

Early development of the facial region in a non-avian theropod dinosaur

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An isolated maxilla of the theropod dinosaur *Allosaurus* from the Late Jurassic (the Kimmeridgian, 153 million years ago) of Portugal is the first cranial remain of a non-coelurosaurian theropod hatchling reported so far, and sheds new light on the early cranial development of non-avian theropods. *Allosaurus* hatchlings seem to have been one-seventh or less of the adult length and are thus comparable in relative size to hatchlings of large extant crocodile species, but are unlike the relatively larger hatchlings in coelurosaurs. The snout experienced considerable positive allometry and an increase in tooth count during early development. The element is especially noteworthy for the abundant and well-developed features associated with the paranasal pneumatic system. Pneumatic structures present include all those found in adult allosaurids and most are even more developed than in adult skulls. Together with evidence on the ontogeny of the tympanic pneumatic system in allosaurids, these findings demonstrate that cranial pneumaticity developed early in theropod ontogeny. The strong development of pneumatic features in early ontogenetic stages of non-avian theropods supports the hypothesis that pneumatization of cranial bones was opportunistic and indicates that heterochrony played an important role in the evolution of craniofacial pneumaticity in this group.

Keywords: Theropoda; *Allosaurus*; ontogeny; craniofacial pneumaticity; heterochrony

1. INTRODUCTION

Non-avian theropod dinosaurs are an important component of Mesozoic terrestrial ecosystems (251–65 million years ago) and have received considerable interest in recent years due to their role as ancestors to birds. However, many aspects of theropod biology and evolution remain poorly understood. This is the case particularly for theropod ontogeny, especially their early development. Despite several recent finds of embryonic or hatchling theropods (Norell *et al.* 1994, 2001; Cohen *et al.* 1995; Mateus *et al.* 1997; Dal Sasso & Signore 1998; Carpenter 1999; Varricchio *et al.* 2002), few studies of ontogenetic changes and developmental mechanisms in theropods have been carried out. Furthermore, most studies dealing with theropod ontogeny have focused on growth, as implied by bone histology (Chinsamy & Elzanowski 2001; Erickson *et al.* 2001; Padian *et al.* 2001, 2004; Ricqlès *et al.* 2001), and accounts of the ontogenetic development of skeletal structures have concentrated on postcranial elements (Dal Sasso & Signore 1998; Varricchio *et al.* 2002). Thus, little is known about the early development of theropod skulls. The only detailed study of cranial ontogeny of non-avian theropods concerns the development of tyrannosaurid skulls (Carr 1999), with the size of the skulls studied ranging from approximately 50% of the adult skull length to fully adult skulls and, thus, covers only late ontogenetic changes in these animals.

The Upper Jurassic locality of Guimarota, Portugal, famous for its abundant and well-preserved microvertebrates (Martin & Krebs 2000), has yielded a small left theropod maxilla of 23 mm total length. This specimen, which represents the first non-coelurosaurian theropod

hatchling skull remain reported so far, is described and its implications for our understanding of the early development of theropod cranial features, especially craniofacial pneumaticity, are discussed here.

2. DESCRIPTION

The element (Institut für Geologische Wissenschaften der FU Berlin, Fachbereich Paläontologie IPFUB Gui Th 4) is well preserved and almost complete, only missing minor parts at the anterior end (figure 1). The maxillary body is low and short relative to the total height of the bone. The ascending process of the maxilla is considerably higher than the maxillary body and has a steeply sloping anterior and a vertical posterior border. The latter defines the anterior margin of a large and obviously high, but short, antorbital fenestra. A well-developed maxillary antorbital fossa is present. Its ventral border is placed at approximately half the height of the subantorbital maxillary body and marked by a notable step, whereas the anterior border along the anterior edge of the ascending process is developed as a bony lamina that slightly overhangs the fossa; the dorsal part of this lamina is broken. A roughly trapezoidal maxillary fenestra is present in the base of the ascending process. The fenestra is very large, being approximately twice as wide as the pila interfenestralis and approximately 18% of the length of the maxilla. Anteroventral to this fenestra, and separated from it by a thin but stout bridge of bone, lies the much smaller, triangular promaxillary foramen in the anteroventral corner of the maxillary antorbital fossa. The margins of both fenestrae are original and not broken, with the exception of a small portion of the pila interfenestralis reconstructed in figure 1c. Dorsal to the maxillary fenestra, a large excavatio pneumatica, of which the

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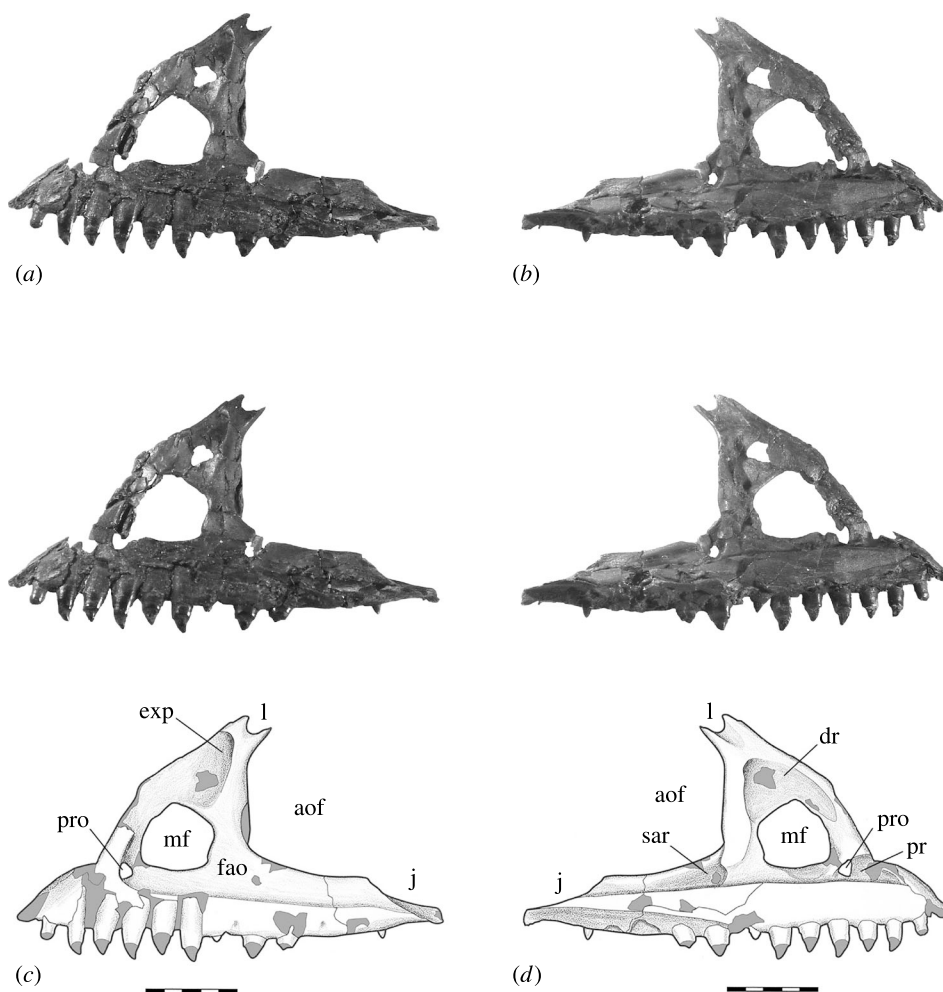


Figure 1. Hatchling allosaurid maxilla (IPFUB Gui Th 4) from the Late Jurassic of Portugal: (a) and (c) lateral view, (b) medial view; (a) and (b) are stereopairs. Shaded sections in (c) and (d) are the damaged areas of the maxilla. Scale bars are 5 mm. aof, antorbital fenestra; dr, dorsal recess; exp, excavatio pneumatica; fao, fossa antorbitalis; j, facet for contact with jugal; l, facet for contact with lacrimal; mf, maxillary fenestra; pr, promaxillary recess; pro, proamxillary fenestra; sar, subantorbital recess.

posterodorsal part is especially sharply defined, is present on the dorsal part of the ascending process (figures 1*a,c*).

From the medial view the alveolar border is thickened, though the thickened area becomes posteriorly narrower (figures 1*b,d*). Interdental plates delimiting the alveoli medially seem to have been present but are poorly preserved; anteriorly, these elements seem to have been largely fused. Several large recesses are present on the medial side. The promaxillary foramen leads into a large triangular fossa that extends from the anteroventral part of the ascending process's base to the anterodorsal section of the maxillary body above the alveolar border. This recess is separated from a small fossa below the anterior part of the maxillary fenestra by a raised bony ridge. A further large, triangular fossa extends dorsally from the maxillary fenestra onto the dorsal part of the ascending process. Finally, a well-developed fossa is also present dorsally above the alveolar border behind the ascending process and becomes posteriorly shallower. Whereas the posterior border of the ascending process is thickened medially, there is a small indentation between this border and the thickened alveolar border through which the posterior recess communicates with the area of the maxillary fenestra.

The contacts with the jugal and the lacrimal are preserved in exquisite detail. The jugal facet is represented by an oblique groove in the posterior end of the maxillary

body, the lateral border of which is more steeply inclined than the medial border. The facet for the anterodorsal ramus of the lacrimal is represented by a saddle-shaped indentation in the dorsal extremity of the ascending process of the maxilla. Medially, a small groove extends from this facet anteroventrally, and its posterior border is thickened to form an oblique ridge.

Thirteen alveoli are present in the maxilla. The teeth in the second to the seventh and the ninth and tenth alveoli seem to represent the same tooth generation; a clear replacement tooth is only present in the eighth alveolus. All tooth crowns are strongly damaged and only the dentine cores of the tips are present, so details of tooth morphology cannot be established.

3. DISCUSSION

(a) *Taxonomic identification and ontogenetic stage*

The presence of both a promaxillary and maxillary fenestra, and the obviously entirely antorbital tooth row, clearly indicates tetanuran relationships for IPFUB Gui Th 4 (Rauhut 2003). Within tetanurans, an excavatio pneumatica on the ascending ramus of the maxilla is only found in sinraptorids and allosaurids within the Allosaurioidea (Witmer 1997a). The element lacks the sinraptorid apomorphies of a greatly enlarged promaxillary fenestra

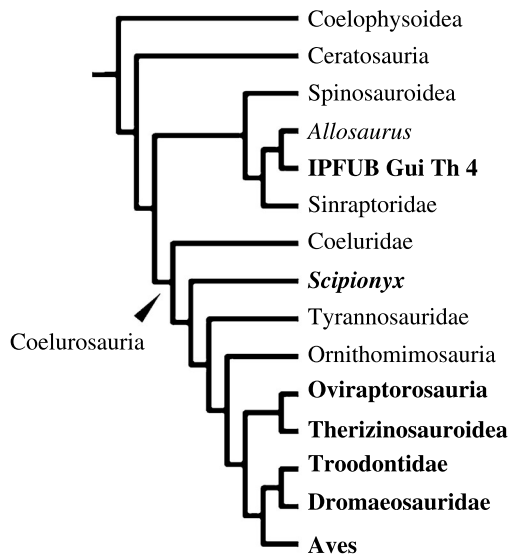


Figure 2. Simplified theropod cladogram indicating the phylogenetic position of the specimen reported here and groups for which embryonic or hatchling cranial material is known (bold). (Based on Rauhut 2003.)

and small maxillary fenestra (Witmer 1997a) and, thus, cannot be referred to the Sinraptoridae. By contrast, *Allosaurus* differs from other allosauroids in its apomorphically large maxillary fenestra (Madsen 1976; Hutt *et al.* 1996; Currie & Carpenter 2000), a character which is also found in IPFUB Gui Th 4. Furthermore, the maxilla from Guimarota can be referred to this genus with some certainty since *Allosaurus* has been reported from roughly contemporaneous beds in Portugal (Pérez-Moreno *et al.* 1999).

The general bone proportions (a short and high maxilla with an almost vertical anterior margin of antorbital fenestra and a low maxillary body; Norell *et al.* 1994; Dal Sasso & Signore 1998) and the striated bone surface (Britt & Naylor 1994) indicate that the specimen represents a very young, embryonic or early post-hatchling individual. This is in accordance with its minute size, since adult *Allosaurus* maxillae have lengths of more than 300 mm (Gilmore 1920; Madsen 1976) and this bone is even larger in other known allosaurids (Currie & Carpenter 2000). All other theropods for which embryonic or hatchling cranial material has been reported (Norell *et al.* 1994; Cohen *et al.* 1995; Dal Sasso & Signore 1998; Varricchio *et al.* 2002) represent advanced coelurosaurians from the Cretaceous period (figure 2); thus, this specimen provides the first opportunity to study aspects of early craniofacial ontogeny in a non-coelurosaurian theropod from the Jurassic period.

(b) Implications for basal tetanuran craniofacial development

Several aspects of the hatchling *Allosaurus* maxilla are noteworthy in respect to tetanuran craniofacial ontogeny. With a total length of 23 mm, the maxilla IPFUB Gui Th 4 is only 8% or less of the size of an adult *Allosaurus* maxilla (figure 3). Allowing for some positive allometry of the maxilla in this taxon, *Allosaurus* hatchlings were probably one-seventh or less of the length of animals at sexual maturity, which compares well with the relative hatchling size of large extant crocodile taxa

(Andrews 1982). By contrast, coelurosaur hatchlings seem to have been relatively larger: the maxilla of an unhatched *Troodon* embryo is only slightly smaller (18 mm; Varricchio *et al.* 2002) than the *Allosaurus* maxilla described here and the same seems to be true for oviraptorosaurs and dromaeosaurids (Norell *et al.* 1994, 2001), although the adults of these taxa are considerably smaller (2 m or less of the total body length) than an adult *Allosaurus* (7–9 m).

The short and high shape of the maxilla IPFUB Gui Th 4 indicates that *Allosaurus* hatchlings had rather short snouts and that the facial region of the skull exhibited positive allometry during early ontogeny. Similar changes have been reported in ornithischians (Coombs 1982; Carpenter 1994; Horner & Currie 1994; Varricchio 1997), but do not seem to occur to the same extent in many coelurosaurians, which tend to have rather long snouts as juveniles (Varricchio 1997; Carr 1999; Varricchio *et al.* 2002). An aspect that is noteworthy is the obvious increase in the number of tooth positions during *Allosaurus* ontogeny. Whereas subadult and adult representatives of this taxon usually have 16 (more rarely 15) teeth in the maxilla (Madsen 1976), IPFUB Gui Th 4 exhibits only 13 tooth positions. Whereas tooth count increases have been reported for several ornithischian clades (Varricchio 1997), it has been argued that theropods exhibit little change in tooth counts, comparable to the situation seen in crocodiles (Varricchio 1997), or that tooth count even decreases during ontogeny (Carr 1999). However, the situation in IPFUB Gui Th 4 indicates that an increase in tooth count during ontogeny probably represents a plesiomorphic feature for dinosaurs, and that constant or decreasing tooth counts during ontogeny occurred in coelurosaur evolution.

The most notable feature of this hatchling *Allosaurus* maxilla, however, is its high degree of pneumatization, as indicated by bony structures associated with the antorbital paranasal sinus system (Witmer 1997b). The antorbital fenestra seems to have been large and the antorbital fossa is well defined. Both the promaxillary and maxillary fenestrae are well developed (figure 1). Indeed, the maxillary fenestra is relatively larger than in any adult non-maniraptoran theropod. The excavatio pneumatica is well developed and sharply defined. This depression is also present in adult allosaurids (Witmer 1997a,b; Currie & Carpenter 2000), but shallower and less well defined (figure 2). From the medial view, the well-developed recess above the maxillary fenestra is especially noteworthy. This recess is absent in adult *Allosaurus* maxillae (Madsen 1976), indicating that the paranasal cavity and its sinus were relatively larger in the hatchling.

The presence of a well-developed paranasal sinus system in such a young, probably early post-hatchling individual is noteworthy. Little is known about the early ontogenetic development of the paranasal sinus system in archosaurs in general, although it was reported that this system develops early in the ontogeny of birds and crocodiles (Witmer 1995). The evidence presented here indicates that paranasal pneumaticity developed early in the ontogeny in theropod dinosaurs and was already well developed in hatchlings. Indeed, some of the pneumatic recesses in the element described, and by inference the associated sinus and its diverticulae, are even more developed than in adult individuals. The same might

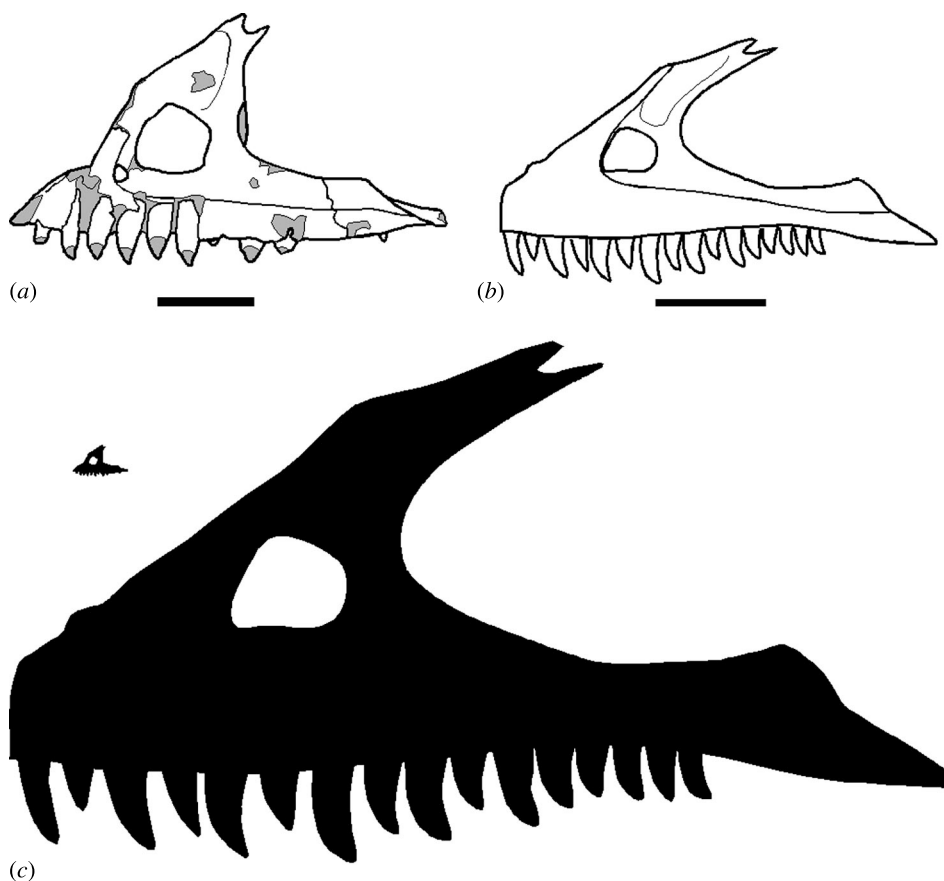


Figure 3. Comparison of the hatchling maxilla IPFUB Gui Th 4 and the maxilla of an adult *Allosaurus fragilis*. (a) Drawing of hatchling maxilla, (b) adult maxilla drawn to same length as (a) to demonstrate differences in proportions, (c) outlines of hatchling (upper left) and adult (lower right) maxillae drawn to the same scale to demonstrate size differences. Scale bars are (a) 5 mm and (b) 100 mm. (b) is based on Museum of the Rockies MOR 693 and Madsen (1976).

apply to the tympanic pneumatic system in allosaurids, as a study of juvenile to adult *Allosaurus* braincases demonstrated that some pneumatic recesses are better developed in juveniles than in adults (Chure & Madsen 1996). After a critical review of the many proposed functions of the paranasal and other cranial pneumatic systems, Witmer (1997a) concluded that opportunistic invasion by pneumatic epithelia (i.e. the invasion and resorption of non-functional tissues by the epithelia) might be a primary reason for the development of pneumatic recesses in bony structures. The present findings strengthen this hypothesis since jaws of a hatchling are certainly exposed to relatively lower loads than the jaws of megapredacious adult allosaurs (Rayfield *et al.* 2001) and, thus, larger recesses are simply developed by resorption of unnecessary bone tissue. It should be noted that the opposite tendency, especially enlargement of the maxillary fenestra in late ontogeny, was noted in a study of tyrannosaur craniofacial ontogeny (Carr 1999). However, this study did not deal with early ontogenetic stages, and different hunting strategies in adult tyrannosaurs (Rayfield 2004) might also have had an influence on the late ontogenetic development of this system.

The strong development of the paranasal pneumatic system in a hatchling theropod has important implications for the evolution of paranasal pneumaticity in theropod dinosaurs. There is a general evolutionary tendency to enlarge the paranasal cavities and increase the amount of associated bony recesses in several theropod lineages (Witmer 1997a,b), including the lineage leading towards

birds. Thus, the observation that parts of the paranasal pneumatic system are more pronounced in a hatchling than in the adult indicates that heterochrony has played an important role in the evolution of these structures. Although heterochrony has been noted as an important aspect of the evolution of other dinosaur clades (Weishampel & Horner 1994; Long & McNamara 1997), little attention has been paid to the importance of these processes in the evolution of non-avian theropods (Weishampel & Horner 1994). Thus, the present findings, in combination with the sparse data available from other studies (Norell *et al.* 1994; Long & McNamara 1997), indicate that heterochrony was probably a widespread phenomenon in the evolution of non-avian theropods.

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