THE UPPER JURASSIC DIAPSID *LISBOASAURUS ESTESI*–A MANIRAPTORAN THEROPOD

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ABSTRACT. *Lisboasaurus estesi* from the Upper Jurassic of Guimarota, Portugal was first described as an anguimorph lizard. Reexamination of the holotype and referred specimens has revealed the presence of thecodont teeth and an antorbital fossa, leading to the conclusion that *L. estesi* represents a small archosaur and not a lizard. Features of the dentition including labio-lingually compressed crowns with unserrated carinae, waisting between the root and the crown, and expanded roots, suggest that *L. estesi* belonged within the troodontid dinosaur–bird clade and, less certainly, within the Avialae (*Archaeopteryx* plus all later birds). It may thus be the earliest avialan. A second species in the genus, *L. mitrocostatus*, is based on indeterminate material and is a *nomen dubium* restricted to the type specimen.

ONE of the most productive localities for Jurassic continental microvertebrates is the lignite mine of Guimarota, near the town of Leiria in Portugal (Kühne 1968). Until recently, the Guimarota lignites were generally interpreted as Lower Kimmeridgian (Upper Jurassic) in age on the basis of the ostracode assemblage (Helmdach 1971*a*, 1971*b*, 1973). However, the plant material suggests a Bathonian to Oxfordian age (Brauckmann 1978), and recent palynostratigraphical studies in the Iberian Peninsula unequivocally support an age not later than Oxfordian for the Guimarota coal seams (Mohr and Schmidt 1988; van Erve and Mohr 1988; Mohr 1989).

The Guimarota lignites are believed to have been laid down in swamps in an upper coastal plain with slight marine influence (Mohr 1989, p. 293). They have yielded a rich assemblage of microvertebrates, including fishes, amphibians, reptiles, and mammals, represented by both dissociated and associated skeletons. Among the lower tetrapods are abundant lizards or lizard-like forms which were described by Seiffert (1973) as scincomorphs (*Saurillus*, *Becklesisaurus*), an anguimorph (*Introrsisaurus*), and a new atypical anguimorph which Seiffert called *Lisboasaurus* and which he suggested might be an aigialosaur/mosasaur relative. As described, *Lisboasaurus* was represented by a small number of jaw fragments and isolated teeth which Seiffert divided between the type species *L. estesi* and a referred species *L. mitrocostatus*. Estes (1983, pp. 116, 118, 133) reassessed all Seiffert's taxa, transferring the Guimarota *Saurillus* and *Becklesisaurus* species to the new genera *Saurillodon* and *Becklesius* respectively; and transferring *Introrsisaurus* to the anguimorph genus *Dorsetisaurus*. Estes (1983, p. 193) removed *Lisboasaurus* from the Anguimorpha and categorized it as Lacertilia *incertae sedis*, with the comment that the holotype maxilla of *L. estesi* had some similarities to those of saurischian dinosaurs.

One of the authors (S.E.E.) has recently reexamined all the material of both species of *Lisboasaurus* in the collections of the Freie Universität, Berlin (= FUB), and the following redescription elaborates on the conclusions of Estes (1983).

SYSTEMATIC PALAEONTOLOGY

Superorder ARCHOSAURIA Osborn, 1902
Order SAURISCHIA Seeley, 1888
Suborder THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
MANIRAPTORA Gauthier, 1986
?AVIALAE Gauthier, 1986 *incertae sedis*
Genus *Lisboasaurus* Seiffert 1973

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Type species. L. estesi Seiffert 1973.

Diagnosis. A small relative of troodontids and *Archaeopteryx* with the following characters: maxilla bearing large pit or diastema in the anterior tooth-row; maxilla with antorbital fossa, but with accessory antorbital fenestra absent or posteriorly placed; maxilla with slender dorsal process excluded from narial margin by tall ascending process of premaxilla; teeth with mediolaterally compressed triangular crowns with lingual groove, expanded roots wider than crowns and with 'waist' between crown and root; teeth with anterior and posterior carinae but no serrations.

Lisboasaurus estesi Seiffert, 1973

Text-figures 1–3.

1973 *Lisboasaurus estesi* Seiffert p. 33, fig. 27.
1983 *Lisboasaurus estesi* Seiffert; Estes p. 193, fig. 54A.

Holotype. FUB Gui.37, a nearly complete right maxilla about 22 mm long and bearing one tooth (Text-figs 1, 2A–D). Subsequent to the reexamination by S.E.E., and prior to photography, the holotype specimen was cleaned of residual matrix and apparently suffered damage to the wall of the antorbital fossa and the posterior end of the tooth-row. The photographs in Text-figure 1 depict it in this condition, while Text-figure 2A–C depicts the lost regions with broken lines.

Diagnosis. As for genus, this being the only valid species.

Locality and horizon. Guimarota lignite mine, 1·5 km SSE of Leiria, Portugal; Guimarota complex of lignitic marls, Oxfordian, Upper Jurassic.

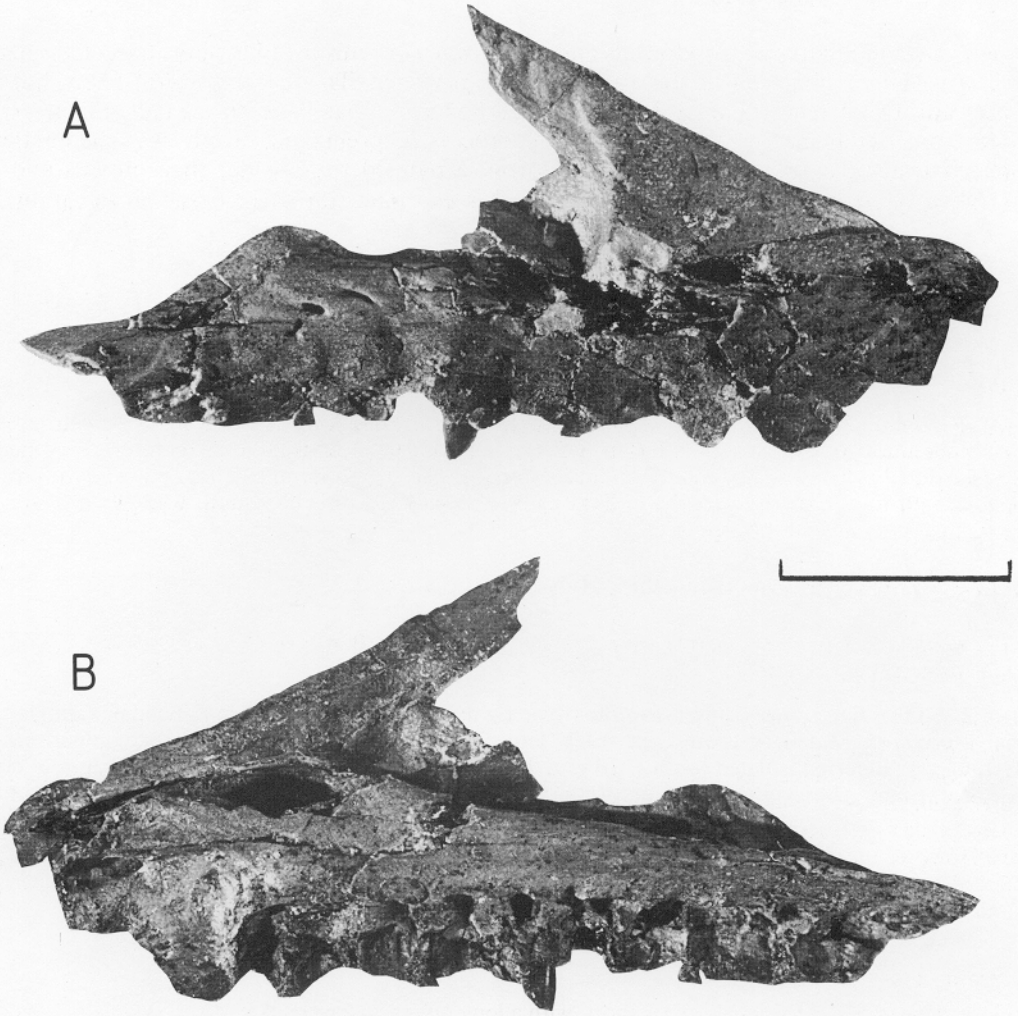
Referred material. A larger left maxilla (FUB field batch no. Jun. 81:13:1; Text-fig. 3A–C) and several isolated teeth (including FUB Gui.L.136, Text-fig. 2E–F) are the only specimens that can certainly be referred here.

In addition to the above jaw material of *L. estesi*, Seiffert referred to it two small blocks containing associated skull and postcranial material (FUB Gui.L.33 and L.177). The preservation of this material is very poor. On the basis of these specimens, Seiffert stated that *Lisboasaurus* had procoelous vertebrae and fused frontals. However there is nothing on these blocks to link them positively with either the holotype maxilla or the referred teeth, and they are not treated as part of the hypodigm of *L. estesi* in the following description and discussion.

Description

The holotype maxilla (Text-figs 1, 2A–C) is short, with a long obliquely-sloping anterior border which is faceted and therefore did not enter the border of the external naris. The presence of a tall ascending process on the premaxilla is implied. The dorsal process of the maxilla is slender and probably only contacted the nasal weakly. The anterior tip of the maxilla is eroded, but there is no evidence that it bore a premaxillary process extending below the naris. The surface of the bone is excavated laterally to give a smooth-walled depression. Seiffert (1973) described this as an anteriorly shifted prefrontal facet, but it is too smooth to be a facet and is the antorbital fossa as noted by Estes (1983). The depression had a thin medial wall (lost after recent preparation), but its borders were damaged so that the shape of the fenestra, which must have lain further back, cannot be reconstructed. No accessory fenestrae are visible in the preserved portion of the fossa wall. Medially this part of the maxilla bears another, shallower depression (Text-fig. 2B) which could be part of a maxillary sinus. This sinus occurs in a comparable position in the maxilla of *Troodon* (Text-fig. 4).

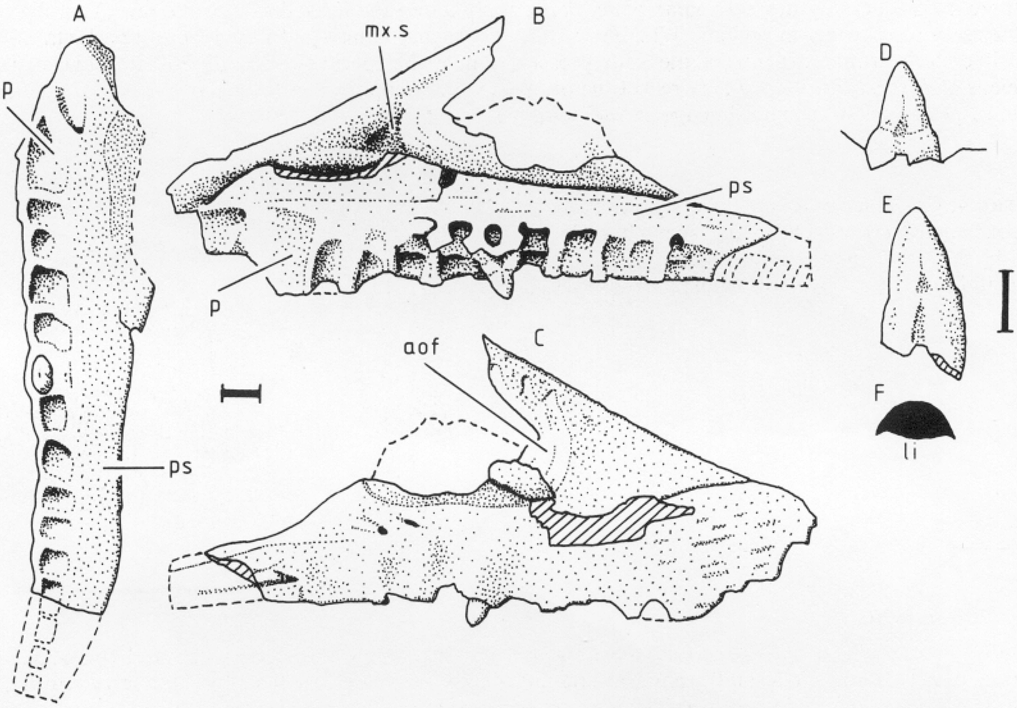
In the holotype maxilla, the dorsal process is separated from the alveolar region by a broad palatal shelf, widest anteriorly, although the medial edge is broken (Text-fig. 2A). Below it, the teeth sat in a deep groove, separated from one another by low ridges of interdental bone. There are spaces for about 13–14 teeth, but the maxilla may be incomplete posteriorly. One tooth is preserved intact (Text-fig. 2D) and its shape, unique in the context of known Jurassic microvertebrates, can be matched by a further set of isolated teeth (e.g. FUB Gui.L.136 in Text-figure 2E). The teeth have mediolaterally compressed triangular crowns with anterior and posterior carinae. The labial surface is more rounded than the lingual one so that, in cross-section (Text-fig. 2F), the carinae appear to curve lingually. There are no serrations. The lingual surface is marked by a basal



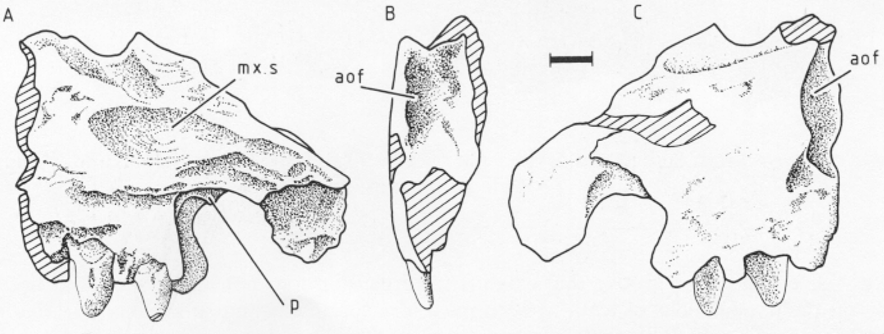
TEXT-FIG. 1. *Lisboasaurus estesi* Seiffert, holotype right maxilla FUB Gui. 37 in A, labial, and B, lingual aspects. Scale bar, 5 mm.

pit which gives rise to a shallow groove that extends towards, but does not reach, the tooth tip. The groove is visible only on the lingual sides of teeth in both maxillary specimens and so the lingual–labial orientation of isolated teeth is not in doubt. The crown is supported by an expanded root which is broader than the crown and there is a clear 'waist' between the two. In the holotype, the root is just visible in the sole preserved tooth which appears to be a partly erupted replacement tooth. This tooth is held in place by a low lingual wall of bone which may represent either a remnant of the alveolar wall or a weak development of this feature. Thus the implantation is thecodont. The expansion of the roots suggests that the roots fully enclosed the replacing teeth.

At the anterior end of the tooth-row of the holotype maxilla, there is a large pit, subdivided into two parts. The smaller anterodorsal section receives the opening of the superior alveolar canal (also visible in the maxilla of *Troodon*, Text-fig. 4). The larger pit is more problematical. It is too smooth to be a facet, or a socket for a large upper caniniform tooth (as suggested by Seiffert 1973 and Estes 1983). It appears to be a true diastema, probably a recess for reception of a lower caniniform tooth.

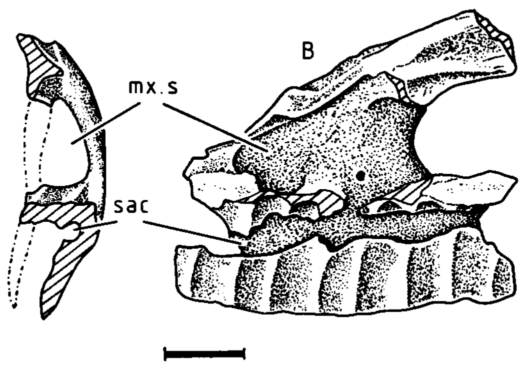


TEXT-FIG. 2. *Lisboasaurus estesi* Seiffert. A–C, holotype right maxilla FUB Gui.37 in A, palatal, B, lingual, and C, labial aspects. D, Maxillary tooth from FUB Gui.37 in lingual aspect (inverted for comparison with Gui.L.136). E, F, Referred isolated tooth FUB Gui.L.136 in E, lingual aspect, and F, cross-section of crown. All scale bars, 1 mm. Abbreviations: aof, antorbital fossa; li, lingual, mx.s, possible maxillary sinus; p, anterior pit; ps, palatal shelf.



TEXT-FIG. 3. *Lisboasaurus estesi* Seiffert, referred left maxilla (FUB field batch no. Jun. 81:13:1) in A, lingual aspect, B, posterior view into anterior wall of antorbital fossa, and C, labial aspect. Scale bar, 1 mm. Abbreviations as in Text-figure 2.

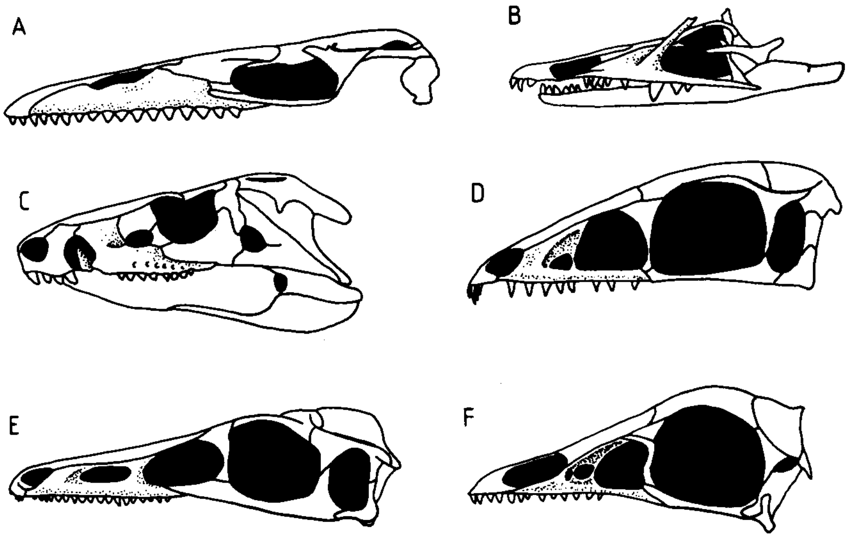
A search through uncatalogued FUB material from Guimarota yielded a second incomplete maxilla (field batch no. Jun. 81:13:1) – a left element somewhat larger than the holotype specimen. This specimen (Text-fig. 3A–C) confirms most features of the holotype – antorbital fossa (Text-fig. 3B–C), maxillary sinus (Text-fig. 3A), anterior pit (Text-fig. 3A), tooth shape and thecodont implantation – and suggests that the holotype maxilla belonged to a juvenile. The thin outer wall of the anterior pit has broken away to give the appearance of a large notch in the tooth-row (Text-fig. 3C). This referred specimen differs from the holotype in one respect, namely that there is considerably more alveolar bone, particularly along the lingual side of the jaw (Text-fig. 3A) so that the teeth are entirely in sockets. Whether or not this lingual bone was formed from interdental plates is impossible to determine because of the poor preservation of the specimen. The difference between the two specimens of *Lisboasaurus estesi* may reflect the ontogenetic development of the alveolar wall or could simply be due to greater post-mortem damage to the holotype.



TEXT-FIG. 4. *Troodon formosus* Leidy, right maxilla in A, reconstructed cross-section (redrawn after Currie 1985, fig. 2) and B, lingual aspect. Scale bar, 10 mm. Abbreviations: mx.s, maxillary sinus; s.a.c., superior alveolar canal.

Systematic position

The holotype maxilla of *L. estesi*, with its long ascending process, antorbital fossa and thecodont tooth insertion, clearly belongs to a small archosaur and not a lepidosaur (see Text-figure 5A for a mosasaur maxilla). Resemblances can be found to the maxillae of several groups of archosaurs with small Jurassic representatives, notably pterosaurs, primitive crocodylomorphs and higher maniraptoran theropods (troodontids and birds). Because the specimens are small and plausibly juvenile, they probably lack the allometric features of larger archosaurs of different groups and tend to have a phenetic resemblance to primitive pterosaurs and primitive crocodylomorphs, most of which occurred significantly earlier than *Lisboasaurus*.



TEXT-FIG. 5. Lateral views of the skulls of A, the mosasaur *Clidastes*; B, the pterosaur *Preondactylus*; C, the crocodylomorph *Protosuchus*; D, the theropod *Compsognathus*; E, the troodontid *Saurornithoides*; and, F, *Archaeopteryx*. (Drawings after A, Russell 1967; B, Wild 1983; C, Crompton and Smith 1980; D, Ostrom 1978; E, Russell 1969; F, Wellnhofer 1974.)

Pterosauria. The maxilla of *L. estesi* resembles that of some rhamphorhynchoid pterosaurs (e.g. the Norian *Preondactylus* Wild 1983) in its long anterodorsal process and the possible presence of a caniniform tooth (Text-fig. 5B). However in rhamphorhynchoids, the caniniform tooth is not at the anterior end of the toothrow, but in the middle, and is separated from the tip of the bone by a long slender process bearing a further series of small teeth. This does not appear to be the condition in *L. estesi*. There are further differences. In *Lisboasaurus*, the dorsal process is faceted and was probably excluded from the narial margin, unlike that of any described rhamphorhynchoid, although the character is present in pteranodonts. The rhamphorhynchoid maxilla is slender and lightly-built and it lacks an antorbital fossa set in the front of the fenestra. Tooth shape also differs; pterosaurs do not have the combination of waisted teeth and sharply expanded roots. One Upper Jurassic genus, *Germanodactylus*, does have teeth with short triangular crowns each with a groove running down one side (Wellnhofer 1970, pl. 10, fig. 2, and D. M. Unwin pers. comm.) but the groove is labial, not lingual as in *Lisboasaurus*, and the maxilla of *Germanodactylus* is of very different shape. In conclusion, *Lisboasaurus* might be an aberrant pterosaur, but as will be argued below, its total suite of characters suggest a closer resemblance to another group.

Crocodylomorph and avialan teeth. Martin *et al.* (1980) and Martin (1983*b*) noted the resemblance of crocodile and Mesozoic bird teeth and suggested that they indicated immediate relationship. Most other workers accept the characters but treat them as convergent (e.g. Gauthier 1986). The teeth of *Lisboasaurus estesi* bear a distinct resemblance to the crocodile-Mesozoic bird tooth type in that they possess expanded roots, waists, and non-serrate carinae. The only group in which these teeth occur in combination with a large antorbital fenestra, are the primitive crocodylomorphs of the sphenosuchian grade and the higher maniraptoran theropod dinosaurs of the Troodontidae and Avialae (birds and relatives).

Crocodylomorpha. At least four genera of crocodile are known from Guimarota, comprising *Machimosaurus*, *Goniopholis*, a *Theriosuchus*-like form, and a *Bernissartia*-like form (Brinkmann 1989). All are typical crocodylomorphs in that they have very reduced or no antorbital fenestrae, and are thus distinct from *Lisboasaurus*. However, members of the primitive pre-crocodyliform grade of crocodiles retain a relatively large fenestra. Most of these are Upper Triassic or Liassic in age, but one, *Hallopus victor*, is from the Upper Jurassic of Colorado (Walker 1970) and hence contemporaneous with *Lisboasaurus*. The only specimen of *Hallopus* lacks cranial material, so comparison must be made with Upper Triassic and Liassic genera. Unfortunately, most of these are represented by specimens which are considerably larger than *Lisboasaurus* and so comparisons of shape are difficult.

The recent evaluation of primitive crocodylomorph relationships by Benton and Clark (1988) places the well-characterized primitive crocodylomorphs in two grades. The basal grade includes *Saltoposuchus* (= *Terrestrisuchus* of Crush 1984). The '*Terrestrisuchus*' material described by Crush (1984) has a much more elongate maxilla than *Lisboasaurus* with an anteroposteriorly long dorsal ramus. The teeth of *Terrestrisuchus* are flattened like those of *Lisboasaurus* but are recurved and serrated. Neither maxilla nor teeth of *Terrestrisuchus* could be confused with *Lisboasaurus* material.

Slightly more advanced crocodylomorphs include the sphenosuchids *Sphenosuchus* and *Hesperosuchus* and the aberrant *Platyognathus*. *Sphenosuchus* and *Hesperosuchus* have teeth with compressed lanceolate crowns, waists and cylindrical roots (Walker 1970, p. 348, fig. 12) which resemble those of *Lisboasaurus*. The teeth of *Sphenosuchus* are serrated, while *Platyognathus* has unique recurved teeth with a polygonal cross-section and a serrated posterior edge (Simmons 1965, pp. 35, 39–40). Unlike *Lisboasaurus*, these Triasso-Liassic forms possess a maxilla with an anteroposteriorly long dorsal process and a posteriorly set fossa associated with the elongate anterior muzzle. *Sphenosuchus* and *Platyognathus* both possess a large anterior mandibular fang which fits into a deep notch in the upper jaw, but in both genera, the notch is at the premaxilla–maxilla junction and not a pocket within the maxilla as in *Lisboasaurus*. This condition is shown well in the more advanced *Protosuchus* (Text-fig. 5C), as described by Crompton and Smith (1980). Thus the teeth of *Lisboasaurus* share some characteristics with those of early crocodylomorphs, but the maxilla shows no special similarity.

Maniraptoran Theropoda. The term Maniraptora was created by Gauthier (1986, p. 30) to define a clade of bird-like theropod dinosaurs and birds. The group, as defined by Gauthier, comprises *Compsognathus* and several minor 'coelurosaurs', the families Caenagnathidae, Elmisauridae, Dromaeosauridae, Troodontidae, and the Avialae (*Archaeopteryx* and all birds). Gauthier (1986) suggested that the Deinonychosauria (Dromaeosauridae + Troodontidae) were the sister-group of the Avialae, but Currie (1987) has argued that the Troodontidae alone are the immediate sister-group of the Avialae, and noted some derived characters which the two groups share uniquely within the Theropoda. The characters of *Lisboasaurus* relate largely to the troodontid-avialan clade which at present has no name. For the purposes of this discussion, the Troodontidae is taken to comprise the genera *Troodon* (= *Stenonychosaurus*, *Pectinodon*), *Saurornithoides*, and *Borogovia* (for recent reviews, see Currie 1987 and Osmólska 1987). All these genera are from the Upper Cretaceous, but if Currie (1987) is correct in arguing that the troodontids are the sister-group to the Avialae then there must have been at least stem-troodontids in the Upper Jurassic, contemporaneous with *Archaeopteryx*.

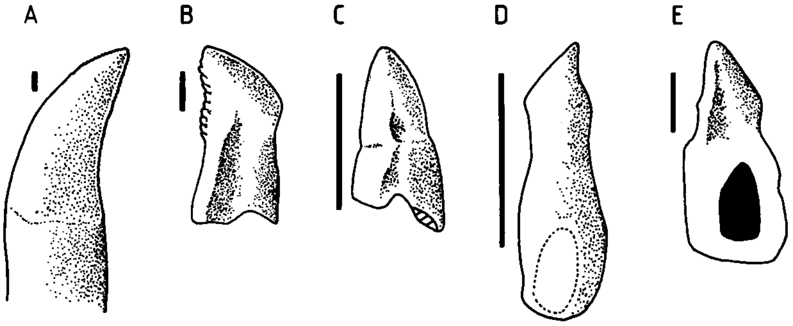
The maxilla of *Lisboasaurus* is very similar in shape to those of small maniraptorans, such as *Compsognathus* (Text-fig. 5D) and *Archaeopteryx* (Text-fig. 5F). As noted in the description, the anterior maxillary teeth of *Lisboasaurus* have compressed asymmetrical cross-section with rounded labial and flattened lingual surfaces and the carinae on the lingual corners. Currie (1987, p. 77) noted this to be a character of the premaxillary teeth of theropods, and it would not be surprising if it extended to the anterior maxillary teeth. Compressed asymmetrical crowns of this type also occur in *Archaeopteryx* (Howgate 1984*b*, p. 656), but carinae are not visible (P. Wellnhofer pers. comm.). The following characters are discussed in the context of the Maniraptora. The condition in troodontids is taken from Currie (1987) and the condition in *Archaeopteryx* is taken from Howgate 1984*a*, *b*, and Wellnhofer (pers. comm.).

The following derived character is shared by troodontids, *Archaeopteryx*, and *Lisboasaurus*.

A. Teeth with constriction between crown and root (Text-fig. 6B–E *contra* the primitive theropod condition, e.g. *Megalosaurus* in Text-fig. 6A).

The following derived character is shared by *Archaeopteryx* and *Lisboasaurus*, but not troodontids.

B. Teeth completely unserrated (Text-fig. 6C–D; Gauthier 1986, p. 12).



TEXT-FIG. 6. Archosaur teeth in lingual aspect. A, *Megalosaurus bucklandi* (original from mandible of holotype, British Museum (Natural History) R.332; serrations present but not visible at this scale); B, *Troodon* (after Currie 1987); C, *Lisboasaurus*; D, *Archaeopteryx* (after Howgate 1984*b*); E, hesperornithid (after Martin 1983*a*). Scale bars, 10 mm (A) and 1 mm (B–E).

Compsognathus lacks serrations on the premaxilla and anterior dentary teeth, but these teeth are recurved, slender-crowned, and also lack carinae. The maxillary teeth of *Compsognathus* have carinae, the posterior carina being serrated (Ostrom 1978). (*Archaeopteryx* and *Lisboasaurus* also share some primitive features *contra* troodontids. They appear to retain a maxillary tooth count of 12–15, whereas troodontids have 19–20 maxillary teeth, but the latter is probably the derived condition. Unlike troodontids, both *Archaeopteryx* and *Lisboasaurus* retain the antorbital fossa, but Gauthier (1986) described this character state as primitive for archosaurs.)

The following derived character is shared by *Lisboasaurus* and troodontids but is not known in *Archaeopteryx*.

C. Maxillary teeth each have a depression at the base of the lingual side of crown which extends as a groove towards the crown tip but does not reach it (Text-fig. 6B–C).

(There are other differences of uncertain polarity in the shape of the crowns, those of *Archaeopteryx* being more recurved (Howgate 1984*a*, *b*) than those of *Lisboasaurus*.)

The following derived characters are shared by *Lisboasaurus* and the Ornithurae (post-*Archaeopteryx* birds), but not troodontids or *Archaeopteryx*.

D1. Maxilla separated from naris by processes of premaxilla and nasal.

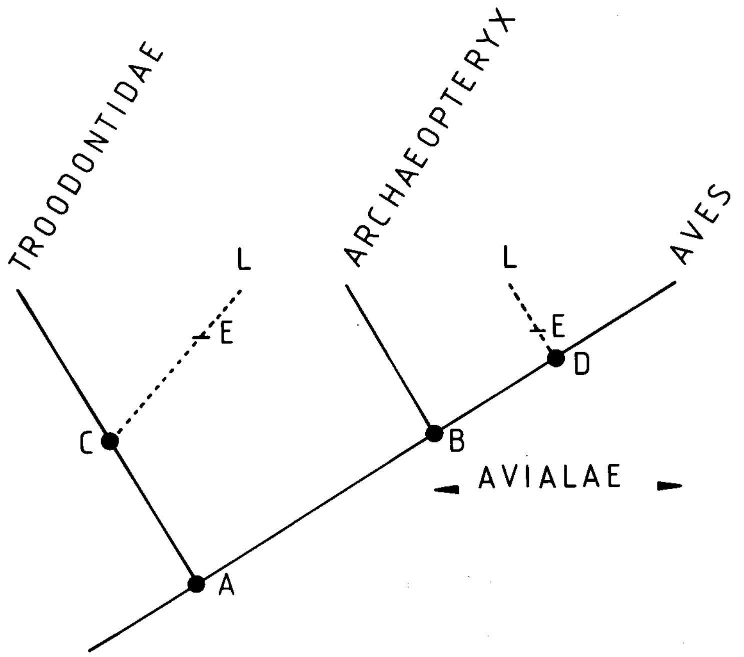
In *Archaeopteryx*, unlike *Lisboasaurus*, the anterodorsal process of the premaxilla is shorter and reconstructions show the maxilla entering the narial margin, a typical saurischian condition (Howgate 1984*a*). Gauthier (1986, p. 15) notes that exclusion of the maxilla from the naris occurs as the primitive thecodontian condition, is lost in Saurischia, but appears as a reversal in ornithomimids and ornithurine (post-*Archaeopteryx*) birds.

D2. Teeth with root wider than crown (Text-fig. 6C, E; Gauthier 1986, p. 12).

The following derived character occurs in *Lisboasaurus* but not in troodontids or *Archaeopteryx*.

E. Large pocket or diastema near anterior end of maxilla suggesting presence of a lower caniniform tooth.

Relationships. If *Lisboasaurus estesi* is a maniraptoran theropod, then character A places it in the troodontid-avialan clade, B places it within the Avialae, while in contradiction, C places it within the Troodontidae. D1 and D2 are weak (because variable) characters which suggest a post-*Archaeopteryx* position in the Avialae and E is a unique character in the context of a troodontid-avialan clade and serves as a defining autapomorphy for *Lisboasaurus*. Text-fig. 7 depicts the alternative relationships of *Lisboasaurus* suggested by these characters. This character distribution suggests that *Lisboasaurus* is a member of the troodontid-avialan clade and could be a primitive avialan. The implications and qualifications to this systematic position are discussed below in the discussion section.



TEXT-FIG. 7. Cladogram depicting the possible relationships of *Lisboasaurus* to troodontid dinosaurs, *Archaeopteryx*, and Aves. Character-states A–E are those described in the text. Abbreviation: L, *Lisboasaurus*.

A NOTE ON '*LISBOASAURUS*' *MITROCOSTATUS*

The material which forms the basis of this species is more problematical than that of *L. estesi*. The holotype dentary (FUB Gui.34) is crushed, but appears to show a type of thecodont implantation essentially similar to that of *L. estesi*. The external surface of this dentary bears a pattern of striate sculpture which is unlike that of any lizard (Estes 1983). Some of the referred teeth resemble those of *L. estesi* but have a short rounded crown (e.g. FUB Gui.L.67). Others, however, have a longer pointed crown (e.g. FUB Gui.18 and 24). This variation suggests that more than one taxon may be represented – a possibility recognized by Seiffert (1970), when he divided the *L. mitrocostatus* material into two subspecies. Estes (1983) suggested that at least some of the *L. mitrocostatus* material might be referrable to the genus *Cteniogenys* which is also known from Guimarota (Seiffert 1973, pp. 13–17). *Cteniogenys* was originally described as a lizard but has recently been shown to be an early choristodere (Evans 1989, 1990). Although superficially similar, the striations on the jaw of *Cteniogenys* are created by a double row of sensory foramina, not the rather irregular sculpturing seen in the *L. mitrocostatus* holotype. The teeth and their mode of implantation are also different, and reference to *Cteniogenys* is highly unlikely. The *L. mitrocostatus* material is too limited to permit firm conclusions, but we agree with Estes (1983) that there is no certainty that the two species are congeneric. In conclusion '*Lisboasaurus*' *mitrocostatus* is, at present, a *nomen dubium* restricted to the holotype dentary, which is not sufficiently determinate to be associated with *L. estesi*, but certainly does not belong to *Cteniogenys* or a true lizard.

DISCUSSION

This study commenced as an assessment of the lacertilian status of *Lisboasaurus estesi*, and the unequivocal conclusion is that the *L. estesi* material is not lacertilian but represents a small archosaur. Our further conclusions must, of necessity, be circumspect for two reasons. The first is the limited nature of the material. Maxillae and teeth can only bear a restricted set of characters and some of these occur convergently in more than one group of small archosaurs. The resemblances of crocodile and Mesozoic bird teeth noted by Martin *et al.* (1980) and Martin (1983*a*, *b*) are generally agreed to be due to convergence (e.g. Gauthier 1986) but are clearly a source of uncertainty when limited material such as *Lisboasaurus* is being studied. However, parsimonious treatment of the available restricted suite of characters does lead to a position in the troodontid-avialan clade with no character contradictions. A less certain parsimonious conclusion, because there is contradiction, is the position within the avialan clade.

A second reason for circumspection is that the early evolution of birds is both poorly known and subject to intense speculation. An Oxfordian relative of *Archaeopteryx* might be the earliest known bird, and yet there is nothing in the morphology of the *Lisboasaurus* fragments that has any bearing on the origin of birds or bird flight. It does, however, serve as a reminder that *Archaeopteryx* was probably only one of an array of similar smaller forms, including stem-troodontids. It is likely that most Jurassic microvertebrate assemblages will prove to contain maniraptoran material which cannot be securely identified as avian or non-avian, the recently described material from the late Jurassic Uncompahgre Formation of Colorado being a case in point (Jensen and Padian 1989). A more precise systematic position for *Lisboasaurus* must await the identification and description of further material from Guimarota.

It would not be too surprising if *Lisboasaurus estesi* were an *Archaeopteryx*-grade maniraptoran. The Solnhofen Limestone represents a coral lagoon floor of Lower Tithonian age (*circa* 150 Ma) in southern Germany. The Guimarota lignite represents a coastal swamp of probable Oxfordian age (*circa* 160 Ma) in Portugal. The two localities are about 1500 km apart and may have been about 1200 km apart in the Jurassic. The presence of similar proto-birds in two contemporaneous continental-coastal localities 1200 km apart within one continent could reasonably be expected.

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