PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

A Metamorphosed Salamander from the Early Cretaceous of Las Hoyas, Spain

Susan E. Evans and Andrew R. Milner

Phil. Trans. R. Soc. Lond. B 1996 **351**, 627-646
doi: 10.1098/rstb.1996.0061

A metamorphosed salamander from the early Cretaceous of Las Hoyas, Spain

SUSAN E. EVANS[1] AND ANDREW R. MILNER[2]

[1] *Department of Anatomy and Developmental Biology, Rockefeller Building, University College London, University Street, London WC1E 6BT, U.K.*
[2] *Department of Biology, Birkbeck College, Malet Street, London WC1E 7HX, U.K.*

CONTENTS

SUMMARY

A salamander, *Valdotriton gracilis* gen. et sp. nov., is described on the basis of six articulated skeletons of small metamorphosed individuals from the early Barremian (Early Cretaceous) La Huérguina Formation at the locality of Las Hoyas, Cuenca Province, Castilla La Mancha, Spain. *Valdotriton* is a relatively plesiomorphic member of the Urodela (crown-group salamanders), but more derived than the Sirenidae and Cryptobranchoidea, in that it possesses a single ossification in place of the prearticular and angular, and it has intravertebral spinal foramina on the anterior caudal vertebrae. It represents a plesion on the stem of the 'internally fertilizing salamander clade' comprising the Plethodontidae, Amphiumidae, Rhyacotritonidae, Proteidae, Dicamptodontidae, Ambystomatidae and Salamandridae.

1. INTRODUCTION

The Caudata – the salamanders and newts – are one of the three surviving clades of amphibians. They are represented by about 350 species distributed in ten families. The majority of caudates are found in Northern Eurasia and North America, the only groups found outside this area being a few members of the Salamandridae in the Atlas mountains of North Africa and a substantial radiation of the plethodontid subfamily Bolitoglossinae in Central and South America (Milner 1983). There is no consensus on the

Phil. Trans. R. Soc. Lond. B (1996) **351**, 627–646
Printed in Great Britain

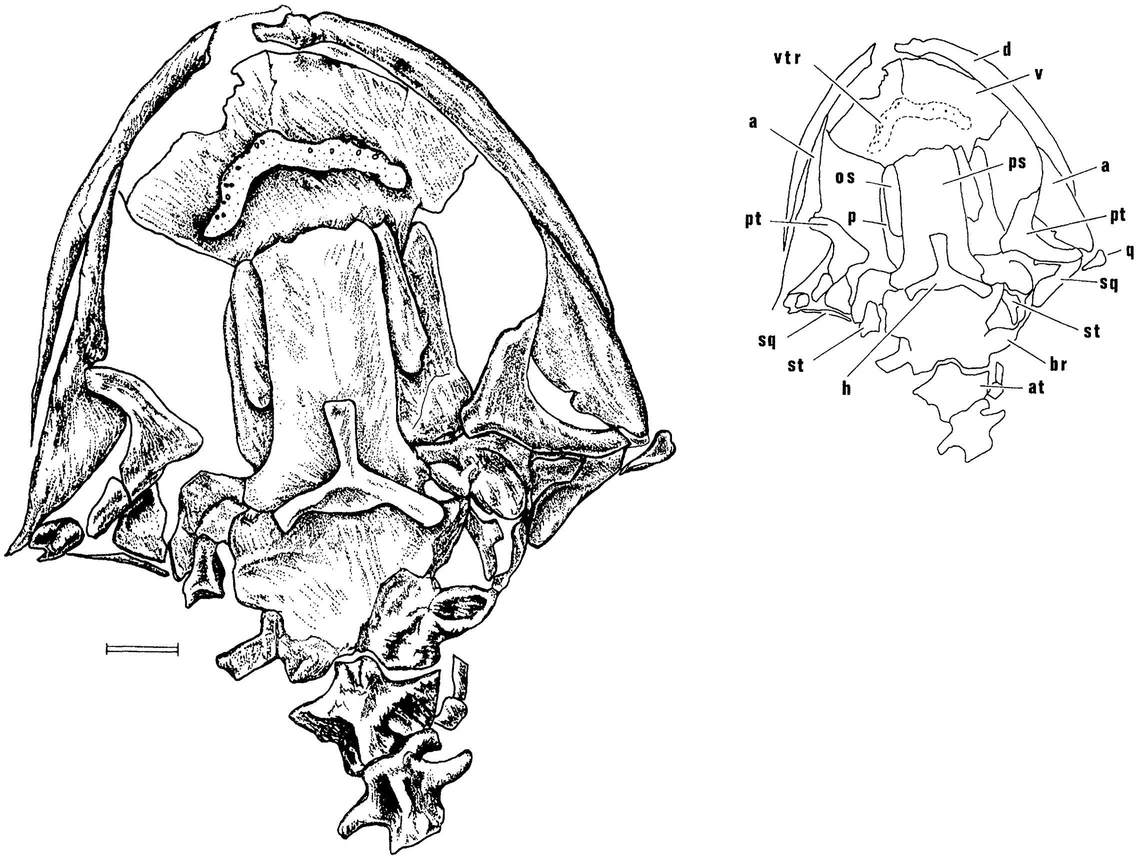

Figure 1. *Valdotriton gracilis* gen. et sp. nov.. Barremian; Las Hoyas, Spain. Holotype, LH 928061b, skull, palatal view. Scale bar = 1 mm.

interrelationships of the families of living salamanders (Edwards 1976; Milner 1983; Duellman & Trueb 1986; Hillis 1991; Larson 1991; Larson & Dimmick 1993; Hay *et al.* 1995), although there is increasing agreement about the relationships of the more primitive forms (see §7).

The fossil record has been of little use in determining the relationships of salamander families. The Caudata have a substantial late Cretaceous and Cenozoic fossil record in Eurasia and North America. From the Campanian (83–65 Ma BP; all figures from Harland *et al.* 1990) onwards, at least some of the extant families have appeared and it is clear that most if not all of the family-level diversification of salamanders had taken place before the Campanian. This phase of salamander evolution is, however, poorly represented in the fossil record and the earliest stages of salamander evolution are not represented at all. Fossil salamanders are not yet known before the Bathonian (170–159 Ma BP; Middle Jurassic), but the group may be theorized to have appeared earlier. If, as preferred here, the Salientia (frogs) are accepted as the sister-group to the Caudata (Milner 1988; Trueb & Cloutier 1991; Milner 1993*a*) then stem-salamanders must have been present in the Lower Triassic (250 Ma BP) contemporaneously with the stem-frog *Triadobatrachus*. The alternative view, that the Caudata and Gymnophiona (caecilians) are sister-taxa, would still necessitate the appearance of salamanders by the Lower Jurassic, contemporaneous with the stem caecilian *Eocaecilia* (Jenkins & Walsh 1993). The record from the Middle Jurassic to the Late Cretaceous is still relatively poor and most of it is based on material collected in the last 20 years. Estes (1981), in a comprehensive review of fossil salamanders, was able to list only five pre-Campanian records of salamanders (apart from the enigmatic *Albanerpeton*) and only two of these, *Karaurus* from the Middle Jurassic of Kazakhstan, and *Hylaeobatrachus* from the Wealden of Belgium, were based on articulated material. Subsequently, several new assemblages of salamander material have been collected and have been or are being described (Estes & Sanchíz 1982; Evans *et al.* 1988; Nessov 1988; Ensom *et al.* 1991; Evans & Milner 1993). They are reviewed in the discussion of this paper. Most are represented by disarticulated elements, but one assemblage, that from the Lower Cretaceous of Las Hoyas in Spain, is composed of articulated skeletons and it is one of the Las Hoyas salamanders that forms the basis of this work.

2. MATERIAL

The rich vertebrate assemblage from the Early Cretaceous locality at Las Hoyas in Cuenca Province, Castilla La Mancha, Spain, was first reported in Sanz *et al.* (1988). The productive horizons are laminated limestones, apparently from a lake bed which was periodically anoxic. The horizons form part of the La Huérguina Formation and are probably of early Barremian age (116–114 Ma BP) and so equivalent in age to the late Wealden of England (Frenegal-Martínez & Meléndez 1995). However, these facies have produced a very different assemblage to that of most other Wealden or Wealden-equivalent localities, not only in the faunal composition but also in the articulated nature of the vertebrate material. The vertebrate assemblage is composed largely of fishes, 13 genera having been reported (Sanz *et al.* 1988; Poyato-Ariza 1989; Poyato-Ariza & Wenz 1995). The only tetrapods to have been described to date are the two birds *Iberomesornis* (Sanz & Bonaparte 1992) and *Concornis* (Sanz & Buscalioni 1992), and the ornithomimosaur *Pelecanimimus polyodon* (Pérez-Moreno *et al.* 1994). Other vertebrates reported from the locality include frogs and salamanders (Evans *et al.* 1995), turtles of problematic identity (Jimenez-Fuentes 1995), lizards (Barbadillo & Evans 1995) and several small crocodiles (Buscalioni & Ortega 1995).

Sanz *et al.* (1988) reported a single unnamed species of neotenous salamander in the Las Hoyas assemblage, but much material has been collected subsequently and three species of salamander or salamander-like amphibian are now known from the locality (Evans *et al.* 1995). One of these is a member of the enigmatic amphibian family Albanerpetontidae. This family appears to represent a fourth lissamphibian group distinct from the salamanders (Fox & Naylor 1982; Milner 1988; McGowan 1994; McGowan & Evans 1995). The two articulated albanerpetontid specimens from Las Hoyas form the basis of the new species *Celtedens ibericus* McGowan & Evans 1995. A second form is the neotenous true salamander reported by Sanz *et al.* 1988 and to be described by the authors at a later date. The third form is a small salamander represented by several metamorphosed specimens. The description of this latter taxon and the discussion of its phylogenetic position form the basis of this paper.

(Institutional abbreviations are as follows. LH: Las Hoyas Collection, currently in the Unidad de Paleontología, Departamento de Biología, Universidad Autonoma de Madrid, eventually to the Museo de Cuenca, Spain. LH-ADR: Las Hoyas Collection, originally part of private collection of Señor Armando Diaz-Romeral, Cuenca, Spain. MC: Museo de Cuenca, Cuenca Province, Spain.)

3. SYSTEMATIC PALAEONTOLOGY

LISSAMPHIBIA Haeckel, 1866
CAUDATA Scopoli, 1777
URODELA Dumèril, 1806
NEOCAUDATA Cannatella & Hillis, 1993
Family Incertae sedis
Genus: *Valdotriton* new genus

Generic diagnosis: as for *V. gracilis*, the only species.

Type species: *Valdotriton gracilis* gen. et sp. nov.

Derivation of name: *Valdo* – of the Wealden. *Triton* (Gk): a newt.

Valdotriton gracilis new species

Holotype: LH 928061a–b, counterparts of a skeleton, missing only part of the tail. Slab b bears the skeleton visible in ventral aspect after preparation (figures 1, 2*a*, 7, 9*bc*, 11*a*). Slab a is a poor impression with only part of the tail visible as original bone.

Specific diagnosis: a primitive crown-group salamander which underwent metamorphosis and grew to at least 40 mm snout–pelvis length. More derived than the sirenid salamanders in the following character: single scapulocoracoid ossification. More derived than the cryptobranchoid salamanders because of the following character: single ossification in the place of the prearticular and angular. More derived than the cryptobranchoid and proteid salamanders because of the following character: intravertebral spinal foramina present in at least nine caudal vertebrae. Primitive characters include: pars dorsalis of premaxilla extending as a spike of bone over the midline of the nasal, suggesting the presence of two anlagen per nasal ossification, vomerine dentition forming a simple transverse band of denticles across the anterior palate, pterygoids present and suturing anteriorly with the posterior ends of the maxillaries, prominent inverted ‘Y’-shaped second basibranchial, 16 presacral vertebrae, double-headed rib-bearers, intravertebral spinal foramina absent from trunk vertebrae. Characters of uncertain polarity include: absence of sculpture on the dermal bones of the skull, vomers lacking anterior fontanelle, neural spines very low with a low backwardly directed spine, terminal phalanges long and slender.

Derivation of name: *gracilis*: lightly built, graceful.

Locality: Las Hoyas fossil site, La Cierva township, about 20 km east of Cuenca, Cuenca Province, Castila La Mancha, Spain.

Horizon: Limestone in Unit III of the La Huérguina Formation, Early Barremian, Lower Cretaceous (Fregenal-Martínez & Meléndez 1995).

Paratypes: LH 2850a–b, counterparts of an almost complete skeleton, in which the dorsal surface of the skull, and a series of caudal vertebrae are well preserved (figures 4, 8*a*).

LH 6021, counterparts of an almost complete skeleton, one showing skull in dorsal aspect (figures 2*b*, 5, 8*c*, 10, 11*b–c*).

MC 6*a–b*, counterparts of a skeleton, skull partly disarticulated but dentition and vertebral column well preserved (figures 2*c*, 3, 8*b*, 9*a*).

Referred material: LH 928001a–b, counterparts of a complete but poorly preserved skeleton, largely visible in ventral aspect. LH-ADR unnumbered, counterparts of anterior half of a skeleton.

4. TAXONOMIC NOTE

Throughout this work, we follow Milner (1988) in restricting the term Urodela to the crown-group salamanders and using the term Caudata for the stem + crown salamanders (i.e. including the

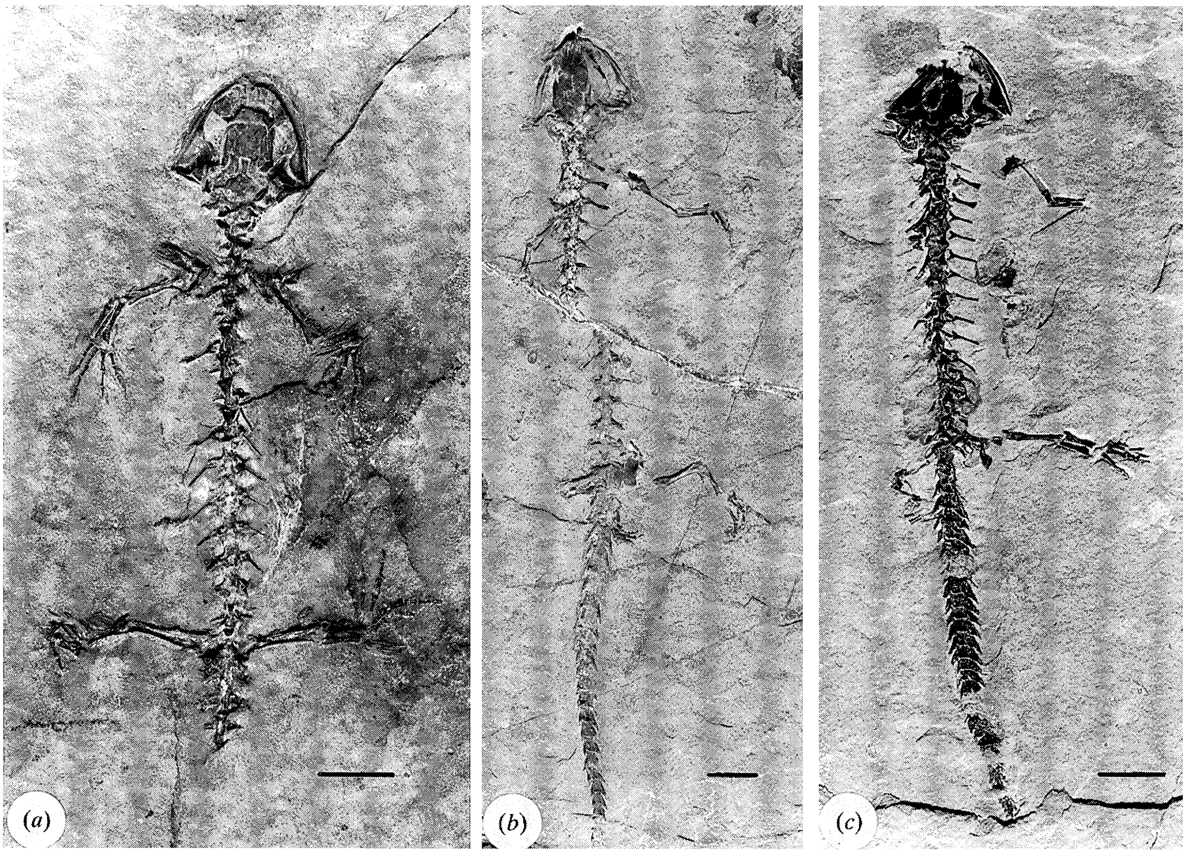

Figure 2. *Valdotriton gracilis* gen. et sp. nov. Barremian; Las Hoyas, Spain. (*a*) Holotype LH928061b, ventral view; (*b*) paratype LH6021a, dorsal view; (*c*) paratype MC6a, ventral view. All scale bars = 5 mm.

Karauridae). This needs to be emphasized because of a taxonomic problem that has recently developed. The history is as follows.

Until 1988, the higher taxonomic terms Caudata Scopoli, 1777 (often attributed to Oppel 1811) and Urodela Dumèril, 1806 were used more or less interchangeably for all living and fossil salamanders. In 1988, A. R. M. published a review of lissamphibian relationships in which it was proposed that separate taxonomic terms should be applied to the 'crown-group' salamanders (all living salamanders and those fossil forms descended from the same common ancestor as the living forms) and the inclusive grouping of 'stem + crown' salamanders (the entire salamander clade down to the dichotomy with the Salientia). Milner (1988) proposed that the name Urodela be applied to the crown-group salamanders, and that Caudata be applied to the stem + crown salamanders. This was based on the precedent of the Caudata being applied to the stem + crown salamanders by Estes (1981) in the definitive review of fossil salamanders at the time, and by Duellman & Trueb (1986) in the most comprehensive text-book on the living amphibians. Both included the acknowledged stem-salamander genus *Karaurus* within the Caudata which was thus an inclusive grouping. Milner (1988) therefore selected Caudata as the label for the inclusive group and Urodela for the crown-group and has continued to use this subsequently (Milner 1993*a*, *b*).

In 1991, Trueb & Cloutier published a detailed analysis of the relationships of the higher groups of lissamphibians. This paper was delayed in publication and the original work largely took place in parallel with Milner's work, although Milner's paper was available before that work was completed. Trueb & Cloutier came to most of the same conclusions as Milner, in that they perceived that distinct names were required for the crown-group salamanders and the stem + crown salamanders, and that Caudata and Urodela were the logical names to use. Unfortunately they selected Urodela as the inclusive (stem + crown) group and Caudata as the crown-group: the precise reverse of Milner's usage. They appear to have been influenced by Carroll (1988) in which the Urodela are made the inclusive taxon for the salamanders. Trueb & Cloutier's taxonomy has been followed by Trueb (1993) and Cannatella & Hillis (1993).

Thus since 1991, there have been two precisely contradictory uses of the taxonomic terms Caudata and Urodela in publication, and this can only result in confusion unless rationalized immediately. This confusion will be minimal for neontologists dealing only in living forms, because the two taxonomic names both broadly apply to the living salamanders. For palaeoherpetologists, however, the confusion will be acute. *Karaurus*, for example, is either a non-urodele caudate (Milner 1988) or a non-caudate urodele (Trueb & Cloutier 1991).

We propose standardization of the use of the these terms as put forward by Milner (1988). This was based on previous usage of the term Caudata in widely used references (Estes 1981; Duellman & Trueb 1986) and

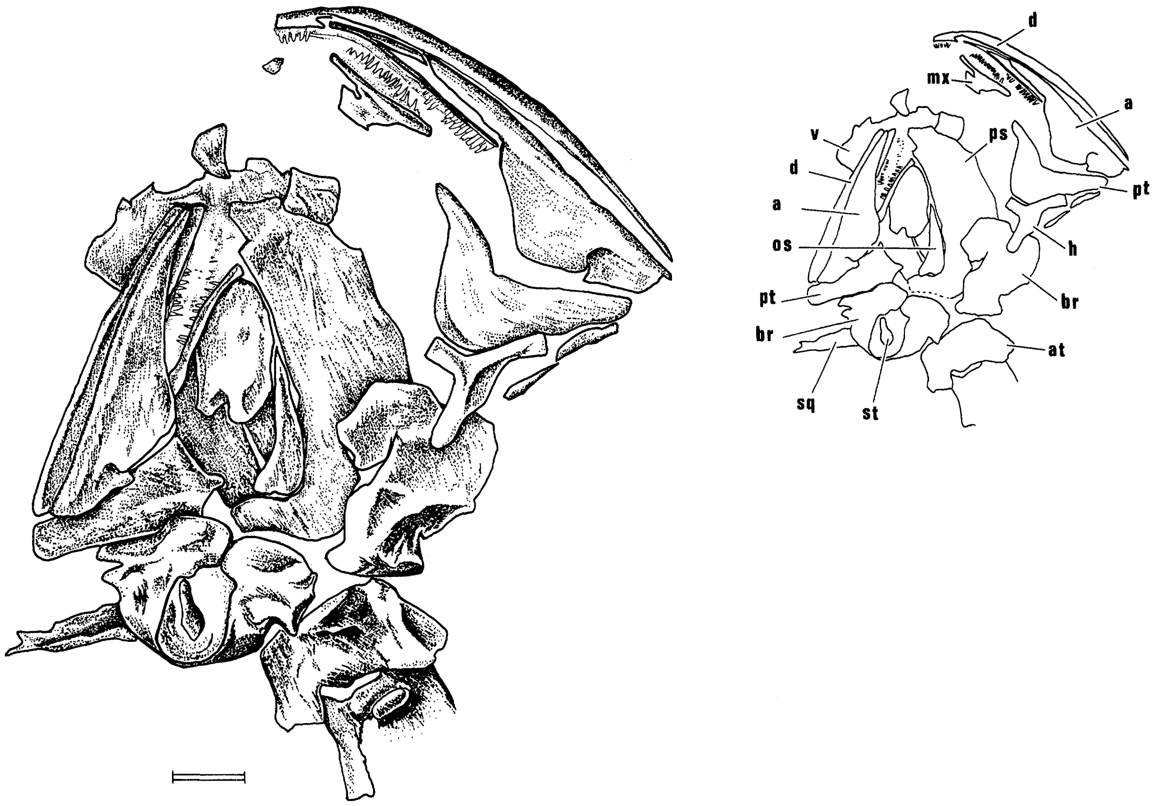

Figure 3. *Valdotriton gracilis* gen. et sp. nov. Barremian; Las Hoyas, Spain. Paratype, MC 6a, skull, palatal view. Scale bar = 1 mm.

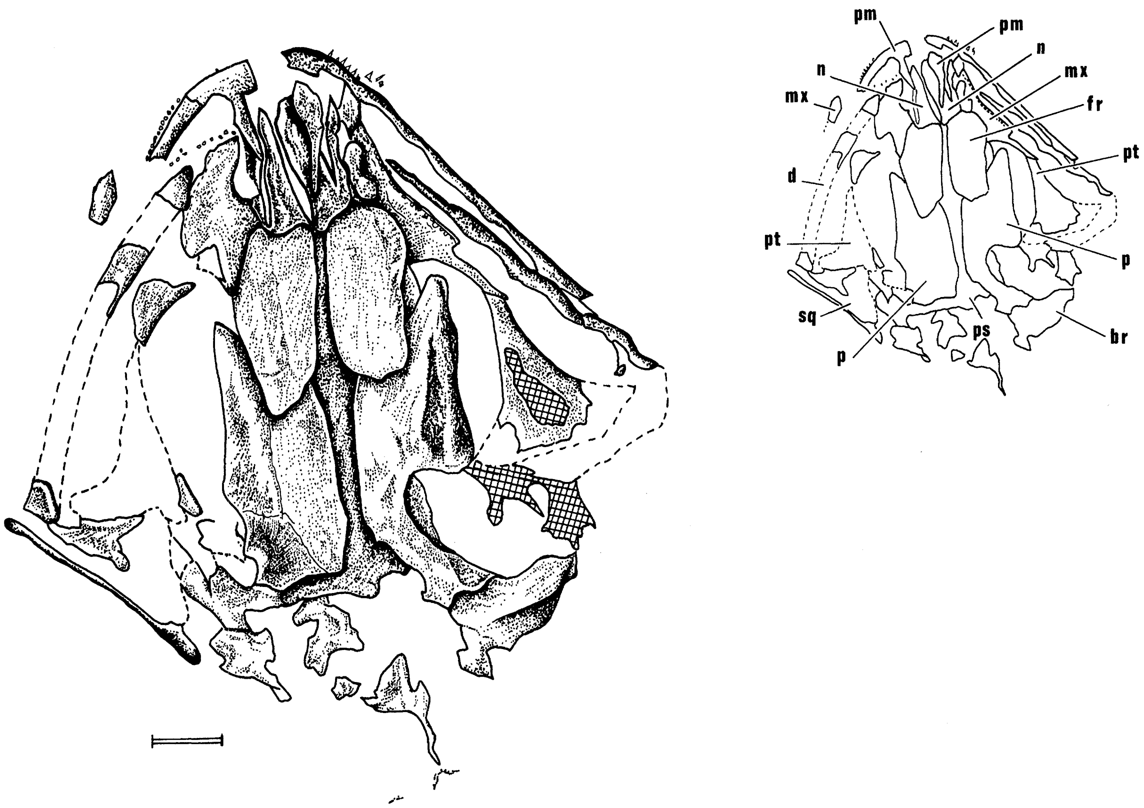

Figure 4. *Valdotriton gracilis* gen. et sp. nov. Barremian; Las Hoyas, Spain. Paratype, LH 2850b, skull, dorsal view. Scale bar = 1 mm.

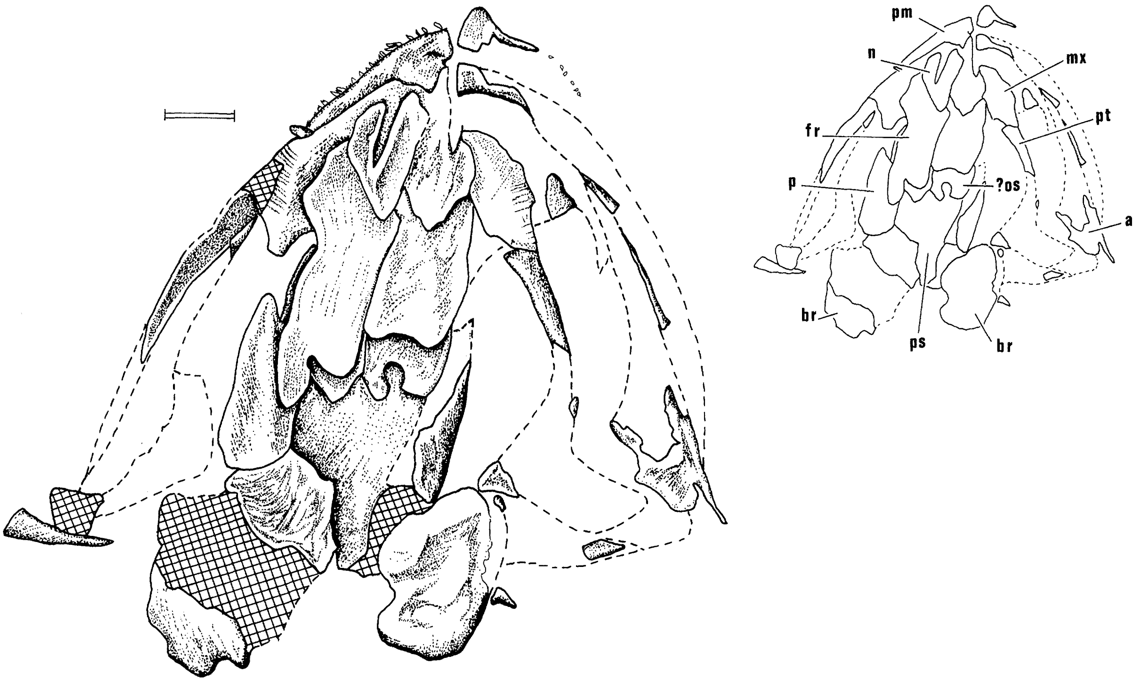

Figure 5. *Valdotriton gracilis* gen. et sp. nov. Barremian; Las Hoyas, Spain. Paratype, LH 6021a, skull, dorsal view. Scale bar = 1 mm.

has three years priority over the usage of Trueb & Cloutier. If there is no standardization, future authors will have to specify persistently the basis of their use of these terms.

5. DESCRIPTION OF *VALDOTRITON*

(*a*) *General features*

The six specimens are all skeletons of small metamorphosed salamanders. Five of them are sufficiently complete to permit the snout–pelvis length to be measured and they are: LH 928001: ca. 28 mm, MC 6: 30 mm, LH 2850: ca. 35 mm, LH 928061: 37 mm and LH 6021: 40 mm. The tail is longer than the trunk (figure 12). They represent metamorphosed individuals because not only are they not perennibranchiate, but the second basibranchial has become modified as an inverted 'Y'-shaped ossification, a post-metamorphosis phenomenon in living salamanders (see below). Although post-metamorphic, the available specimens do not necessarily represent adult individuals. No one specimen shows the full suite of characteristics of this taxon and so we have felt it necessary to designate three paratypes to supplement the holotype. The holotype specimen has a well preserved palate, mandibles, girdles and limbs, whereas the three paratypes provide information on the skull roof, marginal dentition, vertebrae and ribs.

(*b*) *Skull roof*

The dermal bones of the skull are thin and unsculptured. All midline bones are paired and the temporal region is clearly open. The premaxillae are each composed of a wide alveolar region and a long slender pars dorsalis (= dorsal or alary process) which extends back over the nasal (figure 4, 6*b*). The nasals each bear an antero–posterior linear recess on the anterodorsal surface, the dorsal process of the premaxilla sitting in this recess. The lateral margin of the nasal is not visible. The dorsal processes of the premaxillae do not meet or converge medially. Each dorsal process passes along the midline of a nasal. In the living salamanders, this primitive condition occurs in the cryptobranchoids where each nasal develops from two anlage, and the developing dorsal process grows between them before they meet. In more derived living salamanders, the nasal (unless absent) develops only from a lateral anlage and the dorsal process of the premaxilla passes medial to it.

The maxillae bear facial processes of uncertain size, and short posterior processes which do not reach the suspensorium, but articulate with the anterior ramus of the pterygoid (figures 4–5). The presence or absence of septomaxillae and lacrimals has not been established. The prefrontals are long and slender and are anterolaterally directed at the anterior end. Medially, each prefrontal sits in a deep facet formed partly by the nasal and partly by the frontal. The parietals cover the main portion of the skull roof (figures 4, 6*b*). They wedge shallowly between the frontals anteriorly. There are also anterolateral extensions of the parietals lateral to the frontals and forming the anterolateral wall of the braincase.

The cheek region of the skull roof is composed entirely of the squamosals, the quadratojugals being absent (figure 6*b*). The squamosal is never well preserved, but in LH 6021, there appears to be an anterolateral–posteromedial dorsal groove running parallel and close to the posterolateral margin of the

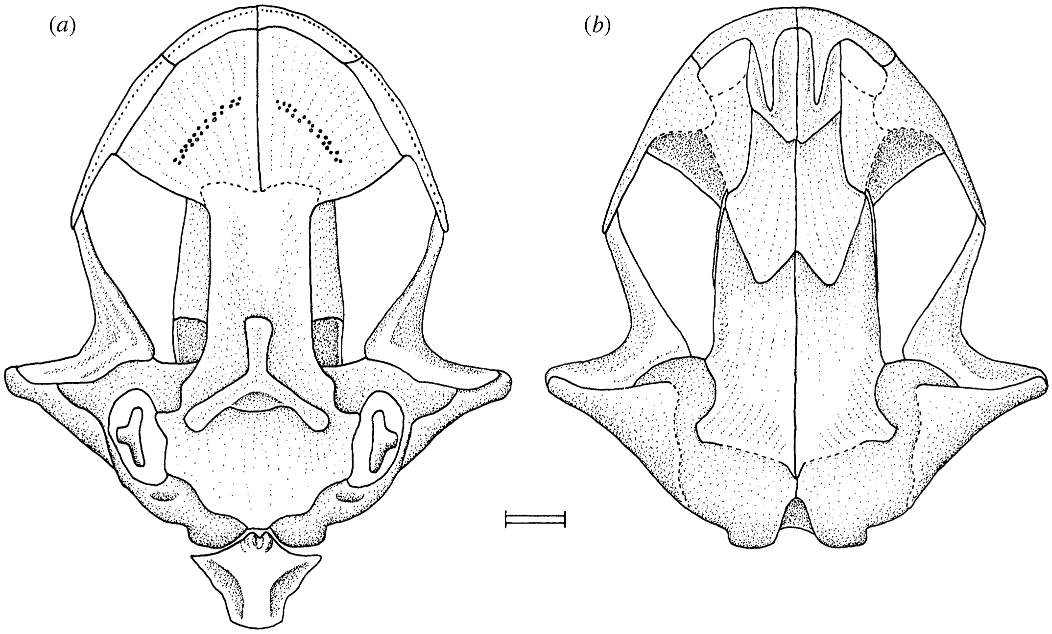

Figure 6. *Valdotriton gracilis* gen. et sp. nov. Reconstructions of skull in (*a*) palatal and; (*b*) dorsal views. Scale bar = 1 mm.

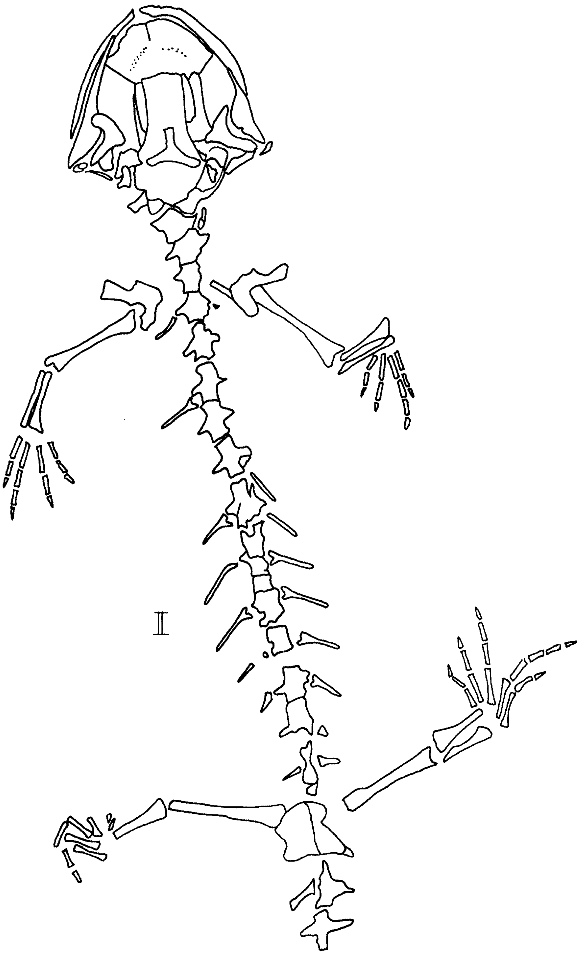

Figure 7. *Valdotriton gracilis* gen. et sp. nov. Barremian; Las Hoyas, Spain. Holotype, LH 928061b, skeleton, ventral view. Scale bar = 1 mm.

parietal. This is interpreted as the groove permitting the adductor musculature to extend to the occipital region, the condition in all modern salamanders but not in *Karaurus* (Ivakhnenko 1978).

(*c*) ***Palate and braincase***

The vomers are broad plate-like structures and border the interpterygoid vacuities anteriorly (figures 1, 6*a*). There is no trace of an anterior fontanelle in the anteromedial region of the palate. The posterior margin of each vomer shows no tendency to curve backwards at its lateral edge. The cultriform process of the parasphenoid is broad and forms the entire underside of the anterior braincase as in modern salamanders (figures 1, 6*a*). The ventrolateral braincase is formed by rectangular orbitosphenoid ossifications articulating between the parietals and the cultriform process. The cultriform process extends ventrally over the posteromedial edge of the vomers (figures 1, 6*a*). The broad basal plate of the parasphenoid extends out to underlie the otic capsules. The pterygoids are Y-shaped ossifications which sutured with the basisphenoid and the quadrate region but did not apparently extend as far as the vomers (figures 1, 3, 6*a*). However in LH 2850 (figure 4) and LH 6021 (figure 5), the palatine ramus of the pterygoid can be seen to extend to form a sutural contact with the posterior extremity of the maxilla. The posterior braincase elements appear to include fully ossified prootics and opisthotics. They border a large fenestra ovalis. The exoccipitals bear prominent flattened condyles.

(*d*) ***Mandible***

Each mandibular ramus comprises a dentary and a single posterior element, apparently a composite prearticular-angular as found in many extant caudate

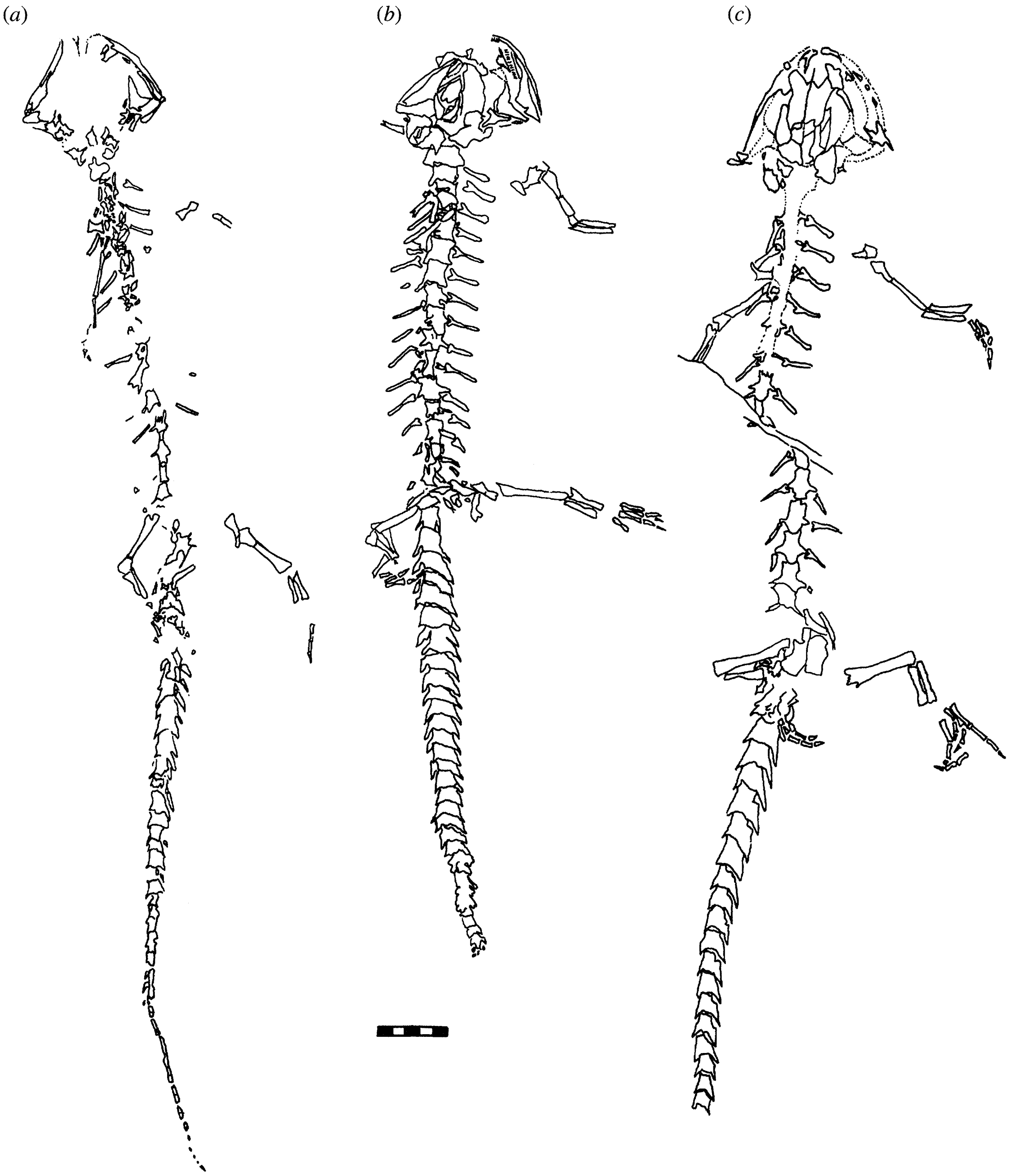

Figure 8. *Valdotriton gracilis* gen. et sp. nov.. Barremian; Las Hoyas, Spain. Paratype skeletons: (*a*) LH2850a; (*b*) MC 6a; (*c*) LH6021a. Scale bar = 5 mm.

families (figures 1, 3). The dentary bears a meckelian groove which is closed anteriorly. It deepens posteriorly and is filled by an anterior extension of the large prearticular-angular. The symphysis is small.

(*e*) *Dentition*

The marginal dentition is present on the premaxillae, maxillae and dentaries (figures 3–5). The marginal teeth are tiny and numerous. The dentary ramus bears a tooth-row of about 60 teeth which is longer than the upper tooth-row, although no premaxilla or maxilla is sufficiently complete to permit useful tooth counts for these elements. The marginal teeth are pointed and pedicellate but it is unclear whether they are unicuspid or bicuspid.

As is typical for frogs and salamanders, the only palatal dentition is borne on the vomers. The configuration is relatively unusual for a metamorphosed salamander in that the vomerine dentition is made up of a gently curved transverse arch of 2–3 closely spaced rows of tiny teeth across the middle region of the vomers (figures 1, 6*a*). It cannot be determined whether the teeth are replaced anterolaterally or posteromedially. This vomerine dentition forms an arch of teeth paralleling the marginal dentition, a configuration generally described as larval when found in modern salamanders, particularly the neotenous cryptobranchids (Regal 1966). Regal categorized the palatal dentition of living salamanders into four types of which his Type 1 dentition (curved vomerine tooth rows parallel to the marginal teeth) was found only in

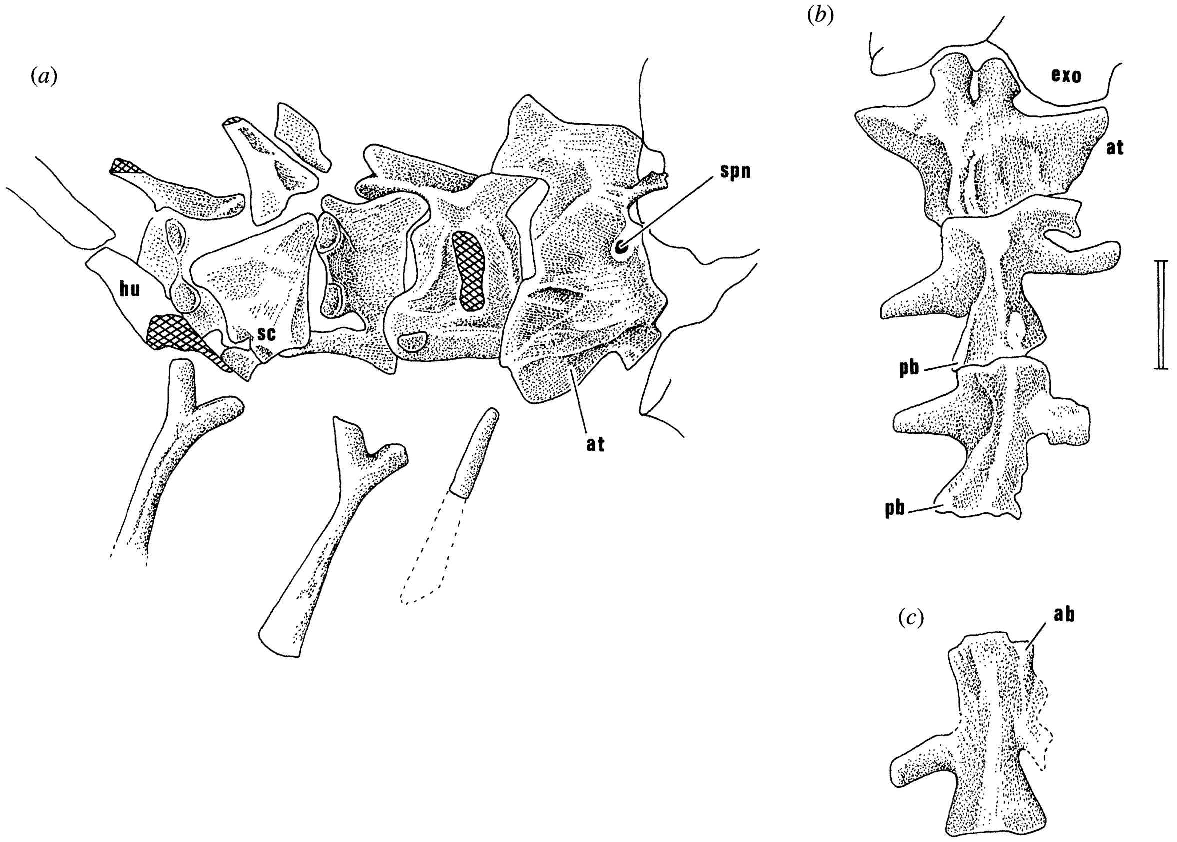

Figure 9. *Valdotriton gracilis* gen. et sp. nov. Barremian; Las Hoyas, Spain. Vertebral structure: (*a*) paratype MC 6a, right ventrolateral view of atlas and first presacral vertebrae; (*b*–*c*) holotype, LH928061b, B, ventral view of atlas and two presacrals; (*c*) presacral vertebra 6. Scale bar = 1 mm.

larvae, neotenous adults and *Dicamptodon* and in a slightly modfied form as two short rows of teeth in *Rhyacotriton*. It thus occurs in some modern metamorphosed forms (*Rhyacotriton* and *Dicamptodon*) argued to be the most primitive of the non-cryptobranchoid metamorphosing salamanders.

(*f*) *Hyobranchial skeleton and stapes*

The hyobranchial skeleton and stapes have the characteristics of those of a metamorphosed salamander. The ceratobranchials are never ossified, the only ossified component of the hyoid skeleton is a characteristic median ossification shaped like an inverted 'Y' when seen in ventral aspect (figures 1, 3, 6*a*). It is situated immediately below the basal plate of the parasphenoid and is the second basibranchial (= os thyroidei). In modern metamorphosed salamanders, such modified basibranchials are present in some genera but absent in others. Özeti & Wake (1969 pp. 99–100, figures 1–4) found that within the Salamandridae, *Chioglossa* possesses a 'inverted Y'-shaped second basibranchial (similar in shape to that of *Valdotriton* but smaller), *Salamandra* species possess a second basibranchial which is a small bar of bone with a tiny anterior medial process, but all other salamandrid genera lose the second basibranchial at metamorphosis. An 'inverted V'-shaped second basibranchial occurs in adults of at least some species of *Ambystoma* (Papendieck 1954 p.173, figure 9), and second basibranchials of various shapes are found in some plethodontid genera but are absent in others (Wake 1966 p. 34, figures 10–11). In comparison with all the above modern forms, the second basibranchial of *Valdotriton* is a relatively large structure with a robust anterior ramus. This may represent a primitive condition for this structure.

The stapes is robust with a large footplate and a short stylus (figures 1, 3, 6*a*).

(*g*) *Axial skeleton*

The vertebral column comprises an atlas, 15 postatlanteal presacral vertebrae (figure 7), 1 sacral vertebra and about 50 caudal vertebrae (figure 8*a*). The vertebrae are notochordal and amphicoelous.

The atlas is not markedly shorter than the postatlanteal vertebrae and is actually longer than the immediately following vertebra (figure 9). The atlas bears a small tuberculum interglenoideum which develops from several components. No specimen presents a clear view of the atlanteal cotyles on each side of the tuberculum but they appear to have been of flattened oval shape. The ventral surface of the atlas bears a squared ventral ridge with ventrolateral flanges (LH 928001). The atlas can be seen to possess spinal nerve foramina in MC 6A (figure 9*a*).

The postatlanteal trunk vertebrae apparently bear no intravertebral spinal nerve foramina, but there are vertebrarterial canals piercing the bases of the rib-

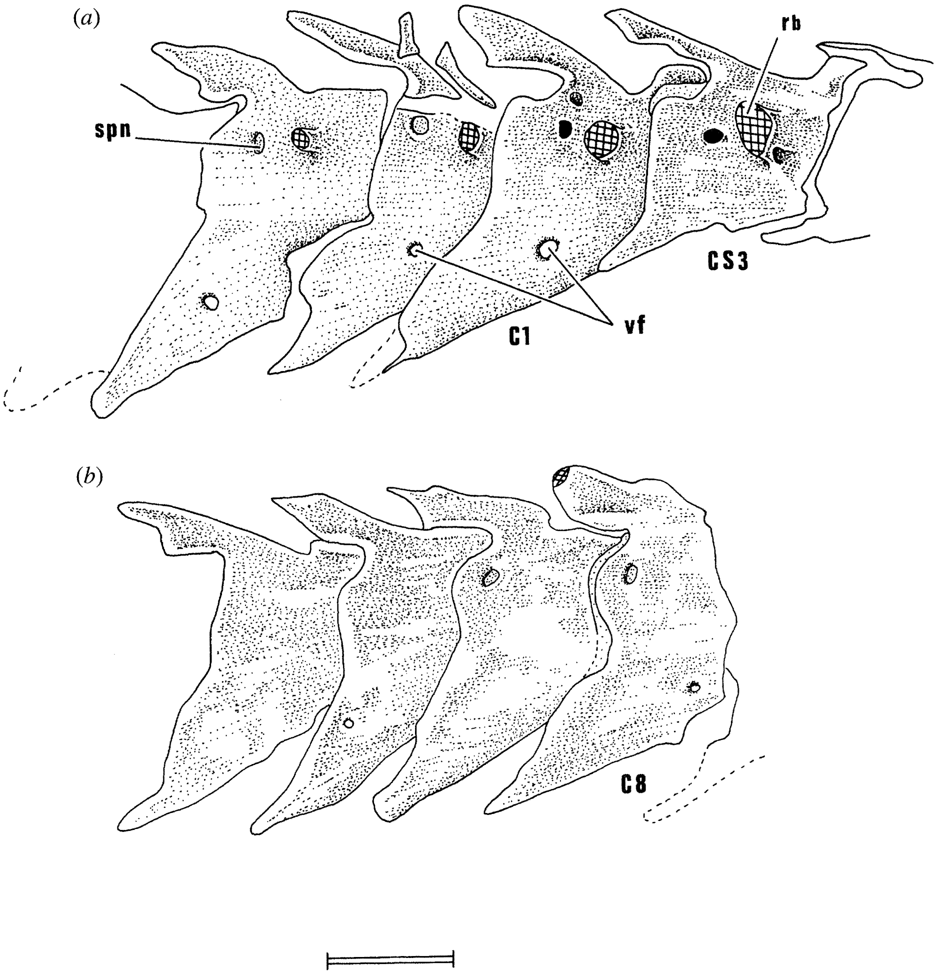

Figure 10. *Valdotriton gracilis* gen. et sp. nov. Barremian; Las Hoyas, Spain. Anterior caudal region of paratype LH 6021: (*a*) series of vertebrae from caudosacral 3 to caudal 3; (*b*) series from caudal 8 to caudal 11. Scale bar = 1 mm.

bearers. The first two postatlanteal vertebrae have posterior basapophyses but no anterior basapophyses (figure 9*b*). The remaining trunk vertebrae bear anterior basapophyses but no posterior basapophyses. The anterior trunk vertebrae are relatively short, less than two-thirds of the length of the posterior trunk vertebrae. The anterior trunk vertebrae are strongly keeled and have short rib-bearers. The posterior trunk vertebrae are without keels and the rib-bearers increase in length, as do the vertebral centra. The rib-bearers are distinctly double-headed throughout the trunk, the two articular facets joined by a thin web of bone. Few neural arches are visible. Those that are visible in profile are dorsoventrally flattened structures, posteriorly forming a low horizontal spine overlapping the following vertebra.

The atlas vertebra does not bear ribs but all succeeding trunk vertebrae do. Trunk ribs are double-headed and the rib heads are widely bifurcate (figures 8*b*–*c*). The first three post-atlanteal vertebrae bear robust ribs, associated with the pectoral musculature. The remaining trunk ribs are relatively long and slender for a salamander. A single stout double-headed sacral rib is visible in two specimens (LH 6021 (figure 11*b*–*c*), MC 6) and it appears that only one sacral vertebra was present.

The tail is longer than the trunk. The sacral vertebra is followed by three caudosacrals. Unlike later caudals, these lack a deep haemal spine, though there is a small haemal spine on caudosacral 3 (figure 10*a*). The caudosacrals still bear transverse processes perforated at the base by vertebrarterial canals. The transverse process are broken but can be seen to be oval in cross section, and decrease in size from caudosacral 1 to caudosacral 3. The following anterior caudals are characterized by thinner transverse processes which are circular in cross section and not perforated at the base (figure 10*a*). The proximal region of the tail is deep, because the individual anterior caudal vertebrae are deep with large haemal arches forming backwardly directed overlapping haemal spines. The neural arches are also backwardly directed and overlapping but are relatively small, and only about half the size of the corresponding haemal arches (figure 10*b*). The distal region of the tail narrows to a slender tip.

The third caudosacral vertebra and the eight succeeding caudal vertebrae each bear a lateral foramen opening behind the transverse process (figure 10*a*). In caudosacral 3, this foramen is situated immediately posterodorsal to the posterior opening for the vertebrarterial canal (figure 10*a*). In each of the eight following caudals, a corresponding foramen

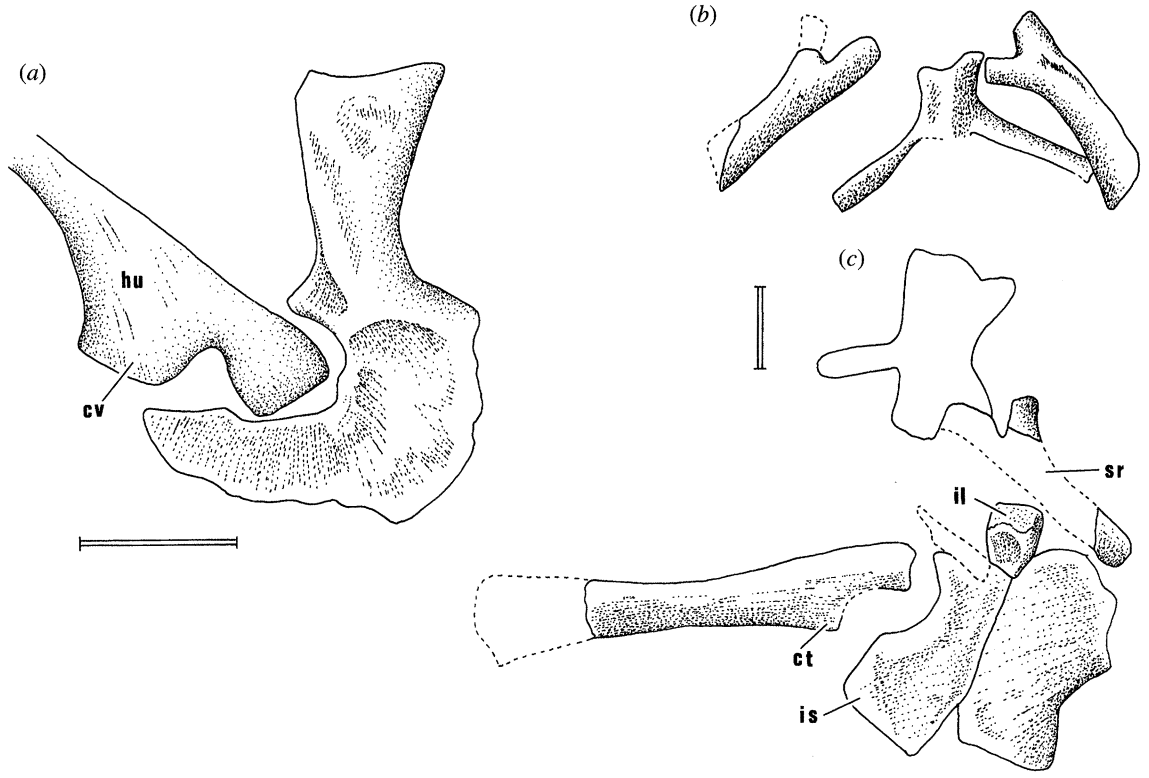

Figure 11. *Valdotriton gracilis* gen. et sp. nov. Barremian; Las Hoyas, Spain. Limb girdles: (*a*) holotype, LH928061b, left pectoral girdle and proximal humerus; (*b–c*) paratype, LH 6021, (*b*) sacral vertebra and ribs of counterpart Lh6020b, (*c*) pelvic girdle and femur on main block LH 6021a. Scale bar = 1 mm.

occurs in the same position, although the vertebrarterial canal is absent (figure 10*b*). These foramina are presumably intravertebral spinal nerve foramina.

(*h*) *Appendicular skeleton*

The appendicular system is only partly ossified, the limb bones having unossified articular surfaces and the pubes, carpals and tarsals not visible and presumed to be unossified (figures 7–8). In comparison with most living salamanders, the manus and pes are relatively large with slender digits (figures 7, 8*c*).

Each scapulocoracoid is a well-ossified single structure with a small blade and a larger coracoid region (figure 11*a*). The humerus is about twice the length of either the radius or the ulna (figure 7). The proximal head is broader than the distal one, but this seems to be largely due to the large crista ventralis orientated at roughly 90° to it (figure 11*a*). The radius is a relatively stout ossification with an expanded distal end. The ulna is uniformly slender. The manus bears four digits with the phalangeal formula 2.2.3.2. visible in the holotype LH 928061 (figure 7). The manual ungual phalanges are long and slender with slightly bifurcated tips.

The pelvis includes well-ossified ilia and ischia but the pubis was apparently unossified. Each ischium is a plate of bone, longer than wide and more or less rectangular but with a concave medial edge (figure 11*c*). The femur is about twice as long as the tibia or fibula. It bears a triangular process for the caudifemoral musculature (figure 11*c*). The tibia and fibula are similar in size but the tibia is slightly expanded proximally. The pes bears five digits with the phalangeal formula 2.2.3.4.2., seen well in the holotype LH 928061 (figure 7). The pedal ungual phalanges are also long and slender, like those of the manus.

(*i*) *Reconstruction*

A reconstruction of the skeleton of *Valdotriton* in dorsal aspect is depicted in figure 12. It is composite, based on the holotype and all three paratypes.

6. TAXONOMIC STATUS OF *VALDOTRITON*

Before discussing the systematic position of this material, it is necessary to demonstrate that it is diagnostically distinct from all other mid-Mesozoic salamanders, both from Las Hoyas and from elsewhere. The following two discussions have this purpose, and are concerned only with demonstrating that *Valdotriton* is a distinct taxon, not with establishing its systematic position.

(*a*) *Comparison with other Las Hoyas Caudata*

Because there is also a small perennibranchiate salamander in the Las Hoyas assemblage, consider-

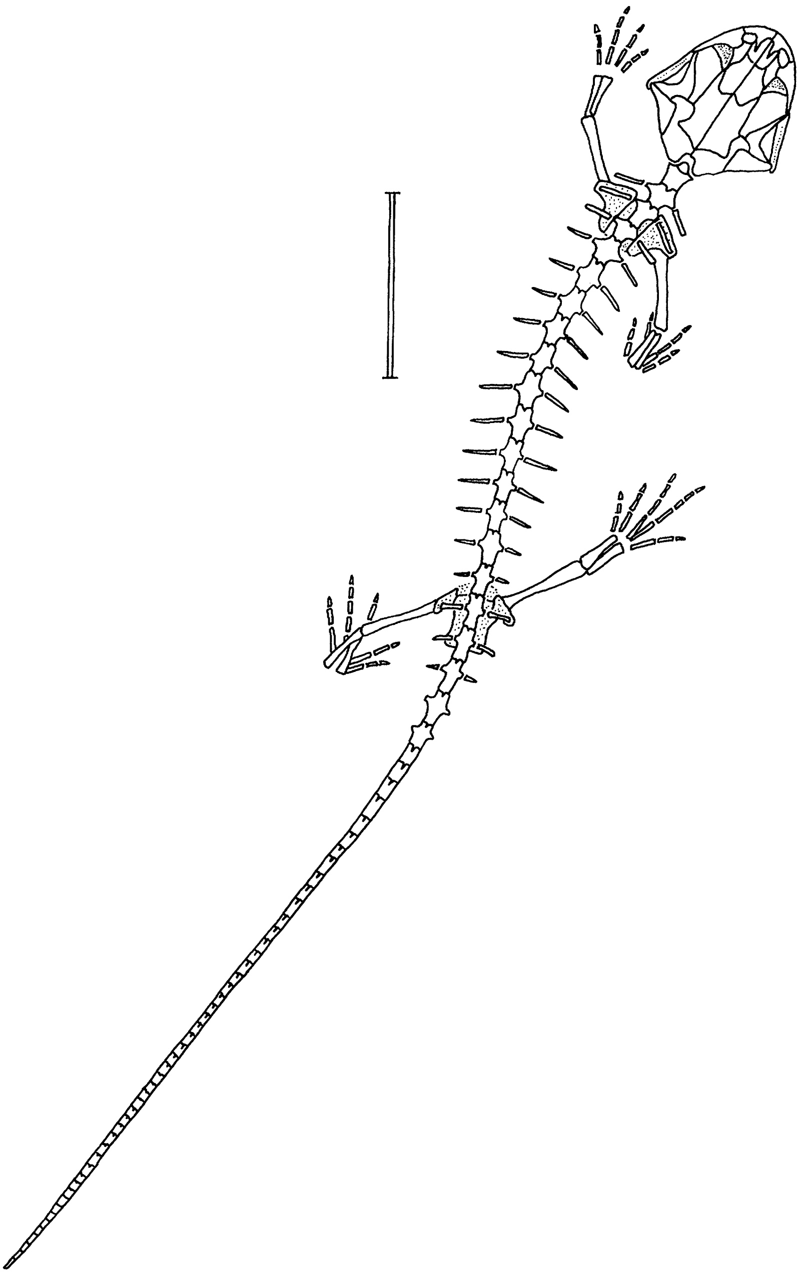

Figure 12. *Valdotriton gracilis* gen. et sp. nov. Reconstruction of skeleton in dorsal view. Scale bar = 10 mm.

ation must be given to the possibility that it represents unmetamorphosed or facultatively neotenous material of *Valdotriton*. Despite the radical nature of skeletal metamorphosis in salamanders, there are some features which do not vary with metamorphosis and can be used in this context. Two specimens of *Valdotriton* have a pedal phalangeal formula of 2.2.3.4.2 (e.g. LH 928061, LH 6021), whereas several specimens of the neotenous form have the formula 2.2.3.3.2 (e.g. LH 002b, LH 6022). Furthermore, *Valdotriton* bears intravertebral spinal foramina in its caudal series, whereas the neotenous form has no spinal foramina at all (e.g. LH 001). These two character differences are independent of metamorphosis and are sufficient to convince us that the neotenous salamanders at Las Hoyas represent a separate taxon from *Valdotriton*.

(*b*) *Taxonomic comparison with Mid-Mesozoic salamander genera*

Salamander material from the Middle Jurassic to the end of the Lower Cretaceous has previously been described under nine genera and ten species. These are reviewed more fully in the discussion, but are compared typologically with *Valdotriton gracilis* in the following paragraph. They are discussed in approximate order of description.

(i) *Hylaeobatrachus croyii*

Hylaeobatrachus croyii Dollo, 1884 is based on a single perennibranchiate specimen described as possessing five fully ossified gill arches (Estes 1981). It bears no resemblance to *Valdotriton*.

Table 1. *The fossil record of salamanders from the Bathonian to the Albian*

(Figures represent estimates of ages in Ma BP for the base of each period, taken from Harland *et al.* 1990.)

	North america	Europe	Asia	Gondwana
ALB 107 Ma	Texas *Prosiren*		Uzbekistan *Horezmia*	
APT 114 Ma				
BARR 116 Ma		Belgium *Hylaeobatrachus* Spain *Galverpeton* *Valdotriton* Salamander 2		
HAUT 120 Ma				Israel *Ramonellus*
VAL 128 Ma				
BERR 135 Ma		England *Batrachosauroidid* Salamander undet.		
TITH 139 Ma				
KIMM 144 Ma	Wyoming '*Comonecturoides*' Salamander undet.		Kazakhstan *Karaurus*	
OXF 152 Ma		Portugal *Marmorerpeton* Salamander undet.		
CAL 159 Ma			Kirghizstan Salamander indet.	
BATH 170 Ma		England *Marmorerperton* Salamanders A+B	Kirghizstan *Kokartus*	

(ii) *Comonecturoides marshi*

Comonecturoides marshi Hecht & Estes, 1960 is a *nomen vanum* restricted to a single femur (Evans & Milner 1993) and cannot be usefully compared to *Valdotriton*.

(iii) *Prosiren elinorae*

Prosiren elinorae Goin & Auffenberg, 1958 has trunk vertebrae which bear neural spines that are longer and less flattened than those of *Valdotriton*. *Prosiren* vertebrae are more robust than those of *Valdotriton* with sharp accessory keels and larger anterior basapophyses.

(iv) *Ramonellus longispinus*

Ramonellus longispinus Nevo & Estes, 1969 was a long-skulled long-bodied form (34+ presacrals) with small fore limbs and a prominent retroarticular process. It bears no resemblance to *Valdotriton*.

(v–vi) *Karaurus sharovi* and *Kokartus honovarius*

Karaurus sharovi Ivakhnenko, 1978 differs from *Valdotriton* in lacking the adductor groove on the dorsal surface of the squamosal, retaining a quadratojugal, possessing a large intervomerine fontanelle, having a second basibranchial with forward directed lateral rami, having heavily sculptured dermal bones and possessing short phalanges and digits (Ivakhnenko 1978). The fragmentary *Kokartus honorarius* Nessov, 1988 also has heavily sculptured dermal bone and appears to be similar to *Karaurus* (Nessov 1988).

(vii) *Galverpeton ibericum*

Galverpeton ibericum Estes & Sanchíz, 1982 is based on a single trunk vertebra bearing intravertebral spinal nerve foramina. Such foramina do not appear to occur in the trunk of *Valdotriton*.

(viii–ix) *Marmorerpeton kermacki* and *M. freemani*

Marmorerpeton kermacki and *M. freemani* (both Evans *et al.* 1988) differ from *Valdotriton* in possessing atlas vertebrae with no intravertebral spinal foramina and with a flattened ventral surface (Evans, Milner & Mussett 1988), lacking any median ridge such as characterizes *Valdotriton*.

(x) *Horezmia gracile*

Horezmia gracile Nessov, 1988 possesses a separate prearticular and angular and a small premaxilla, both characters distinguishing it from *Valdotriton*.

In conclusion, *Valdotriton gracilis* is distinct from all other Jurassic and Early Cretaceous salamanders and hence the new binomen is justified.

7. RELATIONSHIPS OF *VALDOTRITON*

There is at present no agreement on the interrelationships of the families of living salamanders. Cladistically expressed theories of relationship of salamander families have been published by Edwards (1976), Milner (1983), Duellman & Trueb (1986), Larson (1991), Hillis (1991), Larson & Dimmick (1993) and Hay *et al.* (1995). The first three theories have a great deal in common and were based entirely on sets of morphological characters, both skeletal and non-skeletal. Larson's (1991) cladogram was based on ribosomal RNA sequencing without input of morphological data and is substantially different in its rooted topology. It is taken to be superseded by the conclusions of Larson & Dimmick (1993) and Hay *et al.* (1995). The cladograms of Hillis (1991) and Larson & Dimmick (1993) are derived from bootstrap analyses of combined sets of morphological, molecular and cytogenetic data, and represent the most comprehensive interpretations of the available data for living taxa. The recent publication by Hay *et al.* (1995) is based on the largest set of 12S and 16S rRNA sequences yet analysed. In the following account, the attempt is made to place *Valdotriton* in the context of the cladograms of Milner (1983), Hillis (1991) and Larson & Dimmick (1993) which are broadly similar (figure 13*a*–*c*). More limited comparisons are made with Hay *et al.* (1995). This differs radically from the others in the proposed relationships of the higher salamanders (figure 13*d*) which were not discussed in any morphological context. Comparisons are also made with selected fossil taxa which can be related to cladograms based on extant forms.

(*a*) *Caudata*

The Caudata is composed of a series of stem-plesions such as *Karaurus* and *Marmorerpeton* leading to the Urodela. The Urodela or crown-group salamanders (the clade comprising all living forms and all fossil forms falling within that clade) share the presence of an adductor groove over the dorsal surface of the squamosal, the absence of the quadratojugal, and the presence of intravertebral spinal foramina in the atlas vertebra. *Valdotriton* has all these characteristics and is therefore a crown-group urodele. This separates it from caudates such as *Karaurus* which lacks the adductor groove on the dorsal surface of the squamosal and retains a separate quadratojugal ossification, and *Marmorerpeton* which lacks the atlas intravertebral foramina.

(*b*) *Urodela*

There is an increasing consensus that within the Urodela, the Sirenidae are the sister-group to the remaining forms (Milner 1983; Hedges & Maxson 1993, figure 2; Larson & Dimmick 1993, figures 4–5; Hay *et al.* 1995, figure 1). The clade comprising all living non-sirenid salamanders and their immediate fossil relatives was recently named the Neocaudata by Cannatella & Hillis (1993).

The Sirenidae are a group of highly specialized long-bodied neotenous salamanders and few meaningful comparisons can be made between *Valdotriton* and them. *Valdotriton* does have the single scapulocoracoid ossification characterizing neocaudate salamanders, whereas sirenids have separate scapulae and coracoids, argued to be primitive (Milner 1983; Larson & Dimmick 1993). This places *Valdotriton* in the Neocaudata.

(*c*) *Neocaudata*

The neocaudate salamanders all appear to belong to one of two clades. One is the Cryptobranchoidea comprising the families Cryptobranchidae and Hynobiidae. The other lacks a taxonomic name but has been recently referred to as 'the internally fertilizing salamanders' (Larson & Dimmick 1993). In the following discussion it is referred to as the IFS clade. This clade comprises the families Plethodontidae, Amphiumidae, Rhyacotritonidae, Proteidae, Dicamptodontidae, Ambystomatidae and Salamandridae. This dichotomy has been recognized by Milner (1983), Duellman & Trueb (1986), Hillis (1991), Larson & Dimmick (1993) and Hay *et al.* (1995) (figure 13). The Cryptobranchoidea (Hynobiidae and Cryptobranchidae) are primitive in relation to the IFS clade in that they lack intervertebral foramina in the caudal vertebrae, and retain separate prearticular and angular in the mandible, but are derived in that the rib-bearers coalesce into a single structure. *Valdotriton* has the derived conditions of spinal foramina in the caudal vertebrae and a single prearticular-angular ossification, and the primitive condition of double-headed rib-bearers. *Valdotriton* therefore belongs among the IFS clade without any contradictory characters, and there is no basis for associating the genus with the Cryptobranchoidea.

(*d*) *'The IFS clade'*

The interrelations of the higher salamander groups are still problematic and there is no robust hypothesis for their relationships. However, four discrete groups can be recognized in most analyses, namely: (i) the Proteidae; (ii) the Rhyacotritonidae (for *Rhyacotriton* – see Good & Wake 1992); (iii) the Plethodontoidea (Plethodontidae + Amphiumidae); and (iv) the Ambystomatoidea (Dicamptodontidae + Ambystomatidae + Salamandridae) (Milner 1983; Hillis 1991; Larson & Dimmick 1993). The recent analysis of Hay *et al.* (1995) is exceptional in that the Plethodontoidea form a paraphyletic basal grade of the IFS clade and the Proteidae and Rhyacotritonidae emerge from within a paraphyletic Ambystomatoidea. Most problematic is the relationship of the Proteidae to the remaining forms. They have been treated as the sister-group to the remaining higher urodeles by Edwards (1976), Milner (1983), Duellman & Trueb (1986) and Hillis (1991 figure 11), whereas Larson & Dimmick (1993 figures 4–5) place them in a post-plethodontoid position (figure 13) and Hay *et al.* (1995) make them the most derived IFS salamanders and the sister-taxon to the Dicamptodontidae.

(*e*) **Valdotriton** *and the Larson/Dimmick and Hay* **et al.** *trees*

Larson & Dimmick's (1993 figure 5) tree is not identical to their consensus tree (Larson & Dimmick 1993 figure 3) but the differences lie within the family Hynobiidae which is irrelevant to this discussion, and in the resolution of the base of the IFS clade which can be taken into account. Their branch 4 marking the stem of the IFS clade is defined on nine derived characters, two of which are osteological. One (their character O (0 → 1)) is the fusion of the angular and prearticular discussed above, and possessed by *Valdotriton*. The second (BE (0 → 1)) is the reduction of the each nasal to an origin from a lateral anlagen only, the loss of the medial anlagen resulting in the mesial shift of the premaxillary pars dorsalis. This appears not to be present in *Valdotriton*, the pars dorsalis running across the middle of each nasal in a manner found in living forms in which the nasal is produced by two anlage. If this interpretation is correct, then *Valdotriton* lacks one of the two osteological characters defining the IFS clade although it possesses the other character. Its correct position would then be as a plesion on the stem of the IFS clade with no immediate relationship to any of the subgroups.

However one character could contradict this, namely the presence in *Valdotriton* of spinal foramina in caudal vertebrae 3–10 (Character X (0 → 1)). This is a character of some but not all subgroups of the IFS clade. The position of the Proteidae (primitively with no spinal foramina) nested within this group in a non-basal position, means that either convergence or reversal of this character has occurred. Larson & Dimmick's (1993) interpretation is that this character (or more derived developments) has arisen independently at least three times within subclades. This would suggest that *Valdotriton* should belong to one of these subclades (Plethodontoidea, Rhyacotritonidae, Ambystomatoidea) contradicting its position on the stem suggested by the primitive nasal configuration. Alternatively the Proteidae could have lost caudal foramina by reversal so that the basic condition of the IFS clade was to possess them, in which case the position of *Valdotriton* on the group stem could stand. The latter seems more likely and is supported by other primitive features of *Valdotriton* as follows.

1. The second basibranchial is tiny or absent in all living forms studied for this character, whereas it is relatively large in *Valdotriton*.
2. The pterygoid-maxillary bony connection is a more primitive condition than that found in any living member of the IFS clade. In these forms there is either a tenuous cartilaginous connection or no connection at all.
3. The simple arch of vomerine teeth paralleling the anterior marginal dentition is not found in any metamorphosed member of the IFS clade and has been argued to represent a primitive condition still found in salamander larvae (Regal 1966) and the neotenous cryptobranchids. The small size of *Valdotriton* does leave open the possibility that, although post-metamorphic, it is only just so and may still have a larval palatal dentition.

The mitochondrial DNA-based tree of Hay *et al.* was not presented with any analysis of morphological features and does not appear to relate well to known distribution of morphological character-states. However, the IFS clade is present, with the Proteidae as a derived group within it, so that as far as the possible position of *Valdotriton* is concerned, the same conclusions would apply.

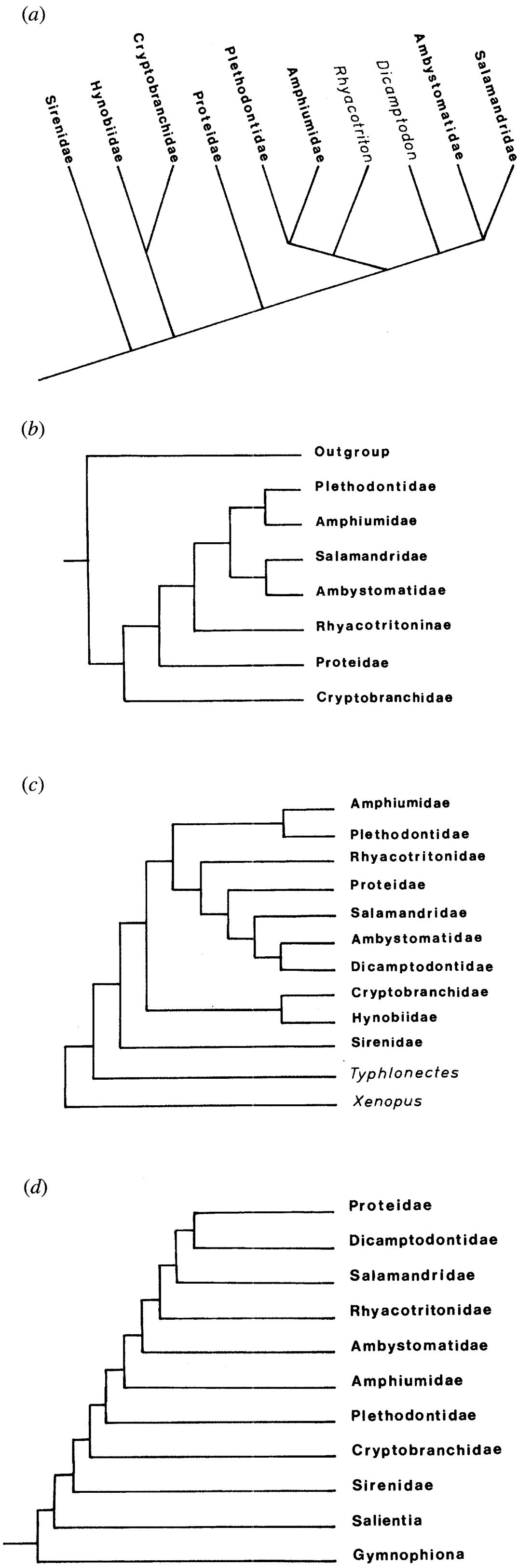

Figure 13. Cladograms of salamander family interrelationships. (*a*) Milner 1983; (*b*) Hillis 1991 figure 11; (*c*) Larson and Dimmick 1993 figure 4*a* (family-level equivalent to figure 5); (*d*) Hay *et al.* 1995 figure 1 (part).

So in the context of the Larson/Dimmick and Hay *et al.* cladograms, the simplest interpretation of the position of *Valdotriton* is that it is a plesion on the stem of the IFS clade possessing some of the IFS osteological characters but not all, and that the absence of spinal foramina in the proteids is a reversal.

(*f*) Valdotriton *and other trees*

The other trees produced by Milner (1983) and Hillis (1991) are either morphologically based or are integrated exercises which produce the same result in one aspect of the internal relationships of the IFS clade, namely that the Proteidae are the sister taxon of all other members of this clade (figure 13*a–b*). The acquisition of intravertebral spinal foramina in at least the caudal vertebra becomes one of the innovations characterizing the (plethodontid + amphiumid + rhyacotritonid + dicamptodontid + ambystomatid + salamandrid) clade, and *Valdotriton* would fall within such a clade. Proteids lack such foramina. Of the other two osteological characters used in the Larson/Dimmick cladogram, the fused angular-prearticular defines the entire IFS clade in the same way, but the loss of the medial nasal anlage becomes complicated by the fact that proteids have lost the nasals entirely and the pattern of this loss may/may not be the same as in the rest of the IFS clade. Morphologically, *Valdotriton* could be argued to be the most primitive member of the post-proteid clade, in retaining both anlage in the nasal, but more derived than proteids in the spinal nerve foramina (figure 14).

(*g*) Valdotriton *and higher salamander families*

It may be briefly noted that there are no derived features to associate *Valdotriton* with any of the other families within the IFS clade. *Valdotriton* lacks intravertebral spinal trunk foramina and this places it outside the Plethodontidae, Ambystomatidae and Salamandridae. It also lacks specific features of any of these families, and would therefore have a gradistic similarity to the Dicamptodontidae and Rhyacotritonidae. The configuration of the nasals, basibranchial, and pterygoid-maxilla connection all suggest that it is more primitive than any of the living post-proteid salamanders.

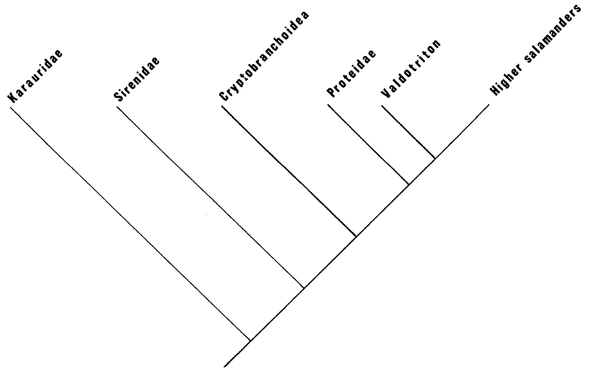

Figure 14. Cladogram showing proposed relationship of *Valdotriton* based on cladogram with core elements as discussed in §7*f*.

We are not in a position to arbitrate between the above discussed schemes of relationship of the families of higher salamanders within the IFS clade and therefore we can only suggest alternative positions for this taxon in alternative cladograms. In the Larson/Dimmick and Hay *et al.* cladograms, *Valdotriton gracilis* is a plesion on the stem of the clade of internally fertilizing salamanders. In the other morphological and integrated cladograms, *Valdotriton gracilis* is a plesion on the stem of the post-proteid clade (figure 14).

The presence of such a form in the Barremian (116–114 Ma BP) of Europe shows that the IFS clade was already in existence and might have begun to diversify. This is not surprising as the previously described contemporaneous form *Galverpeton* appears to belong to one of the more derived families (Plethodontidae, Ambystomatidae, Salamandridae) in which intravertebral foramina were present in the trunk vertebrae.

8. DISCUSSION AND CONCLUSIONS

(*a*) *The early fossil record of salamanders*

The fossil record of the Caudata was last reviewed comprehensively by Estes in 1981. At that time there were relatively few records of salamanders before the Upper Cretaceous. Since then the known fossil record has become much more extensive and the opportunity is taken to present a chronological review of the currently known range of fossils of salamanders from the Middle Jurassic to the end of the Lower Cretaceous (table 1). This review is restricted to undoubted Caudata and the Jurassic-Miocene family Albanerpetontidae is not discussed here. In Estes' (1981) review, they were treated as members of the Caudata and misassociated with material of the caudate *Prosiren*. We follow Fox & Naylor (1982), Milner (1988), McGowan (1994) and McGowan & Evans (1995) in considering their relationship to the Caudata to be unlikely.

(i) *Bathonian (170–159 Ma* BP)

Abundant salamander material is present in the microvertebrate assemblages of England. Elements of large salamanders forming the basis of the genus *Marmorerpeton* were originally described from the Forest Marble of Kirtlington, Oxfordshire (Evans *et al.* 1988) and have subsequently been reported from Watton Cliff and Swyre in Dorset (Evans 1992) and Hornsleasow in Gloucestershire (Metcalf *et al.* 1992). Articulated material of *Marmorerpeton* has also been collected from the Bathonian of Skye in Scotland and is under study by S. E. E. and Dr M. Waldman. The absence of an intravertebral spinal nerve foramen in the atlas suggests that this form may be a stem-salamander, all crown-group urodeles having such a foramen. Two further undescribed salamanders are also present in the Bathonian of the British Isles. A medium-sized, apparently very primitive, stem-salamander, referred to as 'Salamander A' is common at Kirtlington (Evans & Milner 1991) and also occurs at Watton Cliff, Swyre (Evans 1992), Hornsleasow (S. E. Evans & A. R. Milner, personal observation) and Skye

(S. E. Evans & M. Waldman, unpublished data). Some of the maxillary and premaxillary elements attributed to *Marmorerpeton* by Evans *et al.* 1988 probably belong to this form. A small form 'Salamander B' of uncertain relationship is also present at Kirtlington (Evans & Milner 1991), and Hornsleasow (S. E. Evans & A. R. Milner, personal observation).

Bathonian salamanders have also been collected in microvertebrate assemblages from the Kizylsu and Kugart localities, in the northeastern region of the Ferghana Valley in Kirghizstan (Nessov 1988). This material forms the basis of *Kokartus honorarius* Nessov, 1988, described as an early relative of *Karaurus* (see below).

(ii) *Callovian* (*159–152 Ma* BP)

Amphicoelous salamander vertebrae from the Callovian Balabansay Formation of Tashkumyr, Kirghizstan, have been reported by Nessov (p. 477, 1988) but not yet described.

(iii) *Oxfordian* (*152–144 Ma* BP)

Salamander material has been reported from the Oxfordian of Guimarota (Kuhne 1968) and Pedrógao (Thulborn 1973), Portugal, but has not been described. Evans & Milner (1994) noted the Guimarota material to include *Marmorerpeton*.

(iv) *Kimmeridgian* (*144–139 Ma* BP)

The only articulated Jurassic salamander is the single specimen of *Karaurus sharovi* from the Karabastau Formation at Michaelovka in southern Kazakhstan (Ivakhnenko 1978; Nessov 1988). This forms the basis of the family Karauridae. A few isolated salamander elements have been collected from the Morrison Formation at Quarry Nine, Como Bluff, Wyoming in the U.S.A. They include a femur, the type and only specimen of *Comonecturoides marshi* Hecht & Estes (1960), and two types of vertebrae described by Evans & Milner (1993). One of the Como Bluff salamanders had large, heavily constructed vertebrae whereas the other had small delicate vertebrae. None of this described material is determinate but further associated material has been collected which may permit the Morrison salamanders to be characterized (D. Chure, personal communication). The dating of the Morrison horizons remains controversial, but on the basis of work by the U.S. Geological Survey (Turner & Peterson 1992), a Kimmeridgian rather than Tithonian age is now generally accepted for the Upper Brushy Basin Member, the source of the salamander material.

(v) *Tithonian/Berriasian* (*139–128 Ma* BP)

Two types of small salamander, one a batrachosauroidid, have been reported from new microvertebrate assemblages from the Upper Purbeck Beds of Dorset (Ensom 1988, p.149; Ensom *et al.* 1991, p.19).

(vi) *Hauterivian* (*120–116 Ma* BP)

Specimens of a long-bodied, short-limbed salamander from the early Cretaceous of Makhtesh Ramon, Israel, were reported by Nevo (1964) and described by Nevo & Estes (1969) as *Ramonellus longispinus*. This form was originally suggested to be a possible prosirenid by Nevo & Estes (1969) and Estes (1981). With the removal of much of the 'prosirenid' material into the Albanerpetontidae, *Ramonellus* has no obvious similarities to the type *Prosiren* vertebrae, nor to the Albanerpetontidae (now known from complete specimens from Las Hoyas).

(vii) *Barremian* (*116–114 Ma* BP)

More than 30 articulated skeletons of two species of salamander have been collected from the Las Hoyas locality, as noted in the introduction. One is *Valdotriton*, whereas the other species is represented by small perennibranchiate individuals and may be a batrachosauroidid. At least one undetermined caudate larva has also been collected.

(viii) *Barremian/Aptian* (*116–107 Ma* BP)

One of the first articulated Mesozoic salamanders to be collected was the type and only specimen of *Hylaeobatrachus croyii* Dollo, 1884 from the late Wealden of Bernissart, Belgium. This neotenous form was redescribed by Estes (1981) who concluded that it could not readily be associated with any other group of salamanders. A single vertebra, forming the type of *Galverpeton ibericum* Estes & Sanchíz, 1982 has been collected from the microvertebrate assemblage from Galve, Teruel Province, Spain (Estes & Sanchíz 1982, pp. 29–32).

(ix) *Albian* (*107–95 Ma* BP)

Of the original material of *Prosiren elinorae* Goin and Auffenberg, 1958 from the Antlers Formation of Forestburg, Montague County, Texas, the vertebrae including the holotype and an atlas, belongs to a true caudate salamander. The remaining material (dentaries, premaxillae, humeri) which Estes (1969) referred to *Prosiren elinorae* have been argued by Fox & Naylor (1982) to be albanerpetontid elements, a conclusion confirmed by McGowan (1994). Late Albian salamander material is also known from the Khodzhakul Formation in the southwest Kyzylkum desert, Karakalpak region of Uzbekistan (Nessov 1988), and was described by Nessov as a scapherpetontid *Horezmia gracile*.

(*b*) *General conclusions*

Known 20 years ago from only a few specimens, true salamanders are proving to be present in some diversity in mid-Mesozoic Laurasian herpetofaunas from their first appearance in the Bathonian. They ranged at least from Wyoming in the west through to Uzbekistan in the east. The simplest testable assumption is that they were distributed throughout Laurasia from the Middle Jurassic onwards and had already diversified when first represented as fossils. The presence of *Ramonellus* in the Hauterivian of Israel demonstrates that at least one group underwent a range extension into northern Gondwana in the mid-Mesozoic (Milner 1983).

Much of the described or reported material belongs or appears to belong to neotenous forms (*Ramonellus*, *Hylaeobatrachus*, *Horezmia* and much unnamed material) but the karaurids (*Karaurus* and *Kokartus*), *Valdotriton* and *Galverpeton* demonstrate the presence of metamorphosing salamanders in these assemblages. The described material does demonstrate that the range of morphological-ecological types was already approaching that found today. There are metamorphosing 'orthodox' salamanders (*Karaurus* and *Valdotriton*), narrow- headed perennibranchiate forms (*Hylaeobatrachus* and the second Las Hoyas salamander) and long-bodied, small-limbed forms (*Ramonellus*).

All the published Jurassic salamanders and the contemporaneous unpublished material under study by the authors are either clearly stem-forms (i.e. not crown-group Urodela) or, like the possible batrachosauroidids, are of uncertain systematic position. The earliest true Urodela (within the crown-group) are the Lower Cretaceous forms *Valdotriton*, *Galverpeton* and possibly *Ramonellus*. Thus we see some correspondence between the cladograms based on living organisms with fossils clipped on, and the stratigraphical sequence of appearance of forms. It appears that the Caudata are represented by stem-taxa in the Jurassic and basal Urodela from the Hauterivian onwards, and that the modern adaptive radiation was diversifying during the early Cretaceous.

We thank José-Luis Sanz and his group at the Universidad Autonoma, Madrid for inviting us to work on this material. We would also like to thank Señor Armando Diaz-Romeral, and the curatorial staff at the Museo de Cuenca for making specimens available to us for study, and Aysha Raza for assistance in the preparation of artwork. The Las Hoyas research program is supported by EEC Human Capital and Mobility Programme CHRX-cT93 0/64, DYGICYT (Promoción General de Conocimiento) and by Junta de Comunidades de Castilla-La Mancha. This work was funded by grants from the Royal Society, University of London Central Research Fund and NERC award no. GR9/651.

REFERENCES

Barbadillo, J. & Evans, S. E. 1995 IV.6. Lacertilians. In *Las Hoyas. A lacustrine konservat-lagerstätte, Cuenca, Spain. II International symposium on lithographic limestones. Field trip guide book July 16, 1995* (ed. M. N. Meléndez), pp. 57–58. Ediciones de la Universidad Autónoma de Madrid.

Buscalioni, A. D. & Ortega, F. 1995 IV.7. Crocodylomorphs. In *Las Hoyas. A lacustrine konservat-lagerstätte, Cuenca, Spain. II International symposium on lithographic limestones. Field trip guide book July 16, 1995* (ed. M. N. Meléndez), pp. 59–61. Ediciones de la Universidad Autónoma de Madrid.

Cannatella, D. C. & Hillis, D. M. 1993 Amphibian relationships: phylogenetic analysis of morphology and molecules. In *Amphibian relationships. Phylogenetic analysis of morphology and molecules* (ed. D. Cannatella & D. Hillis), *Herpet. Monogr.* **7**, 1–7.

Carroll, R. L. 1988 *Vertebrate paleontology and evolution*. New York: Freeman.

Dollo, L. 1884 Note sur le batracien de Bernissart. *Bull. Mus. d'Hist. Natur. Belg.* **3**, 85–96.

Duellman, W. E. & Trueb, L. 1986 *Biology of amphibians*. New York, St.Louis, San Francisco: McGraw-Hill.

Edwards, J. L. 1976 Spinal nerves and their bearing on salamander phylogeny. *J. Morphol.* **148**, 305–328.

Ensom, P. C. 1988 Excavations at Sunnydown Farm, Langton Matravers, Dorset: amphibians discovered in the Purbeck Limestone Formation. *Proc. Dorset Nat. Hist. Archaeol. Soc.* **109**, 148–150.

Ensom, P. C., Evans, S. E. & Milner, A. R. 1991 Amphibians and reptiles from the Purbeck Limestone Formation (Upper Jurassic) of Dorset. *Contribs Paleont. Mus. Univ. Oslo* **364**, 19–20.

Estes, R. 1969 Prosirenidae, a new family of fossil salamanders. *Nature, Lond.* **224**, 87–88.

Estes, R. 1981 Gymnophiona, Caudata. In *Handbuch der Paläoherpetologie*, vol. 2 (ed. P. Wellnhofer). Stuttgart: Gustav Fischer Verlag.

Estes, R. & Sanchíz, B. 1982 Early Cretaceous lower vertebrates from Galve (Teruel), Spain. *J. Vert. Paleont.* **2**, 21–39.

Evans, S. E. 1992 Small reptiles and amphibians from the Forest Marble (Middle Jurassic) of Dorset. *Proc. Dorset Nat. Hist. Archaeol. Soc.* **113**, 201–202.

Evans, S. E., McGowan, G., Milner, A. R. & Sanchíz, B. 1995 IV.4. Amphibians. In *Las Hoyas. A lacustrine konservat-lagerstätte Cuenca, Spain. II International symposium on lithographic limestones. Field trip guide book July 16, 1995* (ed. M. N. Meléndez), pp. 51–53. Ediciones de la Universidad Autónoma de Madrid.

Evans, S. E. & Milner, A. R. 1991 Middle Jurassic microvertebrate faunas from the British Isles. *Contribs Paleont. Mus. Univ. Oslo* **364**, 21–22.

Evans, S. E. & Milner, A. R. 1993 Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America. *J. Vert. Paleont.* **13**, 24–30.

Evans, S. E. & Milner, A. R. 1994 Chapter 18. Middle Jurassic microvertebrate assemblages from the British Isles. In *In the shadow of the dinosaurs: Early Mesozoic tetrapods* (ed. N. C. Fraser & H.-D. Sues), pp. 303–321. Cambridge University Press.

Evans, S. E. & Milner, A. R. 1995 Early Cretaceous salamanders (Amphibia: Caudata) from Las Hoyas, Spain. In *II International symposium on lithographic limestones; Lleida-Cuenca (Spain). Extended abstracts*, pp. 63–65. Ediciones de la Universidad Autónoma de Madrid.

Evans, S. E., Milner, A. R. & Mussett, F. 1988 The earliest known salamanders (Amphibia: Caudata): a record from the Middle Jurassic of England. *Geobios* **21**, 539–552.

Fox, R. C. & Naylor, B. G. 1982 A reconsideration of the relationships of the fossil amphibian *Albanerpeton*. *Can. J. Earth Sci.* **19**, 118–128.

Fregenal-Martínez, M. A. & Meléndez, N. 1995 I.1. Geological Setting. In *Las Hoyas. A lacustrine konservat-lagerstätte Cuenca, Spain. II International symposium on lithographic limestones. Field trip guide book July 16, 1995* (ed. M. N. Meléndez), pp. 1–10. Ediciones de la Universidad Autónoma de Madrid.

Goin, C. J. & Auffenberg, W. 1958 New salamanders of the family Sirenidae from the Cretaceous of North America. *Fieldiana, Geol.* **10**, 449–459.

Good, D. A. & Wake, D. B. 1992 Geographic variation and speciation in the torrent salamanders of the genus *Rhyacotriton* (Caudata: Rhyacotritonidae). *Univ. California Publs Zool.* **126**, 1–91.

Harland, W. B., Armstrong, R. L., Cox, A. V., Craig, L. E., Smith, A. G. & Smith, D. G. 1990 *A geologic time-scale 1989*. Cambridge University Press.

Hay, J. M., Ruvinsky, I., Hedges, S. B. & Maxson, L. R. 1995 Phylogenetic relationships of amphibian families inferred from DNA sequences of mitochondrial 12S and 16S ribosomal RNA genes. *Molec. Biol. Evol.* **12**, 928–937.

Hecht, M. K. & Estes, R. 1960 Fossil amphibians from Quarry Nine. *Postilla* **46**, 1–19.

Hedges, S. B. & Maxson, L. R. 1993 A molecular perspective on lissamphibian phylogeny. In *Amphibian relationships. Phylogenetic analysis of morphology and molecules* (ed. D. Cannatella & D. Hillis), *Herpet. Monogr.* **7**, 27–42.

Hillis, D. M. 1991 The phylogeny of amphibians: current knowledge and the role of cytogenetics. In *Amphibian cytogenetics and evolution* (ed. D. M. Green & S. K. Sessions), pp. 7–32. San Diego and London: Academic Press.

Ivakhnenko, M. F. 1978 Urodelans from the Triassic and Jurassic of Soviet Central Asia. *Paleont. Zhurnal* **1978**, 84–89. (In Russian.)

Jenkins, F. A. & Walsh, D. M. 1993 An early Jurassic caecilian with limbs. *Nature, Lond.* **365**, 246–250.

Jimenez-Fuentes, E. 1995 IV.5. Turtles. In *Las Hoyas. A lacustrine konservat-lagerstätte Cuenca, Spain. II International symposium on lithographic limestones. Field trip guide book July 16, 1995* (ed. M. N. Meléndez), pp. 55–56. Ediciones de la Universidad Autónoma de Madrid.

Kuhne, W. G. 1968 Contribuicao para a fauna do Kimeridgiano da mina de lignito Guimarota (Leiria, Portugal). 1 – History of discovery, report on the work performed, procedure, technique and generalities. *Mem. Serv. Geol. Portugal* **14**, 7–20.

Larson, A. 1991 A molecular perspective on the evolutionary relationships of salamanders. *Evol. Biol.* **25**, 211–277.

Larson, A. & Dimmick, W. W. 1993 Phylogenetic relationships of the salamander families: an analysis of congruence among morphological and molecular characters. In *Amphibian relationships. Phylogenetic analysis of morphology and molecules* (ed. D. Cannatella & D. Hillis), *Herpet. Monogr.* **7**, 77–93.

McGowan, G. J. 1994 A description of new albanerpetontid material from the Mesozoic of Europe and its bearing on the systematic position of the group. Ph.D. thesis, University of London.

McGowan, G. & Evans, S. E. 1995 Albanerpetontid amphibians from the Cretaceous of Spain. *Nature, Lond.* **373**, 143–145.

Metcalf, S. J., Vaughan, R. F., Benton, M. J., Cole, J., Simms, M. J. & Dartnall, D. L. 1992 A new Bathonian (Middle Jurassic) microvertebrate site, within the Chipping Norton Limestone Formation at Hornsleasow Quarry, Gloucestershire. *Proc. Geol. Assoc.* **103**, 321–342.

Milner, A. R. 1983 The biogeography of salamanders in the Mesozoic and early Caenozoic: a cladistic-vicariance model. In *Evolution, time and space: the emergence of the biosphere* (ed. R. W. Sims, J. H. Price & P. E. S. Whalley), pp. 431–468. London and New York: Academic Press.

Milner, A. R. 1988 The relationships and origin of living amphibians. In *The phylogeny and classification of the tetrapods, volume 1: amphibians, reptiles, birds. Systematics association special volume 35A* (ed. M. J. Benton), pp. 59–102. Oxford: Clarendon Press.

Milner, A. R. 1993*a* The Paleozoic relatives of lissamphibians. In *Amphibian relationships. Phylogenetic analysis of morphology and molecules* (ed. D. Cannatella & D. Hillis), *Herpet. Monogr.* **7**, 8–27.

Milner, A. R. 1993*b* Chapter 38. Amphibian-grade Tetrapoda. In *The fossil record 2* (ed. M. J. Benton), pp. 663–677. Palaeontological Association/Chapman and Hall.

Nessov, L. A. 1988 Late Mesozoic amphibians and lizards of Soviet Middle Asia. *Acta Zool. Cracoviensis* **31**, 475–486.

Nevo, E. 1964 Fossil urodeles in early Lower Cretaceous deposits of Makhtesh Ramon, Israel. *Nature, Lond.* **201**, 415–416.

Nevo, E. & Estes, R. 1969 *Ramonellus longispinus*, an Early Cretaceous salamander from Israel. *Copeia* **1969**, 540–547.

Özeti, N. & Wake, D. B. 1969 The morphology and evolution of the tongue and associated structures in salamanders and newts (Family Salamandridae). *Copeia* **1969**, 91–123.

Papendieck, H. I. C. M. 1954 Contributions to the cranial morphology of *Ambystoma macrodactylum* Baird. *Ann. Univ. Stellenbosch* A **30** 151–178.

Pérez-Moreno, B. P., Sanz, J. L., Buscalioni, A. D., Moratalla, J. J., Ortega, F. & Rasskin-Gutman, D. 1994 A unique multitoothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature, Lond.* **370**, 363–367.

Poyato-Ariza, F. J. 1989 Ictiofauna del Yacimiento de Las Hoyas. In *La fauna del pasado en Cuenca. Actas del I curso de paleontología*, pp. 83–124. Cuenca: Instituto Juan de Valdes.

Poyato-Ariza, F. J. & Wenz, S. 1995 IV.3 Ichthyofauna. In *Las Hoyas. A lacustrine konservat-lagerstätte Cuenca, Spain. II International symposium on lithographic limestones. Field trip guide book July 16, 1995* (ed. M.N. Meléndez), pp. 43–49. Ediciones de la Universidad Autónoma de Madrid.

Regal, P. J. 1966 Feeding specializations and the classification of terrestrial salamanders. *Evolution* **20**, 392–407.

Sanz, J. L. & Bonaparte, J. F. 1992 A new order of birds (Class Aves) from the Early Cretaceous of Spain. In *Papers in avian paleontology, honoring Pierce Brodkorb. Science series no. 36* (ed. K. E. Campbell), pp. 39–49. Natural History Museum of Los Angeles County.

Sanz, J. L. & Buscalioni, A. D. 1992 A new bird from the Early Cretaceous of Las Hoyas, Spain, and the early radiation of birds. *Palaeontology* **35**, 829–845.

Sanz, J. L. & Lacasa, A. 1988 Unusual Early Cretaceous birds from Spain. *Nature, Lond.* **331**, 433–435.

Sanz, J. L., Wenz, S., Yebenes, A., Estes, R., Martinez-Delclos, X., Jimenez-Fuentes, E., Diéguez, C., Buscalioni, A. D. Barbadillo, L. J. & Via, L. 1988 An Early Cretaceous faunal and floral continental assemblage: Las Hoyas fossil site (Cuenca, Spain). *Geobios* **21**, 611–635.

Thulborn, R. A. 1973 Contribuicao para o conhecimento da fauna do Kimeridgiano da mina de lignito Guimarota (Leiria, Portugal). VI – Teeth of ornithischian dinosaurs from the Upper Jurassic of Portugal. *Mem. Serv. Geol. Portugal* **22**, 89–134.

Trueb, L. 1993 Chapter 6. Patterns of cranial diversity among the Lissamphibia. In *The skull, volume 2. Patterns of structural and systematic diversity* (ed. J. Hanken & B. K. Hall) pp. 255–343. Chicago University Press.

Trueb, L. & Cloutier, R. 1991 A phylogenetic investigation into the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). In *Origins of the higher groups of tetrapods: controversy and consensus* (ed. H.-P. Schultze & L. Trueb) pp. 223–313. Cornell, Ithaca and London.

Turner, C. E. & Peterson, F. 1992 Sedimentology and stratigraphy of the Morrison Formation in Dinosaur National Monument, Utah and Colorado. *U.S. Geological Survey, Denver, Annual Report for the Period May 1, 1991 to April 30, 1992.*

Wake, D. B. 1966 Comparative osteology and evolution of the lungless salamanders, Family Plethodontidae. *Mem. S. Calif. Acad. Sci.* **4**, 1–111.

Received 1 *November* 1995; *accepted* 20 *December* 1995

APPENDIX

List of abbreviations used in figures

a	composite angular-prearticular element
ab	anterior basapophysis
at	atlas
br	braincase
C	caudal vertebra
CS	caudosacral vertebra
ct	crista trochantericus
cv	crista ventralis
d	dentary
fr	frontal
h	hyoid element = second basibranchial
hu	humerus
il	ilium
is	ischium
mx	maxilla
n	nasal
os	orbitosphenoid
p	parietal
pb	posterior basapophysis
pm	premaxilla
ps	parasphenoid
pt	pterygoid
q	quadrate
rb	rib-bearer
sc	scapula
spn	spinal nerve foramen
sq	squamosal
sr	sacral rib
st	stapes
v	vomer
vf	vascular foramen
vtr	vomerine tooth row

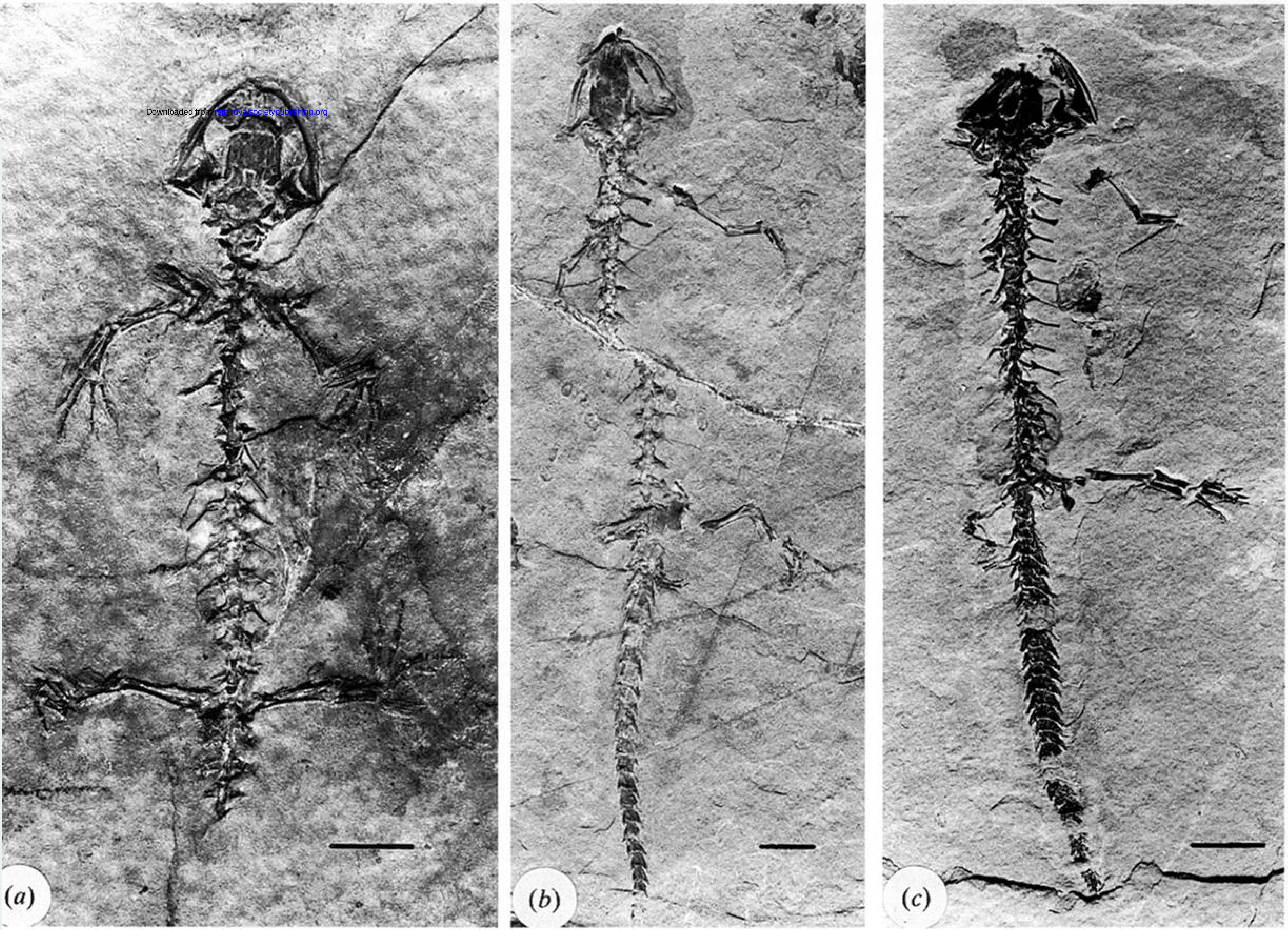

Figure 2. *Valdotriton gracilis* gen. et sp. nov. Barremian; Las Hoyas, Spain. (*a*) Holotype LH928061b, ventral view; (*b*) paratype LH6021a, dorsal view; (*c*) paratype MC6a, ventral view. All scale bars = 5 mm.