

Frontals as Diagnostic Indicators in Fossil Albanerpetontid Amphibians

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Abstract Albanerpetontids are an extinct group of amphibians known from deposits of Middle Jurassic to Miocene age from Euramerica and central Asia. Recent analyses have suggested they are most probably a sister group of frogs and salamanders. Throughout their long history they retain a very conservative body form and are difficult to distinguish from isolated specimens. However, they can be easily diagnosed as albanerpetontids from a collection of unique character states which includes an interdigitating mandibular symphysis; polygonal sculpturing on dermal roofing bones—related to its dermal ossification pattern—; tricusate, non-pedicellate teeth; and a unique atlas-axis complex. A comprehensive comparison of material from different European localities has revealed that the shape of the fused frontal may be a good indicator of genus and even species.

Key words: Albanerpetontids, amphibians, fossils, frontals.

Introduction

Albanerpetontids are structurally virtually indistinguishable. Thus, as currently defined, the genus *Albanerpeton* (Estes & Hoffstetter, 1976) extends from Middle Jurassic to Miocene and is remarkably conservative, but a close comparison of material from different European localities suggests it may be possible to differentiate populations on the basis of frontal shape.

Seven localities have yielded disarticulated albanerpetontid frontals; La Grive–Saint–Alban (Miocene), Upper Milk River, Alberta (Campanian), Uña (Early Barremian), Purbeck (Berriasian), Guimarota (Kimmeridgian), Tashkumyr, Kirghizia, Central Asia (Callovia) and Kirtlington (Bathonian). A further two localities; Las Hoyas, Spain (Late Barremian) and Pietraroia, Italy (Albian) show the frontal within the preserved skull.

Albanerpeton inexpectatum from the Miocene of France has a triangular frontal, widest at its posterior parietal margin, and narrowest and pointed anteriorly. It has almost straight orbital margins, that lie at an acute angle to the midline (Fig. 1A). The orbital margin is roughly half the anterior-posterior length. Anterior to the orbital margin, the articulation facets for the lacrimals are indented on both sides. The anterior process, where the nasals articulate, is relatively long and narrow and is ‘pinched’ into a sharp point. In the smallest specimen, the base width equals the ante-

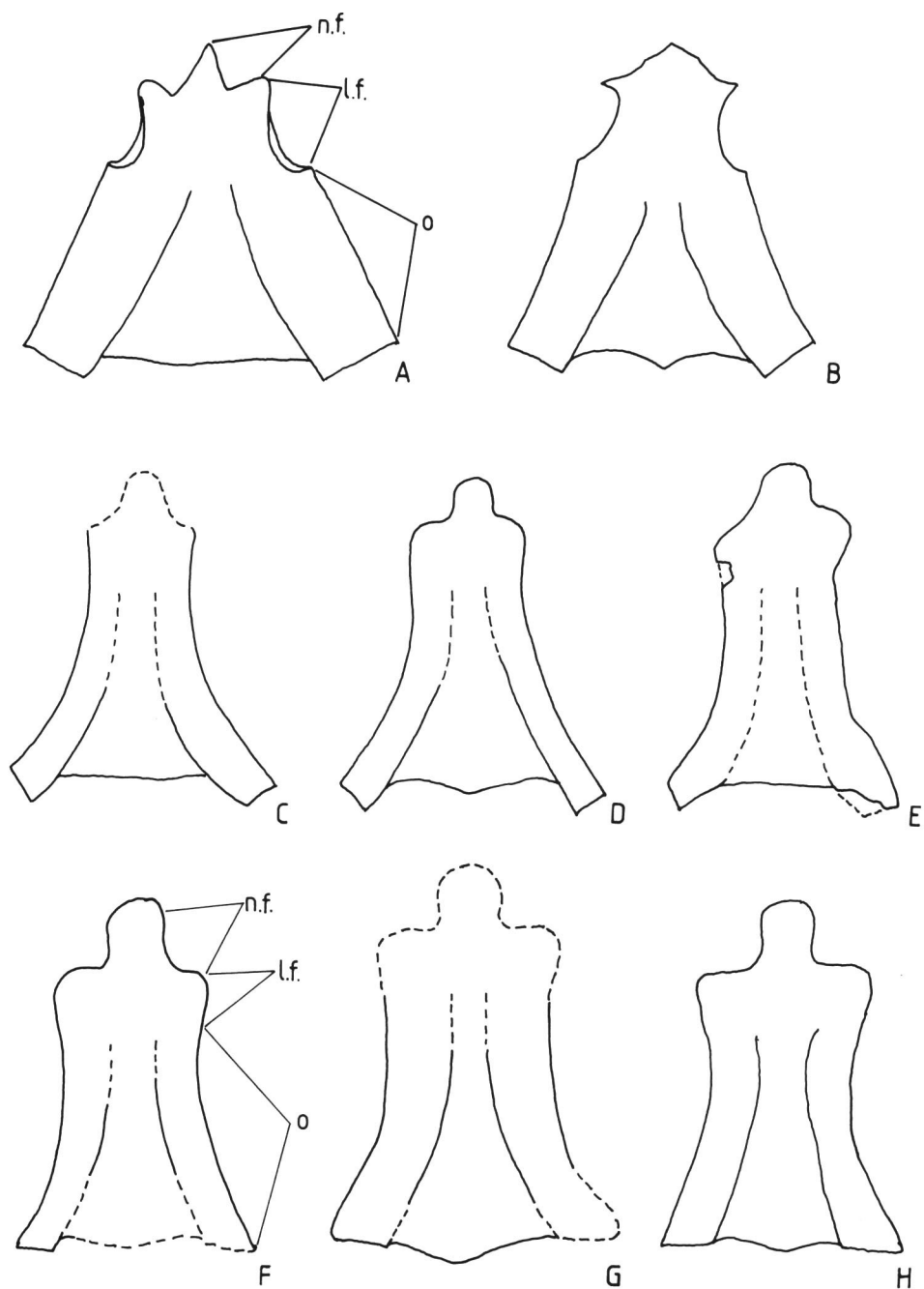


Fig. 1. Outline drawings (not to scale) of frontals from: — A) La Grive – Saint – Alban, *Albanerpeton inexpectatum* – Miocene (after Estes & Hoffstetter, 1976), B) Alberta, *A. galaktion* – early Campanian (after Fox & Naylor, 1982), C) Pietraroia, *Celtdens megacephalus* – Albian, D) Uña, undescribed sp. – Barremian, E) Guimarota, undescribed sp. – Kimmeridgian, F) Purbeck *C. cf. megacephalus* – Berriasian, G) Kirtlington, *C. cf. megacephalus* – Bathonian, H) Las Hoyas, *C. ibericus* – Barremian. Abbreviations used in figure n.f.=nasal facet; l.f.=lacrimal facet; o=orbit margin.

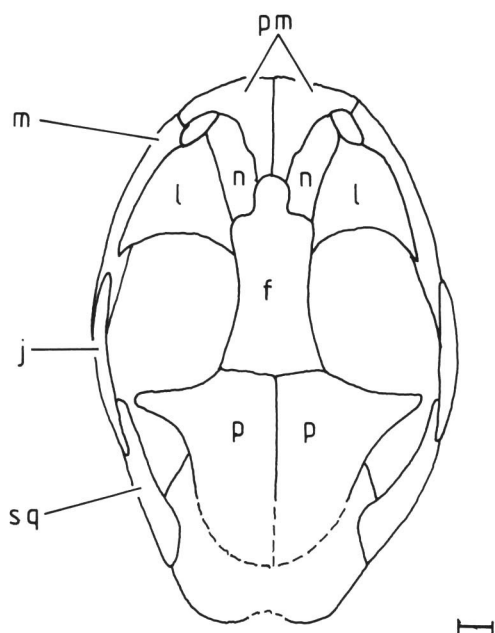


Fig. 2. Reconstruction of skull of *Celteledens ibericus* (after McGowan & Evans, 1995) to show position of frontal relative to other bones in the skull. Scale bar=1 mm. f – frontal; j – jugal; l – lacrimal; m – maxilla; n – nasal; p – parietal; pm – premaxilla; sq – squamosal.

rior-posterior length, but in the larger specimens the base is wider. This suggests a skull that is proportionally wider in larger specimens.

A second frontal type assigned to *Albanerpeton galaktion* is closely similar (Fig. 1 B). It has the characteristic triangular shape and straight orbital margins. However, the orbital margins lie at a less acute angle to the midline by comparison with *A. inexpectatum*, and are proportionally longer. The lacrimal articulation facets are less indented than in *A. inexpectatum* and the anterior process appears shorter and broader but still ‘pinched’.

In older albanerpetontid specimens, from Pietraroia, Uña, Las Hoyas, Purbeck, Guimarota and Kirtlington, the frontal has a very different shape with a wide bulbous, almost circular anterior process and highly curved orbital margins. The frontals are shaped like bells, narrowest halfway along their length (Figs. 1 C, D, H, F, E, G).

This difference is significant and supports the erection of a new genus, *Celteledens* (McGowan & Evans, 1995), for the older material. Figure 2 shows the frontal position relative to other skull elements in the genus *Celteledens*. The characteristic frontal shape of the genus *Celteledens* is seen most clearly in the Pietraroia (Lower Cretaceous, Albian) specimen *Celteledens megacephalus* (McGowan & Evans, 1995). This species becomes the type species of the new genus. Unpublished frontals from

Table 1. Albanerpetontid Frontals: Inter-Lacrimal to Parietal Base Widths.

Specimen Number	Inter-Lacrimal Width (L)	Parietal Base Width (P)	Ratio of L/P as a percentage
<i>A. inexpectatum</i> 1	2.5	6.64	37.7
<i>A. inexpectatum</i> 2	2.64	7	37.7
<i>A. inexpectatum</i> 3	2.5	6.5	38.5
<i>A. inexpectatum</i> 4	2.5	6.43	38.9
<i>A. inexpectatum</i> 5	2.21	5.86	37.7
<i>A. inexpectatum</i> 6	1.64	4.07	40.3
<i>A. inexpectatum</i> 7	2.36	6	39.3
<i>C. megacephalus</i> (Pietraroia) 1	1.68	3.8	44.2
<i>C. ibericus</i> (Las Hoyas) 1	2	3	66.7
<i>C. ibericus</i> (Las Hoyas) 2	1.14	1.82	62.6
Uña 1	0.87	2.07	42.0
Uña 2	0.96	2.3	41.7
Uña 3	1.07	2	53.5
Uña 4	1.07	2.14	50.0
Guimarota*	58	103	56.3
<i>A. galaktion</i> ⁺	22	45	48.9
<i>C. ibericus</i> (Purbeck)	1.43	2.14	66.8

L and P are measured in mm; ⁺taken from a photograph without a scale; *measured from a drawing without a scale; Uña 3 & 4 specimens broken, measurements are reconstructions.

Uña (Lower Barremian) closely resemble the Pietraroia frontal (pers ob.).

Only one of the three known specimens of *Celtedens ibericus*, from the late Barremian of Las Hoyas, Spain, has a frontal well preserved enough to measure accurately. It shares the same basic structure of *C. megacephalus*, but can be distinguished by a greater inter-lacrimal width relative to posterior parietal margin width. This gives the frontals a more waisted appearance. From measurements taken from the frontals of *A. inexpectatum* the inter-lacrimal width relative to the posterior parietal margin width remains constant (range from 37.7 to 40.3) throughout its growth range (Table 1 & Figure 3).

Therefore, the difference in shape between the frontals from Pietraroia and Las Hoyas does not appear to be due to developmental or environmental factors that could result from ecophenotypic differences due to various factors such as diet and temperature. It could be argued that the differences were due to polymorphism, but there are several frontals from Uña (early Barremian) and none show the shape of the Las Hoyas specimen. On this basis, Las Hoyas albanerpetontids may be specifically distinct from those of Pietraroia and Uña.

The frontals from three of the four remaining localities: Purbeck (Berriasian), Guimarota (Kimmeridgian), and Kirtlington (Bathonian), are also basically similar to

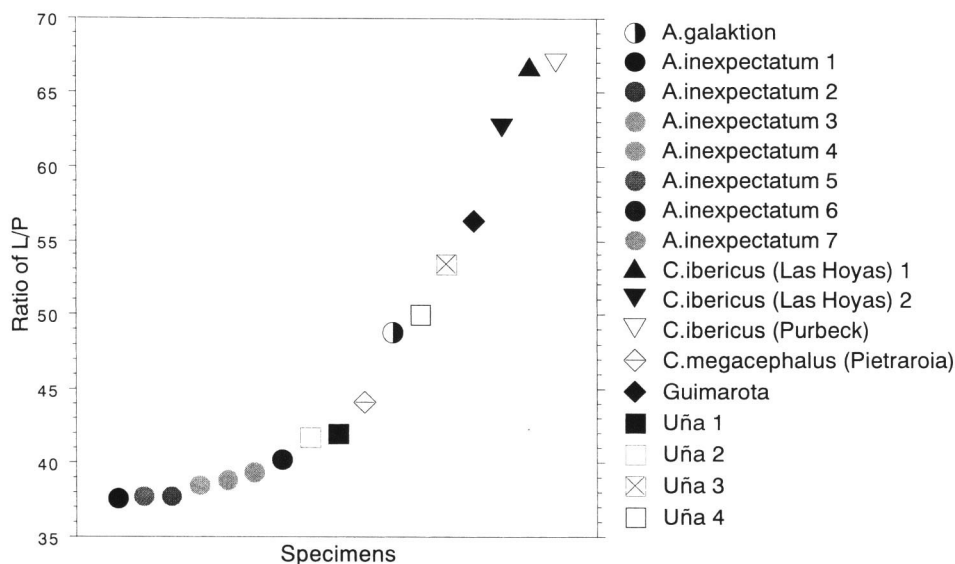


Fig. 3. Distribution of morphologies of albanerpetontid frontals as represented by the ratio of inter-lacrimal width to parietal base width.

those from Pietraroia and Las Hoyas (Fig. 1). However, the curved orbital margins, while running parallel to one another anteriorly, becomes sharply angled posteriorly. The Las Hoyas, Pietraroia and Uña frontals lack this acute lateral angulation. The poor quality of preservation of the Kirtlington and Purbeck frontals make it unwise to use them as the basis of a new species (McGowan, 1996; McGowan & Ensom, 1997). However, there are seven frontals from Guimarota (pers. ob.) that may help to clarify whether this character difference is consistent, and whether a new species or even genus is warranted. The relative positions of the nasal facet and lacrimal facet on a frontal fragment of *Celtdens* from Kirtlington are shown in Figure 4.

Systematic Paleontology

Class Amphibia Linnaeus 1758

Family Albanerpetontidae Fox & Naylor 1982

Contents: Family Albanerpetontidae; Family Prosirenidae Estes 1969 (Part).

Type Genus: *Albanerpeton* Estes & Hoffstetter 1976.

Type species: *Albanerpeton inexpectatum* Estes & Hoffstetter (1976).

Included genera: *Albanerpeton*, *Celtdens*.

Distribution: Middle Jurassic to Miocene of Europe, Early Cretaceous to Palaeocene of North America, Middle Jurassic to Late Cretaceous of Central Asia.

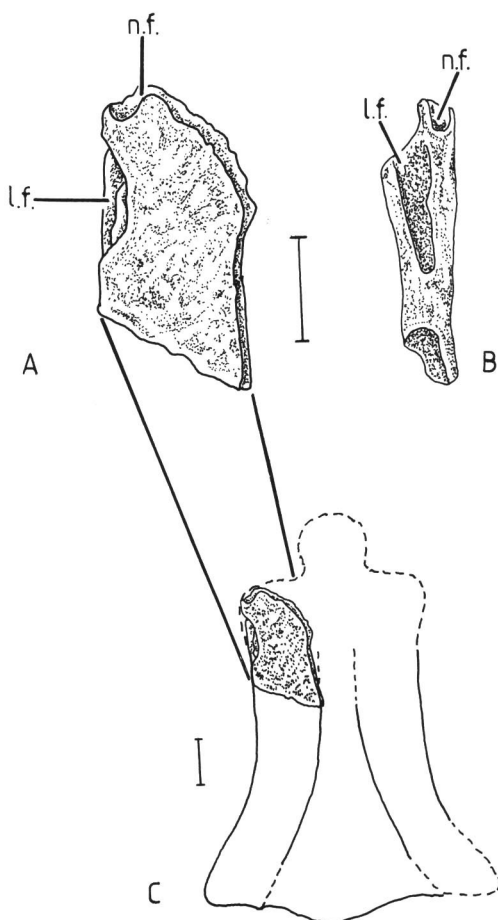


Fig. 4. Frontal fragment (UCK 27) of *Celledens ibericus* from the Bathonian of Kirtlington, Oxfordshire, England. A) Dorsal view, B) Lateral view, C) Position of frontal fragment (UCK 27) in a reconstructed frontal. l.f. – lacrimal facet; n.f. – nasal facet; UCK=University College London, Kirtlington. Scale bars=1 mm.

Diagnosis of family: Small terrestrial amphibians with limbs and a tail; unique polygonal ossification pattern on dermal skull roofing bones which is associated with the polygonal scales that cover the head, body, limbs and at least the base of the tail; unique interdigitating mandibular symphysis; pleurodont, faintly tricuspsate, non-pedicellate teeth; fused frontal; large lacrimal bordering naris and orbit and bearing broad external groove on dorsal surface; parietals with post-orbital process; long needle-like cultriform process on parasphenoid; quadrate-articular joint strongly convexo-concave and lying in horizontal plane; ossified hyobranchus; unique atlas-axis joint in neck, where the atlanto-occipital joint permits movement in the dorsoventral

plane (as in salamanders) and the atlanto-axial joint allows movement in the mesio-lateral plane (unknown in amphibians but similar to mammals); unicipital rib-bearers on amphicoelous monospondylous vertebrae; 20 presacral vertebrae (plus atlas-axis); scapula with long narrow anteriorly projecting scapula blade; humerus with large ball-shaped radial condyle and small ulnar condyle; ossified pubes; tail with more than 24 vertebrae, first seven of which bear transverse processes.

***Albanerpeton* Estes & Hoffstetter 1976**

Type species: *Albanerpeton inexpectatum* Estes & Hoffstetter 1976.

Included species: *Albanerpeton inexpectatum* Estes & Hoffstetter 1976; *Albanerpeton galaktion* Fox & Naylor 1982; *Albanerpeton ?nexusus* Estes 1981.

Distribution: Late Cretaceous (early Campanian to Maastrichtian) of North America, and Miocene of France.

Revised generic diagnosis: As for the family plus; frontal is triangular in shape widest at its posterior parietal margin and narrowest and pointed anteriorly; it has almost straight orbital margins; anterior to the orbital margins the articulation facets for the lacrimals are indented on both sides; the anterior process is narrow and pinched into a sharp point.

***Albanerpeton inexpectatum* Estes & Hoffstetter 1976**

Holotype: LGA-176, a third vertebra co-ossified with the centrum of the second. Middle Miocene, fissure in Milliet Quarry (Paris collection), La Grive-Saint-Alban, France.

Referred material: Many skull elements, vertebrae and limb bones in collections at both Museum National d'Histoire Naturelle, Paris and Université Claude Bernard, Lyon; mandibles in collection at Museum of Comparative Zoology, Harvard University, Cambridge (Mass.), USA.

Distribution: Middle Miocene, La Grive-Saint-Alban, France.

Revised diagnoses: As for the family and genus plus anterior process of the frontal is narrow and spike-like; orbital margin is roughly half the length of the anterior-posterior length of the frontal; sculpture pits deeper and less regular in shape anteriorly and laterally but becoming shallow and more regularly polygonal centrally and posteriorly; in the smallest specimens the base (i.e., posterior parietal margin) is as wide as the anterior-posterior length but in the larger specimens the base is wider.

***Albanerpeton galaktion* Fox & Naylor 1982**

Holotype: UA 16203, a left premaxilla in the collection at University of Alberta, Canada.

Referred material: Specimens from the Upper Milk River Formation, Alberta. Premaxillae UA 16204–16213; maxillae UA 16239–16242; dentaries UA 16217–16223, 16237 and 16238; parietals UA 16214 and 16215; frontal UA 16216; atlantes UA 16224–16235; and numerous uncatalogued premaxillae, maxillae, dentaries, parietals and frontals.

Distribution: Site MR-6, Late Cretaceous (Early Campanian) Upper Milk River Formation, Alberta, Canada. Coordinates on file at the Dept. of Geology, University of Alberta, Canada.

Revised diagnoses: As for family and genus; frontal similar to *A. inexpectatum* but differs in the shape of its anterior process, lacrimal articulations and lengths of its orbital margins; the anterior process appears shorter and broader; the lacrimal facets are less indented (Fig. 1). The orbital margins are still straight edged but lie at a more acute angle than *A. inexpectatum*, and they are longer in proportion to the anterior-posterior length, being more than half the overall length of the frontal (i.e., >55.6%).

***Celtdens* McGowan & Evans, 1994**

Type species: *Celtdens megacephalus* (Costa 1864) (*Triton megacephalus* Costa, 1864; *Heteroclitotriton megacephalus* Kuhn, 1938; *Triturus megacephalus* Kuhn, 1960; *Albanerpeton megacephalus* Estes, 1981).

Diagnosis of genus: As for family plus frontal differs from that of *Albanerpeton* in having a wide bulbous, almost circular anterior nasal process; lacrimal facets not indented; orbital margins curved and longer than half the anterior-posterior frontal length (>60%).

Distribution: Middle Jurassic (Bathonian) to early Cretaceous (Albian) of Europe.

Included species: *Celtdens megacephalus* (Costa, 1864), *Celtdens ibericus* McGowan & Evans 1994.

***Celtdens megacephalus* (Costa 1864)**

Holotype: Almost complete specimen (cat. no. M 542) from the Lower Cretaceous (Albian) of Pietraroia, Italy.

Referred material: Undescribed frontals from the early Cretaceous (Barremian) of Uña, Spain.

Distribution: Early Cretaceous: Barremian of Uña and perhaps Galve II, Spain, and Albian of Pietraroia, Italy.

Diagnosis: As for the family and genus plus frontal has highly curved orbital margins; narrower anterior inter-lacrimal width to posterior parietal margin width than *Celtdens ibericus*.

***Celtedens ibericus* McGowan & Evans 1994**

Holotype: Complete specimen in part and counterpart (Cat. No. LH 6020 A & B) from the early Cretaceous (Late Barremian) of Las Hoyas, Cuenca, Spain.

Referred material: A second complete specimen in part and counterpart (cat. no. LH 030 R A & B) also from Las Hoyas, Cuenca, Spain.

Distribution: Early Cretaceous, Barremian of Spain.

Diagnosis: As for family and genus plus frontal orbital margin differs from *Celtedens megacephalus* in being more curved anteriorly and less curved posteriorly. The inter-lacrimar width is wider in proportion to the base width than that of *Celtedens megacephalus*.

Discussion

As shown above, the frontals of albanerpetontids show diagnostic differences that can be used to separate genera and species. There are clearly two distinct genera; *Albanerpeton* with triangular frontals with a narrow pointed anterior process and straight orbital margins, and *Celtedens* which shows a waisted triangular shape with a bulbous almost circular anterior process and curved orbital margins. Two species are diagnosed on the bases of frontal shape in the genus *Albanerpeton* and two species are diagnosed in the genus *Celtedens*.

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