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Albanerpetontid amphibians from the Lower Cretaceous of Spain and Italy: a description and reconsideration of their systematics

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Albanerpetontids were small, terrestrial amphibians with robust limbs and tails. They are known from deposits from the Middle Jurassic (Bajocian) to the Miocene of Europe, North America and Central Asia. They can be diagnosed by a series of unique derived character states, which include an interdigitating mandibular symphysis, an atlas-axis joint analogous to that of mammals and regular polygonal sculpturing on dermal roofing bones of the skull. They remained remarkably conservative throughout their long history, but the shape of their frontals appears to diagnose genera as well as species. Previous descriptions of albanerpetontids were based on disarticulated remains. Described here in detail are two complete specimens from the Cretaceous (Berriasian) of Spain; one, particularly well-preserved specimen has traces of skin and possibly male courtship glands. A description of the albanerpetontid specimen from the Cretaceous (Albian) of Italy is also given. Previous authors have placed albanerpetontids as either true caudates or as a sister-group of caudates. This new material helps to clarify the systematic position of the group; character analyses show them to be clearly not true caudates but possibly a sister-group of salamanders plus frogs (±gymnophionans). Their relationships with Palaeozoic amphibians remains equivocal with an ancestor most likely to be found in either the microsaurs, or amphibamid or branchiosaurid temnospondyls.
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ADDITIONAL KEYWORDS: Mesozoic – morphology – fossils – *Celtedens* – phylogeny.

INTRODUCTION

The Albanerpetontidae is a group of fossil amphibians, known from deposits of Middle Jurassic to Miocene age, in Europe; Lower Cretaceous to Palaeocene of North America; and Middle Jurassic to Upper Cretaceous of Central Asia. With the exception of a short paper briefly describing this material from Las Hoyas (McGowan & Evans, 1995), all discussions of albanerpetontid morphology and relationships have been based on disarticulated elements (Estes, 1969, 1981; Nessov, 1981; Fox & Naylor, 1982; McGowan, 1996; McGowan & Ensom, 1997, 1998; Gardner & Averianov, 1998) and the poorly described partial skeleton from the Lower Cretaceous of Pietraroia, Italy (Costa, 1864; D'Erasmo, 1914; Estes, 1981; Barbera & Macuglia, 1991).

The genus name *Albanerpeton* was first used to describe a new taxon from the Middle Miocene of La Grive-Saint-Alban, France (Estes & Hoffstetter, 1976). This type species, *Albanerpeton inexpectatum*, was originally assigned to the family Prosirenidae based on 'the presence of a distinctive interlocking mandibular symphysis and faintly tricuspid, non-pedicellate teeth', characters presented as diagnostic of the family (Estes, 1969; p 88). However, the original description of *Prosiren* (Goin & Auffenberg, 1958) based on dorsal vertebrae had not been given due consideration.

The holotype of *Prosiren elinorae*, a dorsal vertebra, from the Antlers Formation (Albian), Texas, USA, was originally assigned to the Sirenidae (Goin & Auffenberg, 1958). However, Estes (1969) described new dissociated vertebrae and skull elements from a neighbouring locality in Wise County, Texas, and suggested that all this new material belonged to the same species, because of the apparent lack of alternative species at this locality. The jaw material was later

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separated from the vertebrae by Fox & Naylor (1982) and placed in the new species *Albanerpeton arthridion*. Estes (1969) relocated *Prodesmodon copei* (originally described as a plethodontid salamander based on its opisthocoelous vertebrae by Estes, 1964) to Prosirenidae on the basis of the similarity of the skull elements including the interlocking symphysis of the dentaries and 'faintly tricuspid, non-pedicellate teeth'. However, vertebrae of *Prodesmodon copei* are remarkably different from *Prosiren elinorae* and were subsequently shown to be similar to the batrachosauroidid salamander *Opisthotriton* (Naylor, 1979) leaving only the associated dentaries referred to the 'prosirenids'. These jaw elements were later attributed to a new species, *Albanerpeton nexuosus* (Estes, 1981).

In 1981, Estes wrote a detailed discussion of the systematics of albanerpetontids [prosirenids] in which he included *Prosiren elinorae* and *Ramonellus longispinus*: an early Cretaceous salamander from Israel (Nevo & Estes, 1969). *Ramonellus* was erroneously linked to prosirenids (albanerpetontids) on the basis of its weakly ossified postcranial skeleton; a condition thought to exist in the partial skeleton of an albanerpetontid from the Lower Cretaceous locality of Pietraroia, Italy (Costa, 1864). However, the Pietraroia fossil is poorly preserved postcranially rather than poorly ossified (see description). The extremely well ossified postcranial skeletons of the Las Hoyas albanerpetontids (see description) support this view.

Nessov (1981) described the first Asian albanerpetontids, from the Upper Cretaceous of Uzbekhistan, Central Asia. These were assigned to a new genus and species, *Nukusurus insuetus*. Nessov attributed this material to the family Albanerpetontidae crediting this new taxon to Fox and Naylor, although Fox and Naylor's study was published the following year. Gardner & Averianov (1998) reported that none of the material assigned to this new taxon could be identified beyond the family level and designated it as *nomen dubium.* This supported the view of McGowan (1994) that the characteristics used by Nessov (1981) in erecting this new genus were indistinguishable from the range of variation seen in other albanerpetontid material from other localities.

Fox & Naylor (1982) highlighted the fact that the type specimen of the Prosirenidae, *Prosiren elinorae*, was a dorsal vertebra. They suggested that subsequent referrals should be based on vertebrae and not other elements such as mandibles. In describing new albanerpetontid material from the Campanian of Alberta, Canada, they showed that the vertebrae of *Prosiren* and *Albanerpeton* were diagnostically different. They assigned *Albanerpeton* to a new family, the Albanerpetontidae, and proposed that the family Prosirenidae should consist of only *Prosiren elinorae* and possibly *Ramonellus longispinus*. They proposed the following features of *Albanerpeton* as diagnostic: the cervical vertebrae, of which the first 'three' vertebrae form a mammal-like 'atlas-axis' complex; the peculiar dentary with its interlocking symphysis; the pleurodont, nonpedicellate, slightly tricuspate teeth; and the unicipital rib-bearing, amphicoelous vertebrae. These characters, plus another ten, making 13 in all, were put forward by Fox and Naylor as evidence that albanerpetontids were not caudates since none of these characters were apparently found in salamanders. They argued that this warranted placing albanerpetontids in a new order, Allocaudata, emphasizing that the relationships of this group to both Palaeozoic and extant amphibians was unclear.

Estes & Sanchiz (1982) disagreed with Fox and Naylor's explanation about the differences between *Prosiren* and *Albanerpeton* vertebrae and with the creation of the family Albanerpetontidae, but they did not discuss this in any detail. Similarly, Duellman & Trueb (1986) continued to use Prosirenidae *s.s.* with no mention of the Albanerpetontidae. Trueb & Cloutier (1991) dismissed the Albanerpetontidae and argued for the 'prosirenids' as true caudates with *Karaurus* as the sister-taxon of Caudata (Urodela).

Milner (1988) followed Fox and Naylor's diagnosis of the Albanerpetontidae as being separate from the Prosirenidae, but considered them to be of 'indeterminate relationship' due to the paucity of material and characters available for analysis at the time. More recently, Evans & Milner (1996) supported this separate plesion of albanerpetontids although they did not discuss it in detail.

The genus *Celtedens* was erected by McGowan & Evans (1995) based on the shape of the frontals, which they suggest as being more robust indicators of specific and generic differences than those used previously (McGowan, 1998). Two species were described within this genus, *Celtedens megacephalus* and *C. ibericus*. The former species includes the holotype, an incomplete articulated specimen from the Albian of Pietraroia, Italy (McGowan & Evans, 1995), disarticulated material from the Bathonian of Kirtlington, England (McGowan, 1996), and the Berriasian of Purbeck, England (McGowan & Ensom, 1997). The latter species is based on the most complete articulated specimens, including the holotype, from the Barremian of Las Hoyas, Spain (McGowan & Evans, 1995).

Based on an incomplete atlantal centrum, Nessov (1997) erected the new genus and species, *Bishara backa,* from the Santonian/?Campanian locality of Baybishe in south central Kazakhstan from the Bostobe Formation. This specimen has apparently been mislaid but has been reinterpreted as a true caudate specimen based on published photographs

(Nessov, 1988 pl.16, Fig. 12; 1997 pl. 10, Fig. 3) by Gardner & Averianov (1998). In addition, Nessov (1997; see also Nessov & Udovichenko, 1986) also described a new species, *Nukusurus sodalis*, based on a single fragmentary dentary from the Coniacian locality of Dzhyrakuduk, in the Kyzylkum desert of north central Uzbekhistan. Gardner & Averianov (1998) reported that the specimen could not be identified beyond the family level and designated it as *nomen dubium*.

With the exception of the poorly preserved partial skeleton from Pietraroia, the Las Hoyas material provides the only complete articulated albanerpetontids. One specimen (LH 6020) has preservation of both hard and soft parts including possible glands in the thighs and polygonal scales that cover the animal from head to tail. The recovery of the articulated specimens from the Lower Cretaceous (late Barremian) of Las Hoyas, Cuenca, Spain has permitted a much more detailed reconstruction and description of albanerpetontids and increases our understanding of the group.

NOTE CONCERNING TERMINOLOGY

I shall use the term Caudata (*sensu* Milner, 1988) to mean the stem group plus the crown group of salamanders and Urodela to mean the crown group only. Evans & Milner (1996) have discussed this standardization of the use of these terms. No phylogenetic meaning is implied here by the use of the term Lissamphibia. It is merely a useful way of addressing the three living orders of Amphibia.

ABBREVIATIONS USED IN FIGURES

a – atlas, ar/art – articular, c – centralia, co – coracoid, cp – cultriform process, d – dentary, dc – carpals, f – frontal, fe – femur, fi – fibula, fib – fibulare, hu – humerus, hyo – hyobranchus, i – ischium, il – ilium, in – intermedium, j – jugal, l – lacrimal, mx – maxilla, n – nasal, p – parietal, pa – parasphenoid, pm – premaxilla, pra – prearticular, pu – pubis, qu – quadrate, r – radius, ra – radiale, rc – radial condyle, sc – scapula, sph – spherules, sq – squamosal, t – tibia, ta – tarsalia, ti – tibiale, u – ulna, ul – ulnare.

SYSTEMATIC PALAEONTOLOGY

CLASS AMPHIBIA LINNAEUS, 1758

FAMILY ALBANERPETONTIDAE FOX & NAYLOR, 1982

The new material from Spain and the Pietraroia specimen can be differentiated from more recent albanerpetontids on the shape of their frontals which differ from those of the genus *Albanerpeton* (McGowan & Evans, 1995; McGowan, 1998). The *Albanerpeton* frontal is strongly triangular, has a narrow, pointed anterior process and relatively straight orbital margins (Estes & Hoffstetter, 1976; McGowan & Evans, 1995). The Spanish and Italian specimens have frontals with a bulbous, almost circular anterior process, and highly curved orbital margins; they are narrowest mid-way along their length. By comparison with the albanerpetontid material from the Miocene of La Grive-Saint-Alban, France (Estes & Hoffstetter, 1976) and modern salamanders, these differences have been interpreted as significant at the generic level (McGowan & Evans, 1995; McGowan, 1998). More subtle differences between the Spanish and Italian specimens (discussed below) suggest that they may be specifically distinct.

Celtedens McGowan & Evans, 1995

Type species: Celtedens megacephalus (Costa, 1864) (*Triton megacephalus* Costa, 1864; *Heteroclitotriton megacephalus* Kuhn, 1938; *Triturus megacephalus* Kuhn, 1960; *Albanerpeton megacephalus* Estes, 1981).
Diagnosis of genus: An albanerpetontid in which the frontal differs from that of *Albanerpeton* in having a wide bulbous, almost circular anterior process; orbital margins curved and longer than half the anterior-posterior frontal length (>60%).
Distribution: Middle Jurassic (Bathonian) to Lower Cretaceous (Albian) of Europe.
Included species: Celtedens megacephalus (Costa, 1864), *Celtedens ibericus* McGowan & Evans (1995).

Celtedens megacephalus (Costa, 1864)

Holotype: Almost complete specimen (M 542) from the early Cretaceous (Albian) of Pietraroia, Italy. Lacks details of postcranial skeleton and palate and premaxilla region.
Referred material: Undescribed frontals from the early Cretaceous (Barremian) of Uña, Spain; disarticulated cranial and postcranial remains from the Middle Jurassic (Bathonian) of Kirtlington, Oxfordshire, England and Cretaceous (Berriasian) Limestone Group, Purbeck, Dorset, England; also disarticulated material from the Cretaceous (Kimmeridgian) of Guimarota, Portugal (McGowan, 1998).
Distribution: Bathonian to Albian of Western Europe.
Diagnosis: As for the genus; the frontal has highly curved orbital margins and a narrower anterior interlacrimal width to posterior parietal margin width in comparison with *Celtedens ibericus*.

Celtedens ibericus McGowan & Evans, 1995

Holotype: Complete specimen in part and counterpart (LH 6020 A & B) from the Lower Cretaceous (late Barremian) of Las Hoyas, Cuenca, Spain. Lacking only the distal part of the tail and details of the palate.

Referred material: Two complete specimens in part and counterpart (LH 030 R A & B; LH 15710 A & B) also from Las Hoyas, Cuenca, Spain.
Distribution: Early Cretaceous (Barremian) of Las Hoyas, Spain.
Diagnosis: As for the genus; plus frontal orbital margin differs from *Celtedens megacephalus* in being more curved anteriorly and less curved posteriorly. The interlacrimal width is wider in proportion to the base width than that of *Celtedens megacephalus*.

DESCRIPTION OF LAS HOYAS ALBANERPETONTIDS

GEOLOGICAL SETTING

The fossil locality of Las Hoyas is situated about 20 km east of the city of Cuenca, in Cuenca Province, Castilla-La Mancha, central Spain (Fig. 1). The area around the fossil site is composed of Mesozoic (Triassic to late Cretaceous) rocks lying on a Palaeozoic base. The fossiliferous beds of Las Hoyas are primarily composed of limestones, which are believed to have formed from alluvial and lacustrine deposits. The outcrop has been correlated with the limestone beds of the La Huérguina Formation from the lowest part of the Lower Cretaceous ('Weald') in the south-western Iberian range (Sanz *et al.*, 1990). Although the Las Hoyas beds have not been precisely dated they are believed to be around late Barremian based on its correlation with the La Huérguina Fm., which has been dated on its rich charophyte assemblage (Fregenal-Martinéz & Meléndez, 1995). For a more complete discussion of the geology, see Sanz *et al.* (1990).

The Las Hoyas locality has yielded a wealth of fresh-water and terrestrial flora and fauna including crustaceans, insects, fish, albanerpetontids, salamanders, frogs, turtles, lizards, crocodiles, dinosaurs and birds (Sanz *et al.*, 1988, 1990; Pérez-Moreno *et al.*, 1994; Evans & Milner, 1996; Evans & Barbadillo, 1997, 1998, 1999).

MATERIAL

LH 6020, the holotype of *Celtedens ibericus* (McGowan & Evans, 1995), consists of both part and counterpart. This is an almost complete specimen seen in ventral view (Fig. 2). The skull is well preserved, however, it appears that the skeleton was dorsoventrally flattened and the bedding plane runs through the bone. The paired parietals, frontal and parts of the upper jaw are clearly seen. Most of the dentition is missing, although a few preserved teeth show the faintly tricuspate shape typical of albanerpetontids. The tail in this specimen is incomplete, but is marginally longer than that of LH 030 R, with only the posterior part missing. Measurements were taken of the skull, limb lengths and overall body dimensions (Table 1). In addition to the skeleton, there has been preservation of some soft structures; surrounding the skeleton are faint remains of skin and lying within the skin of each thigh are remains of what appear to be femoral glands (Fig. 2 and see Dermal Structures description).

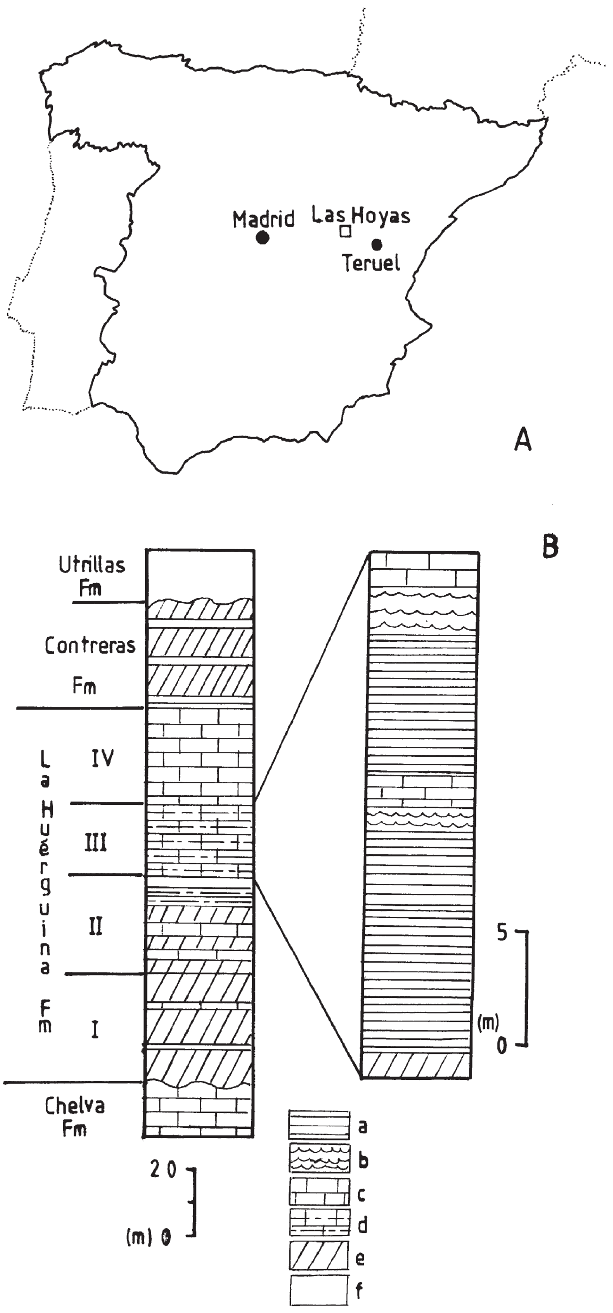


Figure 1. A, The Las Hoyas fossil locality in central Spain. B, Geological section of the Las Hoyas fossil locality (after Sanz *et al.*, 1988). (a) Laminated facies, (b) Flaggy facies, (c) Massive facies, (d) Limestone with laminites, (e) Silt and clay, (f) Sand.

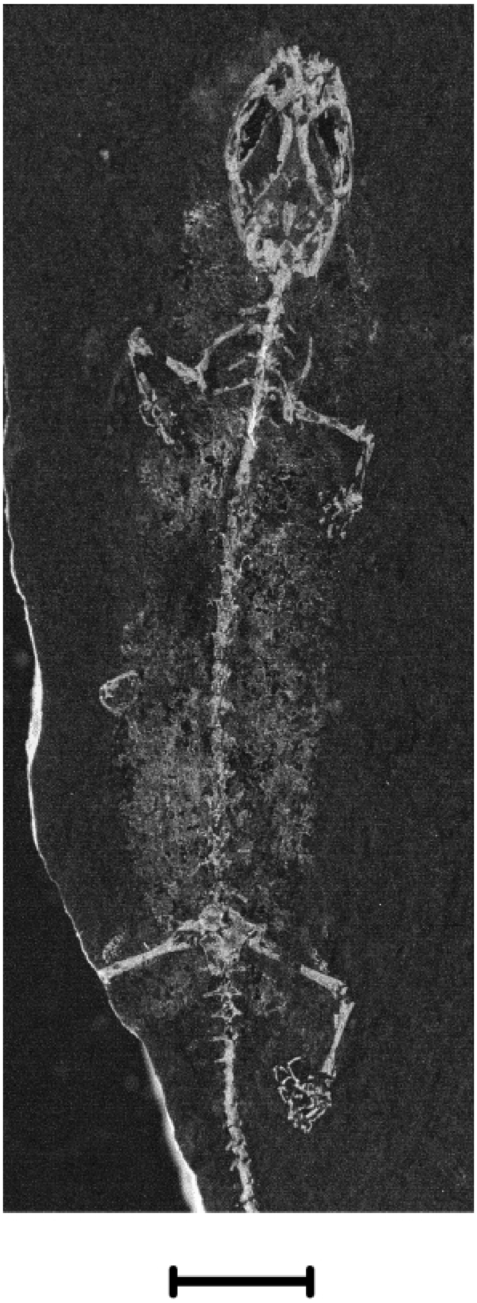


Figure 2. *Celtedens ibericus*, LH 6020, from Las Hoyas, Spain. Shows outlines of dermis. Scale bar = 1 cm.

LH 030 R (A & B) consists of both part (Fig. 3) and counterpart of an almost complete specimen seen in lateral view. Although the skull is poorly preserved, several teeth are visible and are similar to those of other albanerpetontids. Limbs are preserved in part, as are most of the trunk vertebrae, but the tail is incomplete. Body dimensions (Table 1) are similar to those of LH 6020.

LH 15710 is less well preserved than the previous two specimens. It consists of the skull and anterior half of the body up to the 10th thoracic vertebra. No limbs or girdles are preserved. LH15710a shows the unique atlas and axis in articulation with the occiput, but otherwise reveals fewer details than the counterpart. The cranium appears quite solid and well fused, but is too poorly preserved to highlight its finer details. The counterpart, LH15710b, shows clearer details of the skull, which is smaller than the other two specimens, being only 8 mm long.

General features of the skull

The following description is based on LH 6020, unless otherwise stated. The overall length from the anterior edge of the premaxillae to the rear of the cranium is 12.5 mm. The width of the skull, at its widest point between the orbits is 7.5 mm (Figs 4 and 5). The skull is olive-shaped and does not appear to have been distorted during preservation. The premaxillae have long ascending nasal processes and abut medially, but do not appear to be fused as has been noted in some premaxillae from La Grive-Saint-Alban (Estes & Hoffstetter, 1976). The right premaxilla bears five broken teeth with space for three or four more; the left has three to five with spaces for four or five more (Fig. 5), making an estimate of 8–10 teeth in each premaxilla. Only one tooth crown (right premaxilla) has preserved its overall shape and has the slightly tricuspate shape, which is diagnostic of albanerpetontids. Foramina are seen on the labial surface of the premaxillae of LH 15710b.

The maxillae articulated with the premaxillae anteriorly and with the lacrimal anterolaterally. From the level of the lacrimal, the maxillae run posteriorly approximately three-quarters the length of the orbits, forming the ventrolateral margin of the orbits. The maxillae taper posteriorly and bear an articular facet on the dorsal edge (Fig. 6). This facet was probably for the bone (jugal?) that lies immediately above it and, on the part block, is partially in articulation with it (see below).

The lacrimals are relatively large with a convex curved anterior edge, which formed the posterior border of the external naris. The posterior edge of the lacrimal formed the anterior border of the orbit. Laterally, it appears to have articulated with the maxilla and medially with the nasal and frontal. There is no indication of a separate prefrontal, but the large lacrimal may consist of a fusion of the prefrontal and lacrimal proper. There is only one known example of a prefrontal, described by Estes & Hoffstetter (1976) for the *A. inexpectatum* material from the Miocene of France. This prefrontal is solidly fused to the lacrimal of specimen MNHN.LGA 1226. Gardner

Table 1. Body proportions of Las Hoyas albanerpetontids (all lengths in mm)

Specimen	LH 030 R	LH 6020
Snout to vent length	59.5	51
Tail length	16	27
Skull length	13	12.5
Humerus (right)	6	4.5
Humerus (left)	5.75	4.5
Radius & ulna (right)	4.25	4
Radius & ulna (left)	4	3
Femur (right)	7.5	6+
Femur (left)	8.25	6.25
Tibia & fibula (right)	5+	(off block)
Tibia & fibula (left)	5.25	4.25
Number of presacral vertebrae	22	22
Number of caudal vertebrae	13 (incomplete)	24 (incomplete)
Ratios relative to snout to vent length		
Skull	4.5 : 1	4.08 : 1
Humerus	9.92 : 1	11.33 : 1
Radius & ulna	14 : 1	12.75 : 1
Femur	7.2 : 1	8.16 : 1
Tibia & fibula (incomplete)	(incomplete)	12 : 1

(2000) argues that it is this prefrontal that articulates with the frontal not the lacrimal. The preservation of the Las Hoyas specimens does not help clarify the situation.

Medial to the lacrimals are the long, slender nasals, which articulate with the premaxillae anteriorly on the lateral edge of the ascending alary process and with the frontal posteriorly, at the level of the anterior margin of the orbit. The nasal facet on the frontal is damaged, but from disarticulated frontal material from other localities, the nasal probably articulated with a concave facet on the anterolateral edge of frontals. The rounded internasal process can still be determined on LH 15710a and faintly on LH 6020 (Figs 4 and 5). Except for its anterior part, the nasal articulated with the lacrimal laterally. The nasal formed the medial margin of the external naris anteriorly, but did not enter the orbit. Estes & Hoffstetter (1976) described similar bones in *Albanerpeton inexpectatum* as prefrontals. There are several reasons why these long slender bones are best described as nasals and not prefrontals:

i) In their reconstruction of *A. inexpectatum* Estes & Hoffstetter (1976) alluded to the presence of small oval nasals lying medial to their prefrontals (sic), although no such elements were found. They probably based their reconstruction on the drawings of the skull of *Celtedens megacephalus* by Costa (1864) and D'Erasmo (1914) to which it has a certain resemblance. In their figures, both Costa and D'Erasmo showed small oval nasal bones lying medial to the prefrontals. However, it can be seen from Fig. 13 that no small oval bones are apparent in this region of the skull of *C. megacephalus*. In addition, no small oval bones have been described from any other albanerpetontid localities.
ii) The long slender nasals of *C. ibericus* border the external naris but do not enter the orbital margin as would be expected of a bone in the orbital series.
iii) The reconstruction of the La Grive-Saint-Alban material (Estes & Hoffstetter, 1976) shows the lacrimal lying further forward than in the Spanish and Italian specimens. The nasal (their prefrontal), is positioned slightly more to the rear and overlaps the lacrimal. This reconstruction suggests that the lacrimal does not articulate directly with the frontal in the French material although it apparently does in both the Las Hoyas and Pietraroia fossils. An articulation between the frontal and lacrimal is suggested from disarticulated frontals from other localities. These show two articulation facets on the anterolateral margin of the frontal, one is more anterior and lies slightly above the second (McGowan, 1998: Fig. 5). The former is for articulation with the nasal, the latter with the lacrimal.
iv) In extant amphibians, the prefrontals tend to be reduced in size or lost prior to the nasals. Since the small oval nasals described by previous authors do not appear to exist, the long slender bones that articulate

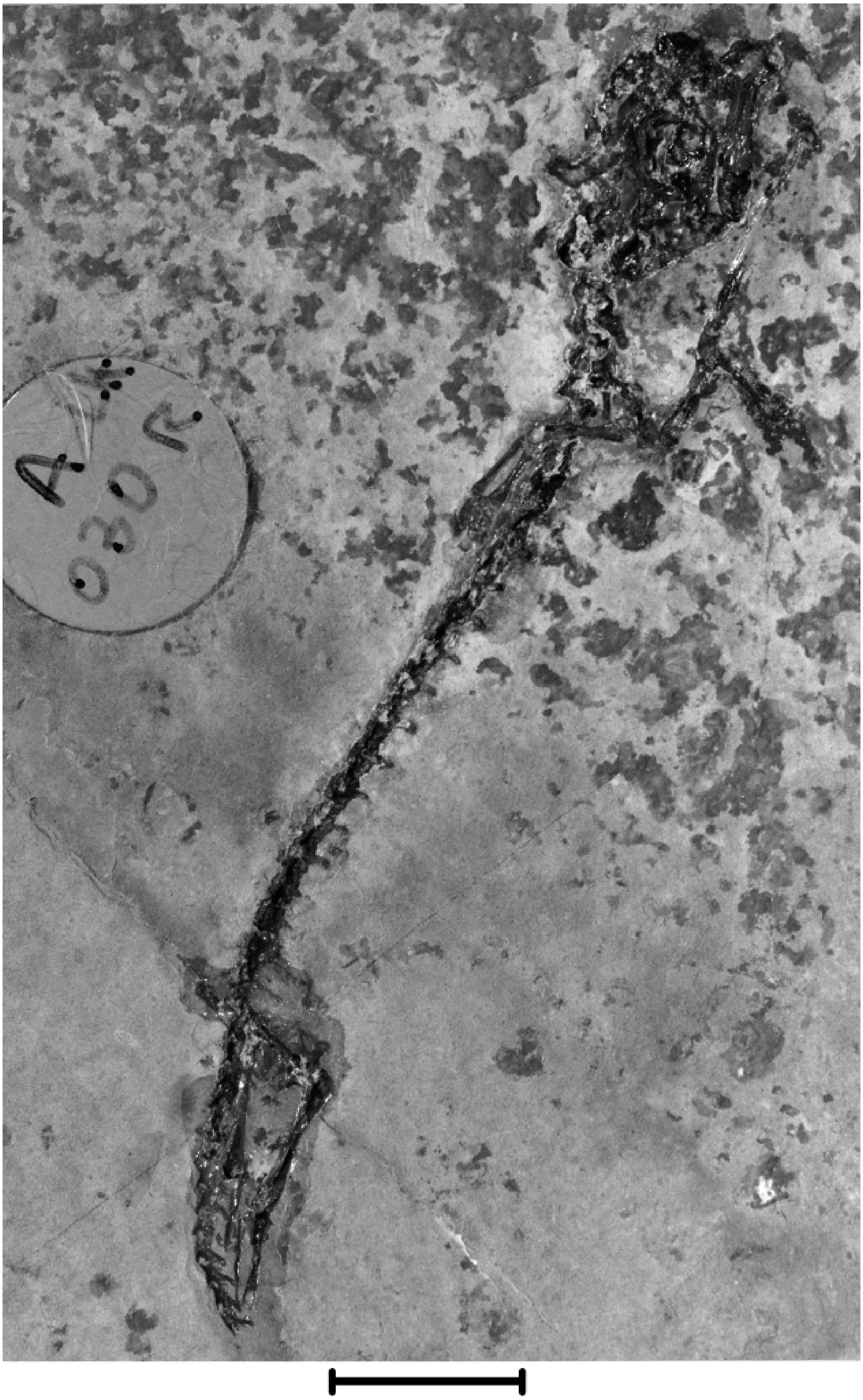


Figure 3. *Celtedens ibericus*, LH 030 RA (part block), from Las Hoyas, Spain. Scale bar = 1 cm.

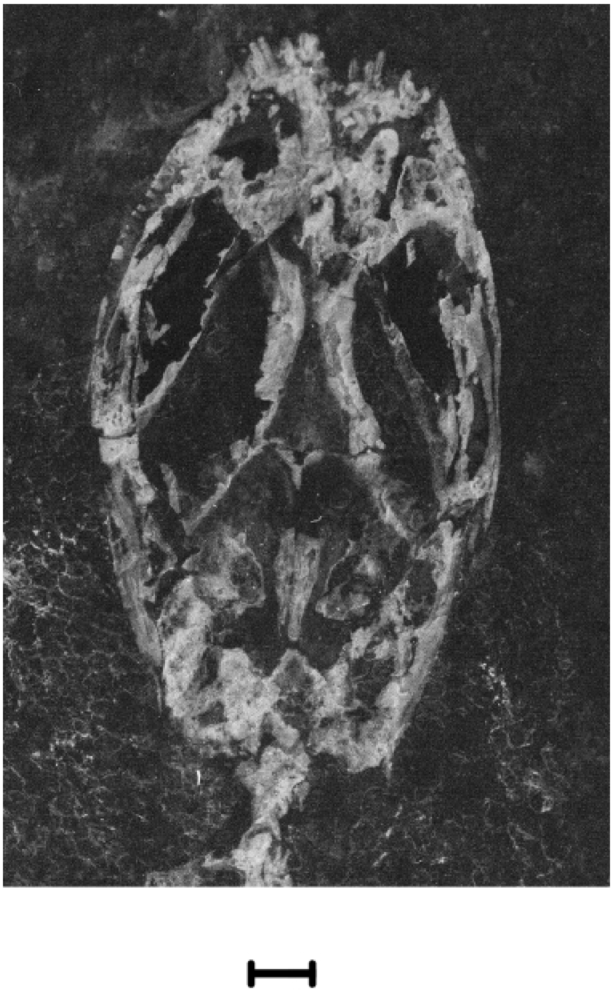


Figure 4. *Celtedens ibericus* skull, LH 6020, from Las Hoyas, Spain. Scale bar = 1 mm.

with the frontals, premaxillae and lacrimals and form a border of the external nares are best interpreted as the nasals.

(v) Prefrontals may exist in albanerpetontids but not as separate bones. From the only known documented prefrontal of *A. inexpectatum* (Estes & Hoffstetter, 1976) it appears that the lacrimals and frontals may be solidly fused together. However, this situation remains unclear in both the Las Hoyas and Pietraroia specimens.

vi) The skulls of albanerpetontids are heavily ossified and show a general reduction of elements and a fusion of bones, the presence of two small bones between the premaxillae and frontal would only serve to weaken the skull at this point. Despite Gardner's (2001) passionate arguements that these two small oval bones should exist there appears to be no logical reason for their presence. Gardner (2000) even suggested that he could see bone material between the right premaxillae and the frontal of LH 6020 based on an examination of a photograph. However, by examining the specimen it is clear that this bone material belongs to the palatine of the palate on that side. The right premaxilla has been anteriorly disarticulated giving the false impression that there is space for a bone between the premaxilla and frontal on that side. The left premaxilla is not disarticulated and clearly shows no space for a small oval bone between it and the frontal. Gardner did not discuss why there was no equivalent bone material on the contarlateral side, which lacks the palatal remains on that side. In addition, the Pietraroia specimen also shows no evidence of a small oval bone. More complete albanerpetontid skulls are required to clarify this interpretation.

Lying medially and forming the medial borders of the orbits is the fused frontal, which articulated with the nasals and probably with the lacrimals anterolaterally (Fig. 5). Posteriorly, the frontal abuts against the paired parietals. There does not appear to have been any overlap between the frontal and the lateral flanges of the parietal, in contrast to the condition in material from other localities, such as La Grive-Saint-Alban (Estes & Hoffstetter, 1976). Under ultraviolet light, faint traces of a hexagonal pattern can be seen through the thin central portion of the frontal (Fig. 4). This hexagonal sculpture pattern reflects the typical pattern of the dermal scales found covering the animal.

Immediately posterior to the frontal are the paired parietals, which abut in the midline with no apparent overlap (Fig. 5). The anterolateral edges of the parietals form the posterior margins of the orbits. The hexagonal pattern seen in the frontal continues onto the anterior half of the parietals.

Lateral to the parietals, on both sides of the skull, are what appear to be the remains of quadrate and squamosal elements (Figs 4 and 5). The quadrates are large and roughly rectangular. They meet the cranium dorsolaterally and the squamosals laterally. The squamosals are relatively narrow anteriorly, but widen posteriorly where they met the cranium. The articulars have close fitting joints with the quadrates, at the level of the posterior borders of the orbits. The joint is clearest on the right (Fig. 5).

Another element, unknown from any previously described albanerpetontid material, is seen medial to the left maxilla, dentary and squamosal. This thin bone articulates with the labial surface of the left maxilla and then runs posteriorly to end just behind the level of the orbit (Fig. 5). The LH 030 R specimen shows a bone in the same position (but in lateral view). This element is narrow and tapers anteriorly where it meets the maxilla, but becomes much wider posteriorly (Fig. 6). A similar element exists in the *Celtedens megacephalus* from Pietraroia, Italy. From disarticu-

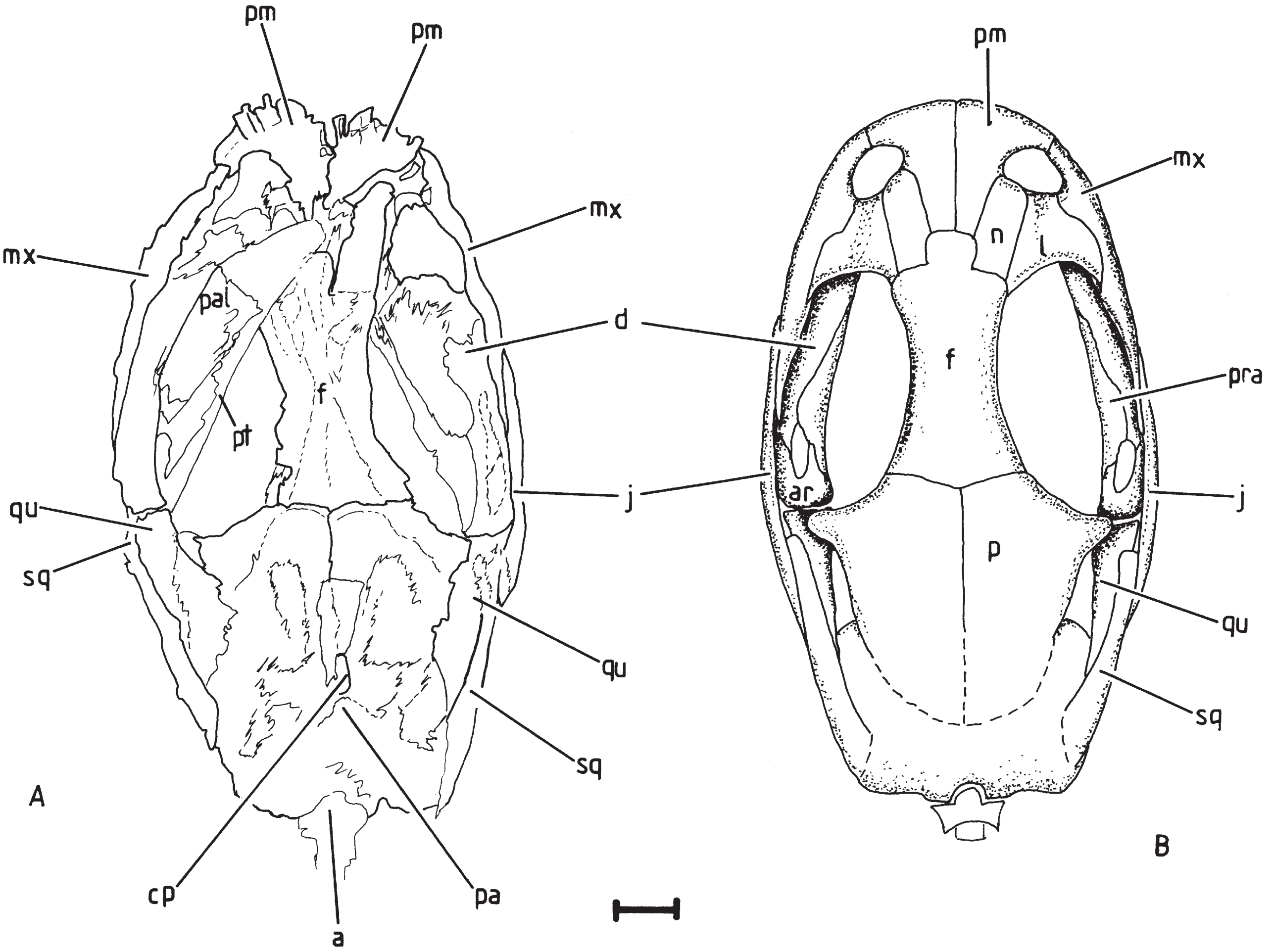


Figure 5. Skull of LH 6020 – the holotype of *Celtedens ibericus*, Las Hoyas, Spain, with a reconstruction on the right. Scale bar = 1 mm.

lated material, from the Miocene of La Grive-Saint-Alban, France, a facet on the posterior margin of the maxilla indicated the presence of another element (Estes & Hoffstetter, 1976; Fox & Naylor, 1982). This element is best interpreted as the jugal and provides the first evidence of the jugal in an albanerpetontid (McGowan & Evans, 1995).

Below the posterior part of the parietal, there is a small median columnar-like bone, which is probably the remains of the cultriform process of the parasphenoid. Immediately behind it lies the triangular parasphenoid, apparently fused to the rest of the braincase. The individual bones of the braincase cannot be identified, since there are no indications of sutures that would distinguish individual elements (Figs 4 and 5).

There appear to have been two palatal elements on each side of the skull, a pterygoid posteriorly and a palatine anteriorly (Fig. 6). The medial palatal element, the pterygoid, is widest posteriorly and has a long narrowing process running anteriorly. The anterolateral palatine, is approximately 2 mm wide and runs anteriorly where it tapers at the anterior level of the frontal. The pterygoid articulates with the palatine along a facet that runs diagonally towards the midline. Both pterygoids appear to have a facet at their most anterior edge, on a level with the anterior edge of the orbit (Figs 2 and 3). The arrangement of these palatal elements suggests the presence of large palatal vacuities.

No palatal elements have previously been described for albanerpetontids. Fox & Naylor (1982) mentioned the presence of palatal elements inferred from a facet on the maxilla. Neither bone is likely to be an ectopterygoid since this bone is much reduced in dissorophoid temnospondyls (Milner, 1993) and is lost or much reduced in living amphibians (Duellman & Trueb, 1986). In addition, there is a tendency to reduce or lose this element before the other two in higher tetrapods (Romer & Parsons, 1978).

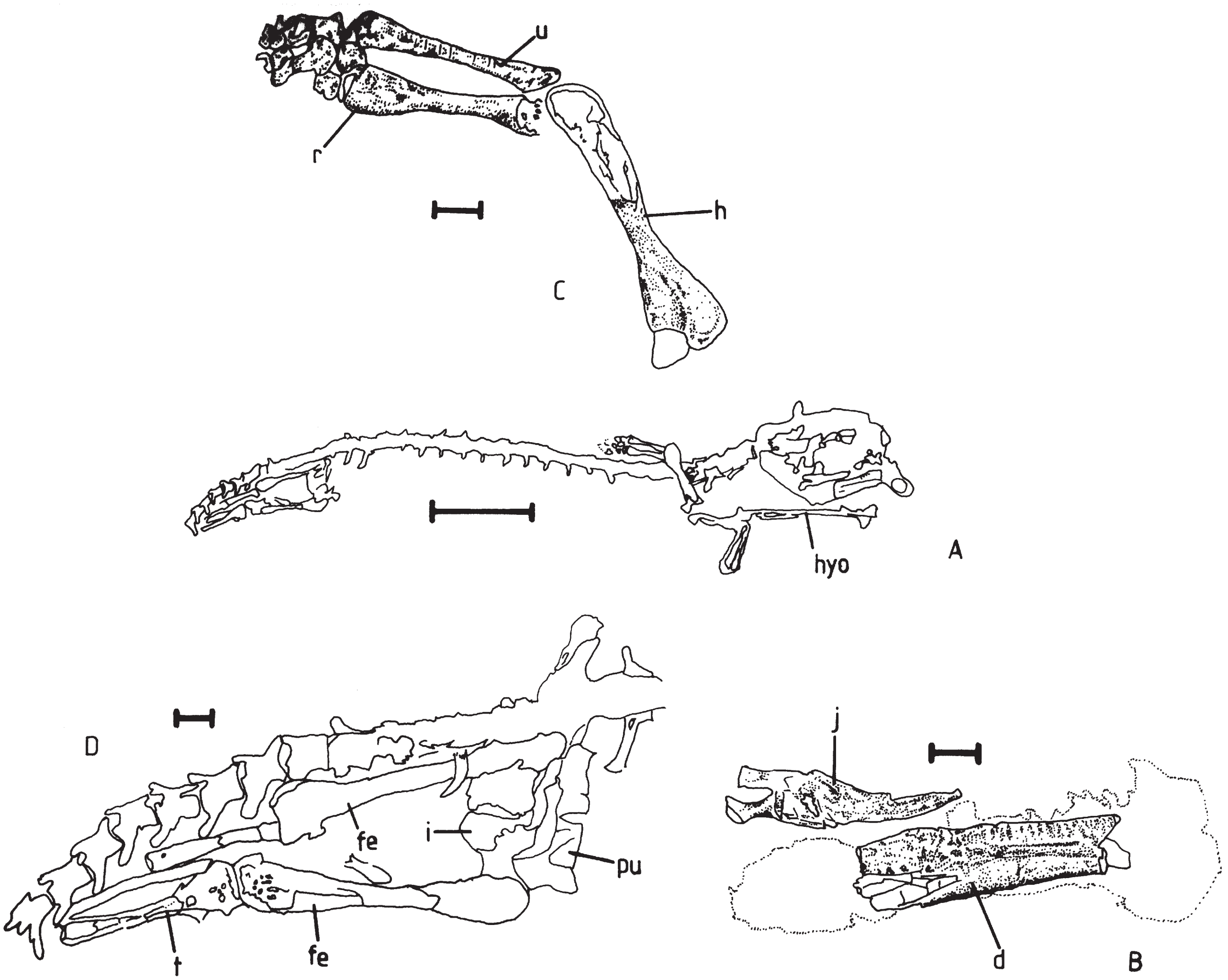


Figure 6. A, Outline drawing of LH 030R. Scale bar = 1 cm. B, Enlarged detail of dentary and jugal. C, Forelimb detail showing humerus, radius, ulna and wrist bones. D, Detail of tail and hindlimbs. B, C & D scale bars = 1 mm.

The dentaries are robust, well ossified and typically albanerpetontid with an estimate of more than 20 teeth per jaw (Fig. 4). Anteriorly, the dentary curves towards the premaxilla. Posteriorly, both dentaries meet the articulars (Fig. 6).

Lying below the skull of LH 030 is the impression of what may have been the hyobranchial apparatus. Lying within this impression are the remains of some bone material. This impression runs from a level just behind the mandibular symphysis to the level of the atlas (Fig. 7). No details of the elements that composed this apparatus can be distinquished.

AXIAL SKELETON

The atlas of LH 6020 is visible in outline (Fig. 5). Its centrum length is 0.5 mm, which is about one quarter of a dorsal vertebra, i.e. ≈ 2 mm. The anterior cotyles lay at roughly 90° to the main axis of the vertebral column. The left cotyle is still in articulation with its corresponding occipital condyle (Fig. 5). The tuberculum interglenoideum is rounded into a single process. The axis is *in situ* behind the atlas, but shows no details. The atlas of LH15710b is 2 mm at its widest point across the condyles; the axis is roughly 1 mm × 1 mm. Together the atlas-axis length of this specimen is 1.5 mm. The overall length of the atlas–axis complex is 1 mm. Neither atlas nor axis bears ribs. The smaller axis element sits neatly behind the atlas on this specimen and supports the reconstructions given previously (Estes & Hoffstetter, 1976; McGowan, 1994, 1996).

In addition to the atlas and axis, there are 20 presacral vertebrae, all possess a pair of unicapitate transverse processes, bearing a pair of ribs (Figs 4 and 5). The ribs are roughly the same length as the

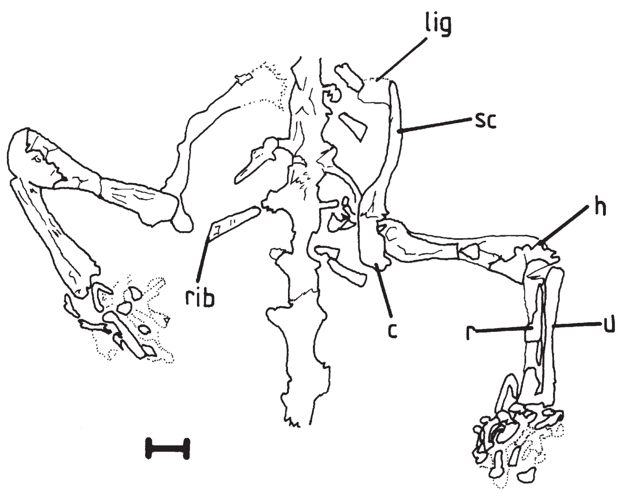


Figure 7. Forelimbs of *Celtedens ibericus* – LH 6020. Scale bar = 1 mm.

centrum (2 mm) and project slightly backwards. They appear spatulate, with the distal ends wider than the proximal. The centra are amphicoelous and hourglass-shaped. The single sacral vertebra is best seen in LH 6020 (see Figs 9 and 10).

Twenty-five caudal vertebrae, with amphicoelous, hourglass-shaped centra bearing haemapophyses, are preserved in LH 6020, although, the tail is incomplete. The length of each caudal centrum decreases from 2 mm to 1 mm between C2 and C24 (C25 is incomplete). The first seven or eight caudals bear transverse processes, which become progressively shorter posteriorly. The eighth caudal vertebra is badly damaged and what seems to be a transverse process could also be the haemapophysis since the vertebral column twists in this region to bring the more posterior vertebrae into lateral view.

FORELIMBS AND PECTORAL GIRDLE

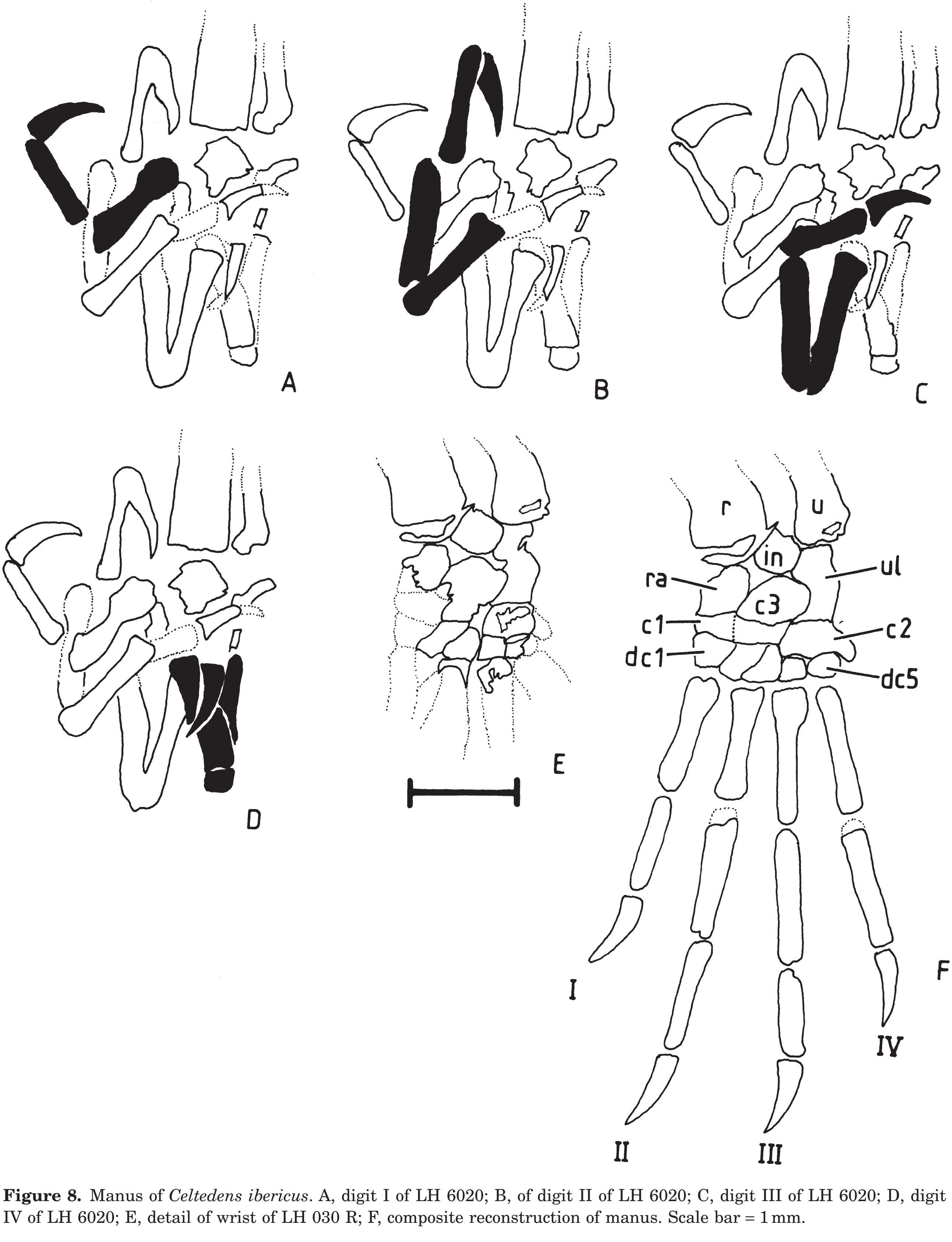
The coracoid is relatively small and forms the anteromedial component of the glenoid fossa. The scapula provides the lateral component. This has a very long narrow blade (Fig. 7). The distal ends of both scapular blades appear to have been attached to either the first or second ribs, possibly by means of ligamentous attachment from the cartilaginous suprascapulae. The presence of a suprascapula is suggested by the slight impression in the matrix at the anterior end of both scapular blades, which may have housed a cartilaginous mass. On the left side, this impression is closely associated with the rib of the second dorsal vertebra. Such an attachment may have given extra support to the pectoral girdle. A similar condition occurs in the pectoral girdle of sirenids where the anteriorly projecting suprascapula attaches to the rib of the third presacral vertebra (pers. obs.).

The humerus of LH 6020 is approximately 4.5 mm long and although only partially preserved, was clearly heavily ossified (Fig. 7). There is a strong ridge proximally that may represent the *crista ventralis humeri*. On the opposite edge, there is apparently no *crista dorsalis humerus*, although this region is damaged. The humeri of LH 030 R, although also damaged, show no trace of a *crista dorsalis humeri*. It is therefore presumed that the humeri of albanerpetontids did not have *crista dorsalis humeri* as is seen in modern salamanders. Towards the distal end of the humerus of LH 6020, the impressions of scales can clearly be seen where the bone of the humerus is missing. Both radius and ulna are approximately 4 mm in length.

The right forelimb of LH 030 R (A) shows a deep fossa in the head of the humerus that presumably accommodated the supracoracoideus muscle. The humeri were well ossified and approximately 6 mm long (Table 2). Distally they had well ossified radial and ulnar condyles. The radial condyle is ball-shaped and roughly twice the size of the ulnar condyle. The right radius and ulna are of similar length, 4.25 mm. The radius is more robust than the ulna (Fig. 6). It is widest at the epiphysis. Both radius and ulna have well-ossified epiphyses. The proximal end of the ulna has a shallow concave fossa for articulation with the ulnar condyle of the humerus.

No Las Hoyas specimen has a complete manus and this has posed problems in its interpretation. However, by using both specimens a composite of the manus has been tentatively reconstructed (Fig. 8).

The carpals are seen most clearly on LH 030, and although poorly preserved, the remains of the digits can be seen in LH 6020. The wrist appears to have retained a primitive arrangement without a great deal of fusion/reduction of elements as seen in modern salamanders and frogs. The wrist clearly consists of separate radiale, intermedium and ulnare proximally. The centralia (c) are less clear. The largest centrale, c3, may or may not be fused to c1 lying immediately below it. Distal to the ulnare is another centrale, c2. This appears to have a possible curved projection, seen only in impression, that partially 'wraps' around one of the distal elements. There are clearly four distal carpals on the part block. These have been numbered dc2–dc5 inclusive. From the outline impression of the carpus on the part block there appears to be space medially to accommodate either another element or an extension of dc2. A tentative reconstruction of three proximal, three medial and five distal elements is given. In LH 6020 the left manus is most complete. The manus is contracted into a balled fist with the digits all curling in the same direction. Digits I and II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dc5
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III
IV

Figure 8. Manus of *Celtedens ibericus*. A, digit I of LH 6020; B, of digit II of LH 6020; C, digit III of LH 6020; D, digit IV of LH 6020; E, detail of wrist of LH 030 R; F, composite reconstruction of manus. Scale bar = 1 mm.

are easiest to interpret and appear to have their full complement of elements, i.e. two and three, respectively; digits III and IV are only faintly preserved and their reconstruction is less certain than the first two digits. They have three and two phalanges, respectively. This gives a phalangeal formula of 2.3.3.2. In the reconstruction of McGowan & Evans (1995), the manus formula was printed incorrectly as (2.3.3.3), however, it was figured correctly as (2.3.3.2).

HIND LIMBS AND PELVIC GIRDLE

The pelvis is comprised of three pairs of elements; pubes anteriorly, ischia posteriorly and bilateral ilia; all were well-ossified (Fig. 9).

The right ischium runs from the level of the anterior cotyle of the first caudal vertebra to the level of the second caudal transverse process. It is subrectangular in shape, widest anteriorly and narrowing only slightly as it runs posteriorly at the level of the ischial process. The anterior and posterior cotyles of the first caudal vertebra can be seen through the damaged left ischium as can the joint between the first and second caudal vertebrae.

The pubes articulate with the ischia at the level of the joint between the sacral and first caudal vertebrae. There is a thin unossified area at the facet between the right pubis and right ischium, which may indicate this area was cartilaginous. Both pubes are roughly one vertebral length long (≈ 2 mm) and lie below the sacral vertebra, whose partial remains can be seen anteriorly (Fig. 9).

Laterally, the ilia are preserved in impression only suggesting that they may have remained cartilaginous at their distal ends (as in modern salamanders; Duellman & Trueb, 1986). There is a thin unossified area at the facet between the right pubis and right ilium, which suggests that this area may have been cartilaginous. A similar but wider strip exists on the left.

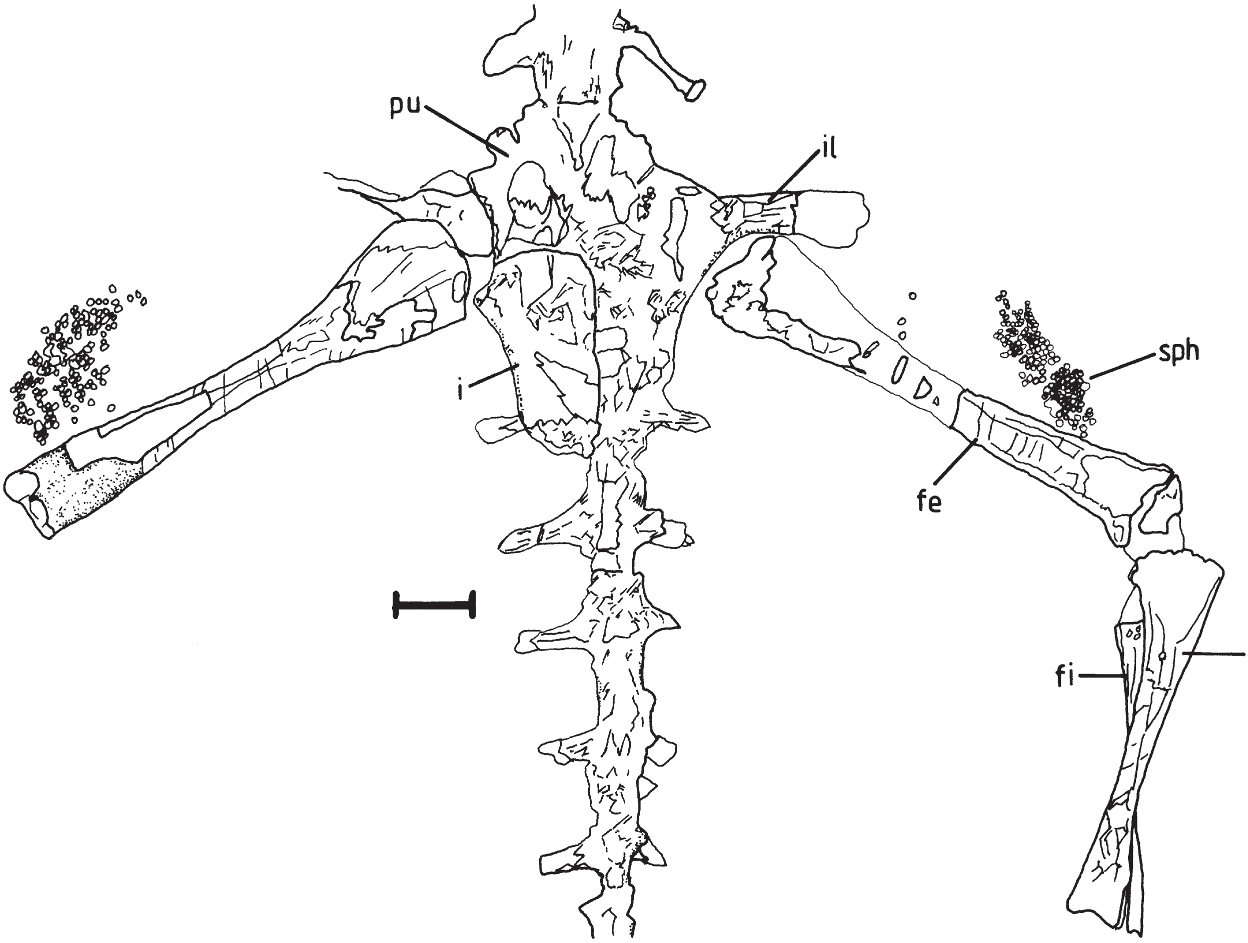

Figure 9. Pelvis and hindlimbs of LH 6020 specimen showing spherules at distal end of each femur (pes is omitted from drawing). Scale bar = 1 mm.

Neither left nor right acetabulum has been well preserved, although the right is marginally better. On this side, there is a slight depression at the anterior end of the ischium, medial to the ischial process, and a shallower depression in the adjacent pubis (Fig. 9). This appears to be the extent of the acetabulum on the right side. If this is correct then the ilium does not contribute to the acetabulum, which would be unusual, but the poor preservation makes interpretation difficult.

The hind limbs are well ossified and consist of the femur (6.25 mm), tibia and fibula (both 4.25 mm) and pes (8.3 mm) (Fig. 9). A faintly tripartite impression on the head of the right femur suggests that the ventral side of the femoral head bore a trochlear groove, which articulated with the ischial process. There is no sign of a trochanter, but from the orientation suggested by the impression, one would expect it to project into the matrix and, thus, be hidden from view.

The left tibia is heavily ossified and sturdier than the fibula. The overall length of both elements is 4.25 mm, but neither show structural details.

The left pes is almost complete and preserved in dorsal view (Figs 10 and 11). Since the majority of the ankle is in faint impression only, the reconstruction is tentative. The digits are curled into a ball as in the left manus with the phalanges curling towards the body. Like the wrist, the ankle shows a primitive arrangement of ossified elements, similar to that seen in ancient amphibians such as *Trematops,* with little or no reduction or fusion of elements as observed in modern salamanders. Three proximal elements are present and articulate with the distal epiphyses of the tibia and fibula, namely the tibiale, fibulare and intermedium. Next come four ossified centralia (c1–c4; Fig. 11), followed by five ossified distal elements, the tarsalia (ta1–ta5; Fig. 11). However, no indication of an ossified pretarsal element was observed. The metatarsals and phalanges were all well ossified. There are five digits present with a phalangeal formula of 2.3.4.4.3. The overall length of the pes including the ankle is roughly 8.3 mm, a reconstruction of the pes suggests that the second and third digits were the longest. Each digit terminated in a robust claw. The claws of phalanges I, II and IV are incomplete and therefore the total length of these two digits can only be estimated.

DERMAL STRUCTURES

Skin

Outlining the skeleton of the holotype specimen are faint remains of its dermal covering. This is better seen under UV light (Fig. 3). This dermal covering consisted of hexagonal scales reminiscent of the ossification pattern seen on certain dermal skull roofing bones. These scales covered the head, body and at least the proximal part of both fore- and hind limbs. On the tail, only the base shows traces of scales. Hexagonal scales can be clearly seen lying within the orbits (Fig. 3), suggesting that albanerpetontids had eyelids, which would support the theory that the animals were largely or fully terrestrial (Estes & Hoffstetter, 1976; Fox & Naylor, 1982; McGowan & Evans, 1995).

Femoral glands

There are over 100 spherules lying distally above the right femur (Figs 9 and 10). These spherules lie beneath the skin just above the knee of the animal. They do not penetrate the outer dermal layer. There are similar remains in a corresponding position on

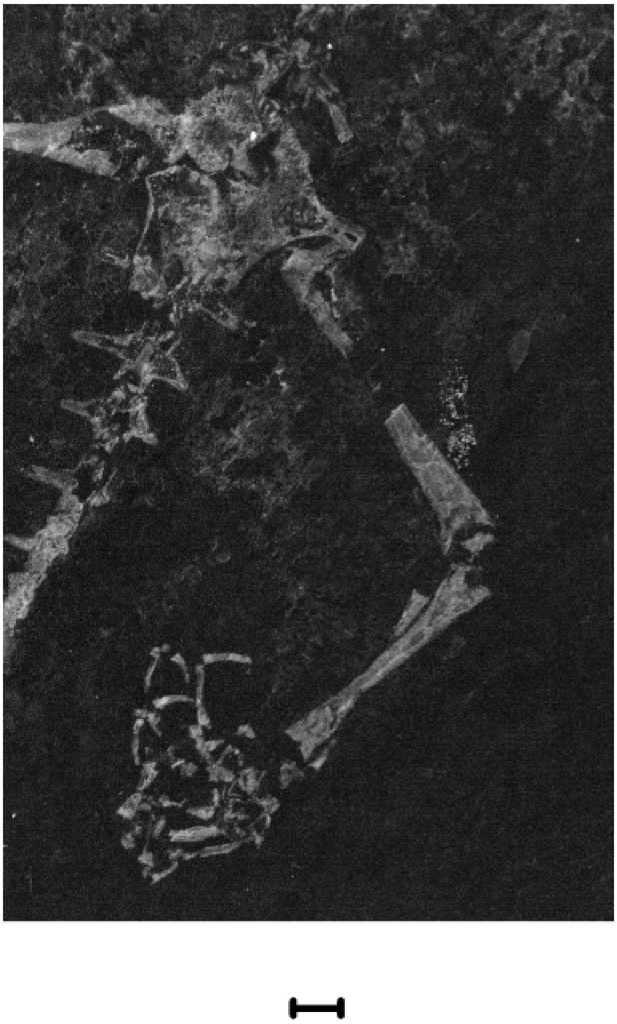

Figure 10. *Celtedens ibericus,* LH 6020, hindlimb and pelvic girdle showing possible courtship glands (spherules). Scale bar = 1 mm.

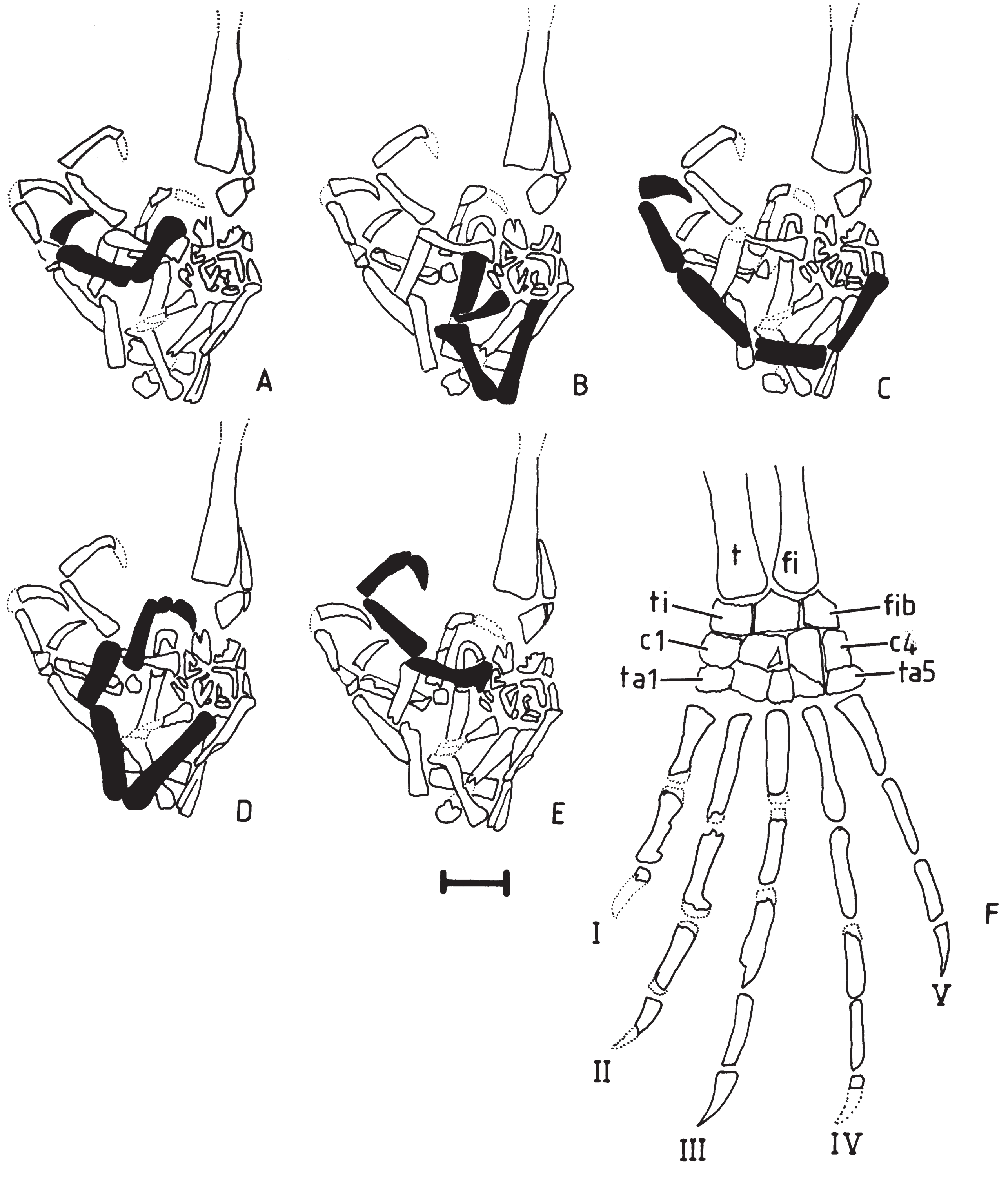
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Figure 11. Pes of *C. ibericus*. A, Digit I; B, digit II; C, digit III; D, digit IV; E, digit V; F, reconstruction from LH 6020. Scale bar = 1 mm.

the left limb. Since these structures lie in a similar position on each hind limb this suggests a functional reason for their presence. They are best interpreted as glands concerned with courtship.

The spherules do not appear to be bone because they have a different texture to the femur lying adjacent to them. It is possible that they are the crystallised remains of glands that lay immediately below the skin. The distribution and shape of these structures suggest that they were branched alveolar or compound alveolar exocrine glands (Romer & Parsons, 1978; p 95).

In modern amphibians, three types of exocrine glands are commonly found: (i) mucous or sebaceous, (ii) poison, and (iii) sex/courtship glands (Noble, 1931).

The mucous variety is commonly used to keep the skin of terrestrial or semiterrestrial amphibians moist. Since adult albanerpetontids were apparently terrestrial, one may expect them to have mucous glands. However, there are two reasons why these glands are probably not mucous:

(i) mucous glands would be expected to be distributed evenly around the body to give overall body coverage; in modern amphibians these are generally simple alveolar type glands, not branched or compound (Romer & Parsons, 1978),

ii) albanerpetontids had a body covering of polygonal body scales that probably helped prevent desiccation.

If these glands were of the poison variety one might expect an associated spine projecting nearby to inject a predator. No such spine can be seen. However, passive secretion of poison is also known (Noble, 1931), so, rejection of poison glands on this basis alone is unwise. However, one would expect to find poison glands on more vulnerable parts of the body, and thus more likely to be seized first by a predator. Therefore, poison glands may be more likely on the distal parts of the limbs, the more distal part of the tail, the head or the animal's flanks. The position of these glands on the proximal part of the hind limb suggests that it is less likely that these glands were poisonous.

The most probable type of gland is the sex or courtship gland. In modern amphibians, there are numerous cases of courtship glands developing in males. In a review of glands found in amphibians, Duellman & Trueb (1986) noted that male plethodontid, ambystomatid and some salamandrid salamanders develop courtship glands during the mating season. *Pseudoeurycea smithii* (a plethodontid) develops mental glands (Trufell, 1954). *Tarichia torosa* (a salamandrid) develops diffuse submandibular glands (Smith, 1941); and *Notophthalmus viridescens* (a salamandrid) develops genial glands on the sides of its head (Hilton, 1902). Some plethodontids also have glands at the base of the tail (Baird, 1951). All of these glands come into contact with the female during courtship or mating (Duellman & Trueb, 1986; p53).

Male salamanders which have been kept in captivity for long periods develop nuptial protuberances on the inner surfaces of their limbs during the mating season. These outgrowths usually consist of keratinized epidermis and are associated with hypertrophied leg musculature (Duellman & Trueb, 1986: 54). Nuptial excrescences have been recorded on the hind limbs of the salamandrid *Notophthalmus* (Hilton, 1902), on the forelimbs of *Pleurodeles* and *Taricha* (Smith, 1941) and on the chest and forelimbs of *Onychodactylus* during the mating season. These keratinized protuberances function in maintaining a grip on the female during amplexus (Duellman & Trueb, 1986: 54).

It is unlikely that the glandular structures in albanerpetontids were used to grip the female because they do not project through the skin (Figs 2 and 4). It is more likely that they secreted either a pheromonal or viscous substance that helped to attract a female or bond the male to the female during amplexus.

DESCRIPTION OF PIETRAROIA ALBANERPETONTID

LOCALITY AND GEOLOGY OF PIETRAROIA

Pietraroia lies about 50 km north-east of Naples in southern Italy (Fig. 12). The fossiliferous beds known as the 'Calcari ad ittioliti di Pietraroia' are limestone deposits from the Lower Cretaceous. This layer has been variously dated as Barremian-Albian or Aptian based on microfossil remains of *Cuneolina* spp., Miliolidae, Textularidae*, Glomospira,* Orbitolinidae and ostracods (Catenacci & Manfredini, 1963; Bravi, 1994). It has been most recently dated as early Albian by Bravi and De Castro (Bravi, 1994) based on a study of the microfossils in the layer immediately below the 'Calcari ad ittioliti di Pietraroia'.

The environment during deposition is believed to have been a shallow water lagoon, which underwent periods of drying out (mud cracks, gas-pits and edgewise breccias) with frequent flooding by the sea (mass-mortalities and ichthyolithic beds) (D'Argenio, 1963; Bravi, 1994). Bravi (1987) has confirmed these observations and also the probability that the basin was intermittently fed by the draining rivers of the surrounding area.

MATERIAL

The material is the holotype of *Celtedens megacephalus*, a single partial skeleton (M 542) from the base of the Albian of Pietraroia, Italy, housed in the

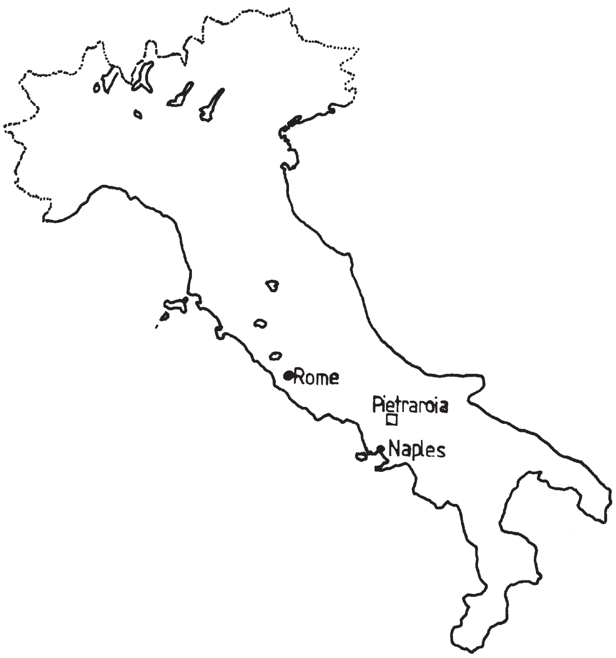

Figure 12. Location of Pietraroia fossil locality in Italy.

Costa collection, Museo Palaeontologia, Universita′ degli studi di Napoli, Italy.

The specimen was first described by Costa (1864) as *Triton megacephalus*. D'Erasmo confirmed this description in 1915. In 1938, Kuhn redescribed the specimen as *Heteroclitotriton* and later in 1960 as *Triturus*. Brame (1973) invalidated the latter assignment. The fossil was more recently reassigned as *Albanerpeton megacephalus* by Estes (1981). McGowan & Evans (1995) nominated this specimen as holotype of the new genus *Celtedens* based on the shape of its frontal.

DESCRIPTION OF PIETRAROIA MATERIAL

The specimen is preserved in ventral view (Fig. 13); no counterpart is known. The anterior of the skull and palate are missing. The vertebrae are very poorly preserved, and several are missing.

In the skull, both premaxillae and the right maxilla are missing. The left maxilla lies under the dentary of that side. The frontal is fused and complete, its anterior shape, however, is obscured both by the nasal and the cultriform process and by crushing of the elements in this region. Posteriorly, the base of the frontal is wider and the flanges more curved than the Las Hoyas specimens. The flanges overlap the parietals laterally. Lacrimals form the anterior frontal orbital margin with the left lacrimal the more complete. The impression of the right lacrimal runs concomitantly with the fragment of that side. The left nasal lies medial to the lacrimal. The parietals are paired and articulate with the frontal anteriorly. Laterally, they form the posterior margins of the orbits. The remaining orbital margin is composed of the frontal (medially), lacrimal (anteriorly) and maxilla (laterally).

The quadrates meet the articulars on both sides. The right quadrate is broken but clearly shows the large convex anterior joint surface (Fig. 13). The squamosals lie lateral to the quadrates and articulate with the braincase posterolaterally.

Lying lateral to the quadrate of the left side is another element that may be a jugal (Fig. 13). A similar element is seen in the holotype of *C. ibericus* (LH 6020) from Las Hoyas. No corresponding element can be distinguished on the right side.

Most of the right dentary is missing. The right articular is visible and articulates with the quadrate. It is partially broken but reveals its highly concave joint surface. The left dentary is more complete but is broken anteriorly. No teeth can be seen in either dentary.

Overlying the rear of the braincase are the fragmentary remains of the ossified hyobranchial apparatus. Anteriorly, lying in the midline above the posterior edge of the parietals, is a small square element with a long columnar process, which runs forward to overlie the anterior edge of the frontal. This is probably the remains of the parasphenoid with a long narrow cultriform process. Amphibamid and branchiosaurid temnospondyls had similarly long and narrow parasphenoids (Boy, 1986, 1987; Milner, 1988).

The atlas and axis cannot be seen, but five trunk vertebrae lie behind the skull. A total of 16 trunk vertebrae are visible although they are poorly preserved and reveal little of their structure. There are clearly several missing vertebrae so a precise count is not possible. Thirteen poorly preserved caudal vertebrae are also visible.

The shoulder girdle is poorly preserved. Fragments of the right scapular blade remain, but no details can be seen. Nothing more of the right forelimb is preserved. The scapula of the left side can be seen only in impression. The left humerus is moderately well preserved distally and bears the characteristic large ball-like, radial condyle (Fig. 13). The head of the ulna is still in contact with the ulnar condyle, but more distally, the bone is preserved only in impression. A part of the radial head remains *in situ*, but like the ulna, is mainly impression distally. Fragmentary remains of the wrist are visible but no details are clear.

None of the pelvis is preserved and only partial fragments of the right femur, fibula, tibia and tarsals remain. No terminal phalanges are preserved.

A reconstruction of an albanerpetontid is given in Fig. 14.

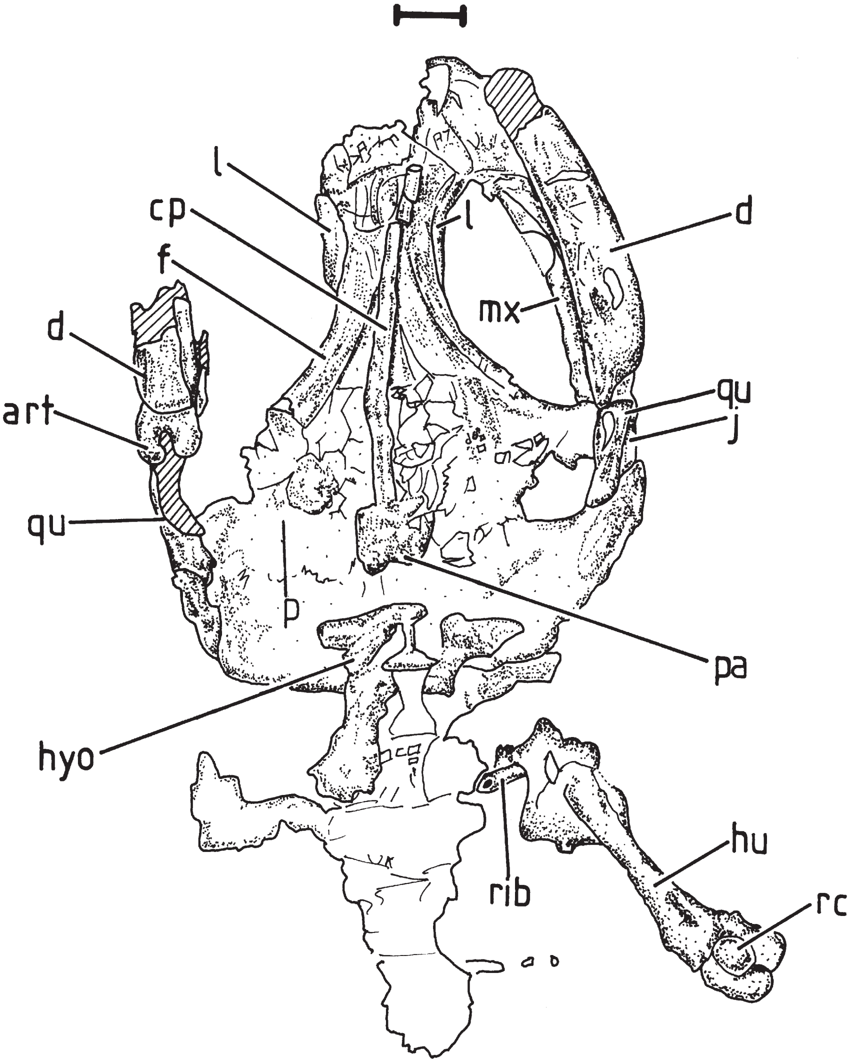

Figure 13. Detail of skull and forelimb of *Celtedens megacephalus* from Pietraroia, Italy. Scale bar = 1 mm.

DISCUSSION

Phylogeny of the albanerpetontids

Several studies have suggested that albanerpetontids may be a sister-group of lissamphibians (Fox & Naylor, 1982; Milner, 1988, 1993; McGowan & Evans, 1995; Gardner, 2001), although others have suggested that albanerpetontids were true caudates (Estes, 1981; Duellman & Trueb, 1986; Trueb & Cloutier, 1991). Of the above studies, only four directly addressed the relationships of albanerpetontids using osteological characters in a cladistic analysis. Milner (1988) did not include albanerpetontids in his final analysis, but suggested that they were probably a sister group to Batrachia, although the paucity of data known for albanerpetontids, at that time, did not help clarify the relationships of the lissamphibians, which was the main point of his thorough study. McGowan & Evans (1995), using a smaller data set than the one used in this present study, reported that albanerpetontids appear to be most closely related to Batrachia ± Gymnophiona.

In contrast, Duellman & Trueb (1986) were still using the Prosirenidae for comparisons with salamanders, even after the clarification given by Fox & Naylor (1982). Consequently, they used bicapitate ribs, as seen in *Prosiren,* but not albanerpetontids. Of the five characters they used to show prosirenids (albanerpetontids) as a sister group of batrachosauroidids, four were reversals. In addition two of the five characters were unknown (the presence of first hypobranchials and ceratobranchials, and the presence of well-developed glomeruli in the kidneys, the latter character being unknown for either of these fossil taxa). The three remaining characters were primitive (the presence of a lacrimal, the presence of an angular and the otic-occipital region co-ossified, the latter being primitive with respect to Lissamphibia). Of the additional seven characters used to include albanerpetontids within the Caudata, two were unknown (the position of attachment of the *levator mandibular* muscle, and the number of chromosomes), one character was speculative (the mode of fertilization, which may be internal if the structures described as courtship glands in this article are valid and thus indicative of amplexus) and, finally, one character was wrong (the presence of bicapitate ribs). This leaves only three valid characters; an alary process on the premaxillae, separate ossifications for scapula and coracoid, and loss of the quadratojugal.

Trueb & Cloutier (1991), classified albanerpetontids as true caudates and proposed two topologies, which placed them either as sister-group to urodeles or as sister-group to the basal caudate *Karaurus* from the Middle Jurassic of Kazahkstan. In the first topology (*Karaurus* + [albanerpetontids + urodeles]), five characters were used to justify albanerpetontid inclusion within the Caudata. One of these (the anterior ramus of the pterygoid lacking a bony articulation), is unknown in albanerpetontids; one is primitive (the presence of an angular); another (an incomplete maxillary arcade), is primitive with respect to Lissamphibia and homoplastic with respect to *Schoenfelderpeton*; one character (the presence of a *tuberculum interglenoideum*), is homoplastic with respect to microsaurs and *Eocaecilia*; and the fifth character (the presence of monocuspid teeth) was incorrect. A single homoplastic character, the prefrontal forming part of the margin of the external naris, was proposed as supporting albanerpetontids as sister taxon to urodeles. However, the present study clarifies that albanerpetontids do not possess a prefrontal. In the second topology (urodeles + [*Karaurus* + albanerpetontids]), albanerpetontids were proposed as a sister taxon to *Karaurus* based on five characters. Two of these (the lateral orientation of the quadrate ramus of the pterygoid and the presence of a stapedial foramen) are unknown for albanerpetontids; one character (the parietal foramen covered by bone), is primitive for lissamphibians; another character (non-pedicellate teeth) was also primitive, and, in addition, *Karaurus* has pedicellate teeth. This leaves only one character (monocuspid teeth) as valid. Therefore, the inclusion of albanerpetontids within the caudates in the studies of Duellman & Trueb (1986), and Trueb & Cloutier (1991) is highly unjustified. A more recent study by Gardner (2001) argued that albanerpetontids were a monophyletic group and a sister-taxon of Caudata plus Salientia.

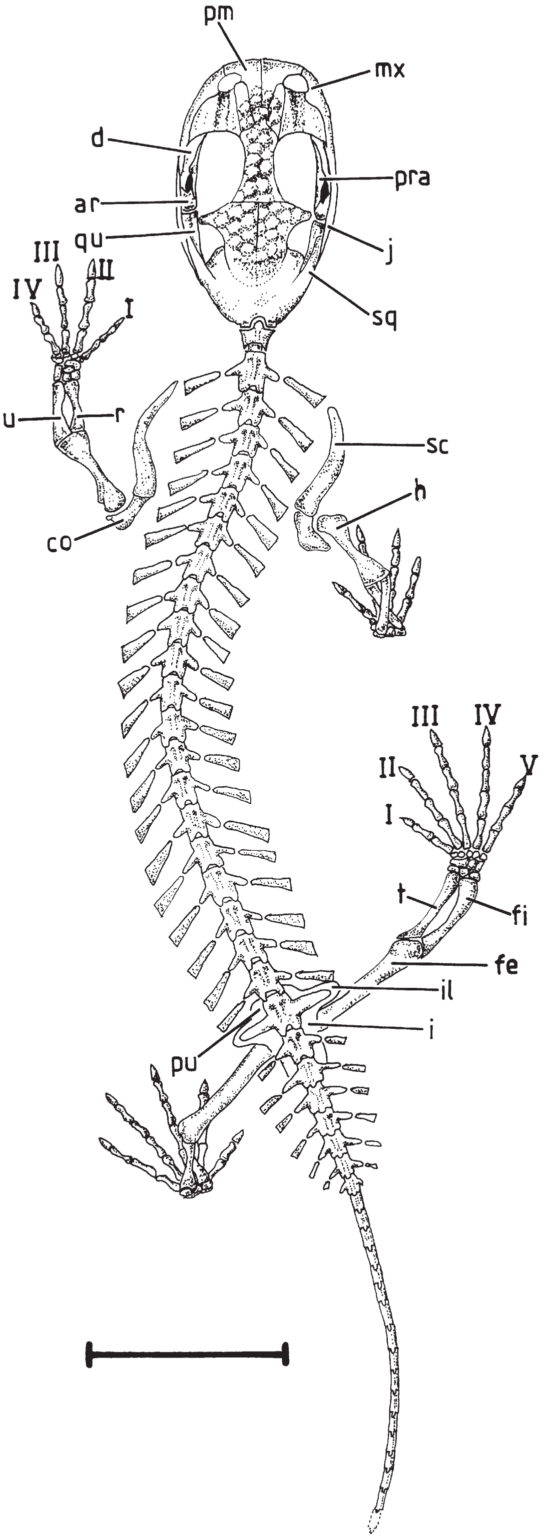

Figure 14. Reconstruction of skeleton of *Celtedens ibericus*. Scale bar = 1 cm.

A cladistic analyses, using both PAUP 3.1.1 (Swofford, 1990) and MacClade 3.07 (Maddison & Maddison, 1992), on an Apple Macintosh G3 computer, and including the 41 characters listed in Appendix 1 and the 20 taxa in Appendix 2, gave equivocal results. Table 2 lists all specimens examined and cited. With all taxa from Appendix 2 included, the analyses produced two equally-parsimonious trees from both Heuristic and Branch and Bound searches using unordered characters (Tree length = 95, consistency index, C.I. = 0.495 and retention index, R.I. = 0.751). A Wagner analysis produced eight equally-parsimonious topologies, which was marginally poorer than the unordered analysis (Tree length = 97, C.I. = 0.485 and R.I. = 0.761). The two trees from the unordered analysis resulted from the placement of a single character, character 12, the presence of a large hemispherical radial condyle. Since microbrachid microsaurs do not show this character, and tuditanids and lissamphibians do, it required reversals in one topology (in microbrachids and hapsidopareiontids: the character status is unknown in brachystelechids) and homoplasy (at nodes 9 and 14 (which included tuditanids)) in the other (data not shown). However, the simplest explanation would be a single evolution at node 8 with a reversal in the microbrachid microsaurs. This analysis did show microsaurs (including gymnophionans) to be a monophyletic assemblage. The Pantylidae were placed as sister group to gymnophionans, with *Rhynchonkos* as sister group to them. The relationships of the remaining microsaurs were consistent with the subordinal hierarchies of Tuditanomorpha and Microbrachomorpha as proposed by Carroll *et al.* (1998) (Fig. 15). A consensus tree of these two equally-parsimonious topologies did not clarify whether the tuditanids or microbrachids were more closely related to the other tuditanomorph microsaurs. However, since the internal relationships of the microsaurs were not the major concern of the present study, further analyses were conducted with several microsaurs removed. To determine if gymnophionans always remained closer to microsaurs than to Batrachia, pantylids, tuditanids or *Rhynchonkos* were used in further analyses. The most-parsimonious trees resulted from using the tuditanids, as primitive microsaurs, and *Rhynchonkos*, recently suggested as a possible ancestor of gymnophionans (Carroll & Currie, 1975; Carroll *et al.*, 1998), as a more derived example. With only the representative taxa included, both Branch and Bound and Heuristic searches for the most-parsimonious tree placed the albanerpetontids as the sister group to Batrachia with Gymnophiona + [*Rhynchonkos* + tuditanids] as the sister group to them (Fig. 16). The single tree produced had a tree length of 86, C.I. = 0.547, and R.I. = 0.715. Removing the tuditanids from the analyses gave a tree length of 83, C.I. = 0.566 and R.I. = 0.707 (Fig. 17). However, using MacClade, placing albanerpetontids as sister taxon to Batrachia + [Gymnophiona + *Rhynchonkos*] only increased the tree length by one step; tree length = 81, C.I. = 0.56, R.I. = 0.71. However, the relationship of microsaurs to gymnophinans was not robust; with *Eococilia* removed from the analysis, microsaurs became a distinct Palaeozoic assemblage, a sister-group to temnospondyls. To further concentrate on the relationships of albanerpetontids, excess temnospondyls were removed. Using only single representatives of the amphibamids and branchiosaurids, a similar picture emerged. Numerous different analyses were made to find the most parsimonious tree. Different representative taxa were used for both the amphibamids and the branchiosaurids. Both Branch & Bound and Heuristic searches produced a single tree, which was not dependent on the representatives of the amphibamids or branchiosaurids used. The tree with the fewest number of steps and the best C.I and R.I. resulted from the use of *Doleserpeton* and *Branchiosaurus* as representatives of the amphibamids and

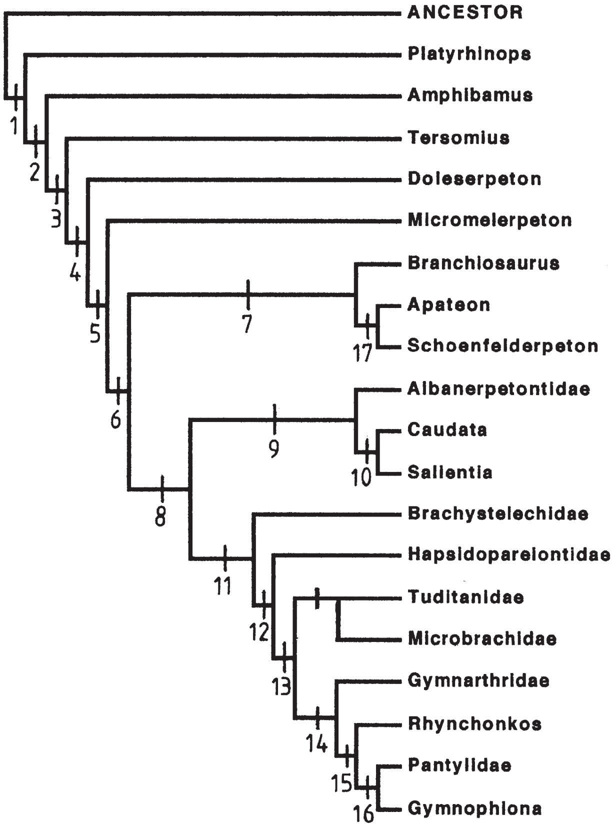

Figure 15. Cladogram 1 showing most parsimonious tree depicting the relationships of taxa used in this study (see Appendix 3 for taxa and character distributions).

Table 2. Specimens examined for comparison of characters with albanerpetontids. LH – Las Hoyas, Museo de Cuenca, provisionally housed in the Unidad de Palaeontologia, Universidad Autonoma de Madrid (Spain); M – Museo Palaeontologia, Universita′ degli studi di Napoli (Italy); UCK – University College London, Kirtlington, London (England); DORCM – Dorset County Museum, Dorchester (England); MNHN-LGA – Museum National d'Histoire Naturelle–La Grive-Saint-Alban Collection, Paris (France); GPIM-N – Geologisches und Paläontologisches Institut der Johannes-Gutenberg-University, Mainz (Germany); PV – National Science Museum, Tokyo (Japan)

Material	Personal observation	Literature citations
Albanerpetontidae		
Celtedens ibericus	LH 6020 (A + B); LH 030 R (A + B)	McGowan & Evans (1995)
Celtedens megacephalus	M 542; UCK1-34 plus many uncatalogued specimens; DORCM GS1-37 plus many uncatalogued specimens	McGowan (1996), (1997)
Albanerpeton inexpectatum	MNHN-LGA 176, plus many uncatalogued specimens	Estes & Hoffstetter (1976); Estes (1981)
Albanerpeton arthridion		Fox & Naylor (1982)
Albanerpeton galaktion		Fox & Naylor (1982)
Albanerpeton nexuosus		Estes (1981)
'Nukusurus insuetus'		Nessov (1981), (1988)
Branchiosauridae		
Branchiosaurus cf. *B. petrolei*	GPIM-N285, N298, N225, N227, N409, N437, N268a + b, N229, N220, N156, N231, N441a + b, N275a + b, N261, N279, N241, N122a + b, PV 18671a + b	Boy (1972); (1978), (1987)
Apateon		Boy (1986), (1987)
Schoenfelderpeton		Boy (1986), (1987)
Amphibamidae		
Doleserpeton		Bolt (1969); Milner (1988), (1993); Clack & Milner (1993)
Tersomius graumanni	GPIM-N892	Boy (1980)
Amphibamus		Bolt (1979)
Platyrhinops		Clack & Milner (1993)
Micromelerpetontidae		
Micromelerpeton credneri	GPIM-N263, N283, N289, N288, N266, N1870, N1874, N1878, N1871, N1880, N1168, N1865, N1884	Boy (1972), (1995)
Microsauria		Carroll *et al*. (1998)
Tuditanidae		Carroll *et al*. (1998)
Pantylidae		Carroll *et al*. (1998)
Gymnarthridae		Carroll *et al*. (1998)
Hapsidopareiontidae		Carroll *et al*. (1998)
Microbrachidae		Carroll *et al*. (1998)
Brachystelechidae		Carroll *et al*. (1998)
Rhynchonkos		Carroll & Currie (1975); Carroll & Gaskill (1978); Carroll *et al*. (1998)
Lissamphibia		
Gymnophiona		Duellman & Trueb (1986); Milner (1988), (1993); Jenkins & Walsh (1993)
Caudata		Carroll & Holmes (1980); Duellman & Trueb (1986); Milner (1988), (1993).
Salientia		Sanchiz (1998); Duellman & Trueb (1986); Milner (1988), (1993); Rage & Roÿcek (1989)

Specimens examined for comparison of characters with albanerpetontids. LH – Las Hoyas, Museo de Cuenca, provisionally housed in the Unidad de Palaeontologia, Universidad Autonoma de Madrid (Spain); M – Museo Palaeontologia, Universita′ degli studi di Napoli (Italy); UCK – University College London, Kirtlington, London (England); DORCM – Dorset County Museum, Dorchester (England); MNHN-LGA – Museum National d'Histoire Naturelle–La Grive-Saint-Alban Collection, Paris (France); GPIM-N – Geologisches und Paläontologisches Institut der Johannes-Gutenberg-University, Mainz (Germany); PV – National Science Museum, Tokyo (Japan).

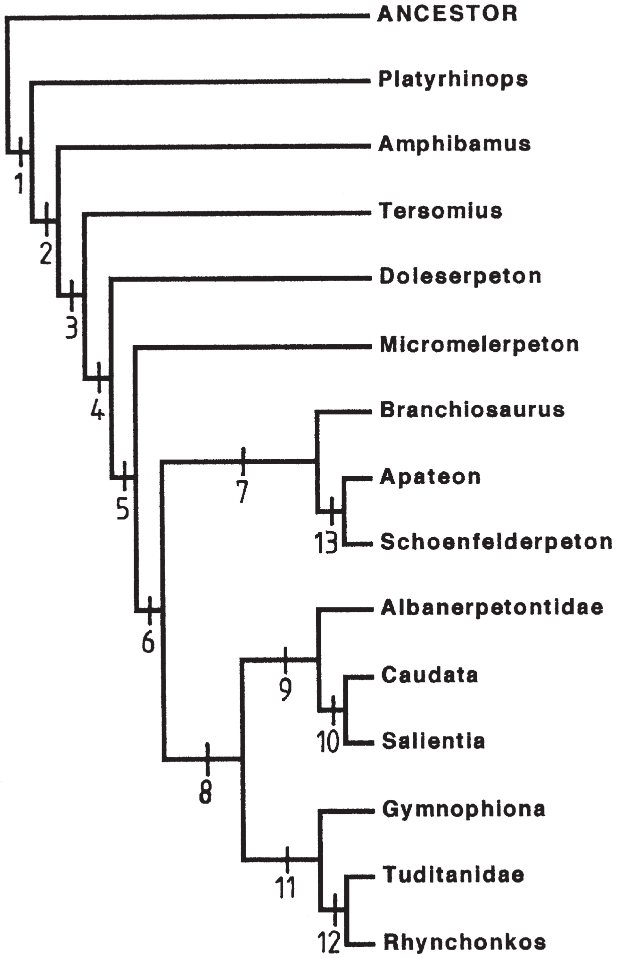
ANCESTOR
Platyrhinops
Amphibamus
Tersomius
Doleserpeton
Micromelerpeton
Branchiosaurus
Apateon
Schoenfelderpeton
Albanerpetontidae
Caudata
Salientia
Gymnophiona
Tuditanidae
Rhynchonkos
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Figure 16. Cladogram 2 showing one of two equally most parsimonious trees with some Palaeozoic taxa removed for clarity (see Appendix 3 for character distributions in each tree).

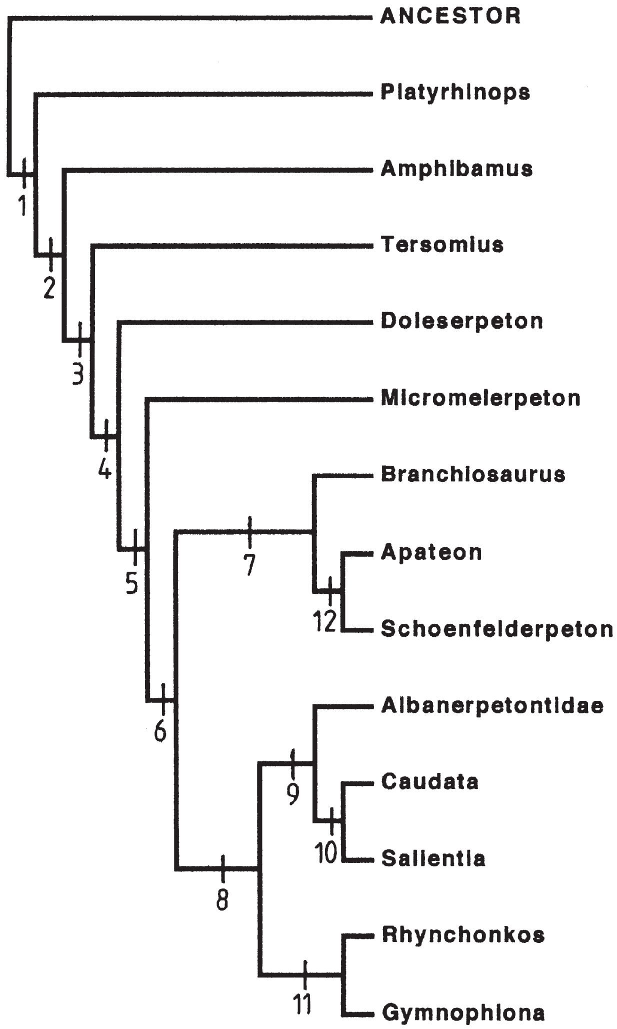
ANCESTOR
Platyrhinops
Amphibamus
Tersomius
Doleserpeton
Micromelerpeton
Branchiosaurus
Apateon
Schoenfelderpeton
Albanerpetontidae
Caudata
Salientia
Rhynchonkos
Gymnophiona
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Figure 17. Cladogram 3 showing one of two equally most parsimonious trees with some Palaeozoic taxa removed for clarity (see Appendix 3 for character distributions in each tree).

branchiosaurids, respectively. The two most equally-parsimonious trees that resulted from PAUP analyses (Fig. 18) gave a tree length of 61, a C.I. = 0.639 and a R.I. = 0.639, which was marginally better than all other analyses (data not shown). The topology in cladogram 3 (Fig. 17) did not require any reversals in albanerpetontids. Although outwith the initial scope of the present study, the finding that gymnophinans may be more closely related to microsaurs than other Palaeozoic amphibians is interesting and requires further examination. From the current analysis it appears that a microsaur–gymnophionan relationship is stronger than a gymnophionan–Batrachia relationship. The latter relationship was primarily based on the loss of bones from the orbital series in the skull, but with the discovery of *Eocecilia* containing a full complement of orbital bones this gymnophionan–Batrachia relationship was weakened. The present results show that the relationships of the albanerpetontids and the lissamphibians are still equivocal. Further analyses and improved fossil data are required to help clarify the phylogeny of these amphibian groups.

If albanerpetontids are indeed related directly to lissamphibians, and since the earliest lissamphibian (*Triadobatrachus*) is of early Triassic age, albanerpetontids must have split from the stem by Permian times and remained an independent lineage throughout the Mesozoic and well into the Tertiary. The oldest know albanerpetontid specimen, a single atlas, still with a notochordal canal, from the Bajocian of southern France (Seiffert, 1969) indicates that the unique neck joint of albanerpetontids was developing around this time. Their unique character assemblage was

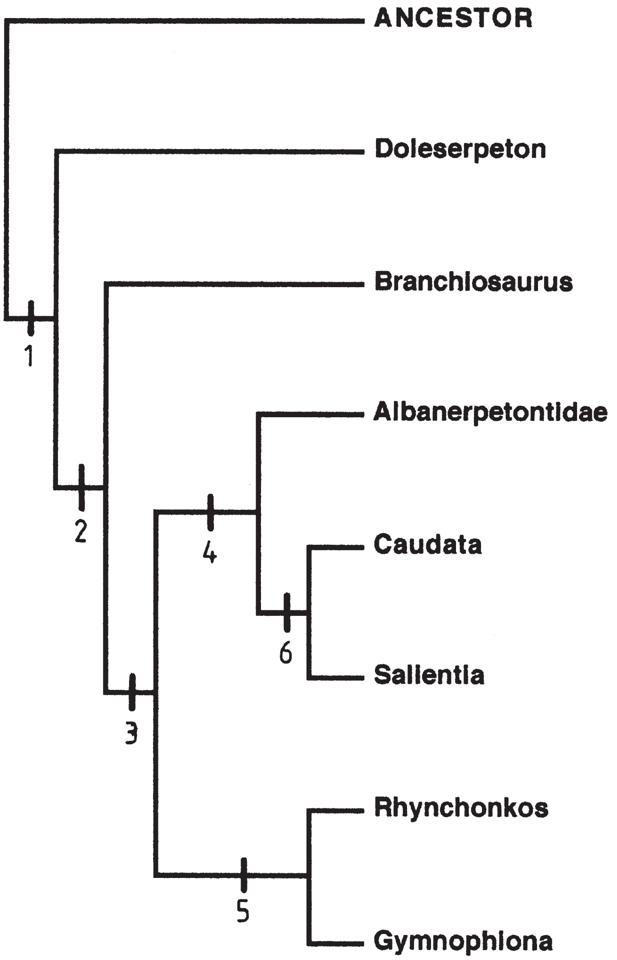

Figure 18. Cladogram 4 showing most parsimonious tree with only single representatives of Palaeozoic taxa included (see Appendix 3 for character distributions in each tree).

already developed by the Bathonian, as indicated from the disarticulated remains from Kirtlington, England (McGowan, 1996) and these characters remained very conservative and relatively unchanged until late Miocene (Estes & Hoffstetter, 1976), their last known appearance. It remains unclear why albanerpetontids disappeared from the fossil record after this period.

CONCLUSIONS

The fossil record of albanerpetontids has been significantly improved with the discovery of the three articulated specimens, referred to *Celtedens ibericus,* from the Cretaceous (late Berriasian) of Las Hoyas, Cuenca, Spain. One specimen has remarkable preservation of the dermis, which shows indications of reticulate body scales, which match the polygonal dermal sculpture pattern of the skull. Within the skin of both thighs are the remains of possible nuptial glands. A re-examination of the Pietraroia albanerpetontid shows that it did not have a weakly ossified postcranial skeleton as previously argued by Estes (1981), but that it was merely poorly preserved. The well-ossified postcranial skeleton of LH 6020 supports this view. The narrow, pointed internasal process and strongly triangular, unemarginated orbital margins that are diagnostic of the genus *Albanerpeton*, contrast with the bulbous, almost circular, nasal process and highly curved orbital margins of the Pietraroia and Las Hoyas specimens assigned to the new genus *Celtedens*.

Some previous studies (Estes, 1981; Estes & Sanchiz, 1982; Duellman & Trueb, 1986; Trueb & Cloutier, 1991) have placed albanerpetontids clearly within Caudata. However, others have questioned this (Fox & Naylor, 1982; Milner, 1988; McGowan & Evans, 1995; Gardner, 2001), and some have suggested they show characters that indicate they are not true caudates and deserve at least sister-group status to salamanders (Nessov, 1981, 1988; Fox & Naylor, 1982; Gardner, 2001). An analysis of the character states of albanerpetontids and comparison with lissamphibians, dissorophoid temnospondyls (proposed as distant relatives of modern amphibians; Milner, 1988, 1993) and microsaurs (suggested as possible lissamphibian ancestors; Carroll & Currie, 1975; Carroll *et al.*, 1998), supports the view that albanerpetontids are distinct from caudates and are the sister-taxon of Batrachia (McGowan & Evans, 1995; Gardner, 2001). In the present analysis microsaurs + gymnophionans were placed as sister-group to lissamphibians, however, this was not a robust construct; with *Eocecilia* removed from the analysis, microsaurs became a distinct Palaeozoic assemblage, a sister-group to temnospondyls. These findings show that the relationships of the palaeozoic amphibians, including microsaurs, to modern amphiians and albanerpetontids are equivocal and further studies are urgently required to help clarify amphibian phlogeny.

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APPENDIX 1

CHARACTERS USED IN CLADISTIC ANALYSES

Character 1 Ribs

Long straight ribs around the body are found in early temnospondyls and Palaeozoic amphibians; short straight ribs first appear in *Balanerpeton* (Milner & Sequiera, 1994).

0, long straight ribs; 1, short straight ribs.

Character 2 Alary process

A broad articulation of the premaxilla with the nasal is the primitive condition; the derived condition is a narrow ascending alary process – first seen in *Archegosaurus* (Temnospondyli) (Milner, 1988).

0, broad premaxilla/nasal articulation; 1, narrow ascending alary process of premaxilla.

Character 3 Tooth crowns

Monocuspid teeth are primitive relative to basal temnospondyls; the derived condition of bicuspid teeth with a lingual and labial cusp first appears in amphibamids. Note, however, the faintly tricuspate teeth of albanerpetontids are not similar to bicuspid teeth because the cusps are not labial/lingual. Brachystelechid microsaurs have spatulate, tricuspate premaxillary teeth (Carroll *et al*., 1998), which may be similar to the tooth crowns of albanerpetontids.

0, monocuspid tooth crowns; 1, bicuspid labial/lingual tooth crowns.

Character 4 Dermal scales

Scales are primitively present in the dermis of early amphibians; loss of these scales is regarded as derived.

0, scales present; 1, scales absent.

Character 5 Teeth

Pedicellate teeth have a distal crown separated from the pedicle by a zone of weakness (either a ring of uncalcified dentine – some frogs; or a ring of fibrous tissue – salamanders, caecilians and other frogs). Pedicellate teeth are regarded as being derived from nonpedicellate teeth.

0, nonpedicellate teeth; 1, pedicellate teeth

Character 6 Vertebral number

Primitive condition is greater than 24 presacral vertebrae – as seen in early temnospondyls; primary derived condition is a reduction to 18–24 presacrals – as seen in dissorophoid temnospondyls; secondary reduction to 16 or fewer – as seen in *Karaurus* and *Triadobatrachus*, a further reduction is seen in frogs (5–8), and an increase (reversal) in salamanders (10–60). Note, however, that reduction of vertebral number occurs independently in several lineages and may not be a strong character. Boy (1987) stated branchiosaurs had mostly 20 presacrals although some had up to 24.

0, > 24 presacral vertebrae; 1, 18–24 presacral vertebrae; 2, ^{2}16 presacral vertebrae; 3, 5–8 presacral vertebrae.

Character 7 Palatal fangs

Their presence is primitive as seen in early temnospondyls; derived condition is replacement of fangs with rows or clumps of teeth (Milner, 1988). *Tersomius* is figured with fangs (Bolt, 1977), *Doleserpeton* is figured and annotated as having fangs, but described as having palatal teeth the same diameter as marginal teeth (Bolt, 1977). *Apateon* and *Schoenfelderpeton* are figured with teeth (not fangs) (Boy, 1986). *Branchiosaurus* is figured without teeth (Boy, 1987). Milner (1988) regarded *Doleserpeton* as having teeth not fangs; however, although Bolt described them as fangs, he drew them as teeth. From Bolt's figure the palatal dentition does suggest they were teeth. In microsaurs, the tuditanid *Asaphestera intermedia* has larger palatal teeth than marginal teeth, but they are not fangs, and *Pantylus cordatus* has large crushing teeth on the palatal bones but not fangs (Carroll *et al*., 1998).

0, palatal fangs present; 1, palatal fangs replaced by teeth.

Character 8 Ectopterygoid

A large ectopterygoid is regarded as primitive – as seen in early temnospondyls; a reduction to a thin strip of bone or complete loss is the derived condition. *Tersomius* was figured with two large fangs on the ectopterygoid (Bolt, 1977). In microsaurs, it is lost in Pantylidae and reduced in hapsidopareiontids, microbrachomorphs and *Rhynchonkos* (Carroll *et al*., 1998).

0, large ectopterygoid; 1, small or absent ectopterygoid.

Character 9 Vertebral type

The primitive condition, as seen in early temnospondyls, is pleurocentra and intercentra of roughly equal size; the primary derived condition, as seen in dissorophoid temnospondyls, is smaller intercentra and large pleurocentra; the secondary derived condition is holospondyly. Note however, that developmental studies of modern amphibians shows the three extant orders to have markedly different development of the vertebrae (Wake, 1970).

0, pleurocentra and intercentra of equal size; 1, smaller intercentra and large pleurocentra; 2, holospondyly.

Character 10 Braincase
Neurocranium and dermatocranium remain separate in the primitive condition, as seen in temnospondyls; the derived condition is a fusion of the neurocranium and dermatocranium, as seen in lissamphibians and microsaurs.
0, neurocranium and dermatocranium are not fused together; 1, fusion of neurocranium and dermatocranium.

Character 11 Basapophyses
Basapophyses are paired raised ridges or bosses seen on the ventral surface of the centrum. They can be in either an anterior or posterior position, but this position is regarded as labile (Wake, 1970). Absence is primitive; presence is derived. It is not known if the parapophyses of gymnophionans are homologous.
0, no basapophyses present; 1, basapophyses present.

Character 12 Radial condyle
Primitively the radial condyle does not differ greatly in size from the ulnar condyle – as seen in temnospondyls; in the derived condition, the radial condyle is enlarged into a large ball. Salamanders, frogs, albanerpetontids, *Eocaecilia micropodia* and many microsaurs all show this condition. This character may not be very robust since large radial condyli are found in other Palaeozoic amphibians such as nectrideans, which may suggest it is an adaptation to terrestriality where the radius is the major weight-bearing bone in the forearm.
0, small radial condyle; 1, large hemispherical radial condyle.

Character 13 Tabular
0, tabular present; 1, tabular absent.

Character 14 Tuberculum interglenoideum
In bicondylar atlantes, the primitive condition is the absence of a median odontoid; the presence of a *tuberculum interglenoideum* on the atlas is regarded as derived.
0, atlas lacks a *tuberculum interglenoideum*; 1, atlas bears a *tuberculum interglenoideum*.

Character 15 Interclavicle
A single median ventral plate of bone in the pectoral girdle first appears in primitive tetrapods. It articulates with the lower ends of the paired clavicles. The primitive condition is a broader than long, well-ossified interclavicle as in early temnospondyls; the derived condition is a loss or extreme reduction in the interclavicle, i.e. *Amphibamus* upwards (Milner, 1988).
0, interclavicle broader than long; 1, loss or extreme reduction of interclavicle.

Character 16 Supratemporal
0, supratemporal present; 1, supratemporal absent.

Character 17 Intertemporal
0, intertemporal present; 1, intertemporal absent.

Character 18 Lacrimal
Presence of a large lacrimal is regarded as primitive; the derived condition is reduced or lost lacrimal. *Apateon*, *Branchiosaurus* and *Schoenfelderpeton* can be regarded as having small lacrimals, as figured by Boy (1986).
0, large lacrimal present; 1, lacrimal absent or very small.

Character 19 Scapulocoracoid
In early primitive tetrapods, e.g. *Eryops,* this endochondral girdle ossified as a single unit and bore the glenoid fossa. In derived amphibians, a second ossification centre arises below the glenoid fossa and is termed the coracoid (procoracoid).
0, co-ossified scapulocoracoid; 1, scapula and coracoid remain separate ossifications.

Character 20 Parasphenoid
In temnospondyls this bears a slender anteriorly projecting cultriform process; used by Milner (1988, 1993) as a synapomorphy of temnospondyls.
0, slender cultriform process; 1, wide anteriorly projecting parasphenoid.

Character 21 Pubes
0, ossified pubes; 1, unossified, cartilaginous pubes.

Character 22 Opercular
The derived condition of an ossified opercular bone found in the oval window is found only in salamanders and frogs. Lack of this ossification is considered primitive. It is not known if the accessory ossicle (AO) seen in some microsaurs (e.g. gymnarthrids, ostodolepids and *Rhynchonkos*) is homologous or analogous with the opercular (Carroll *et al.*, 1998). Therefore, it is treated as unknown in those microsaurs that are known to possess an AO.
0, nonossified opercular; 1, ossified opercular.

Character 23 Postorbital
Presence is regarded as primitive; absence is derived.
0, postorbital present; 1, postorbital absent.

Character 24 Postfrontal
Presence is regarded as primitive; absence is derived.
0, postfrontal present; 1, postorbital absent.

Character 25 Jugal
Presence is regarded as primitive; absence is derived. The jugal is present in *Apateon* (Boy, 1987), not absent as Milner (1988) suggested.
0, jugal present; 1, jugal absent.

Character 26 Hyobranchus
The ceratohyals and basihyals of tetrapods are primitively cartilaginous, e.g. early temnospondyls and amphibamids. The derived condition of ossified ceratohyals and basihyals is found in aquatic paedomorphic forms, e.g. branchiosaurs, and within salamanders in cryptobranchids, hynobiids and sirenids. Ossified elements of the hyobranchus have also been found in albanerpetontids.
0, cartilaginous hyobranchus; 1, ossified hyobranchus.

Character 27 Tooth implantation
The derived pleurodont condition where the teeth are anchored to one side of the inner side of the jaw is considered derived; temnospondyls appear to show an acrodont condition, which is regarded as primitive.
0, acrodont condition of tooth implantation; 1, pleurodont tooth implantation.

Character 28 Ectopterygoid contacting maxilla
Primitively, the ectopterygoid contacts the maxilla laterally as in early temnospondyls. In the derived condition, the ectopterygoid is separated from the maxilla by the subtemporal fenestra as in branchiosaurid temnospondyls. Milner (1993) has used this character state as a synapomorphy of branchiosaurids and lissamphibians, but among Recent amphibians, only frogs possess a subtemporal fenestra, and the ectopterygoid is lost.
0, ectopterygoid contacts maxilla; 1, ectopterygoid separated from maxilla by subtemporal fenestra.

Character 29 Frontal entering orbital margin
Primitively, the prefrontal and postfrontal dermal bones of the orbital series suture with one another, e.g. early temnospondyls. In the derived condition, these bones are reduced, not contacting one another, or lost and the frontal enters the orbital margin.
0, frontal does not enter the orbital margin; 1, frontal enters the orbital margin.

Character 30 Intervomerine pit
Primitively, the vomers, the most anterior dermal bones of the palate, articulate medially without a fenestra. In the derived condition, the vomers are only partially in contact with one another medially, creating a fenestra.
0, no intervomerine fenestra; 1, intervomerine fenestra present.

Character 31 Number of teeth in jaw
Primitively, there are more than 60 teeth in the jaw ramus, e.g. early temnospondyls; the derived condition is a reduction in the number of teeth to fewer than 60.
0, >60 teeth in jaw ramus; 1, <60 teeth in jaw ramus.

Character 32 Frontals
Frontals are primitively wide, paired dermal bones lying either side of the midline of the skull level with the orbits. The derived condition is narrow paired elements.
0, wide paired frontals; 1, narrow paired frontals.

Character 33 Maxilla contacts jugal or quadratojugal
Primitively, the maxilla is braced posteriorly by either the jugal or quadratojugal or both, e.g. most temnospondyls. In the derived condition, the maxilla is free posteriorly as in salamanders (although some plethodontids retain a cartilaginous articulation from the pterygoid) and *Schoenfelderpeton* and *Apateon dracyformis* (Boy, 1986).
0, maxilla in contact with jugal or quadratojugal; 1, maxilla free posteriorly.

Character 34 Palatine, ectopterygoid and pterygoid in contact
Primitively, the palatine is excluded from the interpterygoid vacuity, e.g. the temnospondyl *Dendrerpeton*. The derived condition is regarded when the palatine enters the vacuity margin, i.e. *Trematops* and descendents. This is the condition seen in salamanders, frogs and *Eocaecilia,* but not in the microsaurs. Also seen in *Schoenfelderpeton* (Boy, 1986), *Apateon, Branchiosaurus* (Boy, 1987), *Tersomius* and *Doleserpeton* (Bolt, 1977).
0, palatine, ectopterygoid and pterygoid in contact; 1, palatine enters the interpterygoid vacuity margin.

Character 35 Fangs on vomer
Fangs are present on the vomers of early temnospondyls, which is regarded as the primitive condition. The derived condition is a replacement of the fangs by clumps or rows of teeth or loss of dentition altogether.
0, vomerine fangs; 1, vomerine fangs replaced by teeth.

Character 36 Cultriform process with denticles
Primitively, denticles were present on the cultriform process of early temnospondyls. The derived condition is a loss of denticles from the cultriform process proper, but with possible retention of denticles on the parasphenoid base, e.g. *Apateon*, *Branchiosaurus*, *Schoenfelderpeton* (Boy, 1986, 1987), *Doleserpeton* and *Tersomius* (Bolt, 1977). Both *Eocaecilia* and *Rhynchonkos* had denticles on the cultriform process; neither frogs nor salamanders do.
0, denticles on cultriform process; 1, denticles absent from cultriform process.

Character 37 Supratemporal
Primitively, the supratemporal is as long as broad, e.g. early temnospondyls. The primarily derived condition is when the supratemporal is longer than broad; used by Milner (1993) to define *Schoenfelderpeton* and *Melanerpeton,* secondarily derived condition is the loss of this bone.
0, supratemporal long as broad; 1, supratemporal longer than broad; supratemporal lost.

Character 38 Posterior skull shape
Primitively, the posterior skull is straight or slightly concave; in the derived condition, the shape is convex.
0, posterior skull shape straight; 1, posterior skull shape convex.

Character 39 Coronoid teeth
Primitively, three coronoids were present on the dorsolingual surface of the lower jaw bearing irregular teeth, i.e. early temnospondyls; the primarily derived condition is a reduction of the number of coronoids and a tooth row parallel to the dentary, e.g. only *Rhynchonkos* and some but not all gymnophionans (note: it is not established if this second row of teeth is homologous to the parallel tooth row of early temnospondyls); secondarily derived state is regarded as the loss of the remaining coronoids, e.g. salamanders and frogs.
0, three coronoids bearing irregular teeth; 1, reduced number of coronoids with parallel tooth rows; 2, loss of remaining coronoids.

Character 40 Orbit
Primitively, the orbit of temnospondyls was large; the derived condition of small orbits is seen in gymnophionans and microsaurs.
0, large orbits, 1, reduced orbits.

Character 41 Jaw articulation
The jaw articulation is primitively posterior to the occiput margin, e.g. early temnospondyls and amphibamids (*Tersomius* and *Doleserpeton* as figured by Bolt, 1977); the primary derived condition is a jaw articulation anterior to the occiput, e.g. branchiosaurs, salamanders; the secondarily derived condition is level with the occiput, i.e. frogs only.
0, jaw articulation posterior to occiput margin; 1, jaw articulation anterior to occiput margin; 2, jaw articulation level with occiput.

APPENDIX 2

DATA MATRIX AND SPECIES USED IN THE CONSTRUCTION OF CLADOGRAMS

Species/ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Branchiosaurus	1	1	0	0	0	1	?	1	0	0	0	0	0	0	0	?	1	0	1	0	1	0	0	0	0	1	1	1	1	0	?	0	0	1	1	1	0	0	0	0	1
Apateon	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	1	1	0	?	0	1	1	1	1	0	0	0	0	1
Schoenfelderpeton	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	1	1	0	?	0	1	1	1	1	1	0	0	0	1
Albanerpetontidae	1	1	0	0	0	1	?	1	2	1	1	1	1	1	1	1	1	0	1	0	0	?	1	1	0	?	1	?	1	0	1	0	0	?	?	1	2	0	2	0	1
Tuditanidae	0	0	0	0	0	0	1	0	2	1	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0	1	0	2	1	0	0	1
Pantylidae	0	0	0	0	0	1	1	1	2	1	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	?	2	1	1	1	2
Gymnarthridae	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	0	0	0	?	0	0	0	?	0	0	0	0	1	0	0	0	1	0	2	1	0	1	1
Hapsidopareiontidae	0	0	0	0	0	0	1	1	2	1	0	?	0	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	?	1	0	0	0	1	0	2	1	0	0	1
Microbrachidae	0	0	0	0	0	0	1	0	2	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	?	0	0	0	?	1	0	0	0	1	0	2	1	0	1	1
Brachystelechidae	0	0	0	0	0	1	1	1	2	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	?	0	?	1	?	1	0	0	?	1	0	2	1	?	0	1
Rhynchonkos	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	0	0	0	?	0	0	0	?	0	0	0	?	1	0	0	0	1	0	2	1	1	1	1
Gymnophiona	1	0	1	0	1	0	1	1	1	1	?	1	1	1	1	1	1	1	0	1	?	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	2	1	1	1	1
Caudata	1	1	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	0	1	1	1	0	1	1	1	1	2	0	2	0	1
Salientia	1	1	1	1	1	3	1	1	2	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0	0	1	1	1	2	0	2	0	2
Platyrhinops	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Amphibamus	1	1	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Tersomius	1	1	1	0	1	0	0	1	0	0	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	0	0	0	0
Doleserpeton	1	1	1	0	1	0	1	1	1	0	0	0	0	0	?	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0
Micromelerpeton	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	?	0	?	0	0	0	0	1	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0

APPENDIX 3

CHARACTER DISTRIBUTIONS AT MAJOR NODES AND TERMINAL TAXA IN CLADOGRAMS

Cladogram 1

Node	Characters
1	1, 2, 3, 15, 19, 34
2	5, 8, 31
3	29, 36
4	7, 9^{0-1}, 17, 32
5	3^R, 5^R, 26,
6	6^{0-1}, $9R1^{-0}$, 27, 32^R, 35, 41
7	21^C, 28
8	9^{1-2}, 10, 14, 16, 37
9	11, 12, 13, 15, 22, 23, 24, 26, 39^{0-2}
10	3, 4, 5, 6^{1-2}, 18, 20, 21, 25, 30
11	1^R, 2^R, 19^R, 27^R, 34^R, 36^R, 38
12	$6R1^{-0}$
13	8^R, 29^R, 12^R, 40
14	$9R2^{-1}$
15	39^R
16	8^R
17	33^R
Schoenfelderpeton	37
Tuditanidae	40^R
Caudata	19^{R1-0}, 33
Salientia	6^{2-3},11^R, 14^R, 41^{1-2}
Pantylidae	6, 9^{1-2}, 28, 41^{1-2}
Gymnophiona	1^C, 3^C, 5^C, 13^C, 15^C, 18^C, 20^C, 26^{R1-0}, 27^C, 34^C
Micromelerpeton	7^R, 30^C, 36^R, 37^C
Tersomius	30^C
Amphibamus	6^{C0-1}, 15^C
Platyrhinops	4^C, 15^C

Cladogram 2

Node	Characters
1	1, 2, 3, 19, 34
2	5, 8, 31
3	29, 36
4	7, 9, 17, 32,
5	3^R, 5^R, 26,
6	6^{0-1}, 27, 32^R, 35, 41
7	$9R1^{-0}$, 21, 28
8	10, 12, 13, 14, 15^C, 16, 26^R, 37^{0-2}, 39^{0-1}
9	9^{1-2}, 11, 22, 23, 24, 39^{1-2}
10	3^C, 4^C, 5^C, 6^{1-2}, 18^C, 20^C, 21^C, 25, 30^C
11	2^R, 6^R, 19^R, 29^R, 36^R, 38, 40
12	1^R, 8^R, 13^R, 15^R, 27^R, 36^R
13	33^C
Schoenfelderpeton	37^C
Micromelerpeton	7^R, 30^C, 36^R, 37^C
Tuditanidae	9^{1-2}, 39^R, 40^R
Caudata	19^R, 33^C
Salientia	6^{2-3}, 11^R, 14^R, 41^{1-2}
Amphibamus	6^C, 15^C
Tersomius	30^C
Gymnophiona	3^C, 5^C, 18^C, 20^C
Platyrhinops	4^C, 15^C

Cladogram 3

Node	Characters
1	1, 2, 3, 19, 34
2	5, 8, 31
3	29, 36
4	7, 9, 17, 32,
5	3^R, 5^R, 26,
6	6^{0-1}, 27, 32^R, 35, 41
7	$9R1^{-0}$, 21, 28
8	10, 12, 13, 14, 15^C, 16, 26^R, 37^{0-2}, 39^{0-1}
9	9^{1-2}, 11, 22, 23, 24, 39^{1-2}
10	3^C, 4^C, 5^C, 6^{1-2}, 18^C, 20^C, 21^C, 25, 30^C
11	2^R, 6^R, 19^R, 29^R, 36^C, 38, 40
12	33^C
Schoenfelderpeton	37^C
Rhynchonkos	1^R, 8^R, 13^R, 15^R, 27^R, 34^R
Gymnophiona	3^C, 5^C, 18^C, 20^C
Caudata	19^R, 33^C
Salientia	6^{2-3}, 11^R, 14^R, 41^{1-2}
Micromelerpeton	7^R, 30^C, 36^R, 37^C
Tersomius	30^C
Amphibamus	6^C, 15^C
Platyrhinops	4^C, 15^C

Cladogram 4

Node	Characters
1	1, 2, 8, 17, 19, 29, 34, 36
2	6^{0-1}, 16, 27, 35, 41^{0-1}
3	9^{0-1}, 10, 12, 13^{C}, 14^{C}, 15^{C}, 36^{0-2}, 39
4	9^{1-2}, 11^{C}, 22, 23, 24, 39^{1-2}
5	2^{R}, 6^{2-3}, 19^{R}, 29^{R}, 36^{R}, 38, 40
6	3^{C}, 4, 5^{C}, 6^{1-2}, 18^{C}, 20^{C}, 21^{C}, 25, 30
6	2^{R}, 9^{2-1}, 23^{R}, 24^{R}, 29^{R}, 36^{R}, 38, 39^{2-1}, 40
Branchiosaurus	21^{C}
Gymnophiona	3^{C}, 5^{C}, 18^{C}, 20^{C}
Caudata	19^{R}
Salientia	6^{2-3},11^{R}, 14^{R}, 41^{1-2}
Doleserpeton	3^{C}, 5^{C}, 9^{0-1},
Rhynchonkos	1^{R}, 8^{R}, 13^{R}, 15^{R}, 27^{R}, 34^{R}