

A DISCOGLOSSID FROG FROM THE MIDDLE JURASSIC OF ENGLAND

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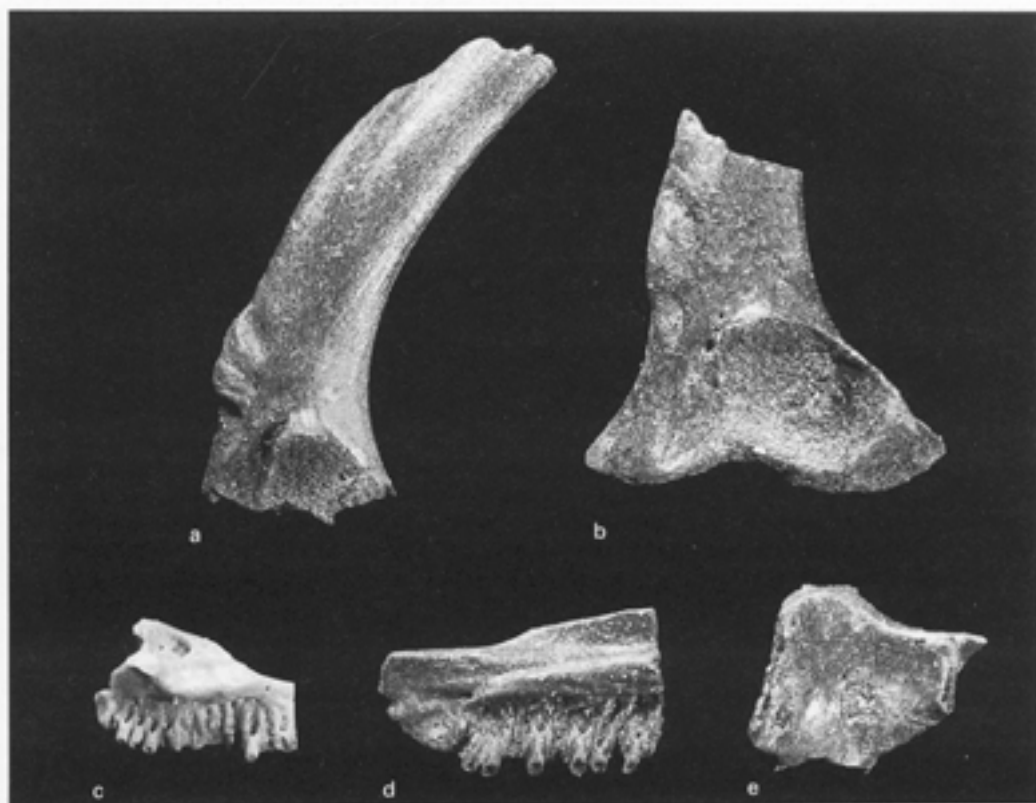
ABSTRACT. A discoglossid frog, *Eodiscoglossus oxoniensis* sp. nov. is described from the Upper Bathonian Forest Marble of Oxfordshire. It closely resembles *Eodiscoglossus santonjae* from the Jurassic-Cretaceous boundary of Spain but can be distinguished by characteristics of the ilium and premaxillary. The *E. oxoniensis* specimens represent the earliest European material critically identifiable as a frog and the earliest discoglossid yet recognised. An association of *Eodiscoglossus* with *Albanerpeton* and a *Marmorerpeton*-like salamander may have characterized certain freshwater ecosystems in Europe for about 50 million years from the Bathonian to the Barremian-Aptian.

THE fossil record of frogs prior to the Cretaceous is poor. The single specimen of *Triadobatrachus* from the Lower Triassic of Madagascar demonstrates that stem-anurans with just a few anuran skeletal characteristics had evolved by the beginning of the Mesozoic (Rage and Roček 1986, 1989; Milner 1988). However, no other Triassic anurans are known and few frogs have been described from Jurassic rocks, although these are all crown-group representatives with the full suite of anuran skeletal characteristics. They are known from eight localities and are reviewed in the discussion (below).

The Middle Jurassic frog material described here was obtained from the microvertebrate assemblage in the Kirtlington Mammal Bed at Kirtlington in Oxfordshire from which Freeman (1979) first recorded frog material. It represents the first discoglossid frog to be reported from pre-Upper Jurassic rocks and also the earliest known critically determinable frog material from Europe. The specimens described and figured here were collected either by Professor K. A. Kermack and colleagues or by Mr E. F. Freeman and have been donated to the Department of Palaeontology, British Museum (Natural History) (BMNH). Mr Freeman is undertaking palaeoecological work with his collections and the specimens collected by him retain his catalogue number (prefixed by EF). Comparative study was also made of *Eodiscoglossus* material at the Museum National d'Histoire Naturelle, Paris (MNHN).

LOCALITY AND HORIZON

The new material was collected from various parts of the Old Cement Works Quarry, near Kirtlington in Oxfordshire, (Ordnance Survey Grid Reference SP 495200; Freeman 1976, 1979; Kermack *et al.* 1987). The techniques of collection and preparation of microvertebrates from this locality were described by Kermack *et al.* (1987). The productive horizon is the Kirtlington Mammal Bed, near the base of the Forest Marble, which is of Upper Bathonian age (approximately 170 Ma; Harland *et al.* 1982). A full account of the local stratigraphy is given by Freeman (1979). The palaeoenvironment appears to have been a shallow non-stagnant water body, with occasional influxes of poorly sorted sediment (Freeman 1979). The Mammal Bed has produced a rich microvertebrate fauna of which only some of the mammals (Freeman 1976, 1979; Kermack *et al.* 1987) and salamanders (Evans, Milner and Mussett 1988) have been described so far.



TEXT-FIG 1. *Eodiscoglossus oxoniensis* n. sp. a, BMNH R. 11700, holotype right ilium in lateral aspect; b, BMNH R. 11720, right ilium in lateral aspect; c, BMNH R. 11703, right premaxillary in lingual aspect; d, BMNH R. 11704, right maxillary in lingual aspect; e, BMNH R. 11707, atlas centrum in dorsal aspect.

SYSTEMATIC PALAEOLOGY

Class AMPHIBIA

Order ANURA

Suborder DISCOGLOSSOIDEI Sokol, 1977

Family DISCOGLOSSIDAE Guenther, 1859

Genus EODISCOGLOSSUS Villalta, 1957

Type species. *Eodiscoglossus santonjae* Villalta, 1957.

Range. Bathonian to Barremian/Aptian; Spain and Great Britain.

Diagnosis. Discoglossid frog resembling *Discoglossus* in one derived character: ilium with dorsal crest and dorsal tubercle; and several primitive characters: 15–18 premaxillary teeth, about 50 maxillary teeth, coronoid process smooth and convex with no notches, anterior vertebrae bearing free ribs and posterior vertebrae bearing no ribs, iliac synchondrosis absent.

Discussion. *Eodiscoglossus* has no apomorphic characters, but is more plesiomorphic than *Discoglossus* in at least three features: pterygoid process of maxillary poorly developed, elongate flattened atlantal cotyles, neural arches lacking upturned flared posterior margins. It is more

plesiomorphic than the similar *Wealdenbatrachus* from the Barremian/Aptian of Uña, in that the ilium bears a single dorsal tubercle whereas *Wealdenbatrachus* has a pair of tubercles in this position.

The diagnosis is based on characters, most of which can be seen in both the Montsech and the British material. It is not entirely satisfactory in that there are no apomorphic characters for the genus, and it is probable that *Eodiscoglossus*, as defined here, is a primitive grade of *Discoglossus*-group discoglossid. However, as *E. oxoniensis* lacks obvious autapomorphic characters and clearly has a close phenetic resemblance to *E. santonjae*, a new genus cannot be justified and it is most practical to place both species in one genus.

Eodiscoglossus oxoniensis sp. nov.

Text-figures 1–4d, 5, 6a–c.

~ *Derivation of name.* From the county of Oxfordshire.

Holotype. British Museum (Natural History) Department of Palaeontology R. 11700, a right ilium lacking the end of the iliac blade and part of the acetabulum (text-figs. 1a, 6a, 6b).

Paratypes. BMNH R. 11701 (EF 75:10:1:6), R. 11720, 2 right ilia with fully preserved acetabular regions (text-figs. 1b and 6c); R. 11702, 11703, 2 right premaxillaries (text-figs. 1c, 2a–c); R. 11704, 11705, 2 right maxillaries (text-figs. 1d, 2e, f); R. 11707, R. 11708, 2 broken atlas centra (text-figs. 1e and a–e).

Referred material. 5 premaxillaries, 33 maxillaries, 9 angulosplenials (including R. 11706), a broken atlas (R. 11721), 30 isolated neural arches (including R. 11709–R. 11712), 7 broken scapulae (including R. 11722, R. 11723), 2 right humerus distal heads (R. 11713, R. 11714), a radioulna (R. 11715), 51 ilia, 2 ischia (including R. 11716 (EF 76:13/14:36:4)) and 10 tibiofibulae (including R. 11718 (EF 75:3:1:10) and R. 11719 (EF 76:4:1:2)).

Locality. Old Cement Works Quarry, Kirtlington, Oxfordshire, England, Ordnance Survey Grid Reference SP 495200.

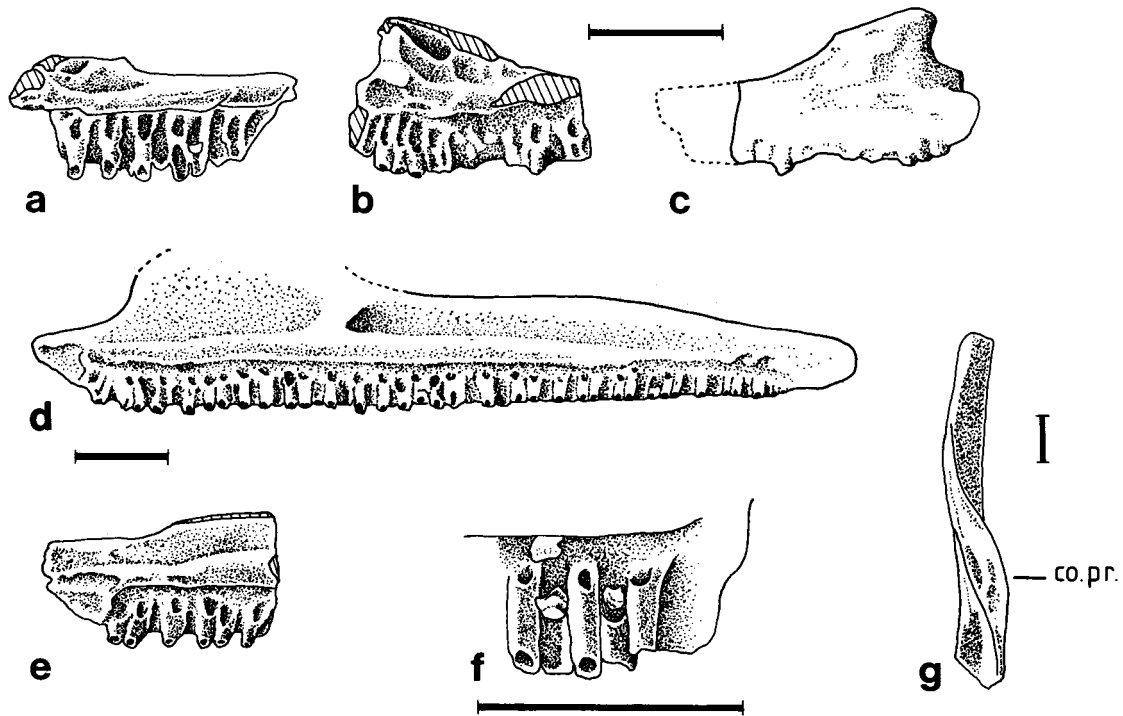
Horizon. Kirtlington Mammal Bed, near base of the Forest Marble, *aspidioides* Zone, Upper Bathonian, Middle Jurassic.

Diagnosis. Species of *Eodiscoglossus* in which the ilium shows the following features in contrast to that of *E. santonjae*: iliac shaft flattened and broad but narrow in cross-section with lateral ridge; little waisting at the junction of the shaft and the acetabular region; dorsal tubercle poorly developed, shallow and flush with the surface of the iliac shaft; supraacetabular fossa deep. The premaxillary of *E. oxoniensis* apparently has a low alary process in contrast to the elongate process of *E. santonjae*. Other bones appear to be indistinguishable in the two species.

DESCRIPTION

General features

The present material comprises about 160 elements as listed above. Scaled against skeletons of *Rana temporaria*, the larger elements belong to medium-sized frogs of 80 mm snout-vent length, although many of the bones derive from smaller animals. There is no more than one morphological type of any given bone and this, coupled with the numbers of ilia (53) and maxillaries (35), strongly suggests that only a single form is present. The bones are either diagnostically discoglossid or consistent with attribution to the Discoglossidae and so unity of the material is assumed.



TEXT-FIG. 2. *Eodiscoglossus oxoniensis* n. sp. *a*, BMNH R. 11702, right premaxillary in lingual view; *b*, *c*, BMNH R. 11703, right premaxillary in *b*, lingual and *c*, labial views; *d*, reconstruction of right maxillary in lingual view; *e*, BMNH R. 11704, anterior region of right maxillary in lingual view; *f*, BMNH R. 11705, detail of partial right maxillary showing pedicels and developing crowns of teeth; *g*, BMNH R. 11706, left angulosplenial in dorsal view. Scale bars = 1 mm. Abbreviation: co. pr. coronoid process.

Skull

Premaxillary (text-figs 1c and 2a-c). Seven specimens were collected, none of which is complete. The premaxillary has a broad pars dentalis with at least 15 tooth positions (about 18 in *E. santonjae*, Vergnaud-Grazzini and Wenz, 1975, p. 22). The lateral region of the pars dentalis is long and the medial region is short, as in other discoglossids including *E. santonjae*. The alary process is low and of moderate width, quite unlike that of other discoglossids including *E. santonjae* in which this process is as tall as the bone is wide (e.g. Vergnaud-Grazzini and Wenz 1975, fig. 1). It is convex anteriorly and concave posteriorly, with a deep medial excavation which probably received a peg of cartilage from the nasal capsule (text-figs. 1c and 2b). At the anteromedial junction of the alary process and the pars dentalis, there is an excavation showing that the alary processes were separated in the midline. The pars palatina (palatal shelf) is narrow laterally and wider medially. At the medial end, it curves sharply backwards into a medial expansion. The end of this expansion is incomplete, so it is not possible to determine whether it was pointed or blunt posteriorly.

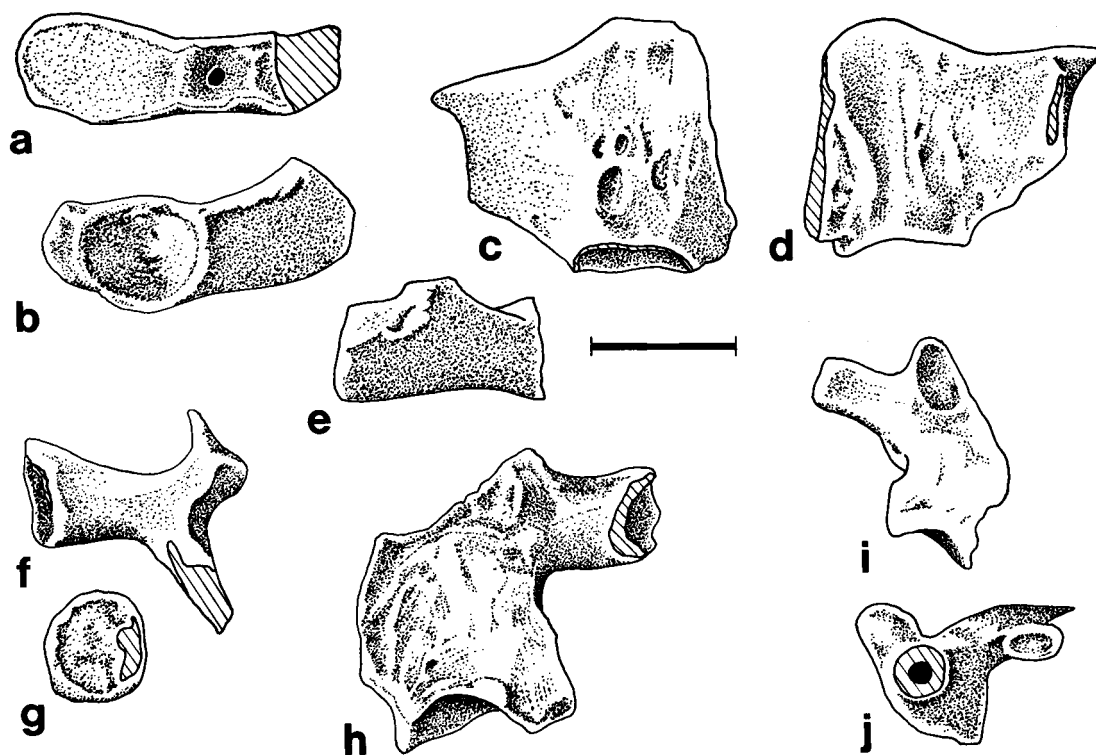
Maxillary (text-figs. 11d and 2d-f). About 35 maxillaries were recovered, none of which is complete. The pars dentalis is long and bears approximately 50 tooth positions, a similar number to that in *E. santonjae*. The pars facialis is long and divided into three regions:

- (i) a straight, narrow anterior process with a medial, slightly concave overlap surface for the premaxillary, anterior to the tooth-row (text-fig. 2e);
- (ii) behind the anterior process, the bone expands dorsally for a short distance back to the leading edge of the orbit;
- (iii) further back, the bone levels off and runs back as a low wall below the orbit.

Medially, at the level of the anterior orbital border, the maxillary bears a depression which opens into a foramen for the superior alveolar nerve. Laterally, the maxillary bears a shallow longitudinal groove at the level of the base of the tooth row. Otherwise the lateral face of the bone is featureless except for several small sensory nerve foramina. The pars palatina, or palatal shelf, begins just behind the anterior process of the bone as a low rounded ridge. Posteriorly, however, this expands into a small narrow shelf – the pterygoid process – where the lateral part of the pterygoid abuts against the maxillary. This process ends at the same level as the tooth row, but the bone continues for a short distance behind the tooth row although the posterior tip is not preserved in our material. The shape of the maxillary bears a close resemblance to that of *Wealdenbatrachus* (Fey 1988, fig. 22).

Dentition (text-fig. 2f). The premaxillary and maxillary teeth are slender and pedicellate. The crowns are always lost on fully erupted teeth but several specimens show isolated crowns either at the tooth bases or moving into position on broken teeth. The crowns are small and bicuspid, and show no other obvious specialization. Hecht (1970) regarded the maxillary of *Eodiscoglossus* as toothless, but the material described by Vergnaud-Grazzini and Wenz (1975, fig. 1) shows that *E. santoniae* has toothed premaxillaries and maxillaries.

Angulosplenial (text-fig. 2g). The angulosplenial is represented by nine specimens. It bears a coronoid process which is a long low convex bulge with no anterior or posterior notches.

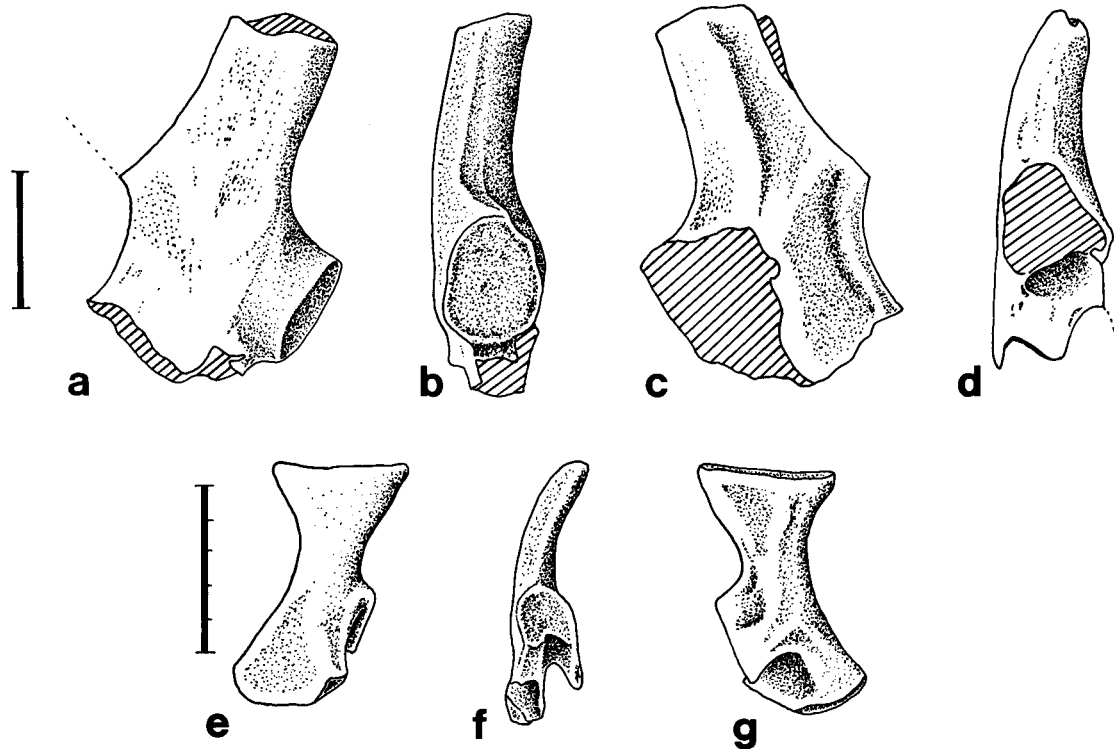


TEXT-FIGURE 3. *Eodiscoglossus oxoniensis* n. sp. a-d, BMNH R. 11707, atlas vertebra in a, anterior, b, posterior, c, ventral and d, dorsal views; e, BMNH R. 11708, atlas vertebra in left lateral view; f, g, BMNH R. 11709, anterior trunk vertebral arch in f, anterior view and g, lateral view of rib facet; h, BMNH R. 11711, posterior trunk vertebral arch in dorsal view; i, j, BMNH R. 11712, posterior trunk vertebral arch in i, dorsal and j, lateral views. Scale bar = 1 mm.

Axial skeleton

Atlas vertebra (text-figs. 1e and 3a-e). Three incomplete atlantal centra were recovered. The atlantal centrum is dorsoventrally flattened. The anterior cotyles are of depressed oval shape. Medially, they are moderately separated by an intercotylar region bearing a small notochordal pit (text-fig. 3a), but with no medial notch as seen from above or below. The long axes of the anterior cotyles are not horizontal but are orientated at a shallow obtuse angle. Posteriorly, there is a small circular cotyle which may be imperforate (R. 11707, 11708) or perforate (R. 11721). The presence of this cotyle implies that the following trunk vertebra is opisthocelous with an anterior condyle. The atlantal centrum is anteroposteriorly short but broad. The ventral surface is smooth except for a few small pits on either side of the midline. The dorsal surface is concave, with weak grooves on either side of a small rounded central ridge. The neural arch pedicel is broad-based but narrows dorsally, leaving an anterolateral notch for the exit of the first spinal nerve, and a long sloping posterolateral border. This atlas with such flattened, slightly separated anterior cotyles corresponds to the type II atlas of Lynch (1971). The distinction between this and the Lynch type III atlas in which the cotyles are confluent, is not always clear. Trueb (1973) identified the atlas of the extant leiopelmatids as type III but now considers them to be type II (pers. comm. in Clarke, 1988). Estes and Sanchíz (1982b) identified the atlas of the Galve material of *E. santonjae* as type III, but it appears to be very similar to the atlantal centrum described here. The degree of separation of the cotyles is apparently variable and not always clear in imperfect material. The apparent difference between the type II atlas of *E. oxoniensis* and the type III atlas of *E. santonjae* described by Estes and Sanchíz may not be of great significance.

Trunk vertebrae (text-fig. 3f-j). No complete trunk vertebrae were collected, although over 30 broken neural arches were recovered. The vertebrae have very narrow pedicels and lightly built arches which are apparently

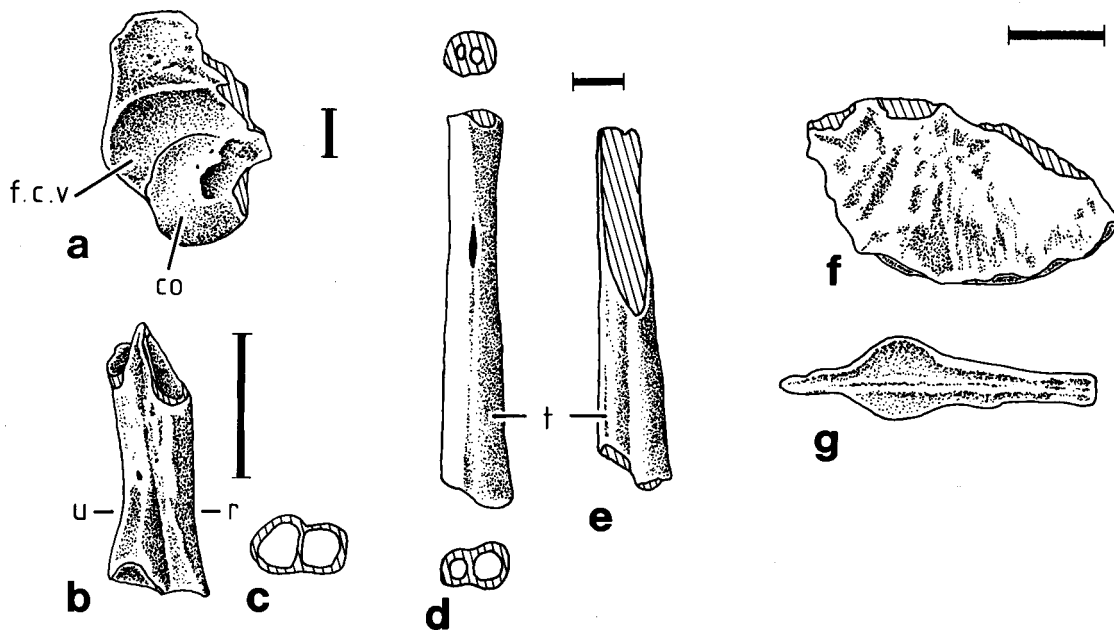


TEXT-FIG. 4. *Eodiscoglossus oxoniensis* n. sp. a-c, BMNH R. 11722, broken left scapula in a, lateral, b, posterior and c, medial views; d, BMNH R. 11723, broken left scapula in posterior view; e-g, *Rana temporaria*, left scapula in e, lateral, f, posterior and g, medial views. Scale bars = 1 mm (a-d), 5 mm (e-g).

easily broken. The neural arches are flattened, with almost horizontal pre- and postzygapophyses. The pedicel is narrow and there is a small horizontal backwardly-directed neural spine between the postzygapophyses (e.g. text-fig. 3*h*, *i*). Between the neural spine and the postzygapophyses, the posterior surface of the arch is excavated into deep pockets for intervertebral ligaments. The neural arches were probably imbricate but there is no suggestion of flaring of the posterior margin as in some discoglossids. Each pedicel bears a slender transverse process, usually broken at the tip. In a few isolated arches, however, the lateral process is expanded distally and bears a pitted terminal surface for the attachment of a free rib (text-fig. 3*f*, *g*). Other lateral processes were not terminally expanded and presumably bore no rib, not even a rudiment (text-fig. 3*i*). In *E. santonjae* and *Wealdenbatrachus*, free ribs are present on the anterior presacrals only and this appears to have been the condition in *E. oxoniensis*. Although no trunk centra are known, the presence of a posterior cotyle on the atlantal centrum means that the first trunk vertebra must have had an anterior condyle and have been opisthocoelous. In the absence of other evidence, all the presacral trunk vertebrae are assumed to have been opisthocoelous. Only three frog families have such presacral vertebrae, namely the Discoglossidae and the pipoid families Rhinophrynidae and Pipidae.

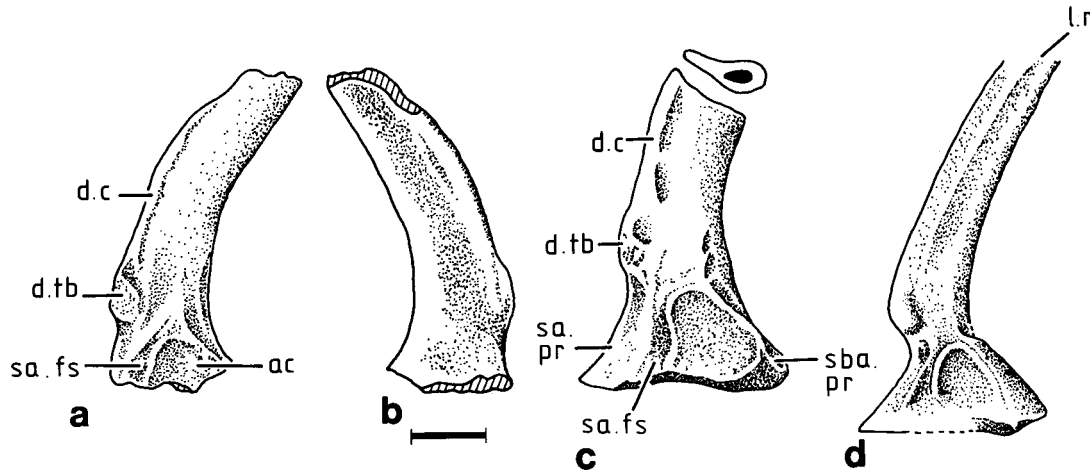
Appendicular skeleton

Scapula (text-fig. 4*a-d*). Of the pectoral girdle elements only 7 broken scapulae have been recovered. They are all too incomplete for the general shape to be determined and a scapula of *Rana temporaria* is figured comparatively (text-fig. 4*e-g*) to clarify the orientation of the fragment figured in text-fig. 4*a-c*. The scapulae appear to have been bicapitate, i.e. with separate articulations for the clavicle (pars acromialis) and coracoid (pars glenoidalis). Although the pars acromialis is not visible on any specimen, it is clear that there is a distinct pars glenoidalis demarcated ventrally by a deep pocket (text-fig. 4*d*) which must have separated the ventral region of the scapula into two heads.



TEXT-FIG. 5. *Eodiscoglossus oxoniensis* n. sp. *a*, BMNH R. 11713, distal head of right humerus in ventral view; *b*, *c*, BMNH R. 11715, left radioulna in *b*, ventral and *c*, cross-sectional views; *d*, BMNH R. 11718, incomplete tibiofibula, midshaft region together with proximal and midshaft cross-sections; *e*, BMNH R. 11719, incomplete tibiofibula, distal shaft region; *f*, *g*, BMNH R. 11716, ischial plate in *f*, right lateral and *g*, ventral views. Scale bars = 1 mm. Abbreviations: co, articular condyle; f.c.v., fossa cubitus ventralis; r, radius; t, tibia; u, ulna.

Fore-limb (text-fig. 5a-c). Of the fore-limb bones, only the distal heads of two humeri (R. 11713 and R. 11714) and a left radioulna (R. 11715) have been recovered. The shape of the humeral heads suggests that both derive from right humeri, but there is little preserved except the hemispherical articular condyle and a deep fossa cubitus ventralis (Estes and Sanchiz 1982b). The radioulna is distinguished from the tibiofibulae by its shorter broader shape (text-fig. 5b, c). There is a prominent radioulnar groove along the visible length of the specimen, a very primitive feature, but as the specimen derives from a very small individual, this may simply reflect immaturity.



TEXT-FIG. 6. *Eodiscoglossus oxoniensis* n. sp. a, b, BMNH R. 11700, holotype right ilium in a, lateral and b, medial views; c, BMNH R. 11701, right ilium in lateral and cross-sectional views; d, *Eodiscoglossus santonjae* MNHN MSE.5, right ilium. Scale bar = 1 mm. Abbreviations: ac. acetabulum; d.c. dorsal crest; d.tb. dorsal tubercle; l.r. lateral ridge; sa.fs. supraacetabular fossa; sa.pr. supraacetabular process; sba. pr. subacetabular process.

Ilium (text-figs. 1a, b and 6a-c). More than 50 ilia were collected, most showing only the thickened acetabular region. Three specimens, R. 11700 (the holotype), R. 11701 and R. 11720 show the important features. The following description uses the terminology of Vergnaud-Grazzini (1966). The iliac shaft is broad, anteriorly recurved and mediolaterally flattened (text-fig. 6c). The dorsal crest is moderately developed and separated from the smooth convex lateral surface by a narrow groove. Posteriorly, at the base of the shaft, the ilium bears an elongate but shallow tubercle (for the *musculus iliofemoralis*), separated from the remainder of the bone by dorsal and ventral pits. The acetabular region is thickened, but its ventral articular surfaces are completely preserved only in two specimens, R. 11701 and R. 11720. The acetabulum is prominent and roughly oval, lying towards the anterior edge of the bone (text-figs. 1b and c). Anterodorsally, a small pit (for the *musculus iliacus internus* Estes and Sanchiz 1982a) separates the acetabular surface from the shaft. Anteroventrally, the bone is drawn out into a small triangular subacetabular process. Posteroventrally, there is a larger supraacetabular process, separated from the acetabulum by a long supraacetabular fossa (text-fig. 1b). The ventral border of the bone is lightly forked, with pitted surfaces for the pubis and the ischium. Medially, the acetabular region shows little detail. There is no evidence of an iliac synchondrosis, although the medial edge of the pubic facet is roughened, suggesting a ligamentous attachment.

In comparison with the ilium of *Eodiscoglossus santonjae* (MNHN MSE. 5) (text-fig. 6d), that of *E. oxoniensis* is similar in general structure but several consistent differences can be itemized.

(i) In cross-section, the iliac shaft of *E. santonjae* is triangular, one corner of the triangle being formed by the prominent lateral ridge which extends up the lateral face of the shaft (text-fig. 6d). In *E. oxoniensis*, there is no lateral ridge and the shaft is narrow in cross-section (text-fig. 6c).

(ii) The shaft of *E. santonjae* is narrow in lateral view whereas that of *E. oxoniensis* is flattened and broad.

(iii) At the junction of the shaft and the acetabular region, the ilium of *E. santonjae* is sharply waisted; this is less marked in *E. oxoniensis*.

(iv) The dorsal tubercle of *E. santonjae* is more prominent than that of *E. oxoniensis*. That of *E. santonjae*

extends well above the surface of the iliac shaft, while the dorsal tubercle of *E. oxoniensis* is shallow and flush with the surface.

(v) The supraacetabular fossa is deeper and more marked in *E. oxoniensis* than in *E. santonjae*.

These features are constant on all the ilia of *E. oxoniensis* recovered and the differentiating characters were constant on those ilia of *E. santonjae* which were examined and serve to distinguish the species.

The ilium of the recently described Cretaceous discoglossid *Wealdenbatrachus jucarensis* (Fey 1988, figs 32–35) is similar in general shape to those of both *Eodiscoglossus* species. In the holotype specimen (Fey 1988, figs. 34 and 35), there is a dorsal tubercle which is prominent like that of *E. santonjae* but there is also an accessory tubercle. This tubercle is not found in either *Eodiscoglossus* species and appears to be the most diagnostic character of *Wealdenbatrachus*. The ilia of the paratype specimens of *Wealdenbatrachus* (Fey 1988, figs. 32 and 33) differ from that of *E. oxoniensis* in that they show greater development of the supra- and subacetabular processes and greater differentiation of the shaft and crest.

Ischium (text-fig. 5f, g). Two specimens of fused ischia were recovered (R. 11716, R. 11717). The compound bone is semicircular with a pitted margin and a pronounced posteroventral ridge radiating out from the acetabular region as in modern *Rana*. The posterior region is not preserved and it is not clear whether there was a posterodorsal expansion or not.

Tibiofibula (text-fig. 5d, e). Ten tibiofibular shafts were recovered (e.g. R. 11718, R. 11719). The larger tibia and smaller fibula are firmly fused, being barely distinct in the central shaft but partly separated by deep grooves towards the proximal and distal ends. The tibiofibulae were long and gracile resembling those of jumping anurans such as *Rana* rather than walking anurans such as *Bufo*.

DISCUSSION

Interrelationships of primitive frogs and the systematic position of E. oxoniensis

The Leiopelmatidae (*Leiopelma*, *Ascaphus*) and Discoglossidae (*Discoglossus*, *Alytes*, *Barbourula*, *Bombina*) are widely perceived as the most primitive families of living frogs. Clarke (1988) has recently completed a 95-character analysis of the osteology of all but one of the living species in these two families (*Bombina fortinuptialis* was not available for study), and has concluded that each family is monophyletic but that their interrelationships are uncertain. The Leiopelmatidae and Discoglossidae are frequently grouped together as the Discoglossoidae or Discoglossodea, but it is not clear whether this group is a monophyletic sister-clade to the remaining frogs or a primitive grade of frog with the Discoglossidae closer to the higher frogs, Sokol (1975, 1977) has argued that the Discoglossoidae are a clade and that the Discoglossidae and Leiopelmatidae share derived characters of the tadpole branchial system, namely (i) absence of the interbranchialis III muscle and (ii) extensive fusions between the copula II and the hypobranchials. No characters to support this relationship have been found in the adults however and in Lynch's cladogram (1973, fig. 3.6), the Discoglossidae share two characters with the higher frogs, namely: (i) presacral column reduced to eight vertebrae or fewer and (ii) *musculus caudaliopuboischiotibialis* lost. Both sets of characters are small and the interrelationship of leiopelmatids, discoglossids, and higher frogs is effectively an unresolved trichotomy.

Clarke (1988) has used his osteological data to analyse the internal relationships of the extant genera and species of the Discoglossidae. He concluded that *Alytes* is the sister-taxon to the other genera and that, within the remaining forms, *Discoglossus* is the sister-taxon to *Barbourula* and *Bombina*. The following discussion of the characters of *E. oxoniensis* is based, where possible, on the derived characters supporting this hypothesis of relationships.

Eodiscoglossus oxoniensis can be placed within the family Discoglossidae on the basis of two derived characters. Neither is unique to the Discoglossidae, but the combination characterizes only this family and one pipid genus, namely *Hymenochirus*.

(i) Opisthocelous vertebrae. These only occur in three anuran families, the Discoglossidae, Pipidae and Rhinophrynidae (Trueb 1973). This Kirtlington material shows no other general features of pipids or rhinophrynids.

(ii) Ilium bearing a dorsal crest. Such ilia are found in the Discoglossidae, Leptodactylidae, Ranidae, and the pipid genus *Hymenochirus*, but the Kirtlington material shows no other characteristics of the latter three taxa.

In Clarke's (1988) hypothesis of relationships based on osteology, the subfamily Discoglossinae (*Discoglossus*, *Bombina* and *Barbourula*) is defined by six osteological characters. One is found in *E. oxoniensis*:

(iii) Occipital condyles with major axes at shallow or steep angle. The occiput of *E. oxoniensis* is unknown but the atlantal cotyles slope upwards at a shallow angle and so presumably the occipital condyles must have as well.

Clarke also defines the Discoglossinae by the presence of neural arches with flared posterior margins but these are not present in *E. oxoniensis*.

Other derived features, which occur in some but not all discoglossines, are also found in *E. oxoniensis*. These characters are not distributed congruently with each other, or with other characters within the Discoglossidae (Clarke 1988), but broadly support a relationship between *E. oxoniensis* and the Discoglossinae:

(iv) Imbricated vertebrae. These are found in most but not all discoglossine species.

(v) Groove at the base of the tooth row on the lateral face of the maxillary. This occurs in *Discoglossus* and one species each of *Bombina* and *Barbourula*.

(vi) Neural spines moderately developed. This occurs in *Bombina* and some *Discoglossus* species.

The Kirtlington material can be associated with the genera *Discoglossus*, *Wealdenbatrachus*, and *Eodiscoglossus* on the basis of one derived character:

(vii) The ilium has a distinct dorsal tubercle, not as well-developed as in *E. santonjae* or the other two genera but more so than in other discoglossids (Estes and Sanchíz 1982a; Fey 1988; Clarke 1988). There are no derived characters which suggest immediate relationship to *Alytes*, *Barbourula* or *Bombina*.

The Kirtlington material can be associated with *Eodiscoglossus* on the basis of one character of uncertain polarity:

(viii) The atlas has extremely flattened anterior cotyles (Estes and Sanchíz 1982b).

As noted under the generic diagnosis, there is no certain derived character shared by *E. santonjae* and *E. oxoniensis*, but the phenetic resemblance is sufficiently great that a new genus cannot be justified. Finally, the Kirtlington material merits a separate species because of the differences in ilium and premaxillary construction listed under the species diagnosis and the descriptions of those elements.

Eodiscoglossus oxoniensis does not provide major new insights into the anatomy of early discoglossid frogs. However, it does combine a derived character of *Discoglossus* (ilium with dorsal tubercle) with a primitive feature that places it outside the *Discoglossus-Barbourula-Bombina* group (neural arches lack flared posterior margin). This suggests that the characters used to define the taxa, based on modern material, have either been subject to convergence or reversal, or their polarity is not fully understood. The new material extends the stratigraphical range of the genus *Eodiscoglossus* and the family Discoglossidae down to the Bathonian, and the geographical range of both taxa to include the British Isles. Finally, although the evidence is not strong, such osteological characters as are present suggest that the *Alytes*-group and *Discoglossus-Barbourula-Bombina* group had already differentiated by 170 Ma.

The fossil record of Jurassic frogs

Jurassic frogs have now been described from six localities and reported from a further two. The sole described Lower Jurassic frog is the type and only specimen of *Vieraella herbstii* from the Roca Blanca Formation of Argentina (Reig 1961; Casamiquela 1965; Estes and Reig 1973). Estes and Reig assigned this genus to the Leiopelmatidae (referred to as the Ascaphidae in that work). However, they noted that the leiopelmatid characters of the specimen were all primitive anuran characters and *Vieraella* could equally be a stem-frog with no immediate relationship to any modern

family. It does not prove the existence of a cladistically defined Leiopelmatidae in the Lower Jurassic.

The only Middle Jurassic specimens described in the literature are a possible anuran omosternum from the Bajocian of Aveyron (Seiffert 1969; but see Estes and Reig 1973 for a critical reappraisal) and the Kirtlington material first reported by Freeman (1979) and described in this paper.

Upper Jurassic frogs have been described or reported from five areas as follows.

(i) In the nineteenth century, the Morrison Formation of Como Bluff, Wyoming, U.S.A. produced a few fragments of frog skeleton including two humeri which have been named: *Eobatrachus agilis* Marsh and *Comobatrachus aenigmatis* Hecht and Estes (reviewed by Hecht and Estes 1960; Estes and Reig 1973). The latter authors concluded that the *Eobatrachus* humerus might belong to a pipoid but could not be determined further, while *Comobatrachus* was indeterminate. Estes and Sanchíz (1982a) noted that the *Comobatrachus* humerus had some resemblances to those of discoglossids. Further frog material was collected from the Morrison Formation between 1968 and 1970 but has not yet been described (Prothero and Estes 1980, p. 484).

(ii) The Matildense Formation of Argentina has produced several specimens of a frog named *Notobatrachus degiustoi*. Principal descriptions are by Reig (1957), Casamiquela (1961) and Estes and Reig (1973). Estes and Reig assigned *Notobatrachus* to the Leiopelmatidae (as the Ascaphidae).

(iii) The lithographic limestones of the Sierra del Montsech, Lérida, Spain, dated as uppermost Jurassic or basal Cretaceous, have produced several specimens of at least two types of frog. Most are of the discoglossid frog, *Eodiscoglossus santonjae*, which has most recently been described or discussed by Hecht (1963, 1970), Estes and Reig (1973), and Vergnaud-Grazzini and Wenz (1975). A single specimen of a second frog, *Neusibatrachus wilferti*, was described by Seiffert (1972) and it can be assigned to the Palaeobatrachidae (Estes and Reig 1973; Vergnaud-Grazzini and Wenz 1975). A third named form, also based on a single specimen, is *Montsechobatrachus gaudryi* (Vidal 1902). This poor specimen is generally agreed to be indeterminate, although some features suggest that it may be a palaeobatrachid (Estes and Reig 1973; Vergnaud-Grazzini and Wenz 1975).

(iv) Anuran material has been reported, but not described, from the Lower Kimmeridgian lignites of Guimarota, Portugal (Seiffert 1973).

(v) New localities in the Purbeck Formation of Dorset, England have recently produced fragments of an anuran which have not yet been determined (Ensom 1988). This material is currently being studied by two of the authors (S.E.E. and A.R.M.).

The fossil record as yet permits us to make very few testable statements about the evolution and diversification of frogs in the Jurassic. It is clear that true frogs were present in the Lower Jurassic, but there is no evidence for differentiation into recognizable modern families at that time. By the Bathonian, discoglossids were not only present but may have begun to differentiate as discussed above. However, because of the uncertainty of the interrelationships of primitive frog families to higher frogs and to each other, we cannot yet say which other frog families might be expected also to be present. By the Jurassic-Cretaceous boundary, differentiation at least into leiopelmatids, discoglossids, and palaeobatrachids had taken place.

Ecology and chronology

The Kirtlington assemblage is incompletely described at present, but preliminary quantification of the amphibian material suggests that it may in future be possible to recognize the associations or communities which included *Eodiscoglossus*. In the samples studied, the *Eodiscoglossus* material could not have come from fewer than 28 specimens (right ilia). The five other amphibians recognized, together with the minimum numbers of individuals represented, are: *Marmorherpeton kermacki* (19 atlantes), *Marmorherpeton freemani* (1 atlas), a third small salamander (4 atlantes) a primitive salamander (340 atlantes) and an albanerpetontid (1 atlas). It appears that the assemblage incorporated a major association of *Eodiscoglossus*, *Marmorherpeton kermacki* and the primitive salamander, with the other forms as exotic elements in the fauna.

This association may have been long-lived, at least at the family level. Estes and Sanchíz (1982b)

described similar material from Galve in Spain, including several specimens each of *Eodiscoglossus*, *Albanerpeton*, and an unnamed *Marmorerpeton*-like salamander. The small salamander *Galverpeton* was represented by only a single specimen. The Galve assemblage is Barremian-Aptian and hence 125–113 Ma in age (Harland *et al.* 1982), so it is possible that an amphibian faunal association of *Eodiscoglossus*, albanerpetontid, and *Marmorerpeton* (or similar forms) may have characterized certain freshwater ecosystems in Europe for over 50 million years from the Middle Jurassic to the late Lower Cretaceous. Testing this association against other faunas might eventually be possible but at present most of the assemblages of Mesozoic lissamphibians from Spain and Portugal (e.g. Guimarota, Uña) are still undescribed.

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Since completion of the manuscript, vertebral material, including a sacrum and urostyle, has been recovered. The trunk centra and sacrum are identical to those figured for *E. santonjae* (Estes & Sanjíz 1982*b*). The urostyle has small anterior transverse processes, as in many recent frogs, and is consistent with attribution to the Discoglossidae.