McGowan 2002; JDG personal observations 2003). Albanerpetontid material from the Early Cretaceous of Sweden has also been tentatively referred to *Celtedens* (Rees and Evans 2002) but is too fragmentary to permit positive identification. *Anoualerpeton* Gardner, Evans, and Sigogneau-Russell, 2003 contains two species, *A. unicus*, the type species, from the Early Cretaceous (?Berriasian) of Morocco and *A. priscus* from the Middle Jurassic of England (Gardner et al. 2003). To date, the former represents the only Gondwanan record of the Albanerpetontidae. Albanerpetontid material has also been reported from Asia (Nessov 1981, 1988, 1997; Skutschas 2007) but the albanerpetontid genus *Nukusurus* Nessov, 1981 from the Late Cretaceous of Uzbekistan and its two species are now considered to be nomina dubia within the Albanerpetontidae (Gardner and Averianov 1998). In addition, *Bishara* Nessov, 1997, based on an incomplete atlantal centrum from the Late Cretaceous of Kazakhstan, has been shown to be an indeterminate caudate, not an albanerpetontid (Gardner and Averianov 1998).

Until recently, only one albanerpetontid specimen had been recorded from the Wealden Supergroup (Berriasian to early Aptian) of Britain. This is an indeterminate, fragmentary left articular from the Barremian Wessex Formation of the Isle of Wight (Evans et al. 2004). It was recovered following screening of a small sample of matrix (ca. 45 kg) taken from the holotype quarry of the allosauroid theropod *Neovenator* Hutt, Martill, and Barker, 1996. The bed concerned, L9 (bed numbering scheme follows Stewart 1978) (Fig. 2) is exposed on the south-west coast of the Isle of Wight. Since that time comprehensive sampling of Wessex Formation strata on the Isle of Wight for the purpose of recovering microvertebrate remains has been undertaken by one of us (SCS). This has

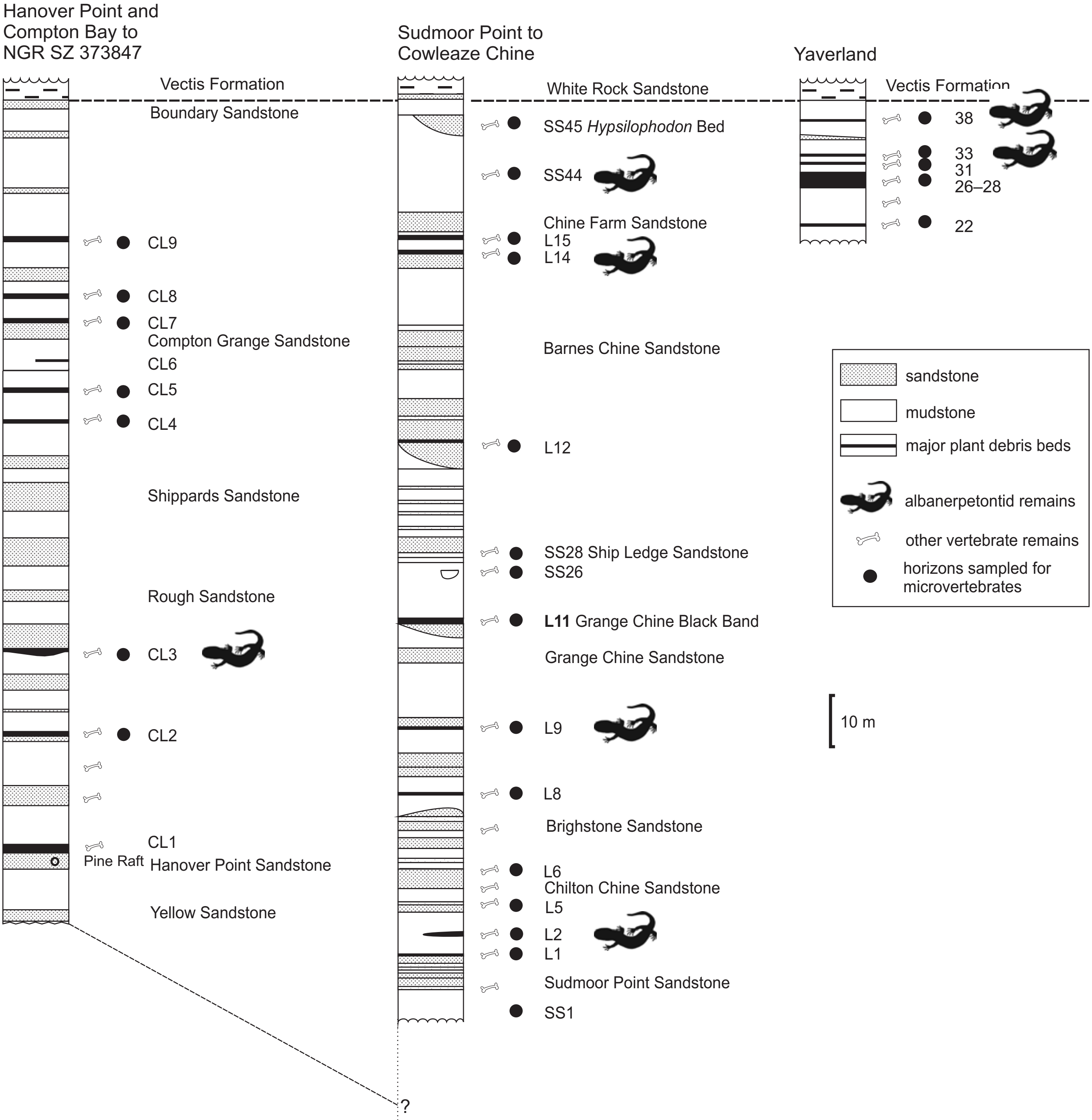

Fig. 2. Schematic lithological logs of the Wessex Formation exposed on the south-west coast (Hanover Point and Compton Bay to NGR SZ 37384, and Sudmoor Point to Cowleaze Chine) and south-east coast (Yaverland), showing horizons from which albanerpetontid remains have been recovered. Refer to Fig. 1 for localities. South-west coast logs from Stewart (1978) and south-east coast log from Radley (1994).

yielded a large number of albanerpetontid bones including jaws and frontals, which have permitted diagnosis of a fourth albanerpetontid genus described here.

Institutional abbreviations.—NHMUK PV, The Natural History Museum, London, UK (note that all specimens registered under the NHMUK PV prefix commence with the letter R and in order to save space and unnecessary repetition in the text only key specimens are identified with the complete institutional abbreviation; others are referred to simply by their R number); DORCM, Dorset County Museum, Dorchester, UK; LH, Las Hoyas collection, Museo de Cuenca, Cuenca, Spain.

Other abbreviations.—NGR, National Grid Reference.

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Geological setting

The Wessex Formation is exposed in coastal sections in Dorset and on the Isle of Wight. On the Isle of Wight the excellent cliff sections, frequently refreshed by erosion, expose about a 180 m thick sequence of interbedded non-marine sandstone, massive, varicoloured mudstone, crevasse splay deposits, calcrete conglomerate, and plant debris beds (sensu Oldham 1976) in which a number of facies associations have been recognized (Stewart 1978, 1981a, b; Daley and Stewart 1979; Insole and Hutt 1994). These strata, which comprise the upper part of the Wessex Formation, are entirely of Barremian age (Allen and Wimbledon 1991). However, the Hauterivian–Barremian boundary probably lies close to the level of the Pine Raft, a collection of large coniferous logs apparently stranded on a point bar (White 1921) (Fig. 2), which is exposed at low water on the foreshore at Hanover Point (NGR SZ 379837) (Harding 1986; Hughes and McDougall 1990) (Fig.1). The Wessex Formation, comprising part of the Wealden Supergroup of southern Britain as a whole, was deposited in the smaller of two sub-basins (the Wessex Sub-basin) that occupied this area during the Early Cretaceous. The high sinuosity river system primarily responsible for deposition of the Wessex Formation flowed from west to east within a confined east-west, fault-bounded valley (Stewart 1978, 1981a; Daley and Stewart 1979; Stoneley 1982; Chadwick 1985; Ruffell 1992; Insole and Hutt 1994; Radley 1994; Wright et al. 1998; Underhill 2002; Sweetman and Insole 2010). The fresh water/terrestrial Wessex Formation is overlain by about 70 m of lagoonal strata, which comprise the upper Barremian to lower Aptian Vectis Formation (Robinson and Hesselbo 2004) (Fig. 2).

The Wessex Sub-basin provided considerable habitat diversity, but seasonal aridity (Ruffell and Batten 1990; Haywood et al. 2004) may have rendered large areas of the floodplain inhospitable at times (Insole and Hutt 1994; Allen 1998; Sweetman and Insole 2010). Aridity also rendered vegetation susceptible to wildfires and the denuded landscape immediately thereafter was vulnerable to erosion by storm waters. The plant debris beds, which have produced the bulk of vertebrate fossils recovered from the Wessex Formation but which make up only about 4% of the succession, represent deposits derived from such local fire and storm events. The fauna present in these beds therefore represents animals that were resident in or visitors to the immediate vicinity rather than those of the hinterland (Insole and Hutt 1994; Sweetman and Insole 2010).

Material and methods

Bulk sediment samples were collected from 27 of the more easily accessible plant debris beds and from a small number of horizons in other facies (Fig. 2). Of the latter, only matrix taken in close proximity to a partial skeleton of an iguanodont dinosaur excavated from a red bed horizon, SS44 at Barnes High (NGR SZ 43787 81026) on the south west-coast (Figs. 1, 2) has produced remains of small terrestrial vertebrates, including those of albanerpetontids. The position of each sample was recorded using GPS and after drying the samples were processed using a bulk wet-screening machine (modified from Ward 1981). After processing, the residues were divided into fractions using a nest of sieves and plant material was removed from these hydromechanically. Fossils were recovered from fractions with a particle size between 500 μm and 2.8 mm using a binocular microscope. Digital images of specimens were obtained using a scanning electron microscope, low acceleration voltages being used in order to avoid excessive charging of uncoated specimens. Measurements were taken digitally using digital image capture, analysis, and processing software (SemAfore version 4.00, Insinööritoimisto J. Rimppi Oy).

Anatomical conventions and terms.— Except for the ilium, osteological terms and measurements generally follow Gardner and Averianov (1998), Gardner (1999c, 2000b); Gardner et al. (2003), and Venczel and Gardner (2005). Orientation of the ilium, which has yet to be determined with certainty for albanerpetontids, and osteological terms used in connection with it, follow Gardner et al. (2010).

Systematic palaeontology

Subclass Lissamphibia Haeckel, 1866

Order Allocaudata Fox and Naylor, 1982

Family Albanerpetontidae Fox and Naylor, 1982

Genus *Wesserpeton* nov.

Etymology: From Wessex, an ancient British kingdom which incorporated the Isle of Wight; and the Greek *erpeton*, meaning creeping animal, also used in the construction of the name of the type genus *Albanerpeton* Fox and Naylor, 1982.

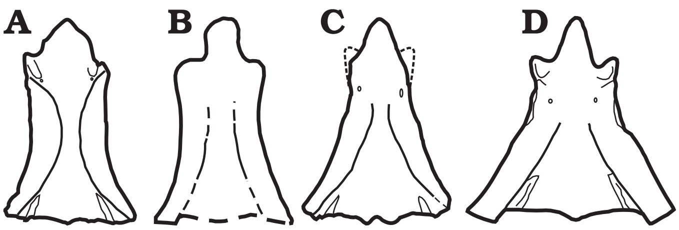

Fig. 3. Outline drawings in ventral view to illustrate generic differences in morphology of azygous frontals of albanerpetontid amphibians. **A**. *Anoualerpeton*, based on type species *Anoualerpeton unicus* Gardner, Evans, and Sigogneau-Russell, 2003, Berriasian of Anoual, Morocco (from Gardner et al. 2003: 307, fig. 2J). **B**. *Celtedens*, based on *Celtedens* cf. *megacephalus* (Costa, 1864) from the Beriasian of the Isle of Purbeck, Dorset, UK (from McGowan 1998a: 186, fig. 1F). **C**. *Wesserpeton evansae* gen. et sp. nov. from the Baremian Wessex Formation of the Isle of Wight, UK, based on holotype, NHMUK PV R36521 (see Fig. 4A) and showing (dashed lines) reconstructed anterolateral processes. **D**. *Albanerpeton*, based on type species *Albanerpeton inexpectatum* Estes and Hoffstetter, 1976, Miocene of Western Europe (from Gardner 1999a: 60, fig. 1L). Images not to scale.

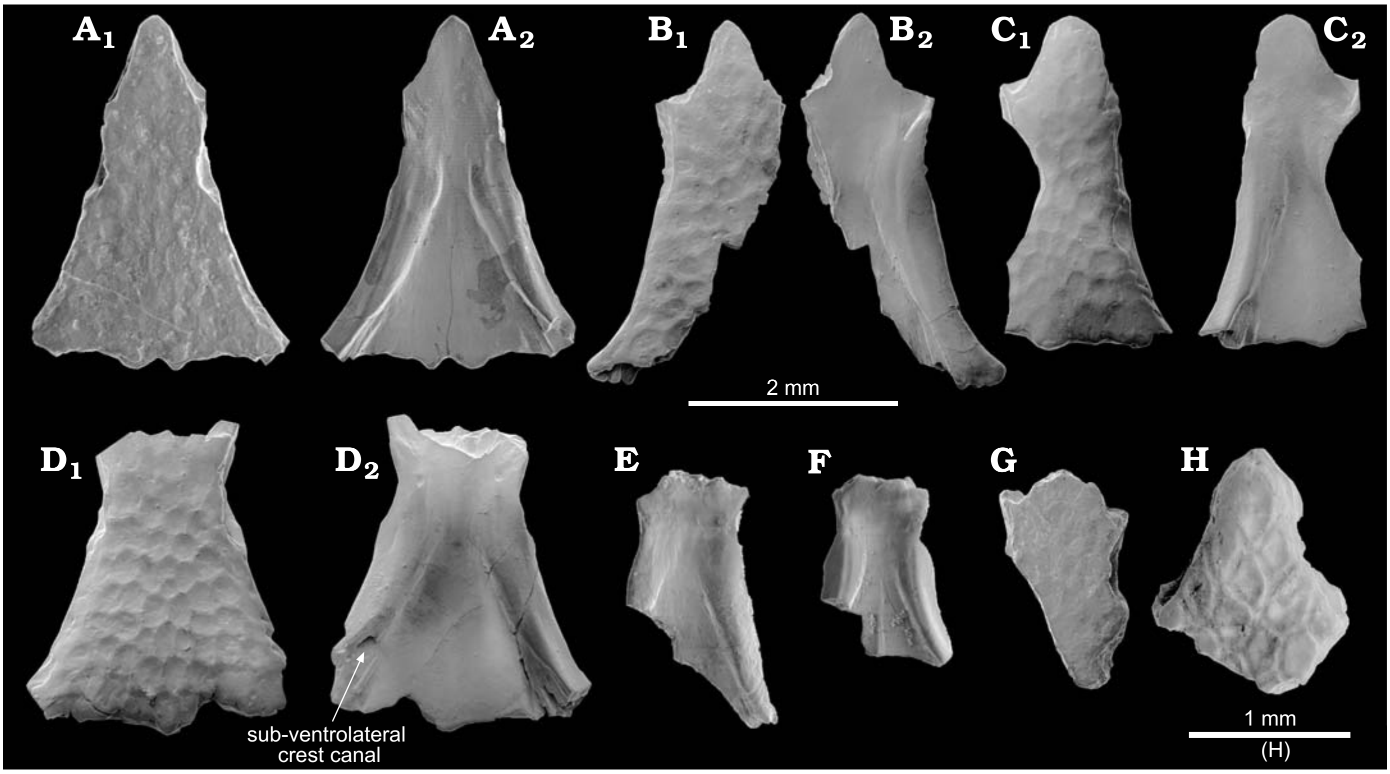

Fig. 4. Scanning electron micrographs of azygous frontals and fragments thereof of the albanerpetontid amphibian *Wesserpeton evansae* gen. et sp. nov. from the Barremian Wessex Formation of the Isle of Wight, UK. All specimens from bed 38, Yaverland, except F, H, which are from bed L2 exposed near Sudmoor Point (Figs. 1, 2). **A**. Holotype specimen, NHMUK PV R36521, in dorsal (A_1) and ventral (A_2) views. **B**. NHMUK PV R36536, in dorsal (B_1) and ventral (B_2) views. **C**. NHMUK PV R36537, in dorsal (C_1) and ventral (C_2) views. **D**. NHMUK PV R36523, in dorsal (D_1) and ventral (D_2) views. Arrow marks the sub-ventrolateral crest canal on the right side of the bone. **E**. NHMUK PV R36538, in ventral view. **F**. NHMUK PV R36539, in ventral view. **G**. NHMUK PV R36540, in dorsal view. **H**. NHMUK PV R36522, in dorsal view, enlarged to show morphology of the internasal process.

Type and only species: *Wesserpeton evansae*; see below.

Diagnosis.—As for species.

Stratigraphic and geographic range.—As for the type species; see below.

Wesserpeton evansae sp. nov.

Figs. 3C, 4–11, 12D.

Etymology: For Professor Susan E. Evans (University College London, UK) in recognition of her outstanding contributions in the field of microvertebrate palaeontology and to our understanding of Albanerpetontidae.

Holotype: NHMUK PV R36521, substantially complete fused frontals (Fig. 3C, 4A, 12D).

Type locality: Yaverland, south-east coast of the Isle of Wight, southern England, NGR SZ 61693 85223 (Figs. 1, 2).

Type horizon: Bed 38 (Radley 1994) occurring about 4 m below the top of the Wessex Formation, Barremian, Lower Cretaceous.

Referred material.—NHMUK PV R36522–36568 and R36595–36611 (Figs. 4–11) complete the hypodigm.

Stratigraphic and geographic range.—Known only from the Barremian Wessex Formation of the Isle of Wight, southern Britain, where it has been recorded from seven horizons (Fig. 2). All figured specimens are from the type locality and horizon with the exception of the frontals NHMUK PV R36539 (Fig. 4F) and R36522 (Fig. 4H) and the dentaries R36553–36558 (Fig. 10M–R) which are all from bed L2 (Fig. 2) exposed high in the cliff at Sudmoor Point (Fig. 1) on the south-west coast, NGR SZ 39458 82709.

Differential diagnosis.—Monotypic albanerpetontid species without any recognized autapomorphies, but which differs from other albanerpetontid genera and species in a unique combination of primitive and derived characters relating to the frontals, premaxilla, maxilla and dentary and to body size.

Frontals: primitively resembles *Anoualerpeton* and *Celtedens*, but differs from *Albanerpeton* in having frontals that are elongate and with the anterior limit of the orbital margin in front of the anteroposterior midpoint of the bone; resembles *Albanerpeton* and differs from *Anoualerpeton* and *Celtedens* in having a more derived, triangular outline of the frontals; differs from *Celtedens* and resembles *Anoualerpeton* and *Albanerpeton* in having a pointed internasal process (primitive).

Premaxilla: differs from *Anoualerpeton* and resembles *Celtedens* and *Albanerpeton* in having suprapalatal pit in premaxilla facing lingually (derived); differs from *Anoualerpeton*, *Celtedens*, and some *Albanerpeton* species, but resembles *A. nexuosum*, *A. inexpectatum*, *A. pannonicum*, and the Paskapoo species in having dorsal edge of premaxilla sutured to nasal in larger individuals (derived); differs from *Anoualerpeton*, *Celtedens*, and some *Albanerpeton* species,

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but resembles *A. inexpectatum*, *A. pannonicum*, and the Paskapoo species in having suprapalatal pit in premaxilla subdivided in at least one third of individuals (derived).

Maxilla and dentary: differ from *Anoualerpeton* and one *Albanerpeton* species (*A. nexuosum*), but resembles other *Albanerpeton* species and *Celtedens* in having dentaries and maxillae with relatively straight occlusal margins and teeth weakly heterodont in size (both primitive).

Body size: differs from *Anoualerpeton*, *Celtedens*, and some *Albanerpeton* species, but resembles *A. arthridion*, *A. pannonicum*, and the Paskapoo species in small body size (derived).

Description

The only complete specimens are "axis" vertebrae among which are NHMUK PV R36534 (Fig. 11C) and R36609 (Fig. 11D), and a humerus NHMUK PV R36610 (Fig. 11F), none of which possesses characters that are diagnostic at the genus or species level. However, the available frontals and jaws document almost all of the structure of these elements and do exhibit diagnostically informative characters. Detailed descriptions are provided and a large number of specimens are figured in order to demonstrate the considerable variation in osteological characters of the new species. Characters described include those that may have no phylogenetic or functional significance but some of which might be thought to in the absence of multiple examples of individual elements. Such descriptions are rarely presented, yet these are informative for recording the range of variability that might be seen in other albanerpetontid taxa if similarly large samples of individual elements were available for those. For ease of reference variations in significant characters of the premaxilla are also set out in Table 1.

Frontals (Figs. 3C, 4, 12D).—The most nearly complete specimen is the holotype NHMUK PV R36521 (Figs. 3C, 4A, 12D). It lacks only the anterolateral processes, the extreme posterior part of the ventrolateral crest on the left side and a smaller fragment from the right side. The two halves are solidly fused medially but posteriorly the suture can be seen in ventral view where it is visible for approximately half the distance to the anterior end. The midline length is 3.4 mm (excluding the posterior protuberances described below) and the width across the posterior margin is estimated (due to breakage) to be 2.6 mm. This yields a ratio of midline length:posterior width of 1.3. It is also possible to estimate the midline length and posterior width in another specimen, R36536 (Fig. 4B). In this specimen the midline length is about 3.6 mm and the posterior width about 2.7 mm giving a midline length:posterior width ratio of 1.33. The internasal process is triangular in dorsal outline and somewhat rounded anteriorly. In those specimens in which the internasal process is preserved, R36521 (Fig. 4A), R36536 (Fig. 4B), R36537 (Fig. 4C) and R36522 (Fig. 4H), it is somewhat variable in terms of both the ratio of midline length:posterior width and in the degree of roundness at the anterior end. This reflects intraspecific variation and not abrasion postmortem. The internasal process bears deep lateral slots for reception of the nasals and in one specimen, R36522 (Fig. 4H), the ventral surfaces of these slots are expanded laterally so that they are visible in dorsal view. The anterolateral processes are distinct from the main body of the bone but are incomplete anteriorly in all specimens. Their morphology can best be seen in R36523 (Fig. 4D) and R36540 (Fig. 4G). Reconstruction of the anterolateral processes suggests they were not as prominent as in some other albanerpetontids (Fig. 3C versus D). The posterior lateral slot for receipt of the posterior end of the prefrontal is also deep. This slot occupies a position between the posterior margin of the anterolateral process and the anterior end of the orbital margin. The dorsal margin of the posterior slot is excavated posteromedially (Fig. $4A_1$). The anterior end of the orbital margin, taken to be the posterior end of the slot for reception of the prefrontal, lies anterior to the midpoint of the bone. R36521 is triangular in outline, with the posterior margin approximately 2.5 times wider than the distance between the slots for reception of the prefrontals. Behind the base of the anterolateral process, the lateral edge of the bone extends posteriorly in a gentle medially concave curve. Anteriorly a tangent to this curve intersects the midline of the bone at about 18° whereas from a position approximately one third of the distance from the posterior margin this increases to about 33°. The posterior margin of the bone is transverse and shallowly anteriorly concave to either side of the midline but is expanded posteriorly either side of that to produce rounded protuberances separated by a U-shaped valley (Fig. 4A). Dorsally, the bone is ornamented with shallow, polygonal pits of variable shape enclosed by a network of narrow ridges. In ventral view, the ventrolateral crests are broadest anteriorly but they do not meet across the midline in any of the available specimens. However, in some, e.g., R36523 and R36538 (Fig. $4D_2$ and E respectively) they approach each other closely. They are strongly tapered posteriorly and bear a shallow groove of variable extent along their ventral surfaces. These grooves do not extend to the posterior end of the ventrolateral crests in any specimen. A minute foramen is present at the anterior extremity of both ventrolateral crests. Neither of these foramina open into the closely adjacent slots posterior to the anterolateral processes and they may be for emissary veins travelling between the intra- and extracranial surfaces via the diploe of the skull (Susan Evans, personal communication 2011). A larger foramen occupies the extreme posterior end of both ventrolateral crests and represents the posterior opening of canals underlying them. The canals are somewhat variable in diameter but can be clearly seen in all broken specimens (e.g., Fig. $4D_2$ arrowed). Anteriorly the sub-ventrolateral crest canals open as slits at the medioposterior extremity of the slots posterior to the anterolateral processes. Posteriorly the crests are strongly convex ventrally and ridge-like in transverse profile. The more lateral part along the orbital margin is bevelled and faces ventrolaterally. Posteriorly the medial face of each ventrolateral crest bears a grooved facet for reception of a complementary process from the parietal. In R36536 (Fig. $4B_2$) the complete left ventrolateral crest bears a sculpted facet at its

Table 1. Ten variable characters recorded for each of the 19 referred premaxillae of *Wesserpeton evansae* gen. et sp. nov. shown in Figs. 5–7. An explanation of the terminology employed and further discussion is provided in the text.

Specimen number	Boss	Supra-palatal pit	Struts surrounding suprapalatal pit	Dorsal opening of palatal foramen, relative to diameter of adjacent tooth shafts	Dorsal opening of palatal foramen, placement	Canal between dorsal and ventral openings of palatal foramen	Additional foramina below pars palatinum	Foramina medial to orbital margin	Facet for premaxillary lateral process of maxilla	Tooth positions
R36524 (Fig. 5A)	prominent high	single	robust medially and laterally	much larger	medial, adjacent to base of medial strut	vertical	absent	7 small	broad and shallow	9
R36526 (Fig. 5B)	distinct low	divided	low medially robust laterally	approximately equal	between struts	oblique	3 large 4 small	1 large 3 small	excavated	9
R36565 (Fig. 6A)	absent	single	robust medially and laterally	much larger	between struts	oblique	1 large 4 small	2 large 1 small	broad and shallow	10
R36566 (Fig. 6B)	absent	single	robust laterally less so medially	approximately equal	between struts	vertical	3 large 5 small	obscured	excavated	9
R36567 (Fig.6C)	absent	single	absent	much smaller	below suprapalatal pit	oblique	1 large 2 small	3 large 2 small	broad and shallow	10
R36568 (Fig. 6D)	indistinct high	single	very low medially and laterally	much smaller	between struts	vertical	3 large 2 small	3 large 1 small	broad and shallow	9
R36569 (Fig. 6E)	absent	divided	absent	approximately equal	below suprapalatal pit	vertical	1 large (as preserved)	1 large 1 small	not preserved	not preserved
R36595 (Fig. 6F)	not preserved	divided	absent	much smaller	below suprapalatal pit	oblique	3 small	2 large 3 small	broad and shallow	7
R36596 (Fig. 6G)	indistinct high	single	robust medially and laterally	approximately equal	base of lateral strut	oblique	1 large	1 small	excavated	not preserved
R36597 (Fig. 7A)	indistinct high	single	robust medially and laterally	much smaller	medial, adjacent to base of medial strut	vertical	1 large (as preserved)	2 large 3 small	not preserved	not preserved
R36598 (Fig. 7B)	distinct very low	single	robust medially and laterally	approximately equal	base of medial strut	oblique	2 large 2 small (as preserved)	1 large	not preserved	not preserved
R36599 (Fig. 7C)	not preserved	single	low medially and laterally	larger	between struts	oblique	obscured	1 small	broad and shallow	?8
R36600 (Fig. 7D)	not preserved	divided	low medially and laterally	approximately equal	base of medial strut	oblique	2 large 5 small	3 large 1 small (as preserved)	excavated	9
R36601 (Fig. 7E)	not preserved	not preserved	not preserved	not preserved	not preserved	oblique	2 large 1 small	not preserved	damaged	9
R36602 (Fig. 7F)	not preserved	not preserved	not preserved	not preserved	not preserved	not preserved	obscured	not preserved	broad and shallow	10
R36603 (Fig. 7G)	not preserved	not preserved	not preserved	not preserved	not preserved	not preserved	obscured	not preserved	broad and shallow lingual rim expanded	9
R36604 (Fig. 7H)	not preserved	divided	robust medially low laterally	smaller	between struts	oblique	3 large	2 large (as preserved)	broad and shallow	10
R36605 (Fig. 7I)	prominent low	divided	robust laterally low medially	approximately equal	between struts	vertical	1 large 6 small	obscured	excavated	?8
R36606 (Fig. 7J)	prominent high	divided	robust laterally less so medially	obscured	obscured	obscured	obscured	2 large	excavated	7

posterior extremity for contact with the parietal. Gardner (1999d) estimated that the snout-pelvic length in albanerpetontids is about ten times the midline length of the frontals. Therefore, those available for *Wesserpeton* suggest a snout-pelvic length of about 35 mm.

Premaxilla (Figs. 5–7).—A substantial number of premaxillae have been recovered. Of these, 19 of the most complete and/or informative with regard to general morphology and intra-specific variation in characters are shown in Figs. 5–7. Two of the most nearly complete specimens NHMUK PV R36524 and R36526 (Fig. 5A and B respectively) document some of the morphological variation observed in this element and provide a framework from which to discuss variations observed in other specimens.

NHMUK PV R36524 (Fig. 5A) is from the right side. It is about 2.6 mm high. The bone is complete with the exception of parts of the left and right sides of the pars palatinum. The medial edge bears an elongate groove, which extends below the labial surface of the bone from a position just above the base of the dorsal boss to the level of the base of the dentition. The lateral extremity of the groove (its base) contains five

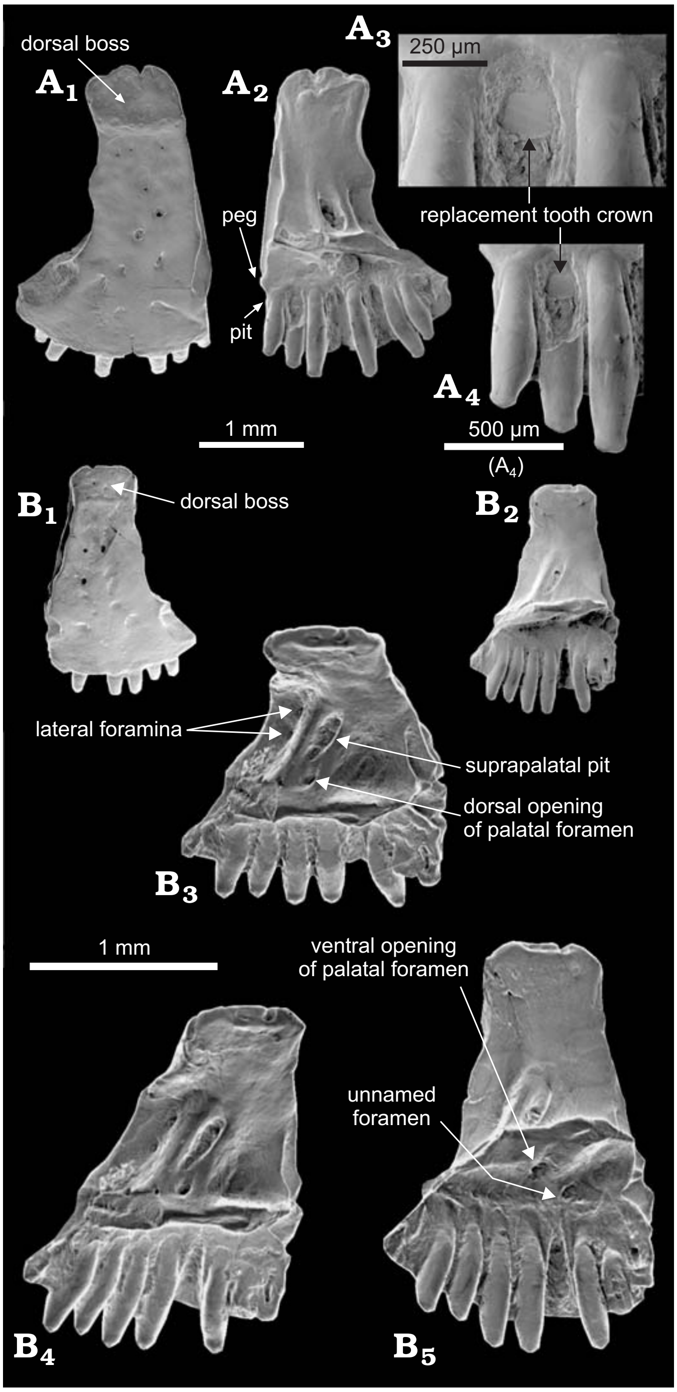

Fig. 5. Scanning electron micrographs of two premaxillae of the albanerpetontid amphibian *Wesserpeton evansae* gen. et sp. nov. illustrating intraspecific variations in morphology discussed in the text. Both specimens from bed 38 of the Barremian Wessex Formation at Yaverland (Figs. 1, 2). **A**. NHMUK PV R36524, right premaxilla in labial (A_1) and lingual (A_2) views; enlargement in lingual view (A_3) to show replacement tooth crown at the base of the 2nd tooth locus; enlargement in lingual view (A_4) to show the first three teeth, resorption pit at the base of the tooth shaft at the 2nd locus and location of the replacement tooth crown. **B**. NHMUK PV R36526, left premaxilla in labial (B_1), lingual (B_2) views; oblique dorsolingual (B_3) and oblique laterolingual (B_4) views, both to show openings and struts on the pars dorsalis; oblique ventrolingual view (B_5), to show the ventral opening of the palatal foramen in the pars palatinum and the location of an unnamed foramen in the pars dorsalis.

evenly spaced and sized foramina and a minute foramen just above the level of the dentition. A pronounced flange separates the labial groove from a lingual groove extending from a position just below the level of the base of the boss to a position approximately one third of the distance from the base of the medial-most tooth to its apex. The ventral extremity of the groove is deepened to form a pit and on the lingual side at the dorsal extremity of the pit there is a small peg (Fig. $5A_2$). Dorsal to this, the groove is continuous dorsally for the rest of its length and is expanded lingually over the medial surface of the pars palatinum. The presence or absence of foramina in this groove cannot be determined because of adhering matrix. In no specimen is there evidence of fusion between the right and left premaxillae but the deep grooves and the ventrolingual pit and prong seen in this specimen suggest a strong interlock between the bones. However, although all premaxillae in which this part of the bone is preserved display grooves of the type described above their morphology is very variable. A detailed description of some of these differences is provided below in connection with R36526. Another noteworthy example of differences in this aspect of the morphology of premaxillae occurs in R36596 (Fig. 6G), which is also from the right side. In this specimen there is a deep labial groove extending from almost the dorsal extremity of the bone to a level equivalent to the base of the dentition. The lingual groove is shallow and narrow, extending only from just above the dorsal margin of the pars palatinum to a similar position to that described above for R36524. It is separated from the labial groove by a considerably more medially expanded flange (Fig. $6G_3$) than that of R36524. Furthermore, R36596 does not possess a pit and peg of the sort seen in R36524 and these are variably present in other specimens.

Labially (Fig. $5A_1$), R36524 bears a pronounced dorsal boss ornamented with shallow polygonal pits similar to those seen on the frontals. The boss is variably developed in other specimens and is absent from some (see Table 1 and Figs. $5B_1$, $6B_2$, C_2, D_2, E_2, G_2, $7A_2$, B_2, I_2, J_2). All specimens show that the remainder of the labial face of the bone is relatively smooth with only minor differences in rugosity and that it is perforated by small, scattered nutritive foramina. The dorsolateral corner of the pars dentalis bears a broad, smooth facet for contact with the overlapping complementary premaxillary lateral process of the maxilla. A shallow laterodorsal notch occupies a little less than half of the dorsal margin of the pars dorsalis on its lateral side. A facet extending along the lateral margin of the notch is labiolingually expanded in the region of the ventral extremity of the boss, reflecting labiolingual thickening of the bone in this region.

Lingually, the apex of the pars dorsalis bears a sculpted facet for reception of the anterior margin of the nasal. This is also variably developed in other specimens, being particularly pronounced in R36597 (Fig. $7A_3$). On the dorsolateral margin of the pars dorsalis on the lingual side there is a distinct but low, lingually convex ridge below the boss. A similar but narrower ridge also extends from the dorsal extremity of the mediolingual groove to the dorsal margin of the pars

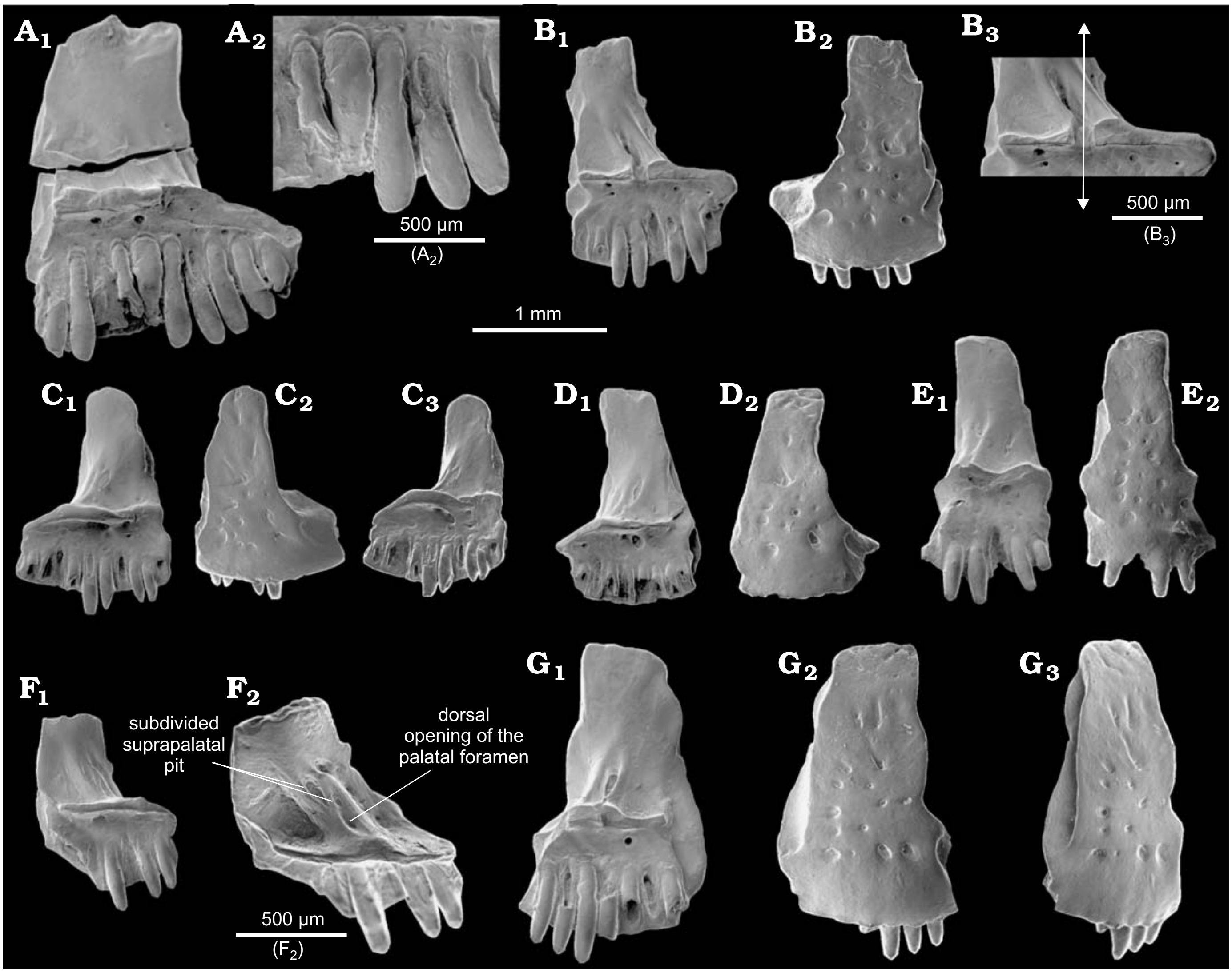

Fig. 6. Scanning electron micrographs of additional premaxillae of the albanerpetontid amphibian *Wesserpeton evansae* gen. et sp. nov. from bed 38 of the Barremian Wessex Formation at Yaverland (Figs. 1, 2), to further illustrate intraspecific variations in morphology and size. **A**. NHMUK PV R36565, right premaxilla, broken transversely through the pars dorsalis and one of the largest recovered; entire specimen in lingual view (A_1); enlargement in lingual view of teeth at positions 4–8 (A_2), to show deformed teeth at 4th and 5th loci. **B**. NHMUK PV R36566, right premaxilla in lingual (B_1) and labial (B_2) views; enlargement (B_3) to show the broken pars palatinum in lingual view, revealing the vertical path (indicated by double-headed arrow) of the canal between the dorsal and ventral openings of the palatal foramen in this specimen. **C**. NHMUK PV R36567, left premaxilla in lingual (C_1) and labial (C_2) views; oblique ventrolingual view (C_3), to show the large ventral opening of the palatal foramen in this specimen. **D**. NHMUK PV R36568, left premaxilla in lingual (D_1) and labial (D_2) views. **E**. NHMUK PV R36569, right premaxilla in lingual (E_1) and labial (E_2) views. **F**. NHMUK PV R36595, right premaxilla in lingual view (F_1); enlargement in oblique mediodorsal and lingual view (F_2), to show subdivision of the suprapalatal pit and the dorsal opening of the palatal foramen. **G**. NHMUK PV R36596, right premaxilla in lingual (G_1) and labial (G_2) views, the latter showing the medially expanded flange in this specimen; oblique mediolabial view (G_3), to show the deep labial slot in the medial margin of the bone.

palatinum. Six minute foramina pierce the bone linguomedial to the narial margin and a more substantial foramen is present at the junction between the pars dorsalis and the lateral margin of the strut surrounding the lateral margin of the suprapalatal pit. In other specimens, e.g., R36526 described below, R36600 (Fig 7D_2) and R36604 (Fig. 7H_1) foramina in this area are larger and fewer in number (Table 1). The lingually opening suprapalatal pit is dorsoventrally elongate and oval in outline, and lies above the 4th and 5th tooth positions (as counted from the medial end following Gardner 1999c). Its medial and lateral margins comprise strongly raised struts rising from the dorsal surface of the pars palatinum. The orientation and height of these struts are very variable; so too is the shape of the suprapalatal pit, which is subdivided in at least one third of the specimens (Table 1) including R36526 described below (Fig. 5B) and others listed in Table 1, e.g., R36595 (Fig. 6F), R36600 (Fig7D_2) and R36604 (Fig. 7H_1). The dorsal opening of the palatal foramen is located at the labial margin of the pars palatinum immediately adjacent to the base of the medial face of the medial strut. In many others it is located between the struts, below the ventral margin of the suprapalatal pit but in one specimen, R36597 (Fig. 7A), there is some ambiguity. In this specimen the undivided suprapalatal pit is large, deep and extends to and below the dorsolabial margin of the pars palatinum. It is possible that in this specimen, as in some other albanerpetontids, e.g., *Albanerpeton pannonicum* Venczel and Gardner, 2005, the dorsal opening of the palatal foramen is located within the floor of the suprapalatal pit. However, this area is obscured by matrix and this condition is not observed in any of the other Wessex Formation premaxillae. A more likely interpretation is that the dorsal opening of the palatal foramen is a very small opening located medially at the base of the medial strut. This placement is seen both in R36524 described here and in a slightly more lateral position in R36600 (Fig. 7D$_2$). In close proximity to this but ventral and slightly lateral to it there is another opening suggesting that in this individual the dorsal opening of the palatal foramen may be divided. Another unusual feature of this specimen is the occurrence of an additional foramen close to the dorsal extremity of the medial strut where it is placed in the centre of the medial surface. In R36524 the dorsal opening of the palatal foramen is somewhat lateromedially elongate and oval in outline. No other foramina are present on the dorsal surface of the preserved part of the pars palatinum. A much smaller foramen, interpreted as the ventral opening of the palatal foramen, lies directly below the dorsal opening at the junction between the pars palatinum and pars dentalis. No other foramina can be seen on the ventral surface of the pars palatinum but the area above the 5th tooth position is obscured by strongly cemented matrix. As in other albanerpetontids, a canal extends through the pars palatinum connecting the dorsal and ventral openings of the palatal foramen. Unlike the situation reported for other albanerpetontids (e.g., Gardner et al. 2003; Venczel and Gardner 2005), in Wessex Formation albanerpetontid premaxillae the orientation of this canal is variable (Table 1). In about half of the specimens, including R36524 (Fig. 5A$_2$) and R36566 (Fig. 6B$_3$), the canal extends vertically through the pars palatinum, as it does in all species of *Albanerpeton* (Gardner et al. 2003; Venczel and Gardner 2005). In the remaining specimens, e.g., R36601 (Fig. 7E$_2$), and as in *Anoualerpeton* (Gardner et al. 2003), the canal instead extends dorsolaterally–ventromedially through the pars palatinum as a result of a more medial placement of the ventral opening of the palatal foramen relative to the dorsal opening. Due to breakage, nothing further can be said about the morphology of the pars palatinum in R36524 other than that it appears to have comprised a lingually broad, horizontal shelf as in other albanerpetontids.

The pars dentalis of R36524 is deep and supports teeth for approximately three quarters of their length from the base to the apex. Nine tooth positions are present of which the 4th, 6th and 9th loci are vacant, the last due to breakage of the tooth. At the 2nd locus the basal part of the tooth on its lingual side is broken away. This reveals a hollow interior at the base of which there is what appears to be a replacement tooth at an early stage of development (Fig. 5A$_3$, A$_4$). The crowns of teeth are entirely discrete from but cemented to the overlying mediolaterally compressed and labiolingually expanded shafts. The shafts have flat medial and lateral surfaces and convex lingual surfaces. They are also labially convex above the ventral margin of the pars dentalis. The shafts thicken labiolingually from their bases towards the ventral margin of the pars dentalis and thereafter rapidly thin labiolingually, but not mediolaterally, as they approach the crowns. The latter are low relative to their mediolateral width and somewhat broader and wider at their bases than the shafts. They are chisel-like along their occlusal surfaces and faintly tricuspid with a central cusp that is slightly higher than the medial and lateral cusps. The crown of the tooth at the 3rd locus appears to be worn as a result of dietary attrition. Other crowns appear unworn.

NHMUK PV R36526 (Fig. 5B) is from the left side. It is about 2.1 mm high, representing a somewhat smaller individual than R36524. This bone is also nearly complete, with the exception of the lateral part of the pars palatinum and a small part of the bone immediately dorsal to it. As in R36524, the medial edge bears an elongate groove that extends below the labial surface of the bone. However in this specimen it extends from the dorsal extremity, where it is shallow. to a position slightly dorsal to the level of the base of the dentition. The lateral extremity of the groove (its base) also contains evenly spaced and sized foramina of which four can be seen but the groove is partially filled with matrix possibly obscuring others. The minute foramen just above the level of the dentition in R36524 is not present in this specimen. The groove, which is shallow dorsally, becomes progressively deeper ventrally. At its ventral extremity it almost entirely covers the 1st tooth position but here the labial roof is excavated laterally to produce a notch. At the ventrolingual extremity of the notch there is a small peg similar to that observed in R36524. As in R36524 a flange creates the lingual surface of the labial groove. However, this is of different morphology: it is entirely confluent with the medial edge of the labial surface of the groove whereas it extends medially beyond it in R36524; it is entirely discrete in R36524 whereas in R36526 it flows into and becomes the lingual surface of the pars dorsalis at about half its height above the pars palatinum (see also the description above of the grooves and flange present in R36596). Lingual to this flange there are what appear in medial view to be two similarly dorsoventrally orientated grooves. The dorsal extremity of the dorsal-most groove marks the point of confluence of the flange with the lingual surface of the pars palatinum. The dorsal groove is deep and very acutely triangular in medial view, the apex pointing dorsally and the base being expanded to excavate the bone between the dorsal and ventral surfaces of the pars palatinum. The ventral groove is in fact connected to the dorsal groove internally by a canal but is separated from it in medial view by a strut extending from the ventral surface of the pars palatinum to the flange separating the labial and lingual grooves. Immediately ventral to the strut the groove is deep but it rapidly becomes shallow ventrally where it

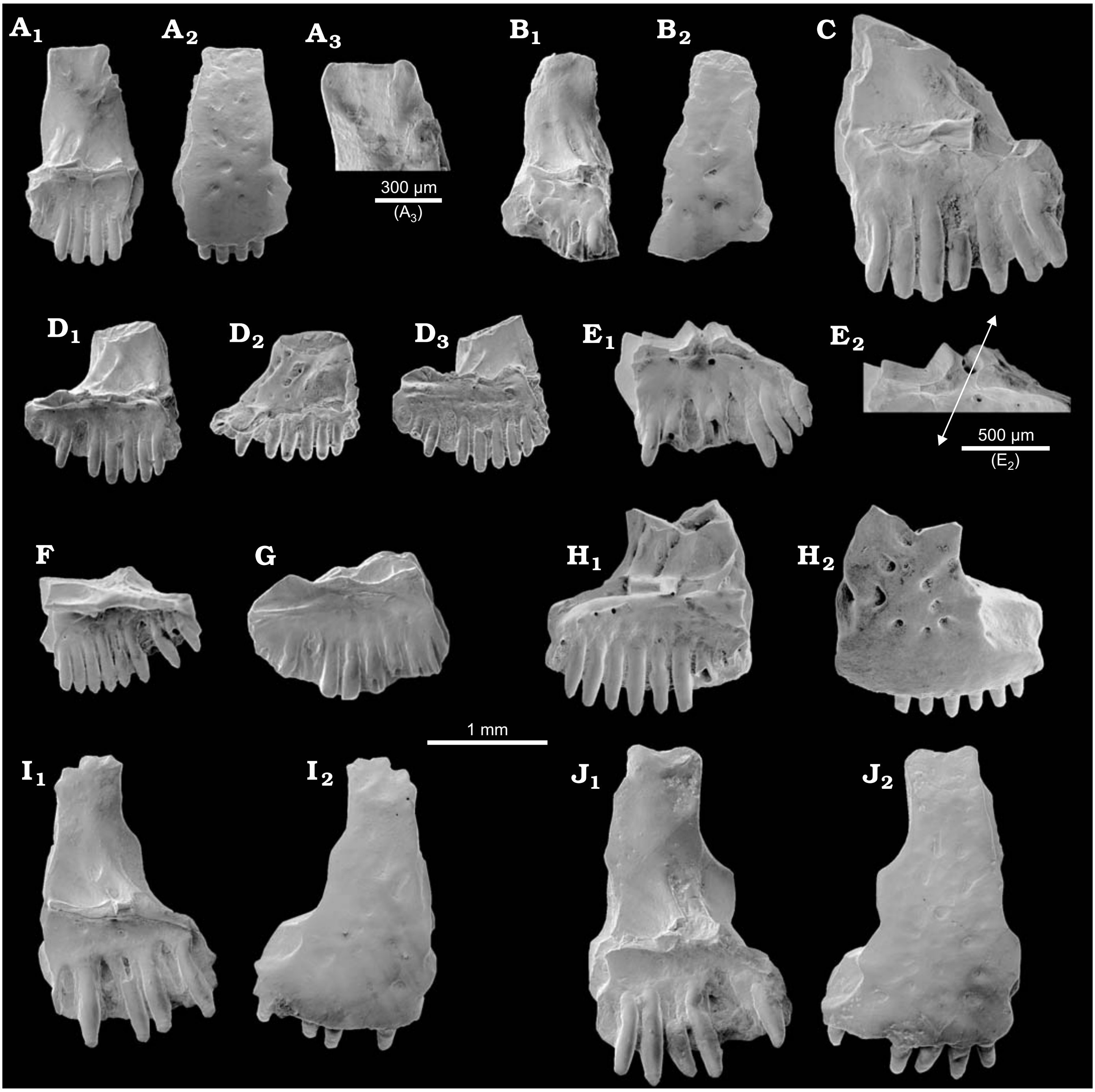

Fig. 7. Scanning electron micrographs of additional premaxillae of the albanerpetontid amphibian *Wesserpeton evansae* gen. et sp. nov. from bed 38 of the Barremian Wessex Formation at Yaverland (Figs. 1, 2), to further illustrate intraspecific variations in morphology and size. **A**. NHMUK PV R36597, left premaxilla in lingual (A_1) and labial (A_2) views; enlargement of the dorsolingual part of the pars dorsalis in lingual view (A_3), to show the V-shaped facet present in this specimen. **B**. NHMUK PV R36598, left premaxilla in lingual (B_1) and labial (B_2) views. **C**. NHMUK PV R36599, large, robust, right premaxilla with mediolaterally wide teeth, lingual view. **D**. NHMUK PV R36600, left premaxilla in lingual view (D_1); oblique dorsolingual view (D_2), to show the palatal foramen, other openings on the pars dorsalis and the articular facet on the dorsal surface of the maxillary process for contact with the maxilla; oblique ventrolingual view (D_3), to show openings in the pars palatinum and pars dentalis. **E**. NHMUK PV R36601, right premaxilla in lingual view (E_1); enlargement to show the broken pars palatinum in lingual view (E_2), revealing the inclined path (indicated by double-headed arrow) of the canal between the dorsal and ventral openings of the palatal foramen in this specimen. **F**. NHMUK PV R36602, right premaxilla in lingual view to show loci for 10 teeth (7^{th} locus is empty, 9^{th} locus is occupied by a broken tooth base and remaining loci have intact teeth). **G**. NHMUK PV R36603, left premaxilla in lingual view to show the dorsally expanded lingual rim of the maxillary process in this specimen. **H**. NHMUK PV R36604, left premaxilla in lingual view (H_1), to show foramina in junction of the pars palatinum with the pars dentalis; and labial view (H_2), to show deep labial foramina in this specimen. **I**. NHMUK PV R36605, right premaxilla in lingual (I_1) and labial (I_2) views. **J**. NHMUK PV R36606, right premaxilla in lingual (J_1) and labial (J_2) views.

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comprises two shallow pits. Foramina are not present in the lingual groove(s).

Labially, R36526 bears a dorsal boss but this is dorsoventrally shorter and less prominent than that of R36524. One shallow polygonal pit is present on the lateral side but otherwise the surface of the boss is rugose and bears a number of minute nutritive foramina. As in other specimens, the remainder of the labial face of the bone is relatively smooth and perforated by small, scattered nutritive foramina. The dorsolateral corner of the pars dentalis bears a facet for contact with the overlapping complementary premaxillary lateral process of the maxilla. Unlike R36524, in which this facet is broad and smooth, that of R36526 is narrow and deeply excavated comprising a pit dorsally at the bottom of which there is a very small foramen. The laterodorsal notch is shallower than that of R36524 but similarly occupies a little less than half of the dorsal margin of the pars dorsalis on its lateral side. It also bears a facet.

Lingually, the apex of the pars dorsalis bears a sculpted facet for reception of the anterior margin of the nasal but this is less pronounced than that of R36524. Unlike R36524, on the dorsolateral margin of the pars dorsalis on the lingual side of R36526 there is only the faintest trace of a lingually convex ridge below the boss. Also in contrast to R36524, there is no ridge extending from the dorsal extremity of the mediolingual groove to the dorsal margin of the pars palatinum. In this specimen only two foramina pierce the bone linguomedial to the narial margin and these are both located at the junction between the pars dorsalis and the lateral margin of the strut surrounding the lateral side of the suprapalatal pit. The suprapalatal pit opens lingually but is subdivided in this specimen. The larger dorsal part is dorsoventrally elongate and oval in outline but is much smaller than that of R36524. The ventral opening is also oval in outline but is only about one third of the size of the dorsal opening. As in R36524 the suprapalatal pit lies above the 4th and 5th tooth positions. Its medial and lateral margins comprise raised struts rising from the dorsal surface of the pars palatinum but in this specimen the lateral strut is substantially more robust than the medial strut. Both lie diagonally ventrolaterally-dorsomedially across the face of the pars dorsalis. In this specimen the dorsal opening of the palatal foramen is located ventral to the suprapalatal pit at the junction with the pars palatinum and between the struts bordering the suprapalatal pit. It is somewhat smaller than the lower opening of the suprapalatal pit and is only about half the diameter of that of R36524. Also unlike R36524, two additional foramina are present at the junction of the pars dorsalis and pars palatinum. Both are small and of approximately equal diameter. One is located at the base of the lateral strut bordering the suprapalatal pit and dorsal opening of the palatal foramen and the other above the 7th tooth position. Lateral to this the bone is broken but a small, circular area of calcite cement suggests that a third foramen may have been present above the lateral margin of the 8th tooth. The ventral opening of the palatal foramen is slightly larger in diameter than the dorsal opening (the opposite condition occurs in R36524) and in this specimen it is located on the pars palatinum. It lies approximately one third of the distance from the junction between the pars palatinum and pars dentalis to the lingual extremity of the pars palatinum. It is located slightly medial to the dorsal opening suggesting that the canal connecting the openings is somewhat dorsolaterally-ventromedially inclined. Variation in the size and location of the ventral opening of the palatal foramen is seen in all specimens (Table 1), no two specimens being exactly the same in this respect. An extreme example is R36567 (Fig. 6C), in which the ventral opening is many times larger in area than the dorsal opening and several times larger than the suprapalatal pit. In R36526 the lateral part of the pars palatinum is broken away and it appears to be abraded medially as no lingually projecting vomerine process of the sort seen in R36603 (Fig. 7G but dorsal view not provided) is present. Between the 3rd and 6th tooth positions, the pars palatinum appears to be complete and is slightly labially excavated below the suprapalatal pit. Two foramina only slightly smaller in diameter than the ventral opening of the palatal foramen are present medially at the junction between the pars palatinum and the pars dentalis. One is placed above and between the 1st and 2nd tooth loci and the other above and between the 3rd and 4th. A third foramen of comparable diameter is similarly placed above the 8th tooth locus. Four additional minute foramina also occur along the junction between the pars palatinum and the pars dentalis. As in R36524, the pars dentalis is deep and supports teeth for approximately three quarters of the distance from their bases to their apices. Also as in R36524, nine tooth positions are present. In this specimen the 1st and 2nd teeth are broken and polishing of the broken ends suggests that breakage may have occurred premortem. The 4th and 9th loci are vacant. The general morphology of the teeth is as described for R36524 but they are somewhat more gracile.

As outlined in the descriptions above, there is considerable intraspecific variation in the premaxilla. To further illustrate this, ten variable characters were chosen and recorded for each of the figured premaxillae (Table 1). Subjective terminology has been used to convey the observed range of variability for each character, but all specimens have been evaluated consistently. In cases where struts surrounding the suprapalatal pit are recorded as absent the pit is invariably located on a swelling on the pars dorsalis. In some cases this is somewhat raised medially and laterally but discrete struts as seen in the described specimens R36524 and R36526 are not present. No attempt has been made to numerically evaluate the areas occupied by the dorsal and ventral openings of the suprapalatal pit and only their relative sizes are recorded. In the table "additional foramina below pars palatinum" refers to those close to and immediately below the junction of the pars palatinum with the pars dentalis. The number recorded does not include minute foramina often present at or immediately below the bases of teeth. In the region close to and immediately below the junction of the pars palatinum with the pars dentalis, as in that medial to the orbital margin on the in-

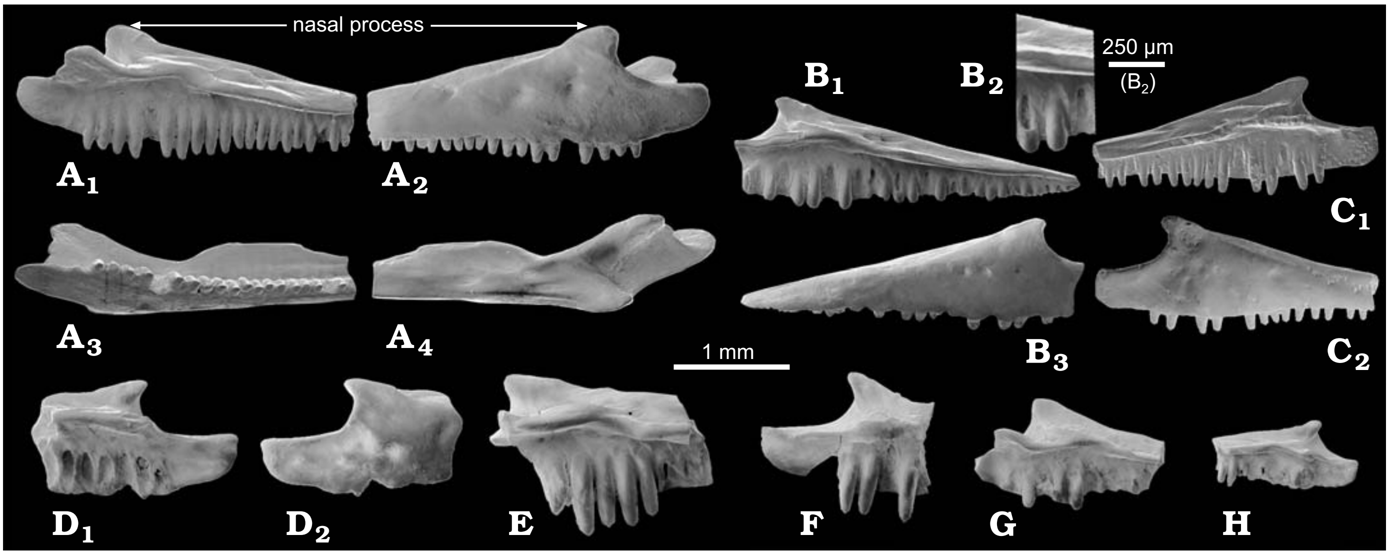

Fig. 8. Scanning electron micrographs of substantially complete and fragmentary maxillae of the albanerpetontid amphibian *Wesserpeton evansae* gen. et sp. nov. from bed 38 of the Barremian Wessex Formation at Yaverland (Figs. 1, 2). **A**. NHMUK PV R36528, right maxilla in lingual (A_1), labial (A_2), ventral (A_3), and dorsal (A_4) views. **B**. NHMUK PV R36527, right maxilla in lingual view (B_1); enlargement in lingual view (B_2), to show a replacement tooth at an advanced stage of development, flanked to the left (anteriorly) by a tooth with large resorption pit and to the right (posteriorly) by a vacant tooth slot; labial view (B_3). **C**. NHMUK PV R36559, left maxilla in lingual (C_1) and labial (C_2) views. **D**–**H**. Fragmentary anterior ends to show differences in morphology and location of the nasal process and other morphological differences discussed in the text. **D**. NHMUK PV R36560, left maxilla in lingual (D_1) and labial (D_2) views. **E**. NHMUK PV R36561, right maxilla in lingual view. **F**. NHMUK PV R36562, right maxilla in lingual view. **G**. NHMUK PV R36563, right maxilla in lingual view. **H**. NHMUK PV R36564, left maxilla in lingual view.

ternal surface of the bone, the size of foramina referred to as "large" and "small" is variable between individual specimens. However, where differently sized foramina are present, they invariably fall into two discrete size categories rendering those recorded as "large" entirely distinct from those recorded as "small". Counts recorded "as preserved" imply that part of the bone that in other specimens may bear foramina is either damaged, missing or partially obscured by matrix. With regard to tooth counts, two are recorded with question marks. In both specimens, the bones are damaged and their counts recorded as "?8". This appears to be a reasonable estimate based on the preserved parts but no complete dentition has yet been recovered in which eight tooth positions are unambiguously preserved.

Maxilla (Fig. 8).—Maxillae are less commonly preserved than premaxillae for uncertain taphonomic reasons. Nevertheless two specimens, NHMUK PV R36528 and R36527, document all characters of this element. These and six further specimens also serve to demonstrate some of the ontogenetic and intraspecific variations that occur.

NHMUK PV R36528 (Fig. 8A) is from the right side and is complete save for a portion of the posterior end. As in other albanerpetontids, the maxilla is an elongate and dorsoventrally low bone. This specimen is 3.0 mm long, but based on the posterior morphology of R36527 (Fig. 8B), it was probably about 4 mm long when complete. The bone is a little under 1.1 mm high measured from the ventral margin of the pars dentalis to the dorsal margin of the nasal process. It includes loci for 21 teeth. Of these, counting from the anterior end (following Gardner 1999c), the 1st, 6th and 19th are vacant. However, a replacement tooth at a very early stage of development is present at the 6th locus and remnants of the base of a ?shed tooth are present at the 19th. In terms of their general morphology, teeth are as described for the premaxilla. Teeth are somewhat variable in size with those occurring anteriorly being larger than those in the posterior half of the dentition. Nevertheless, heterodonty of the sort seen in *Anoualerpeton* (Gardner et al. 2003) and *Albanerpeton nexuosum* (Estes 1964; Gardner 2000a) does not occur. Tooth crowns show variable amounts of wear and some are unworn. The crown of the tooth at the 3rd locus is missing and the apex is rounded. There is also a deep scratch extending anteroventrally-posterodorsally across the lingual side of the pedicel. These features suggest that the crown was lost some time pre-mortem, perhaps as a result of traumatic dietary attrition. The pars dorsalis comprises no more than a low ridge extending along the dorsolateral margin of the bone. Laterally it bears a broad facet for contact with the lacrimal. This commences at the base of the nasal process and extends to the equivalent of approximately half the distance to the posterior end, had the bone been complete. Posteriorly on the dorsal surface there is a facet for articulation with the jugal. This commences slightly posterior to the posterior end of the facet for articulation with the lacrimal and lies medial to it. The nasal process projects dorsally and in this specimen comprises a broad flange with an almost vertical anterior margin forming the posterior part of the external narial opening. The dorsal surface is rounded. In other specimens, e.g., R36559 (Fig. 8C), the anterior surface is posteriorly concave in lateral or medial

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profile. Furthermore, the lateral and medial outline of the nasal process is different in all specimens including those shown in Fig. 8 and in some, e.g., R36560 (Fig. 8D), R36562 (Fig. 8F), and R36564 (Fig. 8H), dorsally it more resembles a peg than a flange. Medially the nasal process bears a further facet for contact with the lacrimal. In the most robust specimen, R36561 (Fig. 8E), this facet extends onto the dorsal surface of the premaxillary dorsal process that is more horizontal in this specimen than that of R36528 which has an anteromedial margin that is more dorsally inclined. The anterior extremity of the nasal process is variably placed; it lies above the 3rd tooth locus in R36528 (Fig. 8A) and R36527 (Fig. 8B); above the 2nd tooth locus in R36560 (Fig. 8D); between the 1st and 2nd tooth loci in R36559 (Fig. 8C); and anterior to the dentition in R36564 (Fig. 8H). Difference in size between R36527 and R36528, in which placement of the anterior extremity of the nasal process is the same, indicates that this variability represents intraspecific variation rather than differences relating to ontogeny. The premaxillary dorsal process comprises a broad, lingually expanded and slightly ventrally concave shelf. As outlined above, it is of somewhat variable morphology, particularly with regard to inclination of the anteromedial extremity. The premaxillary lateral process is a prominent anteriorly projecting flange. It is also somewhat variable in shape and anterior extent but variations are less marked than those of the nasal process. The pars palatinum comprises a lingually expanded shelf, but anteriorly it is deeply indented by the internal narial margin. It also tapers posteriorly. In the central part between the 11th and 17th tooth loci it bears a facet on the medial edge for contact with a palatal bone. Dorsally four large foramina are present. The anteriormost lies dorsally at the base of the very low pars dorsalis. It is slit-like and is placed above the 7th to 9th tooth loci. Ventral to this and towards its posterior end an oval foramen lies above the 9th tooth locus. Posterior and ventral to that location the third foramen lies above the 10th tooth locus. The fourth foramen is placed dorsally above the 13th tooth locus at a similar level to the first but is oval in outline. Ventrally, three large foramina lie at the junction between the pars palatinum and the pars dentalis. They are sub-circular in outline and placed above the 6th tooth locus, between the 10th and 11th tooth loci and above the 17th. A small, irregularly shaped foramen is also present at the base of the 7th tooth. As with the premaxilla, the pars dentalis is dorsoventrally deep supporting teeth for approximately three quarters of the distance from their bases to their apices. It tapers posteriorly reflecting a progressive decrease in tooth height in that direction. The labial surface of the bone is smooth but it is pierced by a row of four very small nutritive foramina. These are located dorsally on the pars facialis above the 3rd, 6th, 9th, and 14th tooth loci.

NHMUK PV R36527 (Fig. 8B) represents an individual of intermediate size, being smaller than that represented by R36561 (Fig. 8E), the most robust specimen, and larger than the smallest represented by R36564 (Fig. 8H). It is substantially complete, lacking only the premaxillary dorsal and lateral processes. It is from the right side, is 3.1 mm long and, as measured for R36528 above, is 0.9 mm high. As in R36528 the labial surface of the bone is smooth but in this specimen it is pierced by a row of three very small nutritive foramina (Fig. 8B$_3$). These are similarly located dorsally on the pars facialis but above the 5th, 7th, and 9th tooth loci. The dental row appears to be complete with loci for 26 teeth (Fig. 8B$_1$). Of these 16 are occupied and although the teeth have been somewhat abraded post-mortem it appears that loci without teeth were vacant pre-mortem. Replacement teeth at an advanced stage of development are present at the 13th, 16th, 18th, and 21st positions. They are identified as such because they almost, but do not completely, fill preexisting slots in the pars dentalis (Fig. 8B$_2$). Otherwise this bone is of similar morphology to that of R36528. Exceptions are the profile of the nasal process (described above) and the number and/or location of foramina perforating the pars palatinum dorsally, and at the junction between it and the pars dentalis ventrally. In this specimen the anteriormost dorsal foramen is anteroposteriorly elongate and located at the base of the pars dorsalis as it is in R36528. Here it extends from a position above the midpoint between the 6th and 7th tooth loci to that between the 8th and 9th. Posterior to this an oval foramen lies more ventrally above the 9th tooth locus. The foramen posterior to this is located between the latter and the posteriormost foramen above the 10th tooth locus. In this specimen it is very small. The posteriormost foramen is located dorsal to the preceding two, it is slit-like resembling the anteriormost foramen and extends from a position above the midpoint between the 10th and 11th tooth loci to that between the 12th and 13th. Despite differences of this sort, all specimens in which the dorsal foramina are preserved show the same general arrangement with the anteriormost and posteriormost foramina being placed dorsal to the two lying between them. The junction between the pars palatinum and the pars dentalis is perforated by at least 11 oval to round foramina. Most are very small but those above the 3rd, 5th, and 9th tooth loci are more substantial. Similar morphological variations are observed in other specimens, including R36559 (Fig. 8C), which is from the left side. As in R36528, this lacks the posterior end and in this case also the premaxillary dorsal process. This specimen is intermediate in size between R36527 and R36228 described above. It is a little less than 2.5 mm long and 0.9 mm high and contains loci for 16 teeth of which 13 are occupied. Based on the posterior morphology of R36527, R36559 may have been about 3.7 mm long when complete. In this specimen all dorsal foramina are oval in outline and the middle two are large and of approximately equal area. Ventrally, only two foramina pierce the area between the pars palatinum and pars dentalis. One is located above the anterior margin of the 1st tooth and the other above the 4th tooth locus.

Dentary (Figs. 9, 10).—Dentary fragments are the most commonly encountered albanerpetontid remains in the Wessex Formation. No specimen is complete, but those available document all aspects of dentary morphology except for the region at the extreme posterior end. In only one specimen is a postdentary bone preserved in association with the dentary, a partial prearticular in R36549 (Fig. 10H), but a number of articulars have been recovered, one of which is almost complete and to which is fused an almost complete angular (see below, Fig. 11I). The most nearly complete dentaries are NHMUK PV R36541 and R36542 (Fig. 9). However, the latter (Fig. 9B) bears a pathology rendering the former the most useful for determining dentary morphology.

R36541 (Fig. 9A) is from the left side. At the anterior end part of the symphyseal region is missing and at the posterior end part of the area for attachment of the postdentary bones is missing. As preserved, the bone is approximately 4.2 mm long and at its posterior end the maximum height is a little less than 0.9 mm, measured from the dorsal margin of the dental parapet to the ventral margin of the bone. It tapers anteriorly and at the anterior end is a little less than 0.6 mm high. The complete dentition comprising 26 teeth is present and all loci are occupied. Counting from the anterior end, teeth at the 2nd, 3rd, and 8th positions have been broken post-mortem, and the crowns of teeth at the 10th and 15th positions have also been damaged post-mortem. Elsewhere teeth show variable amounts of wear attributable to dietary attrition. Those at the posteriormost three positions lack crowns but have polished apices suggesting that the crowns were lost pre-mortem. Three of the teeth bear minor abnormalities: that at the 9th locus has no mesial or distal cuspules and its main cusp is displaced mesially; that at the 12th locus has a minute cuspule just below the crown on the labial surface; and that at the 18th locus has a minute cuspule at the base of the crown on its mesial margin. The 26th tooth is also abnormal in that its base is indented on the mesial margin and swollen distally. This is also seen in an anterior tooth of R36543 (Fig. 10A$_2$). Otherwise, teeth of R36541 are of the type seen in other albanerpetontids and are as described above for the premaxilla and maxilla; however, crown and shaft morphologies of dentary teeth appear to be more variable than those of the premaxilla and maxilla. For example, the crowns of R36557 (Fig. 10Q$_3$) are low and noticeably tricuspid whereas those of R36530 (Fig. 10C$_2$) are taller and less obviously tricuspid. Also, in the former specimen shafts are similar in width to, or mesiodistally narrower than, the crowns throughout their length whereas they are noticeably broader than the crowns in the latter specimen and R36546 (Fig. 10E$_2$), particularly in the region just below the dorsal margin of the dental parapet. In R36541, teeth increase in height from the 1st to the 5th locus and progressively decrease in height posteriorly from the 9th locus. However, along most of its length the occlusal margin is essentially straight as is the dorsal margin of the dental parapet. This renders dentaries of *Wesserpeton* distinct from those of *Anoualerpeton* and *Albanerpeton nexuosum* (Estes 1964; Gardner 2000a; Gardner et al. 2003).

The labial surface is smooth and at the posterior end of the bone there is no trace of a scar for attachment of the external adductor musculature. It bears a single external nutritive foramen located below the 13th tooth locus. However, the number and size of labial foramina are variable as R36549 and R36529 possess two small foramina and R36552 has three minute foramina in the posterior parts of these dentaries (not figured). In R36541 the external nutritive foramen occupies the anterior part of a slit-like anteroposteriorly orientated pit occurring a little more than half of the distance from the dorsal to the ventral margin. Below this foramen, and extending from a position below the 8th tooth locus to the 17th, there is a shallow scar that extends anteroposteriorly along the lateroventral and ventral surfaces of the bone. This marks the site of attachment of the intermandibularis musculature. The symphyseal region has been damaged post-mortem and the symphyseal prongs that interlock in a mortise and tenon fashion with complementary prongs on the opposite dentary as in other albanerpetontids are missing. They are, however, well preserved in other specimens, e.g., R36544, R36530, and R36555. These speci-

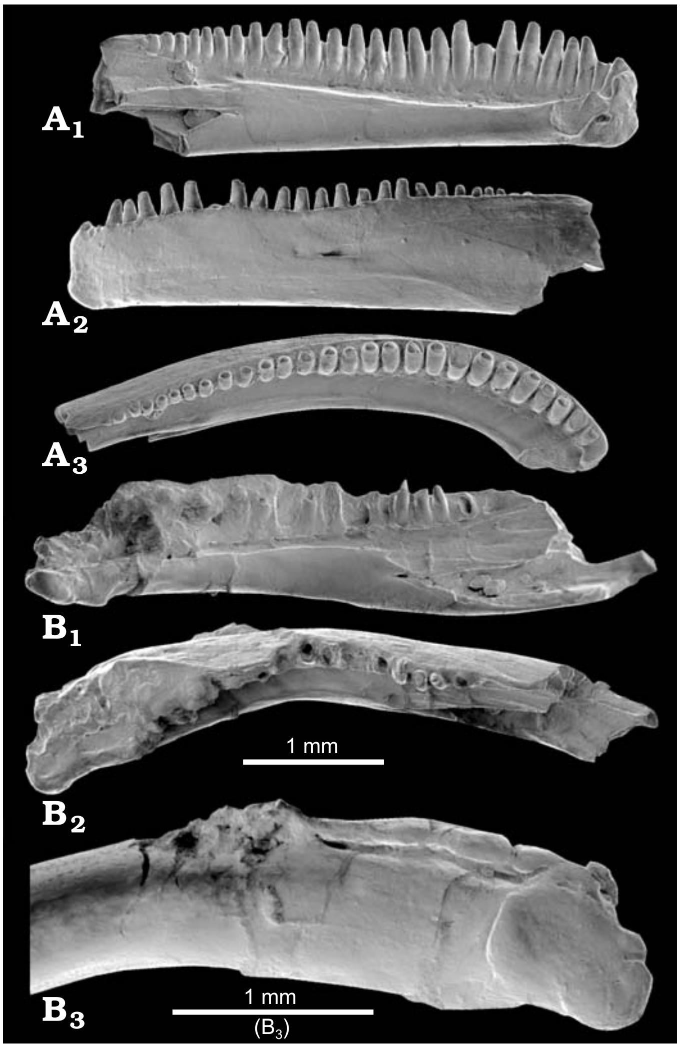


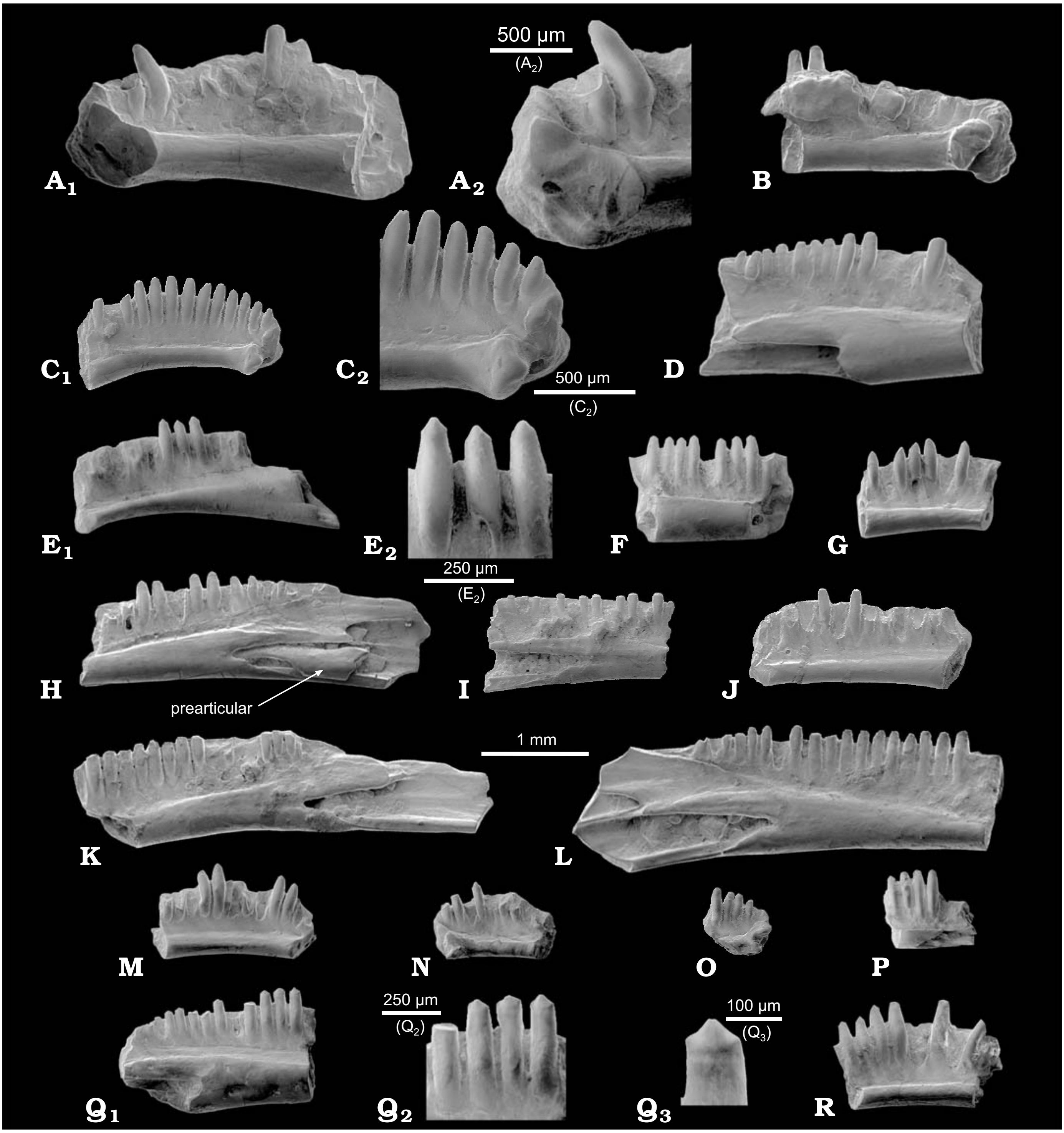
Fig. 9. Scanning electron micrographs of two nearly complete dentaries of the albanerpetontid amphibian *Wesserpeton evansae* gen. et sp. nov. from bed 38 of the Barremian Wessex Formation at Yaverland (Figs. 1, 2). **A**. NHMUK PV R36541, substantially complete left dentary missing most of area for attachment of post-dentary bones in lingual (A$_1$), labial (A$_2$), and dorsal (A$_3$) views. **B**. NHMUK PV R36542, right dentary preserving similar amount of bone, but with pathological anterior portion in lingual (B$_1$) and dorsal (B$_2$) views; enlargement of the anterior end in ventral view (B$_3$), showing bony callous and distortion in region of possible healed fracture and re-modelled symphyseal surface.

mens display some variability in the structure of the symphyseal joint. In R36544 (Fig. 10B) and R36555 (Fig. 10O), both from the left side, two prongs of different size are present, the larger lying dorsally above the smaller. In contrast only one prong is present in R36530 (Fig. 10C), which is also from the left side. The symphyseal face in all specimens is vertical medially and posteriorly. On the posterior surface below the 1st tooth locus in R36541 and similarly placed in other specimens, there is a foramen representing the anterior opening of the Meckelian canal (Fig. 9A$_1$). In dorsal view (Fig. 9A$_3$) the bone is broadly curved, the curvature being greatest along the anterior third of its length. In lingual aspect (Fig. 9A$_1$) the dental parapet is shallow posteriorly and anteriorly but deepens in the region of the tallest teeth. The subdental shelf is labiolingually narrow posteriorly becoming broader anteriorly. The dorsolingual margin is somewhat raised along its length. Ventrally, the subdental shelf is dorsoventrally deep posteriorly but shallows progressively towards the symphysis. No large foramina are present at the junction between the dental parapet and the subdental shelf but numerous minute foramina are present at the bases of teeth. The posterior opening for the Meckelian canal extends anteriorly to underlie the 22nd tooth locus. The lingual margin of the subdental shelf above this bears a facet marking the point of contact with the prearticular. This extends anteriorly terminating below the 20th tooth locus. The remainder of the posterior part of the bone is missing.

R36542 (Fig. 9B) is of note because it bears a pathology resulting from severe trauma and possibly infection at the anterior end of the bone. This is one example of a number of dentaries from both North America and Europe displaying pathologies, and these are the subject of further study by the authors and co-workers. R36542 is from the right side. As preserved, it is approximately 4.8 mm long and at its posterior end the maximum height is a little more than 0.9 mm, as measured for R36541. This bone represents an individual of similar or slightly larger size than that represented by R36541. The greater length of the bone mostly reflects more complete preservation of the posterior end and the presence of abnormal bone growth at the anterior end. In its general morphology R36542 appears to have been similar to R36541 prior to trauma but may have had somewhat fewer teeth. Damage at the anterior end (Fig. 9B$_1$, B$_2$) renders a tooth count here problematic and the injured area posterior to about the 5th tooth locus is obscured by siderite-cemented matrix to about the 10th locus. A tooth count of about 23 seems likely. However, in this specimen, as in R36541, the anterior extremity of the posterior opening for the Meckelian canal extends anteriorly to underlie the 4th tooth locus from the posterior end. This corresponds to the 22nd tooth locus in R36541 for which the total count is 26. Damage to the dentary is primarily restricted to the dental parapet and the anterior end of the bone including the symphysis. Counting from the posterior end, the dental parapet has been displaced lingually and slightly ventrally in the region of the 3rd to 5th teeth. It is more substantially lingually displaced between the 11th and 15th teeth where a fracture between it and the subdental dental shelf has occurred (Fig. 9B$_2$). Anterior to this, part of the dental parapet has broken away and the bone appears to have been fractured dorsoventrally-mediolaterally immediately posterior to the symphyseal prong or prongs. However, abnormal bone growth, which may also reflect sites of infection, renders positive determination of a fracture here problematic. Despite these rather severe injuries, which must have caused feeding difficulties both at the time they were sustained and during the remainder of the animal's life, the individual clearly survived for some considerable time after being injured. The injuries have healed, leaving on the lingual side a flap of bone that projects ventrally from the site of fracture of the dental parapet but which does not adhere to the original bone medial to it (Fig. 9B$_3$). Anterior to this on the ventral surface, bone overgrowth also covers the site of injury adjacent to the symphyseal prong or prongs (Fig. 9B$_3$). Little of the original structure of this area remains and the prong or prongs have been replaced by an anteromedially projecting peg of deformed bone (Fig. 9B$_2$).

Articular and angular (Fig. 11I).—A number of articulars have now been recovered from the Wessex Formation, but most are fragmentary, comprising only the posterior end but in some part of the angular is also preserved. As in other albanerpetontids for which these elements have been described (Estes and Hoffstetter 1976; Estes 1981; McGowan and Ensom 1997; Gardner 1999c; Venczel and Gardner 2005), the angular is fused to the articular with no suture evident in available specimens. The most complete, from the right side, is NHMUK PV R36531 (Fig 11I), which lacks only part of the posterodorsal surface on the lateral side of the articular. This specimen exhibits a vertical surface on the articular for articulation with the quadrate and facet patterns typical of Albanerpetontidae (Evans et al. 2004). The surface for articulation with the quadrate faces posteriorly and, unlike the fragmentary specimen from the Wessex Formation described by Evans et al. (2004), it bears very distinct cotylar

Fig. 10. Scanning electron micrographs of dentary fragments of the albanerpetontid amphibian *Wesserpeton evansae* gen. et sp. nov., A–L from bed 38 Yaverland, M–R from bed L2 near Sudmoor Point (Figs. 1, 2), both horizons within the Barremian Wessex Formation, to illustrate differences in bone and tooth morphology. All in lingual view. **A**. NHMUK PV R36543, anterior part of a right dentary in which the symphyseal end is broken and the anteriormost intact tooth is deformed: entire specimen (A$_1$); enlargement of the anterior end (A$_2$). **B**. NHMUK PV R36544, anterior part of a left dentary to show the two symphyseal prongs present in this specimen. **C**. NHMUK PV R36530, anterior part of a left dentary: entire specimen (C$_1$), to show well preserved anterior teeth; enlargement of the symphyseal region (C$_2$), to show the single prong present in this specimen and the foramen representing the anterior opening of the Meckelian canal. **D**. NHMUK PV R36545, posterior part of tooth-bearing region of a left dentary to show small teeth at the posterior end of the dentition and dorsal part of posterior opening for the Meckelian canal. **E**. NHMUK PV R36546, anterior part of a right dentary with three intact teeth: entire specimen (E$_1$); enlargement to show tooth morphology (E$_2$). **F**. NHMUK PV R36547, fragment from the middle part of tooth-bearing region of a left dentary illustrating →



uniform tooth size along this part of the dentition. **G**. NHMUK PV R36548, fragment from more anterior part of the tooth-bearing region of a left dentary, but lacking symphyseal end. **H**. NHMUK PV R36549, posterior part of a right dentary in which the anterior end of the prearticular is preserved in association, within the posterior opening for the Meckelian canal. **I**. NHMUK PV R36550, posterior part of tooth-bearing region of a left dentary. **J**. NHMUK PV R36551, fragment of tooth-bearing region of a right dentary. **K**. NHMUK PV R36552, right dentary preserving about posterior half of tooth-bearing region and posteroventral part of area for attachment of postdentary bones. **L**. NHMUK PV R36529, left dentary preserving about posterior half of tooth-bearing region and anterior part of area for attachment of postdentary bones. **M**. NHMUK PV R36553, fragment from anterior part of tooth-bearing region of a left dentary in which the posteriormost intact tooth is deformed. **N**. NHMUK PV R36554, anterior part of a right dentary with gracile teeth. **O**. NHMUK PV R36555, anterior end of a small left dentary in which two symphyseal prongs are present. **P**. NHMUK PV R36556, fragment of a left dentary with tall, slender teeth. **Q**. NHMUK PV R36557, posterior part of tooth-bearing region of a left dentary: entire specimen (Q_1); enlargement of the anteriormost three complete teeth (Q_2), which bear crowns that are somewhat anteroposteriorly wider than the shafts; enlargement of the anteriormost tooth crown and apical part of the shaft (Q_3). **R**. NHMUK PV R36558, fragment from anterior part of tooth-bearing region of a left dentary in which teeth have labiolingually expanded shafts.

surfaces. The larger of these is on the lateral side and is dorsoventrally higher than it is mediolaterally wide. The surface on the medial side also comprises a rounded rectangle but the height to width ratio is lower than that of the lateral side, its dorsal margin being placed more ventrally. The dorsal and ventral margins are supported by lips of bone, but these are not present on the lateral and medial margins. The lateral surface (Fig. $11I_1$) bears a deep facet for the posterior process of the dentary. A dorsal groove on this extends from the anterior end for a little over half the facet's length posteriorly. Slightly dorsal to this there is another groove extending anteriorly for about three quarters of the length of the facet and above this there is a similar groove which extends to the anterior limit of the facet dorsally. The posterior margin of the facet demonstrates that the articular was sheathed along most of its length by the dentary. Medially (Fig. $11I_2$) there is a deep groove comprising the posterior part of the adductor fossa. Ventral to this the angular is fused to the articular with no suture being evident. On the posterodorsal surface of this, there is a rather indistinct facet for contact with the prearticular (Estes and Hoffstetter 1976; Estes 1981).

Prearticular (Fig. 10H).—In only one specimen (R36549) is part of a prearticular preserved. This is an anterior fragment that has become lodged in the posterior opening for the Meckelian canal so that its dorsal surface now lies laterally. Little can be said about the morphology of the prearticular because part of what remains is obscured and in addition to the posterior part, the anteroventral part is also broken away. However there is a swelling and thickening of the bone at the posterodorsal part of what remains.

Atlas and "axis" (Fig. 11C–E).—Unlike other lissamphibians in which the atlas is followed by a dorsal vertebra similar in morphology to others in the series, in albanerpetontids there are two joints in the neck. The atlanto-occipital joint permits movement of the head in a dorsoventral plane, as it does in other lissamphibians, whereas that between the atlas and the specialized first post atlantal vertebra (conventionally called the "axis") permits lateral movement (McGowan 1998b). In this respect the first post-atlantal vertebra resembles the axis of amniotes although the two are not homologous.

Of the considerable number of atlantes available, NHMUK PV R36535 (Fig. 11E) is the most informative. As with all other Wessex Formation specimens, it lacks the neural arch and bears only the broken bases of the arch pedicels. Basally at the anterior margins of these and immediately posterior to the dorsal margin of the anterior cotyles there are deep but anteroposteriorly narrow grooves to accommodate the first spinal nerve. Open grooves rather than foramina for the first spinal nerve have also been recorded for *Anoualerpeton priscus* from the Middle Jurassic and *Celtedens* sp. from the Early Cretaceous of Britain (Gardner et al. 2003). As in other albanerpetontids (e.g., Estes and Hoffstetter 1976; Fox and Naylor 1982; McGowan 1996; Gardner 1999c, 2000a), the atlas is wider than it is anteroposteriorly long. The anterior cotyles are shallow and kidney-shaped, and the surfaces for articulation with the occipital bone extend across the ventral surface of the broad interglenoid tubercle. The dorsal and ventral surfaces of the latter are variably pierced by small foramina and some bear no foramina. In R36535 one is present on the left side and one on the right at the posterior margin of the ventral surface of the tubercle. The posterior cotyle bears no notochordal pit and has a dorsal concavity for articulation with a dorsal facet on the anterior cotyle of the "axis" (as further described below). Ventrolaterally the posterior cotyle bears two anterolaterally concave, semilunar facets for articulation with additional and corresponding facets on the anterior cotyle of the "axis". These extend posteriorly, giving the impression in dorsal (Fig. $11E_2$) and ventral view that the posterior cotyle is deeply anteriorly U-shaped.

Two "axes", NHMUK PV R36534 (Fig. 11C) and R36609 (Fig. 11D), document characters of this element and some of the either intraspecific or ontogenetic variation in these characters. Both specimens are very similar in their general morphology to the "axes" of other albanerpetontids (e.g., Estes and Hoffstetter 1976; McGowan 1996, 1998b; McGowan and Ensom 1997). The bone is smaller than the atlas and comprises a centrum with no neural arch or other processes. Posteriorly there is a deep, anteriorly tapering, conical notochordal pit but the notochordal canal does not extend to the anterior end of the bone. The bone surrounding this pit is of even thickness and the cotyle slightly dorsoventrally compressed so that the posterior outline is broadly oval. Foramina are absent from the dorsal surfaces of both specimens, but ventrolaterally towards their dorsal margins both bear minute foramina which do not appear to open in the notochordal pit. Ventrally three small foramina are present in R36534. Two are located in a posterodorsally narrow slit occupying a position close to the midline of the bone at its extreme anterior end. The other minute foramen is located on the midline in the middle of the bone. In R36609 two foramina are present anteriorly as in R36534 but in this specimen they do not lie in a slit. Also in this specimen, there is no third foramen. The anterior surface of R36534, referred to elsewhere as a cotyle but which is functionally a condyle, bears three articulation surfaces. One is placed dorsally and the others ventrolaterally. These articulate, respectively, with the dorsal concavity and the semilunar paired facets of the posterior cotyle of the atlas. In R36534 the anterior cotyle is considerably dorsoventrally higher than that of R36609 although both are of similar width (Fig. $11C_1$, D_1). Also, although both share the same pattern of articulatory surfaces, there are minor differences in their disposition (Fig. 11C, D). Whether or not these differences relate to ontogeny (apart from its anterior width R36609 is in other dimensions smaller than R36534) or to intraspecific variation awaits the recovery of a larger sample of "axes".

Trunk vertebrae (Fig. 11A, B).—Most trunk vertebrae, e.g., NHMUK PV R36607 (Fig. 11A), have the neural arch broken away, but in one specimen, R36608 (Fig. 11B), part is preserved on the right side and the base remains on the left. From the preserved parts it is evident that the neural arch was at least as tall as or possibly slightly taller than the centrum. As in

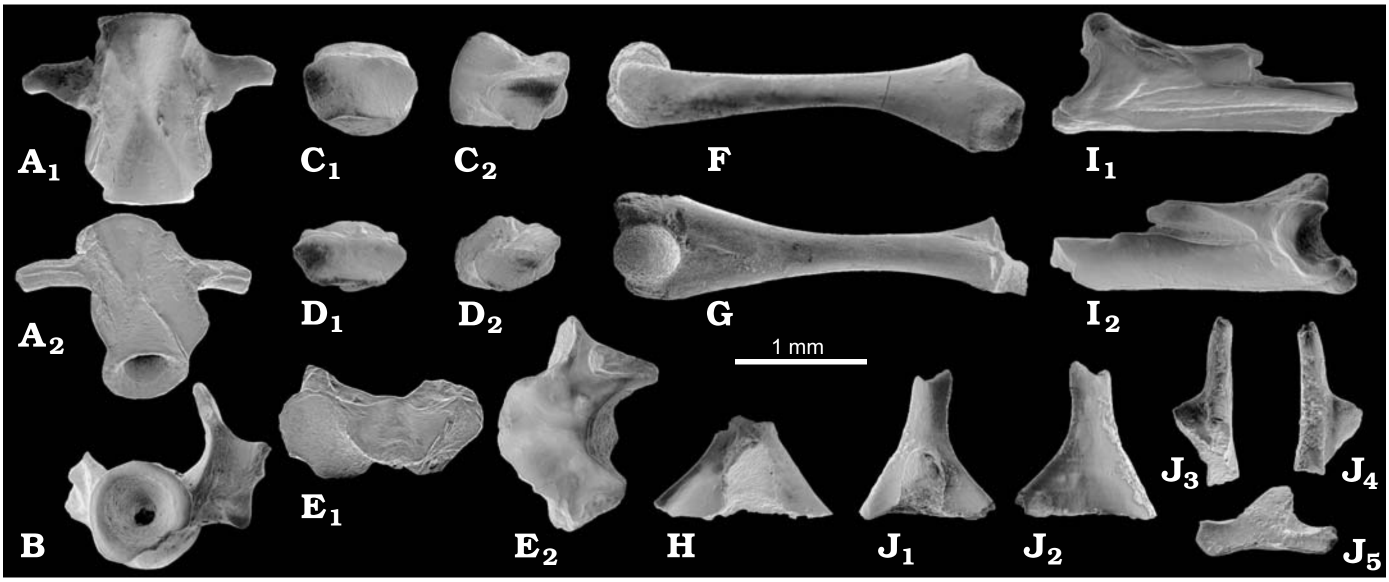


Fig. 11. Scanning electron micrographs of a fused articular + angular and of postcranial bones of the albanerpetontid amphibian *Wesserpeton evansae* gen. et sp. nov., all from bed 38 of the Barremian Wessex Formation at Yaverland. **A**. NHMUK PV R36607, trunk vertebra lacking the neural arch in dorsal (A_1) and oblique posterodorsal (A_2) views. **B**. NHMUK PV R36608, trunk vertebra preserving part of the neural arch, in posterior view. **C**. NHMUK PV R36534, "axis" (i.e., first post atlantal vertebra) in anterior (C_1) and oblique right anterolateral (C_2) views. **D**. NHMUK PV R36609, "axis" in anterior (D_1) and oblique right anterolateral (D_2) views. **E**. NHMUK PV R36535, atlas lacking the neural arch and ventrolateral portion of left anterior cotyle in anterior (E_1) and dorsal (E_2) views. **F**. NHMUK PV R36610, left humerus in medial view. **G**. NHMUK PV R36533, left humerus in ventral view. **H.** NHMUK PV R36611, acetabular part of a right ilium in lateral view. **I**. NHMUK PV R36531, fused right articular + angular in lateral (I_1) and medial ((I_2) views. **J**. NHMUK PV R36532, left ilium lacking dorsal end of the iliac shaft in lateral (J_1), medial (J_2), posterior (J_3), anterior (J_4), and ventral (J_5) views.

other albanerpetontids for which trunk vertebrae have been described (e.g., Estes and Hoffstetter 1976; McGowan 1996; McGowan and Ensom 1997), the centra are amphicoelous and hourglass-shaped, being very narrowly constricted in the centre of the bone, the anterior and posterior cotyles are circular in outline and have thickened rims, and the notochordal canal is anteroposteriorly continuous. In R36608, the transverse processes have been broken off close to their junction with the centrum but the bases can be seen to be anteroposteriorly narrow and dorsoventrally high. In R36607, the transverse processes are intact and, although similar in basal morphology to those of R36608, on R36607 the transverse processes additionally can be seen to be narrow, oval in cross section and unicipital at their lateral extremity. Ventrolaterally two minute foramina are present on the centrum on both the left and right sides of R36607. These are also present on the left side of R36608 but the right side is obscured by siderite overgrowth. In both specimens they are situated equidistant on either side of the anteroposterior mid point of the bone approximately one quarter of the distance from the centreline to the anterior and posterior ends. No other foramina or processes are present.

Humerus (Fig. 11F, G).—Numerous humeri have been recovered, but most lack the proximal end. However, one complete specimen NHMUK PV R36610 (Fig. 11F) and one almost complete specimen R36533 (Fig. 11G) are available. Both are from the left side and are of similar size and morphology. The shaft is slender and elongate and its axis passes through the proximodistal centreline of the humeral ball. The width of the proximal end in ventral view and that of the distal end in medial view are a little more than three times the diameter of the shaft in the middle part of the bone. As in other albanerpetontids (e.g., Estes and Hoffstetter 1976), the humeral ball is fully ossified and larger than the adjacent radial epicondyle and the less perfectly hemispherical condyle on the proximal end for articulation with the scapula. Above the humeral ball there is a deep triangular fossa (the fossa cubitus ventralis of some authors) at the proximal extremity of which there is a small foramen, as also reported for *Albanerpeton inexpectatum* (Estes and Hoffstetter 1976).

Ilium (Fig. 11H, J).—A small number of fragmentary ilia have been recovered, of which the most complete is NHMUK PV R36532 (Fig. 11J). This is from the left side and from which the distal part of the iliac shaft is missing. Unlike some anurans, there is neither a dorsal crest on the shaft nor a dorsal tubercle on the margin of the acetabular region. The shaft is straight and the preserved part shows no evidence of an ovoid or subcircular prominence on its lateral surface as seen in some urodeles (Gardner et al. 2010). The long axis of the shaft is slightly tilted posteriorly relative to the ventral surface (assuming a similar in-life orientation to urodeles), somewhat mediolaterally compressed and oval in cross section. The acetabulum occupies about one third of the acetabular region, which is triangular in lateral and medial outline (Fig. 11J_1, J_2). The acetabulum is elevated on a ramp-like pedestal that is highest adjacent to the base of the iliac shaft (i.e., dorsally). In lateral outline, the acetabulum is dorsoventrally elongated and its dorsal margin is convex. The acetabular surface is shallowly convex and its anterior, dorsal and posterior margins are in the form of a low rim. Relative to the long axis of the shaft, when viewed laterally, the somewhat laterally raised anterior edge of the acetabular region diverges at an angle of about 23°, whereas the more strongly laterally raised posterior edge diverges at about 47°. In another slightly larger specimen, R36611, from the right side and lacking most of the iliac shaft (Fig. 11H), the angles of divergence are about 30° and 55° respectively. The ventral surface, which in life presumably contacted the pubis and ischia as is typical for tetrapods in which the pubis is ossified, is somewhat sinuous, being dorsally concave anteriorly and ventrally convex posteriorly. The medial surface of the acetabular region is smooth, slightly laterally concave and bears a single foramen located somewhat anterior to the midline and about two thirds of the distance from the ventral margin to the base of the iliac shaft.

Discussion

Intraspecific and ontogenetic variation.—The large number of albanerpetontid bones recovered from the Wessex Formation on the Isle of Wight permits documentation of absolute size ranges for elements and variation in certain osteological features. The observed variation, particularly in osteological features of the jaws and frontals (e.g., shape of the internasal process on the frontals; path of the palatal foramen canal and presence of the dorsal boss in premaxillae [Table 1; shape of the nasal process in maxillae), is more extensive than has been documented for other albanerpetontid species (e.g., Estes and Hoffstetter 1976; Gardner 1999c, d, 2000a, b; McGowan 2002; Gardner et al. 2003; Venczel and Gardner 2005). Even so, we have not been able to recognize any distinctive groupings of homologous elements that could be interpreted as representing discrete taxa. For that reason, we: (i) regard the observed variation as a combination of ontogenetic and individual variation; and (ii) conservatively assign all the albanerpetontid specimens from the Wessex Formation to a single species. The combination of primititive and derived frontal and jaw characters listed in the Diagnosis (see above) differentiates the Isle of Wight species at the generic level from the three previously recognized genera (*Albanerpeton*, *Celtedens*, and *Anoualerpeton*). Consequently, we have erected the new genus and species *Wesserpeton evansae* for the Isle of Wight material. It is important to acknowledge that certain of the characters currently used to diagnose and examine relationships among albanerpetontid taxa (including *Wesserpeton*) are known to be variable within some species but not in others. One of these characters, estimation of maximum body size, is also hampered by the near certainty that albanerpetontids, like extant amphibians, probably grew indeterminately and with a growth rate that decreased dramatically as individuals aged. Nevertheless, that subset of characters, in combination with ones that appear to be less variable within species, have proved to be reliable for differentiating taxa for which reasonable sized samples are available (as is the case for the Wessex Formation taxon), and also for yielding relatively robust and repeatable phylogenies.

Abundance and palaeoecology.—Albanerpetontid bones have been recovered from beds throughout the exposed Wessex Formation (Fig. 2) and in two of the beds sampled, L2 (Stewart 1978) on the south-west coast and 38 (Radley 1994) on the south-east coast, they are locally abundant. Where more than one sample has been taken from a bed (e.g., L2, L9, and L14 on the south-west coast and beds 33 and 38 on the south-east coast), samples taken in close proximity to each other have invariably yielded markedly different fossil abundances and different relative abundances of elements of the fauna present. In many cases only one sample has been processed from a given horizon and it is clear that vertebrate remains recovered from these may not therefore accurately reflect the fauna present in the bed as a whole. In extreme examples of this (e.g., bed 38 at Yaverland), one sample produced abundant and diverse vertebrate remains, including the holotype specimen described here, whereas another sample taken from an exposure approximately 20 metres away was entirely devoid of microvertebrate fossils. The lateral difference in fossil abundance within individual plant debris beds reflects a possibly unique taphonomic history for the vertebrate remains they contain (Sweetman and Insole 2010). As a result, statistical analysis of the vertebrate assemblages recovered from individual beds is meaningless and it is not possible to obtain any signal regarding habitat preference for the Wessex Formation albanerpetontid. Nevertheless, after those of diminutive crocodyliforms (Freeman 1975; Sweetman 2011), albanerpetontid remains are the most abundant small tetrapod elements occurring at some horizons. This suggests that *Wesserpeton* was well adapted to, and abundant in, the floodplain environment in which it lived and that it will be recorded from additional horizons following more extensive sampling.

Comments on Early Cretaceous European albanerpetontids.—The recognition of *Wesserpeton* in the Barremian of the Isle of Wight adds to the diversity and geographic range of Early Cretaceous albanerpetontids in Europe (Table 2) and, thus, supports the idea (Gardner and Averianov 1998; Gardner and Böhme 2008) that Europe was an important area for the evolution of albanerpetontids. Besides *Wesserpeton*, at least two species of *Celtedens* are known from the European Early Cretaceous: *C. megacephalus* from the Albian of Italy and *C. ibericus* from the Barremian of Spain (see McGowan 2002). To date, albanerpetontid fossils have been reported from no fewer than 12 Lower Cretaceous localities in western and northern Europe (Table 2). Some of those specimens pertain to *Celtedens* (e.g., material from the Purbeck Limestone Group of southern England). As further discussed in the phylogenetic analysis section, Spanish Barremian frontals from Uña (Wiechmann 2003) and Buenache de la Sierra (Buscalioni et al. 2008) resemble those of *Wesserpeton* (Fig. 12) and it is possible that those represent one or more congeneric species. The Spanish frontals and those of

Table 2. Early Cretaceous occurrences of albanerpetontids in Europe. Taxa flagged with an asterisk denote our suggested identifications, not those of the cited authors. Modified and updated from Gardner and Böhme (2008: table 12.2).

Geological age	Unit, locality and country	Taxa	References
early Aptian	"Calcari ad ittioliti", Pietraroia locality (type locality of *Celtedens megacephalus*) Benevento Province, Italy	*Celtedens megacephalus*	Costa 1864; D'Erasmo 1914; Estes 1981; McGowan 1998a, 2002
Barremian	Wessex Formation, various localities, Isle of Wight, England	*Wesserpeton evansae*	Evans et al. 2004; Sweetman 2006b; Sweetman and Gardner 2008, this paper; Sweetman and Evans in press a
late Barremian	La Huérguina Formation, Buenache de la Sierra locality, Cuenca Province, Spain	cf. *Wesserpeton* sp.* (= "cf. *Albanerpeton* sp." sensu Buscalioni et al. 2008)	Buscalioni and Fregenal-Martinez 2006; Buscalioni et al. 2008
late Barremian	La Huérguina Formation, Las Hoyas locality (type locality of *Celtedens ibericus*), Cuenca Province, Spain	*Celtedens ibericus*	McGowan and Evans 1995; McGowan 1998a, 2002
late Barremian	La Huérguina Formation, Uña locality, Cuenca Province, Spain	*Celtedens ibericus* and cf. *Wesserpeton* sp.* (= *Albanerpeton* sp. nov. sensu Wiechmann 2003)	McGowan 1998a, 2002; Wiechmann 2000a, 2003
late Barremian	unspecified unit, Pio Pajarón locality, Cuenca Province, Spain	Albanerpetontidae indet.	Wiechmann 2003
late Hauterivian–early Barremian	Camarillas and El Castellar formations, various Galve localities, Teruel Province, Spain	Albanerpetontidae indet.	Estes 1981; Estes and Sanchíz 1982; McGowan 1998a; Sánchez-Hernández et al. 2007
late Hauterivian–early Barremian	Blesa Formation, La Cantalera locality, Teruel Province, Spain	Albanerpetontidae indet.	Canudo et al. 2010
Berriasian (and possibly younger)	Vitabäck Clays, Annero Formation, excavation near Vitäback farmhouse, Scania, Sweden	Albanerpetontidae indet.	Rees and Evans 2002
Berriasian	*Unio* Beds and Upper "*Cypris*" Clays and Shales, Peveril Point Member, Durlston Formation, Purbeck Limestone Group, various localities, Isle of Purbeck, Dorset, England	Albanerpetontidae indet.	Underwood and Rees 2002 (text-fig. 2); Evans and McGowan 2002
Berriasian	Cherty Freshwater Member, Lulworth Formation, Purbeck Limestone Group, various localities, including Sunnydown Farm Quarry and Lovell's Quarry, Isle of Purbeck, Dorset, England	*Celtedens* sp. or spp.	Ensom 1998; Ensom et al. 1991; McGowan and Ensom 1997; Gardner 2000a; Evans and McGowan 2002
early–middle Berriasian	upper part of unspecified unit, Champblanc Quarry, near Cherves-de-Cognac, Dépt. Charente, France	Albanerpetontidae indet.	Mazin et al. 2006; Pouech et al. 2006

Wesserpeton differ from those of *Albanerpeton* in relative length (i.e., the length:width ratio). In species of *Albanerpeton* this ratio is close to 1. In the specimens from Uña the average ratio is about 1.35 for the three specimens figured by Wiechmann (2003: pl. 3: 1–3) for which an estimate can be made, and very approximately 1.3 for the composite specimen from Buenache de la Sierra figured by Buscalioni et al. (2008: fig. 8.1). The ratio is also about 1.3 for *Wesserpeton*. This ratio is significant because unlike the angle of intersection of a line drawn parallel to the lateral margin of the bone along one third of its posterior length to the anteroposterior axis of the bone, it serves to distinguish the frontals of *Albanerpeton* (represented by numerous specimens) from those of other taxa with triangular frontals (currently represented by fewer specimens). In contrast to the length:width ratio, in *Albanerpeton inexpectatum*, *Wesserpeton evansae* and in frontals from Spain the above mentioned angle is similar in all taxa. This might give the erroneous impression for specimens lacking the anterior end, e.g., those from Buenache de la Sierra, that the shape of the frontals permits referral of this material to *Albanerpeton*. The above mentioned angle is: 30° for *Albanerpeton inexpectatum* (Fig. 12A); 30° for frontals from Uña (Fig. 12B); 27° for the reconstructed frontals from Buenache de la Sierra (Fig. 12C); and 33° for *Wesserpeton evansae* (Fig. 12D) (an average due to the increasing radius of curvature posteriorly in the posterolateral margin of the frontals of this taxon). Although there are general similarities in the triangular dorsal and ventral outline of frontals from Spain to those of *Wesserpeton*, differences between them (based only on observation of available figures and descriptions as we have been unable to examine the Spanish material directly) suggest that albanerpetontids from Spain possibly referable to *Wesserpeton* are not conspecific with *W. evansae*. The ventrolateral crests in specimens from Uña appear to be narrower and to meet each other anteriorly unlike those of *W. evansae* in which the crests are separated by a valley. The ventrolateral crests in specimens from Buenache de la Sierra also appear to be narrower and less expanded anteriorly. However, in these the crests are separated from each other by a valley as they are in *W. evansae*. In ad-

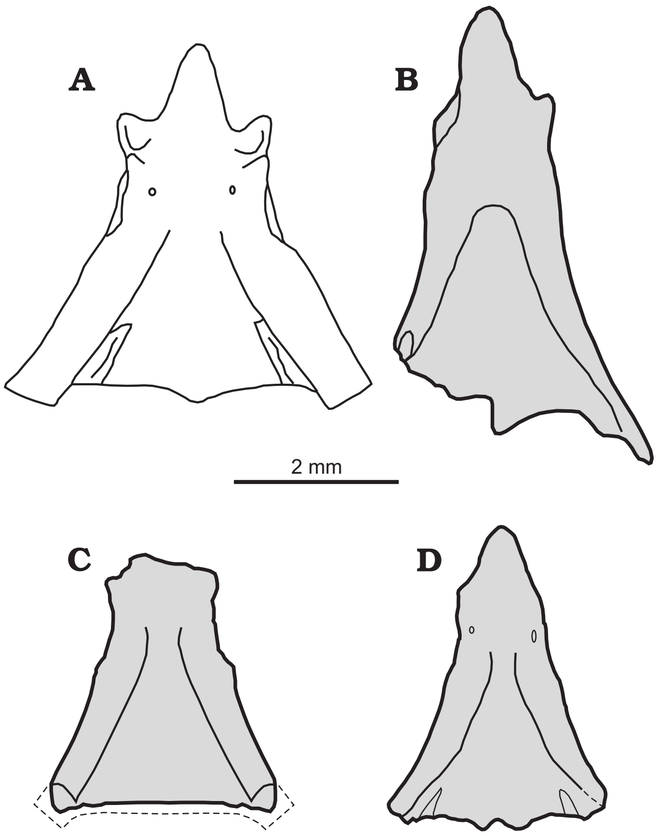


Fig. 12. Outline drawings in ventral view to show similarities and differences in azygous frontals of *Albanerpeton* and three Barremian albanerpetontids. **A**. *Albanerpeton*, based on type species *Albanerpeton inexpectatum* Estes and Hoffstetter, 1976, Miocene of Western Europe (from Gardner 1999a: 60, fig. 1L). **B**. Cf. *Wesserpeton* (= *Albanerpeton* sp. nov. sensu Wiechmann [2003: tafel III, fig. 1]), Barremian of Uña, Spain. **C**. Cf. *Wesserpeton* (referred to cf. *Albanerpeton* sp. by Buscalioni et al. [2008: 698, fig. 8.1]), Barremian of Buenache de la Sierra, Spain. **D**. *Wesserpeton*, based on holotype NHMUK PV R36521 (see Fig. 4A), Barremian of the Isle of Wight, England (this paper). Images at same magnification.

dition, all of the Spanish frontals appear to be somewhat larger than those of *W. evansae* (Fig. 12). The premaxilla of the albanerpetontid from Uña (Wiechmann 2003: pl. 7: 9) also differs from those of *W. evansae*. The Uña specimen has 11 tooth loci whereas the highest count from the many specimens of *W. evansae* is 10 (Table 1, and uncatalogued specimens). The differences in morphology between the frontals from Uña and Buenache de la Sierra suggest that more than one species not referable to *Celtedens* may be present in the Barremian of Spain. However, in view of the variation in osteological features of the frontals of *Wesserpeton* outlined above, these differences may reflect intraspecific variation in characters of the frontals of a single Spanish Barremian albanerpetontid. The identities of other European specimens are less clear and this situation is not likely to improve until a detailed taxonomic study of European Early Cretaceous albanerpetontids is undertaken.

That the albanerpetontids from Uña and Buenache de la Sierra are not conspecific with *Wesserpeton evansae* is supported by other data. Among small terrestrial taxa, including the lepidosaur *Meyasaurus* and the plagiaulacoid multituberculate mammal *Eobaatar*, genera common to the Early Cretaceous of both Britain and Spain (Sweetman 2009; Sweetman and Evans 2011b), no conspecific taxa have yet been recorded. This is indicative of a substantial interval of geographical isolation and endemism during the Late Jurassic and Early Cretaceous reflecting the existence of marine barriers separating Britain from Iberia (e.g., Blakey 2010, but see conclusions below). These would have substantially restricted if not prevented the dispersal of small terrestrial tetrapods between the two areas for considerable intervals of time.

Wesserpeton currently represents the youngest British record of Albanerpetontidae. After deposition of the Wealden Supergroup, marine conditions prevailed until the Paleocene, but during the Eocene and early Oligocene there were long intervals when environmental conditions appear to have been ideal for albanerpetontids. Vast amounts of sediment deposited in these environments has been processed for the recovery of microvertebrate remains, especially mammal teeth (e.g., Hooker 2010 and references therein), but one study of upper Eocene strata at Hordle Cliff, Hampshire, southern England (Milner et al. 1982) resulted in the recovery of a large number of bones, including elements of four frogs and three salamanders. Other small non-mammalian tetrapods including lissamphibians have also been recorded from the Isle of Wight (Rage and Ford 1980; Meszoely et al. 1984). However, albanerpetontid remains have yet to be reported from the Paleogene of Britain. Furthermore, a recent search of non-mammalian microvertebrate remains recovered in the late 1970s and early 1980s from a number of potentially suitable sites on the Isle of Wight (collections held by NHMUK) failed to reveal any bones referable to Albanerpetontidae (SCS personal observations 2010). For reasons that remain unclear it appears therefore that albanerpetontids may not have been resident in southern Britain during the Paleogene. Miocene strata are absent from Britain and if deposited have been removed by erosion. Pliocene deposits are of restricted extent in Britain and for the most part represent shallow marine environments. Very rare frog remains and a single salamander limb bone have been recorded but these records date from the latter part of the 19th Century (Newton 1891).

Phylogenetic analysis

Relationships within the Albanerpetontidae have been examined in four earlier cladistic analyses (Gardner 2002; Gardner et al. 2003; Wiechmann 2003; Venczel and Gardner 2005). These analyses are broadly comparable, because they used many of the same characters and taxa (see summary by Gardner and Böhme 2008). The key patterns are that the three previously recognized genera are all demonstrably monophyletic and that *Anoualerpeton* is the sister-taxon of *Celtedens* + *Albanerpeton*. Two new analyses were run using PAUP (Swofford 2002; see Appendix 1 for details): the first included *Wesserpeton* and the second both *Wesserpeton* and an unnamed para-contemporaneous taxon from Uña, Spain. In his unpublished PhD dissertation, Wiechmann (2003) proposed a species name for the latter taxon, but because that name has not been published, we use the informal term "Uña albanerpetontid".

The first analysis yielded eight most parsimonious trees of 50 steps each. The strict consensus tree is shown in Fig. 13, a simplified tree is shown in Fig. 14, and levels of support for clades are reported in Table 3. As in previous analyses, monophyly of *Anoualerpeton* and *Albanerpeton* is supported, although bootstrap and decay values are not strong (Table 3). Monophyly of *Celtedens* is assumed (see also Gardner 2002; Gardner et al. 2003; Venczel and Gardner 2005) based on the apparently unique presence of a bulbous internasal process on the frontals (e.g., McGowan and Evans 1995; McGowan 1998a, 2002). Wiechmann's (2003) unpublished cladistic analysis identified a bulbous internasal process as an unequivocal autapomorphy for *Celtedens* under both ACCTRAN and DELTRAN optimizations. We regard *Wesserpeton* as a monotypic genus and, by default, monophyletic, because in our analysis it falls outside any of the three previously recognized albanerpetontid genera.

All eight trees in the first analysis show the same pattern of inter-generic relationships (Fig. 14): *Anoualerpeton* (*Celtedens* + [*Wesserpeton* + *Albanerpeton*]). This resembles most previous arrangements (Gardner et al. 2003; Wiechmann 2003; Venczel and Gardner 2005; Gardner and Böhme 2008) in that *Anoualerpeton* retains its basal position, but differs in that *Celtedens* now occupies an intermediate position along the stem as *Wesserpeton* is now the new sister taxon of *Albanerpeton*. The clade *Celtedens* + (*Wesserpeton* + *Albanerpeton*) and the less inclusive clade *Wesserpeton* + *Albanerpeton* have modest bootstrap (70% and 74%, respectively) and decay (1 step for both) values. Each of the two clades is supported by one unequivocal synapomorphy that appears in all eight trees under both ACCTRAN and DELTRAN optimizations (Fig. 14). A lingually facing suprapalatal pit in the premaxilla [26(1)] is synapomorphic for *Celtedens* + (*Wesserpeton* + *Albanerpeton*), whereas frontals with a triangular outline [21(1)] are synapomorphic for *Wesserpeton* + *Albanerpeton*. Two equivocal synapomorphies may also support these clades. A vertically oriented canal between the dorsal and ventral openings of the palatal foramen in the premaxilla [27(1)] is synapomorphic for *Celtedens* + (*Wesserpeton* + *Albanerpeton*) according to ACCTRAN, but only for *Albanerpeton* according to DELTRAN. This synapomorphy is problematic, because the orientation of the palatal foramen canal cannot be scored in any *Celtedens* premaxillae available to us and the derived condition is present only in some, but not all, *Wesserpeton* premaxillae. The second equivocal synapomorphy is small body size [25(1)], which according to ACCTRAN supports the node for *Wesserpeton* + *Albanerpeton*; that arrangement requires several subsequent changes within *Albanerpeton* in order to accommodate interspecific variation in body size within that genus. The alternative

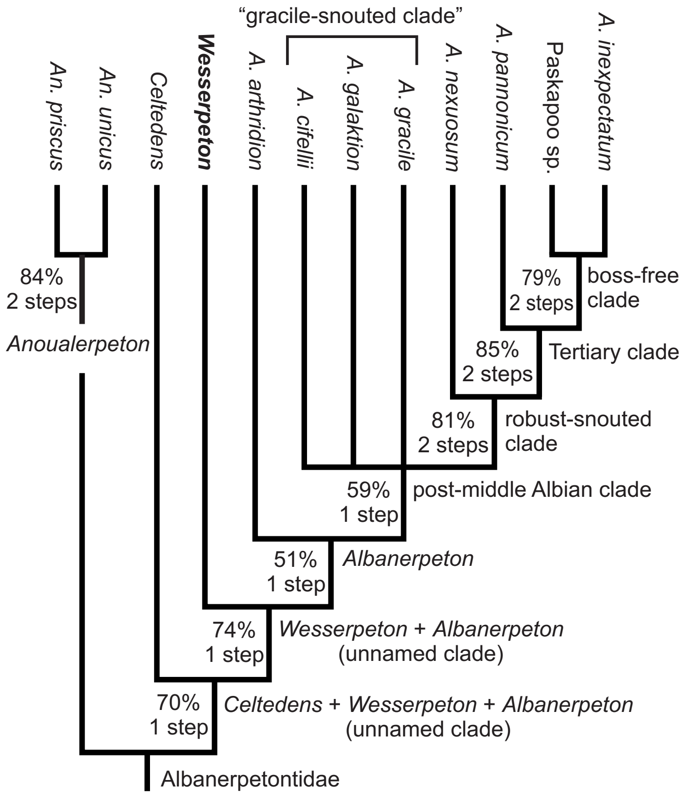


Fig. 13. Strict consensus of eight shortest trees generated in our first analysis, showing hypothesized relationships within Albanerpetontidae, with *Wesserpeton* placed as the sister of *Albanerpeton*. Indices of support for clades (see also Table 3) are to the left of each node; upper value is the bootstrap value (%) for 2000 replicates and lower value is the decay index (steps). Tree statistics (uninformative characters excluded) are as follows: tree length = 50 steps; CI = 0.683, HI = 0.317, and RI = 0.797.

DELTRAN pattern postulates that small body size arose independently in *Wesserpeton* and three times within *Albanerpeton*, once each in *A. arthridion*, *A. pannonicum*, and the unnamed Paskapoo species.

Monophyly of *Albanerpeton* is supported by two unequivocal frontal synapomorphies under both ACCTRAN and DELTRAN optimizations: frontals only moderately elongate [22(1)] and anterior limit of orbital margin on frontals in line with or behind the anteroposterior midpoint of the bone [28(1)]. Relationships within *Albanerpeton* and the distribution of apomorphies supporting its less inclusive clades essentially are unchanged from the most recent previous cladistic analysis (Venczel and Gardner 2005). Relationships among the three Late Cretaceous congeners (*A. cifellii*, *A. galaktion*, and *A. gracile*) continue to be unresolved (see also Gardner et al. 2003; Wiechmann 2003; Venczel and Gardner 2005); this is the only source of topological variation among the eight shortest trees generated in our analysis and it does not affect the pattern of inter-generic relationships.

Previously, triangular frontals [21(1)] also were considered diagnostic for *Albanerpeton* (e.g., McGowan and Evans 1995; McGowan 1998a, 2002; Gardner 2000b, 2002). *Wesserpeton* has triangular frontals, but other aspects of its fron-

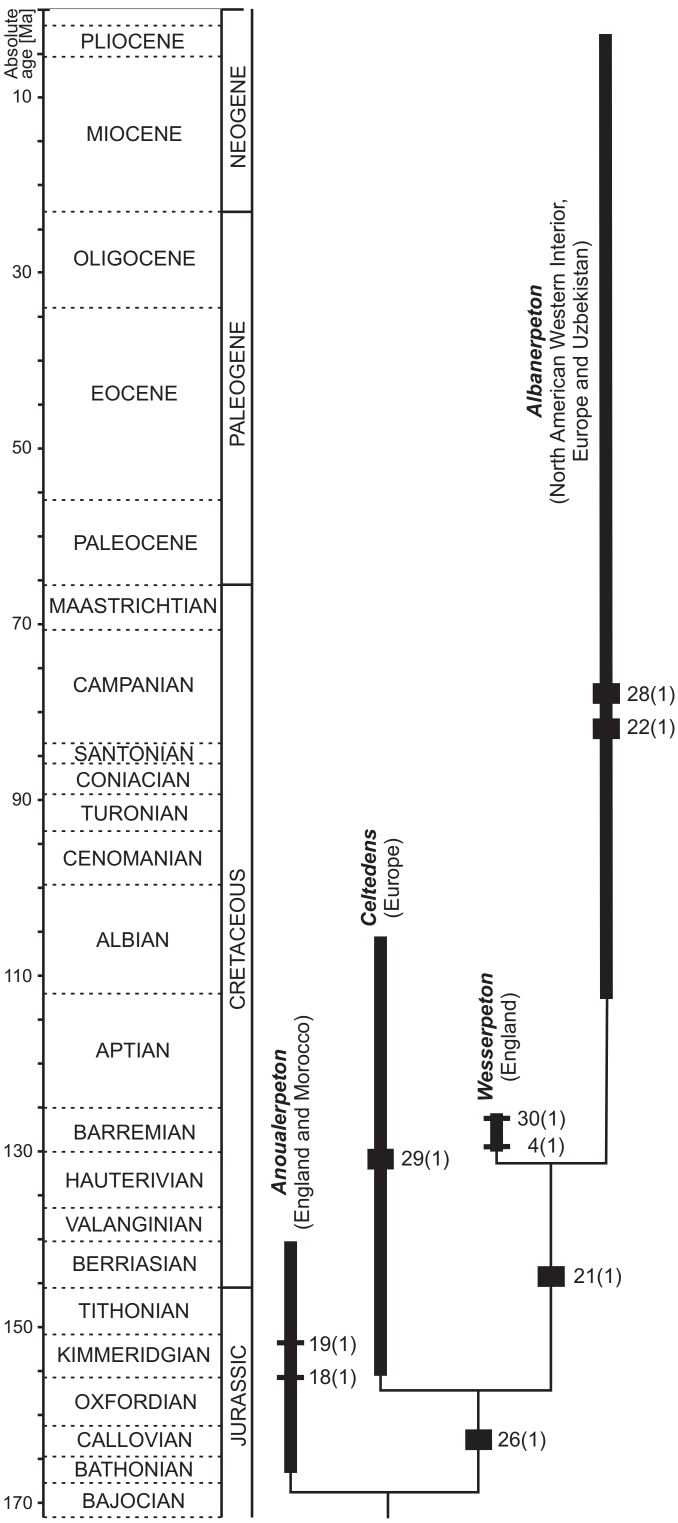


Fig. 14. Simplified, strict consensus tree showing hypothesized relationships among the four albanerpetontid genera, constrained against the geological time scale (absolute ages based on Gradstein et al. 2004: fig. 23.1) and reporting apomorphies (see list of characters in the Appendix 1) for each genus and more inclusive clades. Only unequivocal apomorphies (i.e., ones recovered in all eight of the shortest trees, under both ACCTRAN and DELTRAN optimizations) are mapped onto the tree. Autapomorphies are designated by a thick bar and convergences are designated by a thin bar.

tal structure, specifically that the frontals are elongate [22(0)] and that the anterior limit of the orbital margin lies in front of the anteroposterior midpoint of the bone [28(0)], are primitive for albanerpetontids. This mix of primitive and derived frontal features nests *Wesserpeton* within Albanerpetontidae, as sister taxon of *Albanerpeton*. Because *Wesserpeton* lacks the full suite of derived frontal features seen in existing species of *Albanerpeton*, we do not regard *Wesserpeton* as a member of that genus. We place the base of *Albanerpeton* at the node for the clade containing *A. arthridion*, *A. inexpectatum* (type species), and all other albanerpetontids most closely related to those species. Our concept of *Albanerpeton* is consistent with how most workers (e.g., McGowan and Evans 1995; McGowan 1998a, 2002; Gardner and Averianov 1998; Gardner 1999b–d, 2000a, b, 2001, 2002; Venczel and Gardner 2005; Folie and Codrea 2005; Skutschas 2007) have viewed that genus since 1995 when *Celtedens* was named.

In Wiechmann's (2003) cladistic analysis, the Uña albanerpetontid occupied the same position as *Wesserpeton* does in our first analysis. That is not surprising, because it is evident from Wiechmann's description (2003: 82–83) and drawings (2003: pl. 3: 1–4) that the frontals from Uña are similar to those of *Wesserpeton* (see also the earlier discussion here and Fig. 12B, D), and that both exhibit the same mix of primitive and derived features. Based in part on the observation that the Uña albanerpetontid had frontals that were triangular (like *Albanerpeton*) and did not have the bulbous internasal process of *Celtedens*, Wiechmann (2003) included it in *Albanerpeton*. For the reasons given in the previous paragraph and earlier, we exclude the Uña albanerpetontid from *Albanerpeton*. Considering that the material reported by Wiechmann (2003) compares favourably with material of *Wesserpeton*, is also Barremian in age, and originates from a geographically close locality, the Uña albanerpetontid might well be congeneric with *Wesserpeton evansae*. However, for the reasons set out above, we do not consider it to be conspecific with *W. evansae*.

In order to test the relationships of the two Barremian albanerpetontids, we re-ran our analysis with the Uña albanerpetontid included and scored for the 18 characters that we could confidently determine from Wiechmann's (2003) description and figures. This analysis yielded 24 shortest trees of 50 steps (i.e., same length as the first analysis). The strict consensus tree (Fig. 15A) has essentially the same pattern as the first analysis, except that the two Barremian albanerpetontids form an unresolved trichotomy with *Albanerpeton*. Three arrangements are each seen in eight of the shortest trees Fig. 15B–D, respectively): (i) Uña albanerpetontid (*Wesserpeton* + *Albanerpeton*); (ii) *Wesserpeton* (Uña albanerpetontid + *Albanerpeton*); and (iii) (Uña albanerpetontid + *Wesserpeton*) + *Albanerpeton*. The last arrangement is particularly interesting, because it implies a close relationship between the two Barremian albanerpetontids. We cannot comment further on the identity of the Uña albanerpetontid, because we have not seen the relevant specimens firsthand and they have not been described or figured in sufficient detail.

Table 3. Bootstrap and decay values for less inclusive clades within the Albanerpetontidae for the first analysis in branch-and-bound searches for trees up to two steps longer than the minimum of 50 steps. The strict consensus of the eight shortest trees is shown in Fig. 13. Monophyly of the "gracile-snouted clade" is not supported in this analysis (see also Wiechmann 2003; Venczel and Gardner 2005), but is included for comparison with earlier analyses (Gardner 2002; Gardner et al. 2003) that initially supported monophyly of that clade.

Clade	Bootstrap value (percent for 2000 runs)	Percentage of trees recovering clade		
		minimum 50 steps (8 trees)	min +1 ≤ 51 steps (50 trees)	min +2 ≤ 52 steps (166 trees)
Anoualerpeton	84	100	100	97
Celtedens + *Wesserpeton* + *Albanerpeton*	70	100	84	61
Wesserpeton + *Albanerpeton*	74	100	68	56
Albanerpeton	51	100	78	66
post-middle Albian clade	59	100	94	79
"gracile-snouted clade"	51	38	36	37
robust-snouted clade	81	100	100	96
Tertiary clade	85	100	100	97
boss-free clade	79	100	100	95

Our analyses provide some limited new insights into the evolutionary history of Albanerpetontidae. Based on our hypothesis of relationships (Fig. 14) and first occurrences in the fossil record, the following minimum ages of divergence for less inclusive clades within the Albanerpetontidae can be estimated: (i) late Bathonian for the split between *Anoualerpeton* and the other genera, based on the occurrence of *An. priscus* in the late Bathonian of England (Gardner et al. 2003); (ii) Kimmeridgian for the split between *Celtedens* and *Wesserpeton* + *Albanerpeton*, based on the occurrence of an unnamed *Celtedens* species of Kimmeridgian age in Portugal (Wiechmann 2003); and (iii) Barremian for the split between *Wesserpeton* and *Albanerpeton*, based on the occurrence of the former on the Isle of Wight. Estimated minimum origins of late Bathonian for *Anoualerpeton* and Kimmeridgian for *Celtedens* are unchanged from previous studies (Gardner et al. 2003; Gardner and Böhme 2008). With the recognition of *Wesserpeton* as the sister-taxon of *Albanerpeton*, the inferred origin for *Albanerpeton* is pushed forward from the previous estimate of Kimmeridgian (Gardner et al. 2003; Gardner and Böhme 2008). However, the oldest occurrence of *Albanerpeton* (in the sense that we view the genus) remains that of *A. arthridion* from the latest Aptian or earliest Albian of Oklahoma, USA (Gardner 1999d), which means that according to the time scale of Gradstein et al. (2004), about the first 10 million years of the fossil record for *Albanerpeton* still remains undocumented.

Wesserpeton exhibits a suite of primitive and derived features that nest it within the Albanerpetontidae, stemward of *Anoualerpeton* (basal position) and *Celtedens* (intermediate position), and as the sister of *Albanerpeton*. The sequential placements of *Anoualerpeton*, *Celtedens*, and *Wesserpeton* + *Albanerpeton* in the cladogram are consistent with the first appearances of each genus in the fossil record (see above). Although *Wesserpeton* and *Albanerpeton* are placed in the cladogram as sister taxa, the former can be viewed as documenting a transitional stage in the evolution of albanerpetontid frontals, from the more primitive condition seen in *Anoualerpeton* and *Celtedens* (i.e., elongate, hourglass-shaped, orbital margin accounts for more than one-half length of bone) to the more derived *Albanerpeton*-style frontal. *Wesserpeton* indicates that the triangular frontal shape evolved first, by at least Barremian time, followed later by shortening of the frontal and the orbital margin forming a larger percentage of the lateral edge of the frontals. The sequence in which the last two derived conditions appeared and when they appeared are unknown, but both were present by at least the Aptian–Albian boundary when the oldest unequivocal *Albanerpeton* frontals (*A. arthridion*; Gardner 1999d: text-figs. 2N, O, 4) are encountered in the fossil record.

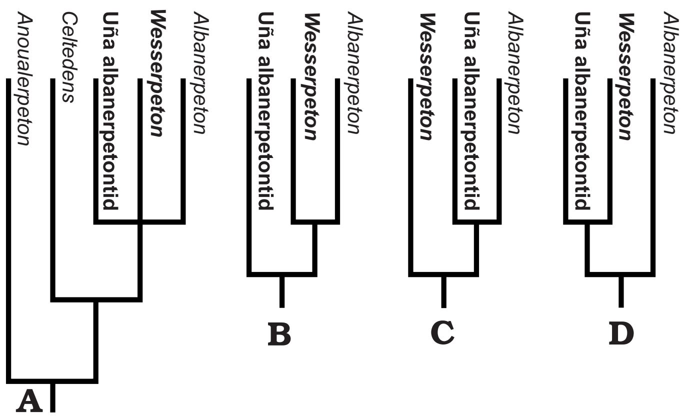


Fig. 15. Simplified versions of strict consensus and topological variants seen in the 24 shortest trees generated in our second analysis, showing alternative hypotheses of relationships among *Albanerpeton*, *Wesserpeton*, and the Uña albanerpetontid. **A**. Strict consensus: unresolved trichotomy among *Albanerpeton*, *Wesserpeton*, and Uña albanerpetontid. **B**. Topological variant 1: Uña albanerpetontid is sister of *Wesserpeton* + *Albanerpeton*. **C**. Topological variant 2: *Wesserpeton* is sister of Uña albanerpetontid + *Albanerpeton*. **D**. Topological variant 3: *Albanerpeton* is sister of *Wesserpeton* + Uña albanerpetontid. Each topological variant was found in one-third of the shortest trees. Tree statistics (uninformative characters excluded) are as follows: tree length = 50 steps; CI = 0.683, HI = 0.317, and RI = 0.806.

Conclusions

The Barremian Wessex Formation of the Isle of Wight has yielded abundant albanerpetontid bones. Despite considerable intraspecific variability (particularly in characters of the premaxilla) they display a unique combination of primitive and derived characters relating to the frontals and jaws permitting recognition of a new genus, *Wesserpeton*, the fourth to be described. *Wesserpeton* has triangular frontals, but other aspects of its frontal structure, specifically that they are elongate and that the anterior limit of the orbital margin lies in front of the anteroposterior midpoint of the bone, are primitive for albanerpetontids. *Wesserpeton* therefore represents an intermediate stage in albanerpetontid evolution and documents the transition of albanerpetontid frontals morphology from the primitive condition seen in *Anoualerpeton* and *Celtedens*, in which the frontals are elongate and hourglass-shaped, to the derived condition seen in the frontals of *Albanerpeton*, which are triangular but anteroposteriorly foreshortened. Inclusion in the phylogenetic analysis of characters of frontals from the Barremian of Uña, Spain suggests a close relationship between this Spanish albanerpetontid and *Wesserpeton*. This would imply at least intermittent faunal interchange between Britain and Iberia during the Late Jurassic and/or Early Cretaceous. Recent palaeogeographic reconstructions place substantial marine barriers between Iberia and Britain at this time but palaeontological evidence now suggests that these reconstructions are too simplistic. The occurrence of congeneric but not conspecific taxa among the small Barremian terrestrial vertebrates of Britain and Spain, including possibly *Wesserpeton*, appears to confirm that faunal interchange did take place. However, this must have occurred some time before the Barremian and was then followed by an interval of endemism. The occurrence of *Wesserpeton* with triangular but otherwise primitive frontals suggests that acquisition of a triangular shape preceded shortening of the bone and that this evolutionary trait was acquired in western Eurasia some time prior to the Barremian. The inferred split between *Albanerpeton* and *Wesserpeton* at or before the Barremian in western Eurasia raises the possibility that *Albanerpeton* evolved in that region from a *Wesserpeton*-like ancestor, then subsequently migrated to North America where it is first recorded (*A. arthridion*) in the Aptian–Albian of the southern USA. *Wesserpeton* represents the youngest British record (Barremian) of Albanerpetontidae, although the clade is known to have persisted on continental Europe until the late Pliocene. The oldest verified occurrences for albanerpetontids (see summary by Gardner and Böhme 2008: 193) are founded on two early Bathonian specimens: an atlantal centrum from Gardies, France (Seiffert 1969; Estes 1981), and an articular from Hornsleasow Quarry, mainland England (Evans and Milner 1994). An older, Early Jurassic (?Sinemurian–Pliensbachian) occurrence for the clade has been suggested (Skutschas 2007; Averianov et al. 2008; Gardner and Böhme 2008) based on two atlantal centra from the Kayenta Formation of Arizona, USA. Originally described as salamander atlantal centra (Curtis and Padian 1999), their attribution to an albanerpetontid has yet to be confirmed.

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Appendix 1

General information.—The two analyses presented here are expanded from Gardner (2002), Gardner et al. (2003), and Venczel and Gardner (2005); our methodology and assumptions generally follow those previous analyses.

Taxa.—Both of our analyses include a hypothetical "all zero" ancestor used to root the tree and the same 11 terminal taxa (two species of *Anoualerpeton*, *Celtedens*, and eight species of *Albanerpeton*) that were included in the analysis by Gardner and Venczel (2005). In addition, our first analysis added *Wesserpeton* and the second analysis added both *Wesserpeton evansae* the "Uña albanerpetontid", which Wiechmann (2003) interpreted as a new (but not as yet formally named) species of *Albanerpeton*.

Characters.—In both analyses, characters 1–27 and 29–31 are unchanged from Venczel and Gardner (2005: appendix). Character 28 from the analysis of Venczel and Gardner (2005; see also Gardner et al. 2003) has been deleted, because it is now clear that the supposedly unique pattern of frontal-prefrontal articulation reported by Gardner (2000: fig. 2A) for *Celtedens* was based on his mis-interpretation of a frontal from Purbeck, England. In its place, we substitute a replacement character 28 that describes the relative length of the orbital margin along the frontals; this character previously was discussed by McGowan (1998a) and Gardner (2000), and was used in Wiechmann's (2003) cladistic analysis. The anatomical breakdown of characters is the same as in Venczel and Gardner's (2005) analysis: premaxillae (n = 17), characters 1–14, 26, 27, 30; maxilla and dentary (n = 6), characters 15–20; frontals (n = 7), characters 21–24, 28, 29, 31; and body size (n = 1), character 25. Character descriptions are presented below.

1. Build of premaxilla: 0, gracile; 1, robust.
2. Ratio of height of premaxillary pars dorsalis versus width 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 sutured with anterior end of nasal; 1, premaxillary pars dorsalis minimally overlaps and strongly sutured 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.

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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. Dorsally projecting process on dentary immediately behind 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 fused frontals: 0, "short", length . width; 1, "long", length > width.
24. Form of ventrolateral crest on large, fused 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, dorsolaterally-ventromedially; 1, vertically.
28. Position in frontals of anterior end of orbital margin relative to anteroposterior midpoint of frontals: 0, in front of; 1, in line with or behind.
29. Dorsal or ventral outline of internasal process on frontals: 0, tapered anteriorly; 1, bulbous.
30. Suprapalatal pit variably divided: 0, undivided; 1, divided in about one-third or more of specimens.
31. Flattened ventromedian keel extending along posterior two thirds of fused frontals: 0. absent; 1, present.

Data matrix.—Matrix modified from Venczel and Gardner (2005: appendix) by replacing previous character 28 (see above) and by adding two Barremian taxa (*Wesserpeton evansae* and "Uña albanerpetontid"). Symbols: ? = unknown; 9 = inapplicable; a = polymorphic for states 0 and 1.

Terminal taxa	Characters							
	00000 12345	00001 67890	11111 12345	11112 67890	22222 12345	22223 67890	3 1	Percent missing or inapplicable
Hypothetical ancestor	00000	00000	00000	00000	00000	00000	0	0
Anoualerpeton priscus	0?0??	?0?00	00000	00110	00110	00?00	0	19
Anoualerpeton unicus	01000	00000	00?00	??110	00000	00000	0	10
Celtedens	000??	?0?00	0????	0000?	00000	1?010	0	32
Albanerpeton arthridion	00000	00000	0000?	00000	11001	11100	0	3
Albanerpeton gracile	00000	00011	10000	00001	11000	11100	0	0
Albanerpeton galaktion	00000	00012	10010	?0000	11010	11100	0	3
Albanerpeton cifellii	00020	00011	1000?	?????	?????	11?0?	?	45
Albanerpeton nexuosum	11110	10111	01001	00110	11110	11100	0	0
Albanerpeton inexpectatum	11111	91211	00001	11001	12120	11101	0	3
Albanerpeton pannonicum	11110	00011	00001	00001	12121	11101	1	0
Paskapoo species	11111	91011	00101	00001	1?101	11101	0	6
Wesserpeton evansae gen. et sp. nov.	0a010	000aa	00?0a	0000a	10001	1a001	0	3
Uña albanerpetontid	000?0	00?00	0????	?????	10000	1?00?	0	42