FULENGIA, A SUPPOSED EARLY LIZARD REINTERPRETED AS A PROSAUROPOD DINOSAUR

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ABSTRACT. The skull of *Fulengia youngi* Carroll and Galton, a supposed lizard from the Upper Triassic/Lower Jurassic of China, is re-examined and compared with contemporary prosauropod dinosaurs. On the basis of its teeth, and the construction of the maxilla and mandible, the skull of *Fulengia* is reinterpreted as that of a juvenile prosauropod dinosaur. It most closely resembles specimens of *Gyposaurus sinensis* Young, now generally acknowledged to be juveniles of the common Lufeng anchisaurid *Lufengosaurus*. *Fulengia youngi* is formally proposed to be a junior synonym of *Lufengosaurus huenei*. The earliest unequivocal fossils of lizards are of Upper Jurassic age.

IN 1977, Carroll and Galton announced the discovery of a 'modern' type of lizard from the Late Triassic of China. The specimen formed part of the collections of the Catholic University of Peking (CUP), which are now housed in the Field Museum of Natural History, Chicago, USA. The specimen, CUP 2037, was originally catalogued as a juvenile of the prosauropod dinosaur *Yunnanosaurus huangi* by Simmons (1965, p. 63) but Carroll and Galton (1977) reinterpreted it as the skull of a lizard and renamed it *Fulengia youngi*.

Prior to the description of *Fulengia*, the earliest true lizards were those of the Upper Jurassic of Europe, America, and China (see Estes 1983, for a full list). The Upper Triassic kuehneosaurs, considered by some authors (Robinson 1962, 1967; Colbert 1966, 1970; Carroll 1975) as true lizards, have more recently been regarded as an independent radiation (Hoffstetter 1962, 1967; Kluge 1967; Evans 1980, 1984, 1988; Gauthier 1984; Benton 1985). Likewise, the Upper Permian genera described by Carroll (1975) have subsequently been argued to lack the character-states diagnostic of lizards (Evans 1980, 1984, 1988; Benton 1985). All of these genera retain primitive diapsid character-states including: paired median skull-roofing elements; complex palatal dentition; toothed parasphenoid; large lacrimal; simple subpleurodont teeth; and amphicoelous vertebrae. The genus *Fulengia*, by contrast, was described as having several derived lacertilian character-states including: fused median roofing bones; small lacrimal; serrated pleurodont teeth, procoelous vertebrae; and, in reconstruction, a temporal region closely resembling that of a modern iguanid lizard. This combination of derived character-states and early geological age made the specimen of great potential significance to those studying the evolution of squamates. However, having examined the holotype and other associated specimens from the same assemblage, we conclude that the original interpretation (Simmons 1965) was more nearly correct and that *Fulengia* is the skull of a juvenile prosauropod dinosaur.

LOCALITY AND HORIZON

The specimen was recovered from the Deep Red Sequence of the Lower Lufeng or Fengjiahe Formation (previously the Lower Lufeng Series), at TaTi in Yunnan Province. This horizon was originally interpreted as late Upper Triassic (Young 1946, 1951; Simmons 1965) but there is a recent consensus amongst Chinese workers that it is Lower Jurassic in age (Chen *et al.* 1982; Sun *et al.* 1985; Sun and Cui 1986). Cooper (1982) comes to the same conclusion from faunal evidence.

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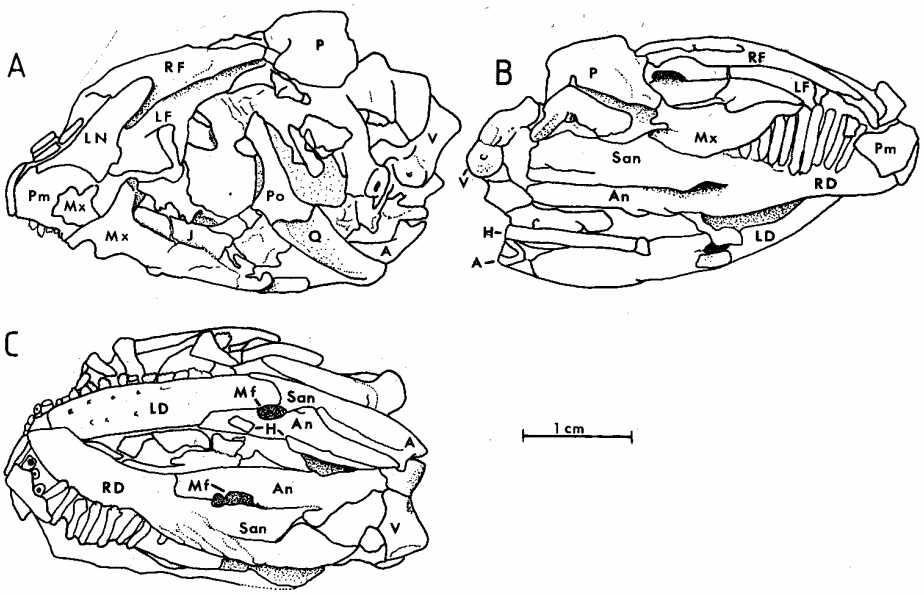


TEXT-FIG. 1. '*Fulengia youngi*', CUP 2037, holotype, in A, left dorsolateral view, B, right ventrolateral view, C, ventral view. Abbreviations: A, articular; An, angular; D, dentary; F, frontal; H, hyoid; J, jugal; L, left; Mf, mandibular fenestra; Mx, maxilla; N, nasal; P, parietal; Pm, premaxilla; Po, postorbital; Q, quadrate; R, right; San, surangular; V, vertebra.

HOLOTYPE SPECIMEN (CUP 2037)

The holotype of *Fulengia* is a small, very mineralized nodule. The specimen comprises a small skull, just under 4 cm long, with a single associated vertebra. Parts of the skull roof, jaws, antorbital, and temporal regions are preserved. In many places, bone junctions are very difficult to identify, particularly where already fragmented bones have been superimposed. No further preparation has been possible. The general outlines of the specimen, as figured by Carroll and Galton (1977, fig. 1) are correct, but we disagree with some aspects of their interpretation (ibid. figs. 1 and 2) with respect to the identification of bones and the position of suture lines (text-fig. 1).

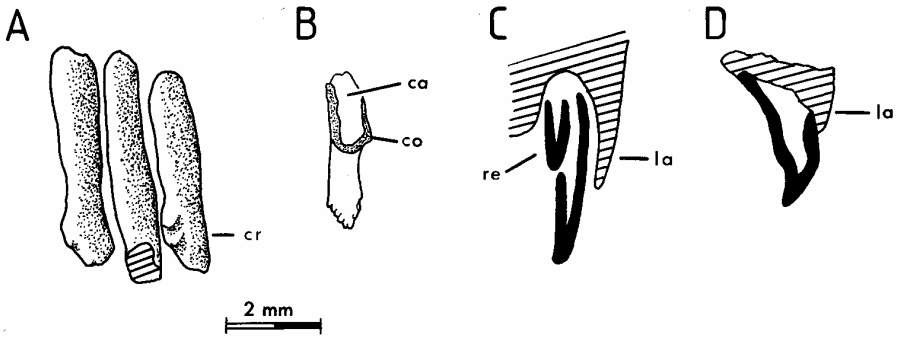
Carroll and Galton (1977) gave six characters which support the hypothesis that *Fulengia* is a lizard:

a, pleurodont teeth with iguanid-like serrations, suggesting an early herbivorous specialization;
b, small lacrimal;
c, absence of a posterior jugal process;
d, configuration of the bones in the temporal region, and the expanded quadrate;
e, median frontal and parietal;
f, association of the above characters with a procoelous vertebra.

These characters bear re-examination:

a. Serrated, pleurodont teeth. The tooth crowns are small, spatulate, and finely serrated, with yellowish enamel. The bases are long and smoothly rounded, as seen where the lateral wall of the maxilla has been broken away on the right side (text-fig. 2A), This is unusual for pleurodont teeth. Iguanid teeth detached from the jaw have a flattened labial surface which is eroded where the tooth contacts the bone (text-fig. 2B, D; Edmund 1969). The smoothly rounded bases accord better with a thecodont implantation (text-fig. 2C) and the spatulate crowns of *Fulengia* resemble most closely those of small contemporary prosauropods (see below).

b. Small lacrimal. As interpreted by Carroll and Galton (1977, fig. 1*a*), *Fulengia* differs from *Kuehneosaurus* and other primitive reptiles in having a reduced lacrimal like that of modern lizards and early sphenodontids. However, their proposed suture line between the lacrimal and maxilla does not exist. The 'small lacrimal' is,



TEXT-FIG. 2. Dentition and tooth implantation. A, maxillary teeth of '*Fulengia*', CUP 2037, in lateral (labial) view; B, maxillary tooth of *Iguana* in labial view; C, cross-section of the thecodont tooth of a crocodile, showing a mature tooth being reabsorbed by a replacement (simplified from Romer 1956, fig. 206*b*); D, cross-section of the pleurodont tooth of an iguanid lizard, *Ctenosaura* (redrawn from Edmund 1969, fig. 10E). Abbreviations: ca, cavity; co, area of contact with jaw; cr, crown; la, labial wall; re, replacement tooth.

in fact, the narrow ascending process of the maxilla (text-fig. 1A) which separates the deep anterior region, shown by the long roots and deep premaxilla (text-fig. 1A), from the shallower posterior section. The shape of the maxilla thus resembles that of the Lufeng prosauropods (text-fig. 4A, B) more closely than that of lizards.

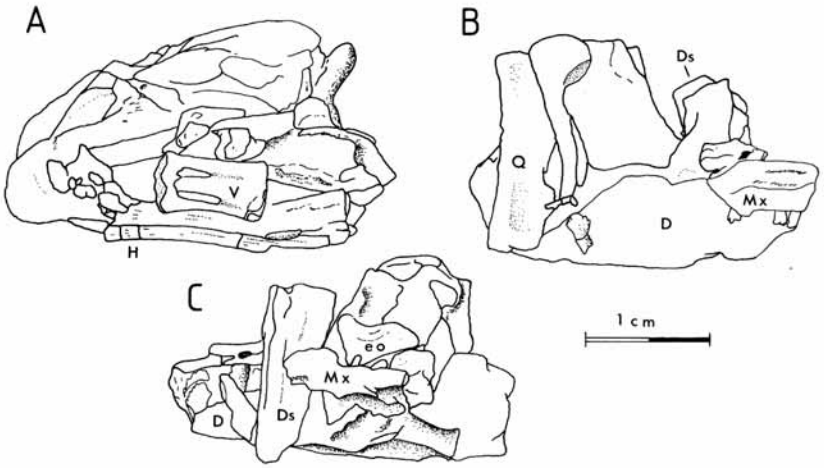
c. Absence of a posterior jugal process. The body of the left jugal is separated from the maxilla by a straight suture (text-fig. 1A). The telescoping of the skull has left the postorbital region unnaturally short and almost certainly carried the jugal further forward than its original position. Dorsally, the jugal is extended into a postorbital process, but ventrally it ends abruptly. Carroll and Galton (1977) interpret this as natural and reconstruct the jugal with a smooth posterior border, but the edge is broken, not smooth. Immediately behind the break, there is a bone fragment which we interpret as the base of a quadratojugal process.

d. Configuration of the bones in the temporal region, and the flared quadrate. The elements identified by Carroll and Galton (1977) as squamosal and supratemporal are bone fragments which, in a telescoped skull, cannot be identified with any assurance. The most obvious bones are the postorbital and the quadrate. The quadrate appears to be short and flared in a manner more closely resembling that of a lepidosaur than an archosaur. However, the dorsal head is obscured by the postorbital and matrix and the proportions may not be as they appear, particularly as a second specimen, CUP 2038*b* (text-fig. 3B), has a quadrate which is similar at its ventral end but more elongate dorsally.

e. Median frontal and parietal. Carroll and Galton (1977, fig. 1*a*, *b*) identify two superimposed plates of bone as the left and right halves of a median frontal bone, but they appear to be separate left and right ossifications (text-fig. 1A, B). The right has a straight medial edge. The parietal region is too distorted for accurate interpretation.

f. Procoelous vertebrae. A single elongated vertebral centrum is preserved in association with the holotype skull (text-fig. 1A–C). One end, to the left, is convex with a small central pit; the other end, to the right, is slightly concave with a central pit. The ventral surface is lightly keeled. There is no neural arch and no evidence to determine which end is anterior and which posterior. The vertebra could as easily be opisthocoelous as procoelous, and, in fact, resembles the axis of *Yunnanosaurus robustus* as figured by Young (1951, pl. 7) (text-fig. 4C).

None of the lizard-like features of CUP 2037 can be confirmed by us. There is no reduced lacrimal, the jugal may possess a posterior process, and the frontals are paired. The temporal region and the parietal(s) are too crushed for interpretation, and the quadrate is incompletely exposed. The dentition and the vertebra are equally or more consistent with identity as a tiny prosauropod dinosaur. This alternative is explored after discussion of CUP 2038.



TEXT-FIG. 3. *Lufengosaurus huenei*, CUP 2038. A, CUP 2038a; B, C, reversed sides of CUP 2038*b*. (NB, CUP 2038 comprises two distinct specimens, here designated *a* and *b* for ease of references.) Abbreviations: D, dentary (larger individual); Ds, dentary (smaller individual); eo, possible exoccipital; H, hyoid; Mx, maxilla; Q, quadrate; V, vertebra.

ADDITIONAL MATERIAL (CUP 2038)

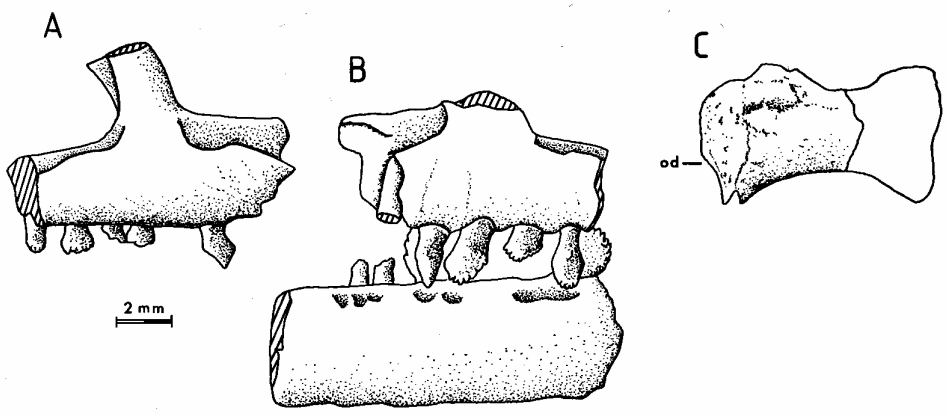
A search through the CUP Lufeng collection yielded two small nodules from TaTi, collected at the same time as the *Fulengia* holotype and placed together under the next catalogue number (2038). Like the holotype, they are catalogued as *Yunnanosaurus huangi*. The specimens resemble *Fulengia* in their size and general preservation (creamish-white and highly mineralized), and may be part of the same accumulation, but the bones are dissociated and represent more than one individual (text-fig. 3). Simmons (1965) suggests that such nodules are coprolitic in origin, but this is uncertain. Much of CUP 2038 is very difficult to interpret. CUP 2038*a* (text-fig. 3A) is a jumble of bone fragments, amongst which only a vertebra and a hyoid element (?ceratobranchial) can be identified with any assurance. CUP 2038*b* is better and includes a quadrate, a possible exoccipital, maxillary fragments, and the dentaries of two different-sized individuals (D and Ds, text-fig. 3B, C). The teeth are identical to those of *Fulengia*, but the jaw fragments show them to be thecodont, as inferred from the holotype. The ventral part of the quadrate is of similar proportions to that of *Fulengia*, but the main body is taller (text-fig. 3B), supporting the interpretation that the quadrate of the holotype is partially obscured.

SYSTEMATIC POSITION AND RECONSTRUCTION

Several aspects of the structure of CUP 2037 identify it as a prosauropod dinosaur.

a. Possession of an antorbital fenestra close to the naris. As described above, the maxilla of CUP 2037 is a long straight bone with a narrow ascending process separating the deep anterior region from the shallow posterior ramus (text-fig. 1A). The posterior border of the ascending process is depressed like that of material referred to *Gyposaurus* (text-fig. 4A, B). There the depression continues on to the surface of the posterior ramus (covered by the jugal in CUP 2037) and borders the antorbital fenestra. The antorbital fenestra is a character of the Archosauria including the Proterosuchidae (Benton 1985, p. 125), and an antorbital fenestra positioned close to the naris is a character of the Archosauria excluding the Proterosuchidae (Benton 1985, p. 126).

b. Thecodont teeth. Within the sauropsid amniotes, this is a character of the Archosauria. The smooth exposed roots of CUP 2037 resemble those of thecodont teeth (text-fig. 2C), not the



TEXT-FIG. 4. A, right maxilla of the prosauropod dinosaur *Lufengosaurus* (*Gyposaurus*) *huenei*, CUP 148-4-2006*a*; B, left maxilla and dentary of *Lufengosaurus* (*Gyposaurus*) *huenei*, CUP 148-4-2006*a*; C, axis vertebra of the prosauropod dinosaur *Yunnanosaurus robustus* (redrawn from Young 1951, pl. 7). (NB, CUP 148-4-2006 comprises five parts representing at least two individuals of different age; CUP 148-4-2006*a* is part of the smaller individual.) Abbreviation: od, odontoid.

attachment faces of the roots of pleurodont teeth (text-fig. 2B, D). CUP 2038 has identical teeth which are certainly thecodont.

c. Mandibular fenestra. Carroll and Galton (1977) noted that the massive jaws of *Fulengia* distinguish it from known lizards; they are more consistent with the deep jaws of prosauropods. In their figures (1977, 1*c*, *e*), Carroll and Galton depict an opening in each mandible at the junction between the dentary, angular and surangular, but do not show such an opening in the reconstruction. These openings are present on both mandibles (text-fig. 1C) and match the structure and position of the small mandibular fenestrae of *Lufengosaurus* (Young 1941*a*). The presence of such mandibular fenestrae is a character of the Archosauria (excluding the Proterosuchidae) (Benton 1985, p. 126).

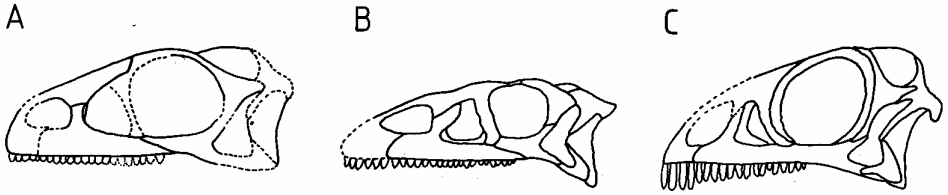
d. Dentition. The spatulate tooth crowns with pointed tips and up to eight serrations per side most closely resemble those of anchisaurid prosauropods (Galton 1985*a*, fig. 5D–H; text-fig. 4). The length of the teeth is also characteristic. Among the herbivorous archosaurs, such deep rooted anterior maxillary teeth are most consistent with the condition found in sauropodomorphs (sauropods and prosauropods).

e. Hyoid skeleton. The robust hyoid elements of CUP 2037 (text-fig. 1B), identified as ceratobranchials by Carroll and Galton (1977, fig. 1), are relatively large for a lizard but correspond to the large ceratobranchials of prosauropods such as *Plateosaurus* (Galton 1985*b*).

The dominant sauropsids of the Lufeng Formation are a group of prosauropod dinosaurs: *Lufengosaurus huenei* (Young 1941*a*); *Gyposaurus sinensis* (Young 1941*b*); *Yunnanosaurus huangi* (Young 1942); *Lufengosaurus magnus* (Young 1947); and *Yunnanosaurus robustus* (Young 1951). All five have been recorded from TaTi (Simmons 1965). They form a size series from the tiny *Gyposaurus sinensis* to the large *Lufengosaurus magnus*. A detailed analysis of the Lufeng material led Rozhdestvensky (1965) to conclude that they form an ontogenetic series of a single species, a view supported by Galton (1976) and Galton and Cluver (1976). The senior name for this species is *Lufengosaurus huenei* and it is placed in the family Anchisauridae (Galton 1985*a*). Cooper (1981) concluded that the Lufeng anchisaurids could be accommodated within the contemporaneous genus *Massospondylus* but has not been followed in this by Galton (1985*a*) who retained the generic name *Lufengosaurus*. Galton (1985*a*), however, split the Lufeng prosauropods into two groups on the basis of dental morphology. *Lufengosaurus* (including *Gyposaurus*) was placed in the

Anchisauridae (defined by possession of denticulate teeth without wear facets). *Yunnanosaurus* formed the basis of a new family Yunnanosauridae (teeth with wear facets but no denticles).

More recently, Z. Yang (= C. C. Young, 1982*a*, *b*) has described some tiny dinosaur jaw fragments from the Lufeng. He placed *Tawasaurus minor* from Heiguopeng (Yang 1982*a*) in the Fabrosauridae and *Dianchongosaurus lufengensis* from Zhangjiawa (Yang 1982*b*) in the Heterodontosauridae. However, Dong (pers. comm. to Sun *et al.* 1985) is sceptical about Yang's attribution of this material to the Ornithischia and we would agree with him. Reference to Yang's figures (1982*a*, pls. 1 and 2; 1982*b*, fig. 2) suggests that both specimens have small serrated teeth which bear a close resemblance to those of *Lufengosaurus* (*Gyposaurus*) and *Fulengia*. It may be that both of Yang's specimens are juvenile prosauropods. The two localities are less than one kilometre from TaTi. Further discussion of the relationships of these specimens is beyond the scope of this work and has no direct bearing on the conclusions outlined below.



TEXT-FIG. 5. A, reconstruction of the skull of '*Fulengia*', CUP 2037, in lateral view; B, lateral view of the skull of the prosauropod *Lufengosaurus huenei* (from Young 1942, fig. 4, and Galton 1985a, fig. 4C); C, lateral view of the skull of the prosauropod *Massospondylus* (simplified from Cooper 1981, fig. 1*a*).

There are no unambiguous character-states supporting the lizard status of *Fulengia* and it may be noted that no further supposed lizards have been identified in the Lufeng fauna (Sun *et al.* 1985). The presence of thecodont teeth, in conjunction with mandibular and antorbital fenestrae, supports the hypothesis that *Fulengia* is an archosaur. In its dental characteristics and in the structure of the maxilla, jugal, and mandible, *Fulengia* most closely resembles the Lufeng prosauropod material referred to *Lufengosaurus* and its junior synonym *Gyposaurus*. Text-fig. 5A shows a new reconstruction of CUP 2037 as a prosauropod, in comparison with *Lufengosaurus* (text-fig. 5B) and *Massospondylus* (text-fig. 5C). It is easily accommodated in Rozhdestvensky's (1965) ontogenetic series and represents a stage slightly younger than that of the smallest specimens of *Gyposaurus sinensis*. We therefore formally propose *Fulengia youngi* to be a junior synonym of *Lufengosaurus huenei*. CUP 2038 (in particular CUP 2038*b*), formerly catalogued as *Yunnanosaurus huangi*, belongs here also. As noted above, Cooper (1981) has proposed that the genus *Lufengosaurus* is a junior synonym of *Massospondylus*. This is a problem beyond the scope of the present paper and does not affect our conclusion with respect to *Fulengia*.

With the reinterpretation of *Fulengia* as a prosauropod, the earliest described lepidosaurs which can be referred unequivocally to the Squamata are from the Upper Jurassic of Europe, North America, and Asia (Evans 1984, 1988; Benton 1985). The earliest known lizard from the People's Republic of China is *Yabeinosaurus* from the Upper Jurassic deposits of Tsaotzushan and Liaoning (Estes 1983).

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