

A STEM-GROUP CAECILIAN (LISSAMPHIBIA: GYMNOPHIONA) FROM THE LOWER CRETACEOUS OF NORTH AFRICA

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ABSTRACT. Of living amphibian groups, the limbless burrowing caecilians are amongst the most highly specialised, but are the least known. Their fossil record is extremely poor, leaving unresolved questions as to their origins, relationships and early distribution. We describe here caecilian remains from a Lower Cretaceous (Berriasian) microfossil locality near Anoual, Morocco. This material represents the second oldest record for the group, after the Jurassic *Eocaecilia* of North America, and the earliest caecilian record for Gondwana. It forms the basis of a new genus, *Rubricacaecilia*, which appears slightly more derived than *Eocaecilia*, but lacks major features of crown-group taxa. We support the use of Apoda Oppel, 1811 for the crown-group alone, and Gymnophiona Rafinesque 1814 for the clade comprising stem-group taxa + Apoda.

KEY WORDS: Amphibia, Lissamphibia, Gymnophiona, Cretaceous, Africa, palaeontology.

LIVING amphibians fall into three major groups: the frogs (Salientia), the newts and salamanders (Caudata) and the limbless caecilians (Gymnophiona). The latter form a group of poorly known, but highly specialised taxa, mostly tropical and burrowing, represented today by six families: the Rhinatrematidae (South America), the Ichthyophiidae (India, Sri Lanka, and South East Asia), the Uraeotyphlidae (India), the Scolecomorphidae (Africa), the Caeciliidae (America, Africa, India, Seychelles), and the semi-aquatic Typhlonectidae (South America). They total about 33 living genera with *c.* 160 species (M. Wilkinson, pers. comm. Feb. 2000), of which the majority are included within the derived, but probably paraphyletic (Nussbaum and Wilkinson 1989; Wilkinson and Nussbaum 1999), Caeciliidae. Recent cladistic analyses identify rhinatrematids as the least derived, and link ichthyophiids and uraeotyphlids as sister taxa. Caecilians (used throughout to indicate both crown- and stem-group taxa) differ from most other amphibians in being elongate with *c.* 70–283 vertebrae (Nussbaum and Naylor 1982), in having a reduced eye and specialised tentacular organ, and, with some exceptions, in having a heavily roofed skull (unlike the reduced open skull of frogs and salamanders) which is used as a digging tool (Wake 1993).

The fossil record of caecilians is very poor. Until recently, it was limited to a few isolated vertebrae from the Palaeocene of Brazil (Estes and Wake 1972; Rage 1991) and Bolivia (Rage 1986, 1991) and from the Late Cretaceous (Cenomanian) of the Sudan (Werner 1994; Evans *et al.* 1996). All of these vertebrae, however, closely resemble those of living taxa, particularly in having the enlarged anterior basapophysial projections that appear to characterise the crown-group (Estes and Wake 1972). Apart from the palaeobiogeographic interest, these fossils add relatively little to our understanding of the evolution of the group as a whole. Of greater significance was the recovery of *Eocaecilia* from the Lower Jurassic Kayenta Formation of northern Arizona, USA (Jenkins and Walsh 1993). *Eocaecilia* has yet to be fully described, and detailed work is ongoing, but it is clear that *Eocaecilia* is very much more primitive than any known taxon, living or fossil, particularly in the retention of limbs and tail, and in the structure of the vertebral column.

Here we describe new caecilian material from an earliest Cretaceous (Berriasian) microvertebrate assemblage from Morocco, North Africa. The material is disarticulated, but referable elements (including those of the jaw, atlas and trunk vertebrae) show that the Moroccan form falls into the temporal (Early Jurassic – Late Cretaceous) and, to a lesser degree, morphological gap between *Eocaecilia* and crown-group caecilians, and thus contributes to our understanding of the post-Jurassic history of the group.

GEOLOGY AND MATERIAL

The Moroccan microvertebrate locality of Anoual is situated in the eastern High Atlas Mountains, 100 km east of the city of Anoual, close to a fort called Ksar Met Lili. The site was sampled during a 1983 field expedition by the Museum national d'Histoire Naturelle, Paris and the Moroccan Ministry of Mines and Energy, with further collecting in 1986 and 1988.

The Couches-Rouges of the High Atlas form a continuous sequence from Middle Jurassic (Bathonian) to Lower Cretaceous (Aptian) (Sigogneau-Russell *et al.* 1990). The calcareous lens containing the microvertebrate assemblage is about 200 mm thick and covers an area of about 200 square metres. It has been dated on the basis of calcareous nannofossils (holococcoliths) which suggest an earliest Cretaceous (Berriasian) age (Sigogneau-Russell *et al.* 1990; Duffin and Sigogneau-Russell 1993). The lens (continental facies) is sandwiched between marine beds, suggesting that it formed part of a deltaic sedimentary environment close to the sea. Altogether some 700 kg of calcareous sediment have been treated with acetic acid, and about two-thirds of the resulting residues have been sorted for microvertebrates and plant remains. The deposits are extremely rich and the preservation is good, although the vertebrate remains are all small, disarticulated and rather friable. The bones are usually broken, but show little sign of polishing or abrasion, suggesting they were deposited under relatively quiet conditions. The site has proved to be a rich source of Early Cretaceous mammals (Sigogneau-Russell 1988, 1991*a, b*, 1992, 1995), and has yielded a diversity of other small vertebrates including selachians (Duffin and Sigogneau-Russell 1993), lizards (Richter 1994; Broschinski and Sigogneau-Russell 1996), two sphenodontian taxa (Evans and Sigogneau-Russell 1997), dwarf or embryonic/hatchling dinosaurs, frogs, the first Gondwanan record of the enigmatic salamander-like Albanerpetontidae, and the caecilian described here (Sigogneau-Russell *et al.* 1998).

The presence of a caecilian amongst the Anoual microvertebrate material is indicated by characteristic elements such as the pseudodentary and pseudangular. Other elements (vertebrae, palatine, possible limb bone) have been attributed by virtue of their general resemblance to the bones of either living caecilians, or the basal caecilian *Eocaecilia* (or a combination of both). In each case, these elements are quite distinct in their morphology from the corresponding elements of either frogs or albanerpetonid amphibians (SE, pers. obs.), the only other lissamphibians in the Anoual assemblage. Together, they form a consistent set of elements, resembling those of known caecilian taxa and varying in similar ways (e.g. the differences between anterior and posterior vertebrae). There is nothing to suggest that more than one taxon is represented.

Institutional abbreviations. CAS, California Academy of Sciences; MCM, collections of the Museum national d'Histoire Naturelle, Paris, France; UCMP, University of California, Berkeley, Museum of Paleontology; UCMVZ, University of California, Berkeley, Museum of Vertebrate Zoology.

SYSTEMATIC PALAEOLOGY

LISSAMPHIBIA

GYMNOPHIONA Rafinesque, 1814

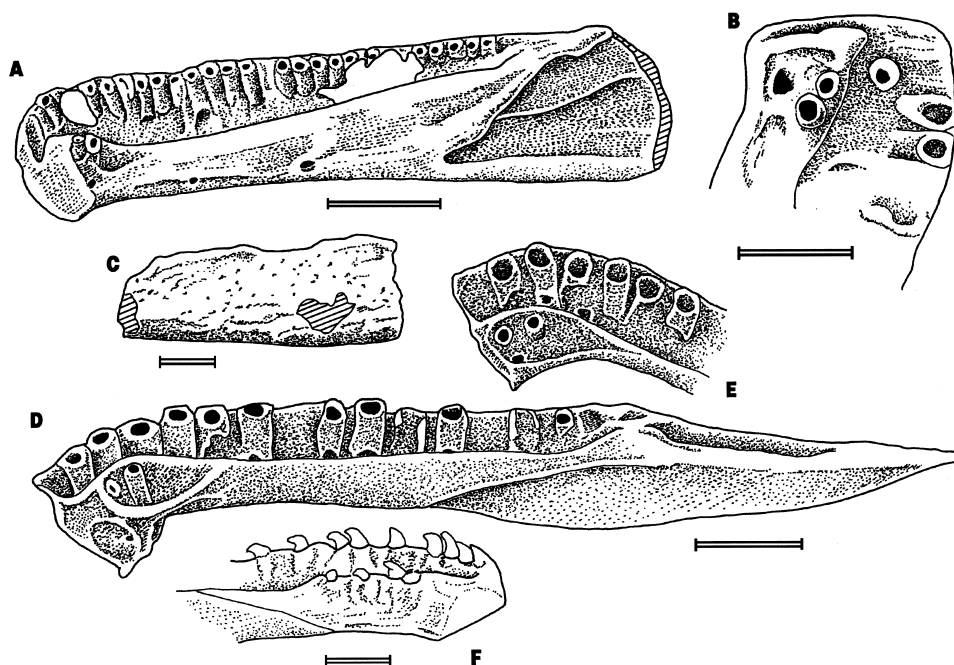
Genus RUBRICACAECILIA gen. nov.

Derivation of name. From *rubrica* (L), meaning red earth, with reference to the Couches Rouges from which the assemblage comes, and caecilia.

Rubricacaecilia monbaroni gen. et sp. nov.

Text-figures 1A-C, 2-5, 6A-F, 7A-B

Derivation of name. To recognise the contribution of the Swiss geologist M. Monbaron whose specialist knowledge of the region contributed to the discovery of the Anoual locality.



TEXT-FIG. 1. A–C, *Rubricacaecilia monbaroni* gen. et sp. nov. A–B, MCM 171, holotype right pseudodentary; A, lingual view; B, occlusal view of symphyseal region and splenial teeth. C, MCM 172, partial left pseudodentary; lateral view. D–E, UCMP 140422, the recent caecilian *Typhlonectes natans*; D, pseudodentary in dorsolingual view; E, detail of D showing symphyseal region and splenial teeth. F, CAS 20926, the recent caecilian *Ichthyophis mindanaoensis*; pseudodentary, lingual view of symphyseal region showing longer splenial tooth row. White areas on these and subsequent figures of fossil material show the position of tightly adherent sand grains which cannot be removed without damage to the specimens. Scale bars represent 1 mm.

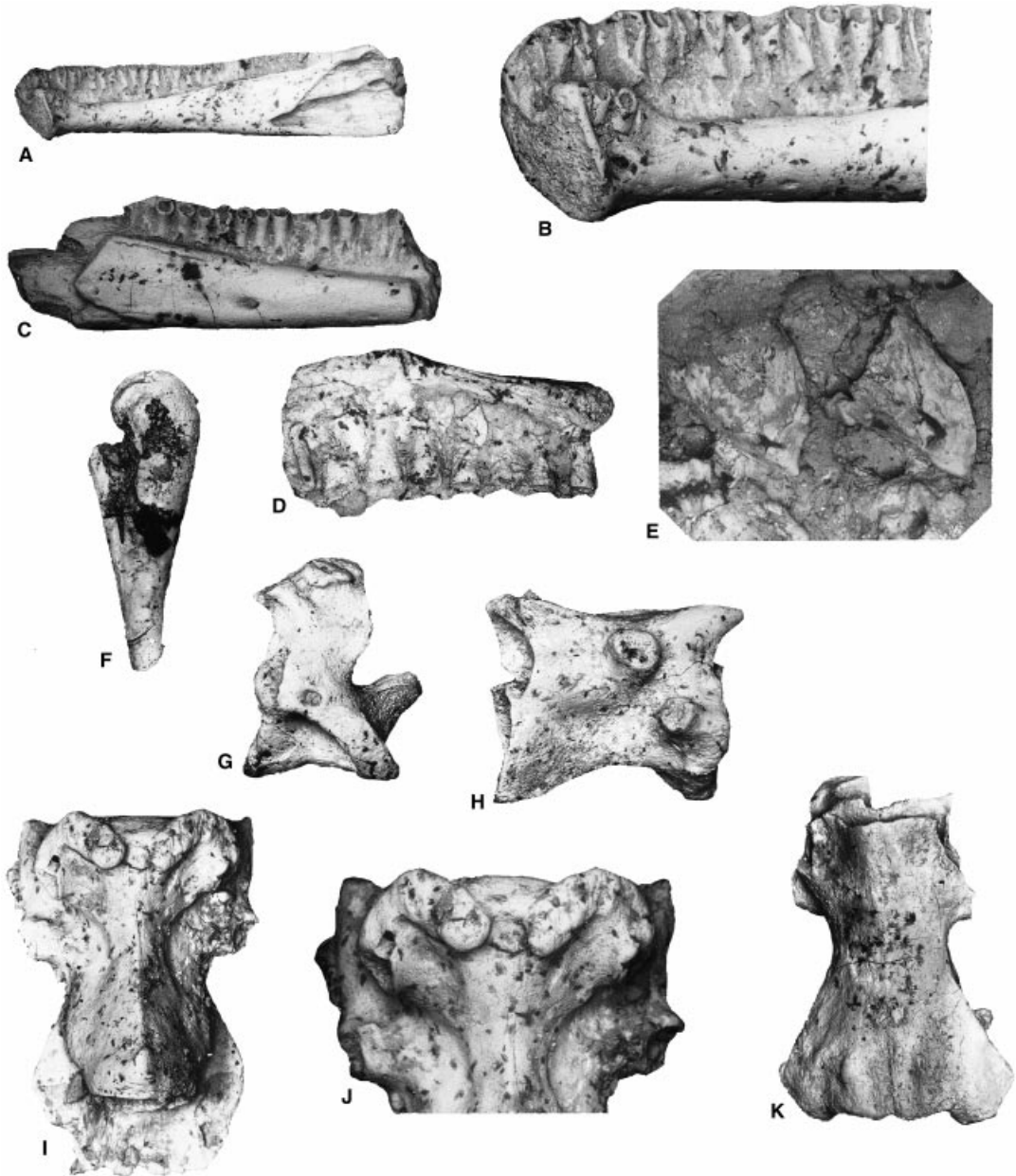
Holotype. A nearly complete right pseudodentary, MCM 171.

Type locality and horizon. Ksar met Lili, 100 km east of the city of Anoual, Morocco; Couches Rouges, Lower Cretaceous, Berriasian.

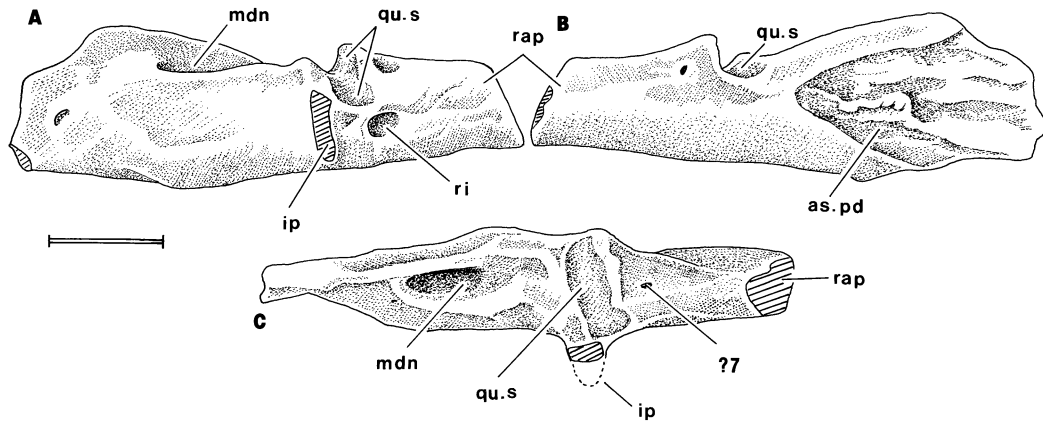
Referred material. MCM 172–173, partial left pseudodontaries; MCM 56, a partial right pseudangular; MCM 174, a partial palatine; MCM 175, an atlas; MCM 1–2, 176–181, postatlantal vertebrae.

Diagnosis. A small (c. 200 mm) primitive caecilian characterised by the combination of the following features: a pseudodentary with c. 28 narrow and close-packed pedicellate teeth, a long closure of the Meckelian fossa (up to tooth position 24), subdivision of the posterior Meckelian fossa by a horizontal shelf, only two teeth in the splenial tooth row; palatine teeth blade-like; internal process of pseudangular small; vertebrae with prominent anterior basapophyses, but lacking enlarged anteroventral basapophyseal processes.

Remarks. *Rubricacaecilia* differs from the Jurassic *Eocaecilia* in having only two teeth in the splenial tooth row (c. 25 in *Eocaecilia*; R. L. Carroll, pers. comm. to SE, Nov. 1999), in having a longer region of closure of the Meckelian fossa, in the structure of the pseudangular (smaller and more posteriorly placed internal process), and in having a more prominently developed ventral keel on the vertebral centra. It differs from all currently known crown-group caecilians, living and fossil, in retaining a tuberculum interglenoideum on the atlas (a feature of the salamander cranio-vertebral joint; Wake 1970) and in lacking anterior processes on the basapophyses. Separate generic status is therefore justified.



TEXT-FIG. 2. *Rubricacaecilia monbaroni* gen. et sp. nov., Couches Rouges, Anoual, Morocco. A–B, MCM 171, holotype, right dentary. A, lingual view; $\times 10$. B, detail of A, showing symphyseal region; $\times 29$. C, MCM 173; partial left dentary, lingual view; $\times 20$. D, MCM 174, left palatine, lingual view; $\times 20$. E, detail of D, showing replacement tooth crowns embedded in matrix; $\times 90$. F, MCM 3, tentatively attributed left femur, showing trochanteric crest; $\times 10$. G, MCM 175, atlas, right lateral view to show tuberculum interglenoideum; $\times 20$. H, MCM 177, anterior trunk vertebra, right lateral view; $\times 20$. I, MCM 181, posterior trunk vertebra, ventral view; $\times 20$. J, detail of I, showing basapophyses and parapophyses; $\times 29$. K, MCM 176, posterior trunk vertebra, dorsal view; $\times 20$.



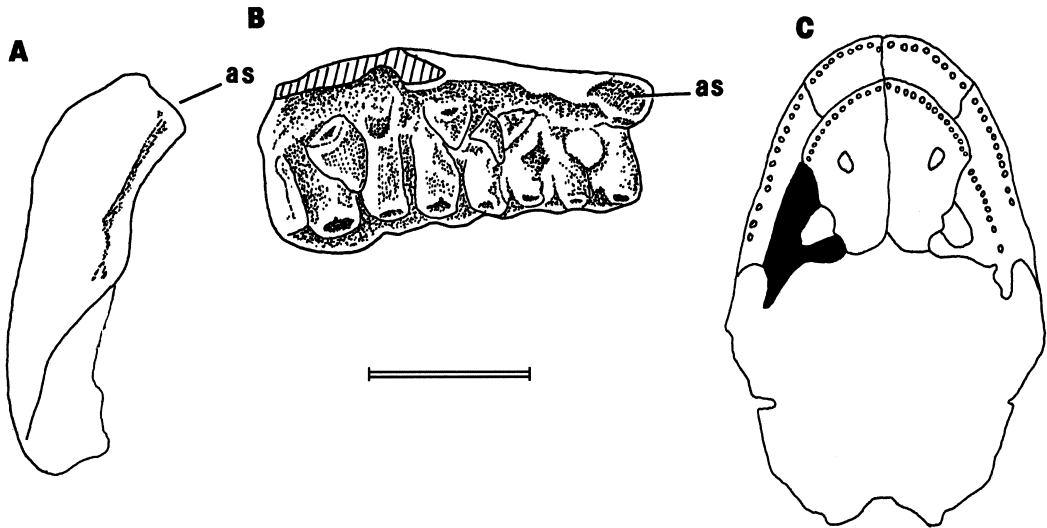
TEXT-FIG. 3. *Rubricacaecilia monbaroni* gen. et sp. nov., MCM 56, right pseudangular. A, medial view; B, lateral view; C, dorsal view. Scale bar represents 1 mm.

Description

Pseudodentary. The lower jaw of caecilians is made up of two elements, the anterior pseudodentary and the posterior pseudangular, each compound (Wake and Hanken 1982). Three specimens of the pseudodentary have been recovered (MCM 171–173). MCM 171 is a nearly complete right bone (Text-figs 1A–C, 2A–C). The alveolar margin carries around 28 close-packed pedicels that are narrow but deep. None of the crowns is preserved. The Meckelian fossa has a long closure (up to tooth position 24), the incisure and facet for the pseudangular lying towards the rear of the bone. The posterior part of the Meckelian fossa is divided into upper and lower parts by a narrow shelf. Anteriorly, the symphyseal surface is shallow and the symphyseal shelf bears two small ‘splenial’ teeth. Laterally, the bone is marked by grooves and many foramina (Text-fig. 1C). Similar foramina are found in living taxa and carry a rich supply of sensory nerves and blood vessels.

Based on the length of the pseudodentary (5–6 mm), and assuming a primitive terminal mouth, rather than a more derived subterminal one, the total jaw length was probably around 8 mm, a length associated with living taxa having a total body length of around 200 mm (SE, pers. obs.).

Pseudangular. This distinctive caecilian element provides attachment for jaw muscles and also the joint surface for the quadrate. The Anoual material has yielded a single right bone (MCM 56, Text-fig. 3A–C). In medial view (Text-fig. 3A), the bone presents a roughly oblong structure, deepest anteriorly where it met the pseudodentary and tapering slightly into the long retroarticular process. The anterior part of the bone is excavated from above by a large opening (prearticular foramen of Bemis *et al.* 1983) for the entrance of the mandibular ramus of the trigeminal nerve and accompanying vessels. According to Bemis *et al.* (1983), the resulting fossa also provides a surface of insertion for parts of the external adductor musculature. The opening is flanked labially by a low crest, presumably also for adductor muscle attachment. About two-thirds of the distance from the anterior tip, a broken surface marks the base of the internal process (seen to project slightly in dorsal view; Text-fig. 3C). This feature is prominent in living caecilians and provides attachment for craniomandibular ligaments (Bemis *et al.* 1983) and some fibres of the pterygoideus muscle (Wilkinson and Nussbaum 1997). Behind the process there is a large foramen that carried the intermandibular nerve and vessels into the surrounding soft tissues (Wilkinson and Nussbaum, 1997). Anterolaterally (Text-fig. 3B), the most obvious feature is a large, triangular articular surface for the pseudodentary. The posterior limit of this facet lies just anterior to the level of the quadrate articular surface. In dorsal view (Text-fig. 3C), the mandibular nerve foramen and associated fossa are seen clearly. Behind the foramen is a short but wide quadrate surface that extends a short distance onto the posteromedial surface of the bone, but is essentially a dorsal feature. In lateral and medial views (Text-fig. 3A–B), the quadrate surface forms a U-shaped notch flanked anteriorly and posteriorly by raised edges. As in modern caecilians (Bemis *et al.* 1983), the arrangement suggests that little anteroposterior movement was possible at this joint. The retroarticular process, a distinctive feature of caecilian mandibles, is long, strongly developed, but straight (i.e. not dorsally arched; see below). In living taxa, it provides attachment for muscles that both open (depressor mandibulae) and close (pterygoideus, interhyoideus) the lower jaw (Bemis *et al.* 1983; Nussbaum 1983: see Discussion)



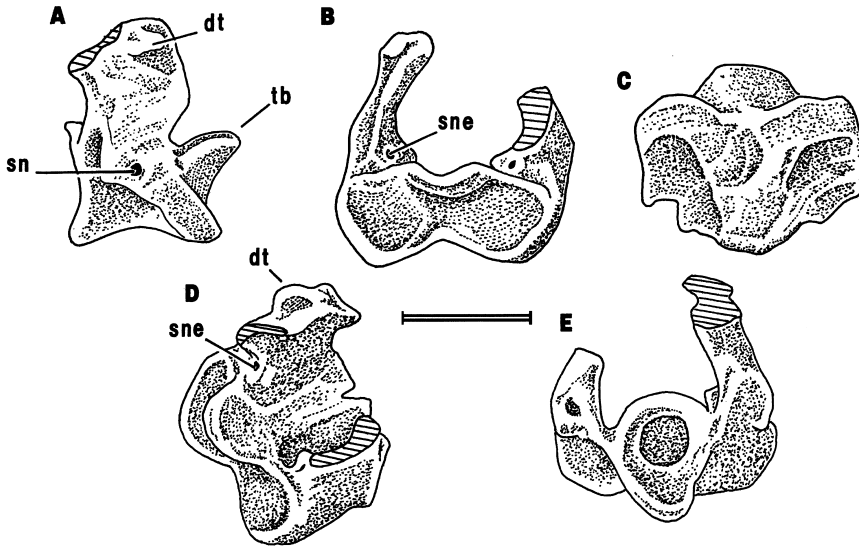
TEXT-FIG. 4. A–B, *Rubricacaecilia monbaroni* gen. et sp. nov., MCM 174, left palatine. A, dorsal view; B, medial view; C, palatal view of a generalised caecilian (redrawn from Taylor 1969, fig. 1; not to scale) with the area of the palatine shown in black. Scale bar for A–B represents 1 mm.

Palatine. A single additional toothed element (MCM 174, Text-figs 2D–E, 4A–B) clearly represents part of the upper dentition of a non-albanerpetontid lissamphibian (pedicellate teeth), but differs strikingly from any element in a frog (the dental elements of which are well-represented at Anoual). The bone has a smooth lateral surface, except for a very narrow anterodorsal groove that curves slightly dorso-medially, and a medial tooth row consisting of eight tooth bases of slightly larger diameter than those on the pseudodentary. At one end there is a discrete medial joint surface, behind which the edge of the bone is smooth and concave. Several replacement tooth crowns are preserved *in situ* at the base of the pedicels (Text-figs 2D–E, 4B). They are mediolaterally compressed and blade-like, like those of most living caecilians (Wake and Wurst 1979). No supplementary cusps are visible, but they may simply be obscured.

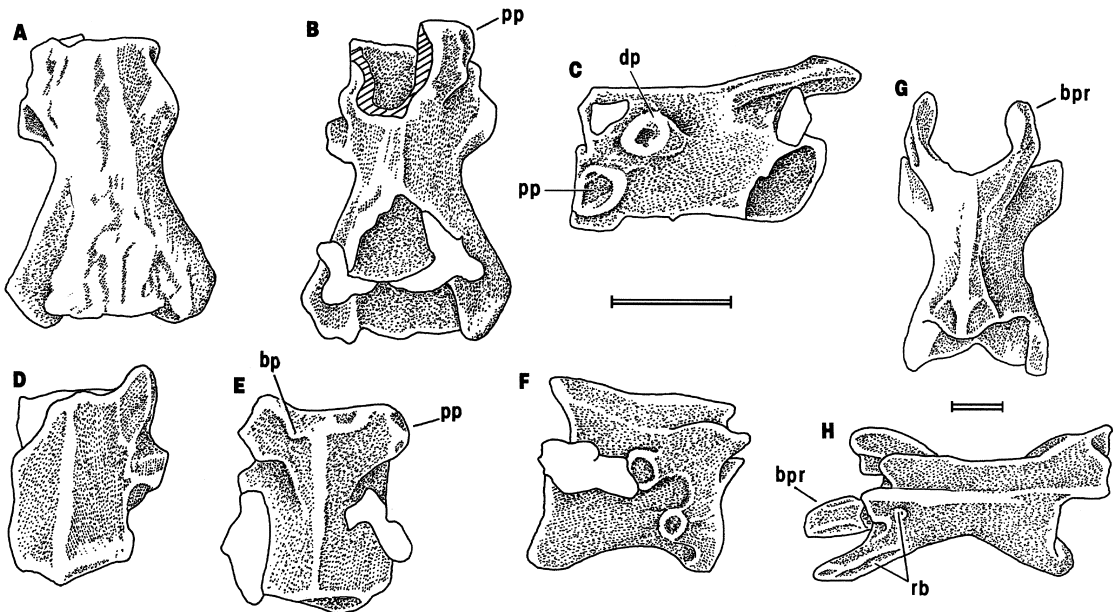
MCM 174 cannot, by its shape, be the premaxilla and must therefore be either the maxilla or palatine. These two elements are fused in the adults of living caecilians (Wake and Hanken 1982; Reiss 1996), but they remain separate in *Eocaecilia* (Jenkins and Walsh 1993). The lateral surface of MCM 174 is strongly angled so that its vertical face is almost at right angles to the medial flange. This feature, and the absence of any lateral nutrient foramina, suggests the bone is part of a palatine. Under this interpretation, it would be a left element, the anterior sutural surface being for the vomer while the concave free medial margin would have formed part of the choana (Text-fig. 4c). The absence of any lateral sutural surface suggests the bone remained free of the maxilla throughout life.

Atlas. The atlas is represented by a single specimen (MCM 175) which preserves a complete centrum but only part of the right neural arch pedicel (Text-figs 2G, 5). The bone is strikingly similar to that of the Jurassic *Eocaecilia* (Jenkins and Walsh 1993; F. Jenkins, pers. comm. to SE, Dec. 1999). The anterior aspect of the centrum (Text-fig. 5B) bears two anteriorly facing ovoid cotyles for articulation with the occipital condyles, but the articular surface extends continuously across the midline. There is a prominent median dorsal tuberculum interglenoideum (Text-fig. 5A, tb), a feature absent in all crown-group caecilians (Text-fig. 7). Laterally, the neural arch pedicel is perforated by a spinal nerve foramen, the short exit canal running obliquely anteromedial to posterolateral (Text-fig. 5A–B, D). In posterior view (Text-fig. 5E), the atlas centrum is seen to be amphicoelous, but the notochordal canal does not penetrate the anterior face of the bone. In ventral view (Text-fig. 5C), the anterior articular region is seen to be heavily buttressed by a thickened rim. The neural arch is broken, but on the right side the dorsolateral surface bears a small, anteriorly directed tubercle (Text-fig. 5A, dt), presumably for epaxial muscle attachment.

Post-atlantal vertebrae. Eight vertebrae are known (MCM 1, 2, 176–181), representing different regions of the body and differentiated mainly by their length/width ratios. Wake (1980) showed that vertebral length in caecilians (*Dermophis*) increases through the first part of the series (reaching close to maximum length around vertebra 20) and begins to decrease again from around vertebra 80 onwards. The Anoual vertebrae also show an increase in length



TEXT-FIG. 5. *Rubricacaecilia monbaroni* gen. et sp. nov., MCM 175, atlas vertebra. A, right lateral view; B, anterior view; C, ventral view; D, dorsolateral view; E, posterior view. Scale bar represents 1 mm.



TEXT-FIG. 6. A-F, *Rubricacaecilia monbaroni* gen. et sp. nov., vertebrae. A-C, MCM 176, posterior trunk vertebra: A, dorsal view; B, ventral view; C, left lateral view. D-F, MCM 177, anterior trunk vertebra: D, dorsal view; E, ventral view; F, right lateral view. G, the recent caecilian *Dermophis mexicanus*; UCMVZ 894, trunk vertebra, ventral view. H, the recent *Typhlonectes natans*, UCMP 140122, trunk vertebrae, dorsolateral view. Scale bars represent 1 mm (scales for A-F and G-H respectively).

(Text-figs 2H–I, K, 6A–F). The centra are notochordal and amphicoelous. The neural arch is wide and flat, with broad horizontal zygapophyses. As in living taxa (Wake 1980), anterior neural arches bear a low midline ridge (Text-fig. 6D), but this is lost in more posterior vertebrae (Text-figs 2K, 6A). The neural arch shape as a whole also changes, being short and parallel-sided with a slight posterior spur in anterior vertebrae, but more posteriorly flared with a nearly straight posterior margin further along the column (Text-figs 2K, 6A, D). These more posterior vertebrae are conspicuously waisted behind the level of the diapophysis. Laterally, prominent diapophyses and parapophyses are present on most vertebrae for the two-headed ribs (Text-figs 2H, 6C, F). No postatlantal vertebra shows any trace of a spinal nerve foramen. In ventral view, the centra bear a low midventral keel (Text-figs 2I, 6B, E). Anteroventrally, the parapophyses can be seen to stem from a median prominence which also bears anterior basapophyses (Text-figs 2I–J, 6B, E). However, these basapophyses lack the enlarged flange-like anterior processes that characterise crown-group caecilians (Taylor 1977a; Text-fig. 6G–H).

Limb element. One of the most problematic elements in the Anoual amphibian collection is MCM 3, the proximal head of a left femur with a small head and a strong hooked trochanteric crest (Text-fig. 2F). Its morphology is strikingly different from that of frog femora and most closely resembles that of a salamander, but no other salamander elements have been identified from the locality (among more than 100 amphibian bones). The most obvious candidate would be the Anoual albanerpetontid, which is relatively common (Sigogneau-Russell *et al.* 1998), but a trochanteric crest has not been observed in any member of this group (SE, pers. obs.), with both associated and dissociated material available. In contrast, the Jurassic *Eocaecilia* not only retained limbs, but the described femur of this genus bears a trochanteric crest like that of salamanders (Jenkins and Walsh 1993). This raises the possibility that the Anoual femur belongs to *Rubricacaecilia*, although this identification is obviously tentative.

DISCUSSION

Comparison

Knowledge of living caecilian osteology is patchy, and the following comparisons are made in the realisation that future work may reveal a more complex pattern of variation for crown-group taxa than is outlined here. With that caveat, *Rubricacaecilia* appears to show a unique combination of characters which place it between the Early Jurassic *Eocaecilia* and more derived caecilians, known from the Late Cretaceous onwards. These features relate to the number and form of the main dentary tooth row, the ‘splenial’ tooth row, and the structure of the pseudangular, palatine, atlas and vertebrae.

Marginal dentition. The pseudodentary tooth count (one ramus) in living caecilians ranges from 6–38, with no obvious pattern between families (Taylor 1968, 1969, 1977b; Wilkinson and Nussbaum 1997). The count of 28 pseudodentary teeth in *Rubricacaecilia* thus lies within the upper range of living taxa, and contrasts with that of *Eocaecilia* in which there are around 40 tooth positions (R. L. Carroll, pers. comm. Nov. 1999). In both primitive taxa, however, the tooth pedicels are small and columnar, with a relatively narrower diameter than those of most crown-group caecilians (the derived Seychellian caeciliid *Praslinia* is an exception; M. Wilkinson, pers. comm. Nov. 1999). In this respect, the teeth of *Eocaecilia* and *Rubricacaecilia* resemble those of frogs and caudates.

Splenial teeth. Symphyisial, or ‘splenial’ teeth are a feature of most caecilians. Generally speaking, tooth number decreases crownward, but there is considerable variation within groups (Taylor 1968, 1969, 1977b): rhinatrematids, 9–18; ichthyophiids, 0–29 (*I. singaporensis* has only three and *Caudacaecilia*, none); uraeotyphlids, 5–9; scolecomorphids, none; and typhlonectids, 1–21. Within caeciliids, splenial tooth numbers range from 0–4 (*Boulengeria*, *Caecilia*, *Gymnophis*, *Herpele*, *Hypogeophis*, *Idiocranium*, *Osaecilia*, *Schistometopum*, *Siphonops*), or 0–17 (*Geotrypetes*, *Grandisonia*) (Taylor 1968, 1969). The high splenial tooth count in *Eocaecilia* (25, R. L. Carroll, pers. comm. Nov. 1999) and the very low number in *Rubricacaecilia* (2) thus lie at opposite ends of the range.

Closure of the Meckelian fossa. In living caecilians, the degree of anterior closure of the Meckelian fossa varies, but it is generally quite short, with the suture for the pseudoangular passing obliquely, but smoothly, posterodorsal to anteroventral. The long closure in *Rubricacaecilia* differentiates it from other

taxa except *Eocaecilia* and the derived lungless typhlonectid *Atretochoana* (Wilkinson and Nussbaum 1997).

Tooth morphology. According to studies by Wake (1976), Wake and Wurst (1979) and Wilkinson and Nussbaum (1999), the primitive caecilian tooth tip morphology (and that found in rhinatrematids and ichthyophiids; M. Wake, pers. comm. 2000) is that of a compressed tip with a small lateral secondary cusp. *Eocaecilia* has this small lateral cusp but the only teeth preserved on the Moroccan material are those on the referred palatine. These are mediolaterally compressed and blade-like (Text-fig. 2E). There is no evidence of the subsidiary cusp but it may be obscured in the view preserved.

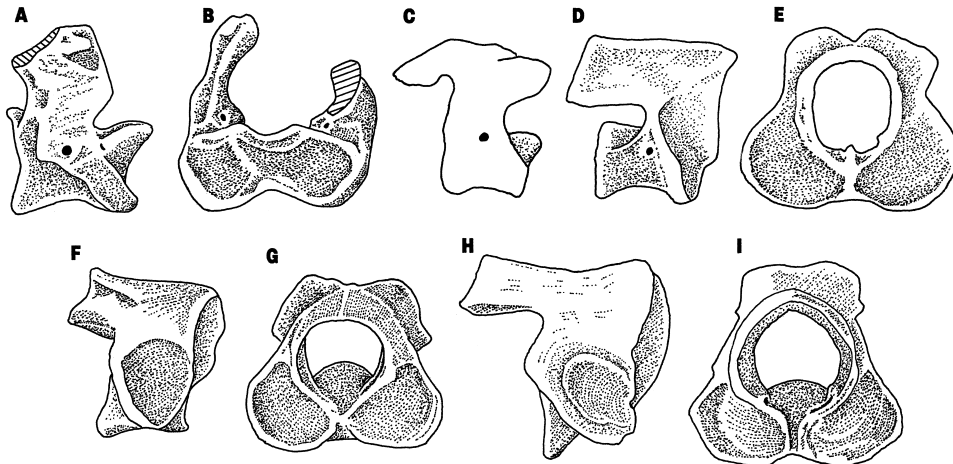
Pseudangular. The features of the pseudangular of *Rubricacaecilia* are typical of caecilians from *Eocaecilia* onwards. However, the bone of the Moroccan genus resembles that of basal crown-group caecilians (rhinatrematids) more closely than that of *Eocaecilia* in several features: the smaller internal process (at least at the base); shorter, deeper and more dorsally placed quadrate surface; and in the position of the internal process (level with the quadrate surface as opposed to well anterior to the surface in *Eocaecilia*). In fact, there are no major structural differences between the pseudangular of *Rubricacaecilia* and that of a living rhinatrematid such as *Epicrionops*. Bemis *et al.* (1983) and Nussbaum (1983) described two components to the caecilian jaw closing mechanism. The first is a retention of the ancestral condition in which the mandibular adductor muscles, operating in front of the jaw joint, pull the mandible upwards. However, there is an additional component whereby one of the ventral constrictor muscles, the interhyoideus posterior, aided by the pterygoideus muscle, pulls posteroventrally on the elongated retroarticular process causing the jaw to pivot around the quadrate joint. The muscle acts in opposition to the depressor mandibulae and closes the jaw. In rhinatrematids, this mechanism is only partially developed, as evidenced by the open temporal fossa (for the original jaw adductors), relatively large adductor insertion, and straight retroarticular process. The interhyoideus is relatively small. In more crownward families, the temporal fossae are closed (reflecting the reduction of the adductor mass) while the retroarticular process is further elongated and dorsally curved. The changed angle of the retroarticular process allows a greatly enlarged interhyoideus muscle to pull almost horizontally along the axis of the body. Bemis *et al.* (1983) concluded that this dual mechanism permits maximum bite forces with minimal widening of the head, an obvious advantage for burrowing animals.

The retroarticular process of *Rubricacaecilia* is horizontal like that of rhinatrematids. In addition, the presence of a crest and fossa flanking the mandibular opening suggests that the adductor muscles remained quite powerful. Thus *Rubricacaecilia* presumably possessed a combination of primitive and novel jaw closing systems.

Palatine. In all crown-group caecilians, the maxilla and palatine are fused to form a single bone (Wake and Hanken 1982; Reiss 1996). Since non-fusion is found in *Eocaecilia* (Jenkins and Walsh 1993), it is likely to be primitive. The presence of a free palatine in *Rubricacaecilia*, if correctly attributed, would therefore be plesiomorphic.

Atlas: tuberculum interglenoideum. The tuberculum interglenoideum is a feature of the atlas of salamanders and of the extinct lissamphibian clade Albanerpetontidae, as well as some microsaur and other Palaeozoic amphibian taxa. The tuberculum is absent in frogs (including stem-group taxa like *Czatkobatrachus*; Evans and Borsuk-Bialynicka 1998) and was either never developed or lost at a very early stage. It is also absent in all crown-group caecilians (Text-fig. 7D–I), but its occurrence in *Eocaecilia* (Jenkins and Walsh 1993; Text-fig. 7C) suggests it was a feature of the early members of the stem-group. Its presence in *Rubricacaecilia* supports this conclusion. In this respect, caecilians, salamanders and albanerpetontids together differ significantly from frogs.

Atlas: cotylar position. In *Eocaecilia*, the atlantal cotyles face directly forwards. In ichthyophiids and uraeotyphlids, the condition is similar although there may be limited extension onto the lateral surface (Text-fig. 7D–E). Lateral extension is greater in more crownward taxa so that in, for example, caeciliids and



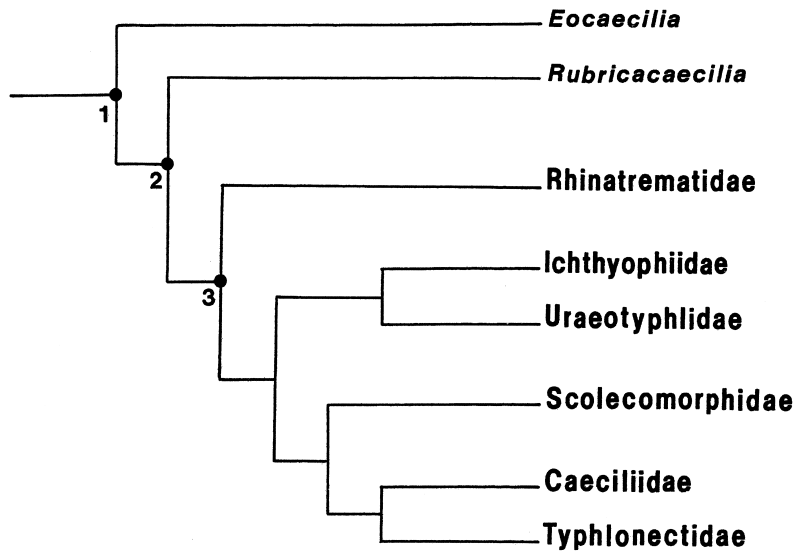
TEXT-FIG. 7. Gymnophionan atlantes. A–B, *Rubricacaecilia monbaroni* gen. et sp. nov., MCM 175. A, right lateral view; B, anterior view. C, *Eocaecilia macropoda* Jenkins and Walsh, 1993 (taken from a photograph supplied by F. Jenkins); MCZ 9231A, outline right lateral view. D–E, *Ichthyophis mindanaoensis*, CAS 20926. D, right lateral view; E, anterior view. F–G, *Dermophis mexicanus*, UCMVZ 894. F, right lateral view; G, anterior view. H–I, *Typhlonectes natans*, UCMVZ 140122. H, right lateral view; I, anterior view. Drawings not to scale.

typhlonectids, the surface for the occipital condyle is wrapped around the anterior and lateral surfaces of the bone (Text-fig. 7F–I). There is a tight fit between the atlas and occipital condyles in gymnophionans (M. Wilkinson/D. Gower, pers. comm. Nov. 1999), and the lateral extension in more derived taxa may strengthen the arrangement for burrowing. The cotyles of *Rubricacaecilia* are like those of primitive taxa in facing fully forwards.

Another difference between the cotyles of *Rubricacaecilia* and those of crown-group caecilians is the extension of the articular surface across the midline. In recent caecilians, the cotyles are discrete (Text-fig. 7), while the condition in *Eocaecilia* resembles that of *Rubricacaecilia* (F. Jenkins, pers. comm. Dec. 1999).

Atlas: spinal nerve foramen position. The posterolateral rotation of the atlantal cotyles in derived caecilians affects the position and orientation of the canal for the spinal nerve. In *Rubricacaecilia*, *Eocaecilia* and *Ichthyophis*, the exit foramen for the spinal nerve is clearly seen on the lateral surface of the neural arch pedicel (Text-fig. 7A, C–D). In more derived taxa, the foramen lies behind the cotyle and is therefore hidden in lateral view (Text-fig. 7F, H).

Vertebrae: basapophyseal processes. The vertebrae of crown-group caecilians are characterised by prominent anteroventral extensions of the basapophyses into bilateral flanges (Estes and Wake, 1972; Text-fig. 6G–H) which are associated with specialised hypaxial musculature (Naylor and Nussbaum 1980). These, in turn, are associated with the peculiar locomotor form that characterises crown-group caecilians (with some exceptions; e.g. aquatic typhlonectids). Vermiform bending movements of the vertebral column and associated axial muscles occur independently of (and within) the sheath of skin and more superficial trunk muscles. Summers and O'Reilly (1997) concluded that this form of locomotion was present in the last common ancestor of crown-group caecilians. If so, then the extended basapophyseal processes may characterise crown-group taxa and their immediate ancestors. These processes are absent in *Eocaecilia* and also in *Rubricacaecilia*, although the presence of anterior basapophyses in the Anoual vertebrae provides support for the view that the enlarged anterior processes of caecilians may be homologous to the anterior basapophyses of salamanders. Small anterior basapophyses are also present in albanerpetontids but are absent in frogs, including the stem-group taxa *Triadobatrachus* (SE, pers. obs.) and *Czatkobatrachus* (Evans and Borsuk-Bialynicka 1998).



TEXT-FIG. 8. Summary cladogram showing the hypothesised relationships of living and fossil caecilian groups (redrawn mainly from Wilkinson and Nussbaum 1999). Node 1, Gymnophiona (splenial teeth in pedicellate jaw; loss of neural spine; no transverse processes); Node 2, unnamed clade (reduced tooth count on pseudodentary; ventral keels on postatlantal vertebrae); Node 3, Apoda (elongated anterior basapophyseal processes; loss of tuberculum interglenoideum). Only characters discussed with respect to *Rubricacaecilia* are noted.

Rib facets. Caecilian vertebrae differ from those of salamanders and albanerpetontids in lacking elongated rib-bearers. There is variation in modern caecilians with respect to the shape and prominence of the rib processes, and variation also occurs along the length of the vertebral column within individuals (Wake 1980). In *Rubricacaecilia*, the diapophysis lies on a short cylindrical base at or just below the posteroventral margin of the prezygapophysis while the parapophysis lies on a small ventrolateral prominence and forms a small, laterally directed spur. The arrangement is similar in *Eocaecilia* (F. Jenkins, pers. comm. Dec. 1999), although small intercentra are also retained in the Jurassic form. There is no way to determine whether these intercentra were also retained in *Rubricacaecilia*.

Vertebrae: ventral crests. Prominent midventral crests on the anterior vertebrae are a feature of crown-group caecilians (Wake 1980) and provide attachment for elements of the hypaxial musculature. They are absent in *Eocaecilia* (Jenkins and Walsh 1993), but clearly developed in *Rubricacaecilia* (Text-fig. 6B, E).

Relationships

With so little of the animal known, it is not profitable to run a cladistic analysis for *Rubricacaecilia*. Recent analyses of living caecilians support the view that Gymnophiona is monophyletic, with Rhinatrematidae as the sister group of all remaining living taxa (Text-fig. 8; Wilkinson and Nussbaum 1999). *Eocaecilia* is clearly the outgroup to this clade. The presence of a tuberculum interglenoideum, the absence of the distinctive anterior processes on the basapophyses, and the possible retention of limbs suggests placement of *Rubricacaecilia* outside the crown-group. The reduced tooth count on the pseudodentary and midventral crests on the anterior vertebral centra suggest a position closer to the crown than *Eocaecilia*, but the reduced splenial tooth row must be regarded as autapomorphic because it is much longer than this in many crown-group taxa. On current evidence, therefore, we conclude that *Rubricacaecilia* is a stem caecilian that lies as a sister taxon to the crown-group. We see no evidence to support sister-group relationship with *Eocaecilia* since the only shared character states are primitive.

With caecilians, we now have a situation similar to that in other lissamphibian groups where both crown and stem-group taxa can be identified. In frogs this is dealt with by the use of the term Anura for the crown-group and Salientia for stem + crown (Milner 1988). Caudata and Urodela serve the same function respectively for salamanders (Milner 1988). Trueb and Cloutier (1991) used the term *Gymnophiona Rafinesque*, 1814 for the clade as a whole, with Apoda Oppel, 1811 for the crown-group alone. Under this definition, *Eocaecilia* and *Rubricacaecilia* would be gymnophionans but not apodans.

With some notable exceptions (e.g. Carroll and Currie 1975; Carroll and Holmes 1980; Laurin and Reisz 1996), most recent analyses of living amphibian relationships (both morphological and molecular) have supported the monophyly of Lissamphibia (e.g. Parsons and Williams 1963; Duellman and Trueb 1986; Milner 1988, 1993; Trueb and Cloutier 1991; Hedges *et al.* 1993; Feller and Hedges 1998). Within Lissamphibia, most workers using morphological characters have supported a frog-salamander sister group relationship, with *Gymnophiona* separating earlier (e.g. Duellman and Trueb 1986; Milner 1988; Trueb and Cloutier 1991; McGowan and Evans 1995). In contrast, several molecular studies have found support for a salamander-caecilian sister group relationship (e.g. Larson and Wilson 1989; Hedges *et al.* 1990; Hay *et al.* 1995; Feller and Hedges 1998). The basal members of each of the major clades are clearly important to this discussion, but we need to identify basal lissamphibians in order to polarise such characters as the possession of a tuberculum interglenoideum or of basapophyses.

Biogeography

Living caecilians are predominantly a Gondwanan group, distributed in South and Central America, Africa, and India, as well as parts of South East Asia. On this basis, Duellman and Trueb (1986, p. 485) hypothesised that the group must have been already widespread in Gondwana by the Late Jurassic–Early Cretaceous, prior to the breakup of the southern landmass. The fossil record of caecilians is minimal, but the discovery of a basal caecilian (*Eocaecilia*) in the Lower Jurassic of North America offers the possibility of a Pangean distribution of caecilians by the end of the Triassic. Feller and Hedges (1998) proposed a Laurasian origin with dispersal from North America into South America and Africa before the break up of Pangea, but the group could equally have originated in Gondwana and radiated north. The first record of a crown-group caecilian (interpreted from the presence of extended basapophyseal processes), is provided by a small number of isolated vertebrae from the Wadi Milk Formation, Sudan (Werner 1994; Evans *et al.* 1996), dated as Cenomanian, some 40 million years later than *Rubricacaecilia*. On present evidence, we do not know whether *Rubricacaecilia* is representative of the morphological stage reached by Gondwanan caecilians at the beginning of the Cretaceous, with the diversification of the crown-group occurring only later, or whether it was already a relict taxon, with crown-group taxa occurring elsewhere. For this we need more material.

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APPENDIX

Abbreviations used in the text. as, articular surface on palatine for vomer; as.pd, articular surface for pseudodentary; bp, basapophysis; bpr, basapophysial process; dp, diapophysis; dt, dorsal tubercle of atlas; ip, internal process; mdn, entry foramen for mandibular branch of trigeminal nerve and blood vessels; pp, parapophysis; qu.s, quadrate articular surface; rap, retroarticular process; rb, rib attachment points; ri, foramen for exit of intermandibular ramus of trigeminal nerve; sn, spinal nerve exit foramen; sne, spinal nerve entry foramen; tb, tuberculum interglenoideum; ?7, foramen which may carry chorda tympani branch of seventh nerve.