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Theropod teeth from the basalmost Cretaceous of Anoual (Morocco) and their palaeobiogeographical significance

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Abstract – The theropod teeth from the Berriasian (Early Cretaceous) site of Anoual (N Morocco) are described. The assemblage is important in that it comes from one of the very few dinosaur sites of this age globally and the only one for the whole of Gondwana. The theropod teeth from Anoual are morphologically diverse. Most of the material possibly belongs to the clade Dromaeosauridae, which would be an early occurrence for this taxon. The palaeogeographic position of Anoual enables it to provide data on the dispersal events that affected terrestrial faunas during Mesozoic times. A Laurasian influence is evidenced by the presence of Velociraptorinae and, on the whole, the theropod fauna from Anoual provides support for the existence of a trans-Tethyan passage allowing terrestrial faunal interchanges during Late Jurassic and/or earliest Cretaceous times. Additionally, Anoual records the existence of diminutive theropods. However, it cannot yet be determined whether the small size of the specimens is genetic or ontogenetic.

Keywords: dinosaur, Cretaceous, palaeogeography, Africa, Europe.

1. Introduction

The so-called site of Anoual is located in the eastern High Atlas Mountains (northern Morocco; Fig. 1), east of the eponymous city, in the lenticular Ksar Metlili Formation. It has yielded an extremely diverse microvertebrate fauna, including fishes, amphibians, turtles, sphenodontians, squamates, archosaurs and mammals (see Knoll, 2000; Evans & Sigogneau-Russell, 2001; Gardner, Evans & Sigogneau-Russell, 2003; Jones, Evans & Sigogneau-Russell, 2003 and references therein). The age of this assemblage is well constrained as Berriasian by the combined dating provided by nannoliths and a charophyte (Sigogneau-Russell, Monbaron & Kaenel, 1990; Mojon, Haddoumi & Charrière, 2005). Considerable attention has been drawn to the mammalian component of this assemblage, which is not surprising, as it stands as the best Mesozoic mammalian fauna in Gondwana in terms of abundance of specimens and taxonomic diversity (see Sigogneau-Russell *et al.* 1998 and references therein; Sigogneau-Russell, 1999*a*, *b*, 2003; Hahn & Hahn, 2003). In contrast, no detailed work has been dedicated to the dinosaurian representatives, which is particularly unfortunate as the evolution of dinosaurian faunas at the dawn of the Cretaceous is presently very poorly known on a global scale (Weishampel *et al.* 2004). Thus, with respect to Africa, there is simply no other dinosaurian site of definitive Berriasian age. The aim of this paper is to present a detailed survey of the theropod teeth from Anoual.

2. Material and methods

The microvertebrate remains from the 'synclinal d'Anoual' (SA) are housed in the Muséum national d'Histoire naturelle (Paris). They were obtained by Dr D. Sigogneau-Russell (Muséum national d'Histoire naturelle, Paris) after acid dissolution of limestone blocks collected at the site in the 1980s and sifting and sorting of the residue under a binocular microscope.

Theropod teeth are, in general, morphologically conservative and typically possess few discrete characters that can be used to identify them confidently. Their detailed systematic study was initiated by Currie, Rigby & Sloan (1990) and is presently based on a small number of relatively simple characters such as cross-sectional shape, the respective positions of mesial and distal carinae, denticle morphology and density, and tooth size. These characters have, at least partly, evolved in correlation with functional necessities and were doubtless strongly subject to homoplasy. In addition, morphological variation in theropod teeth, even within a single jaw, is presently not well appreciated. Nevertheless, recent studies suggest that statistical tools can help to discriminate between theropod teeth of similar gross morphology (see Smith, Vann & Dodson, 2005; but also Samman *et al.* 2005; Smith, 2005, 2007).

The present identification was limited to four categories: Theropoda indet., Maniraptoriformes indet., Maniraptora indet. and Velociraptorinae indet. All suprageneric taxa used in this paper follow Sereno (unpub. data, 2005: http://taxonsearch.org/dev/file_home.php), with adoption of the phylogenetic schemes of Holtz, Molnar & Currie (2004) and

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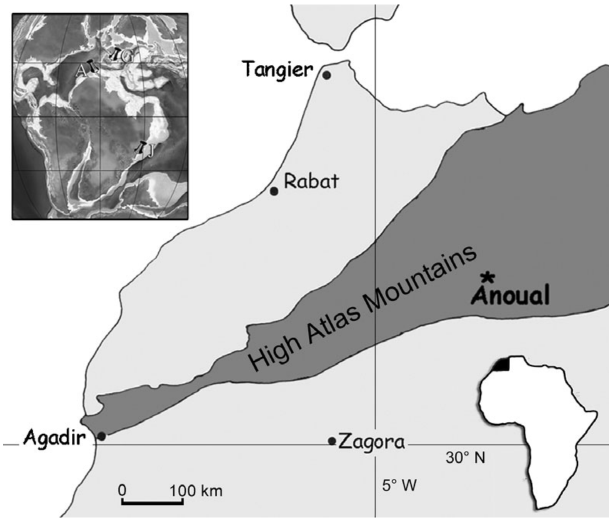

Figure 1. Map showing the position of the Anoual locality. The lower right corner inset shows the position in Africa of the region depicted in the main map (from Sigogneau-Russell *et al.* 1998, fig. 1). The upper left inset is a palaeogeographic map of the Early Cretaceous (120 Ma) from Blakey (unpub. data, 2001: http://jan.ucc.nau.edu/~rcb7/globaltext2.html), in which pins point to the position of the Anoual (A), but also Galve (G) and Jema River (J) sites. A detailed stratigraphic section of the Red Beds of the Anoual Syncline showing the position of the fossiliferous lens of the Ksar Metlili Formation is available in Sigogneau-Russell, Monbaron & Kaenel (1990, fig. 10).

Holtz & Osmólska (2004) for taxa more basal than Coelurosauria, that of Hwang *et al.* (2004) for taxa within Coelurosauria exclusive of those within Dromaeosauridae, and that of Makovicky, Apesteguía & Agnolín (2005) for Dromaeosauridae. Particular emphasis was placed on the following key characters:

(a) teeth without serrations: Maniraptoriformes indet. (e.g. Hwang *et al.* 2004, supplementary data; Makovicky, Apesteguía & Agnolín, 2005, supplementary information);
(b) teeth with distal serrations but lacking mesial ones: Maniraptora indet. (e.g. Ruiz-Omeñaca & Canudo, 2003);
(c) teeth with mesial denticles smaller than distal ones (DSDI $\gg 1$): Velociraptorinae indet. (e.g. Rauhut & Werner, 1995; Rauhut, 2002; Currie & Varricchio, 2004).

The teeth that were overly fragmentary and lacking diagnostic characters were identified only as Theropoda indet. All of the teeth described here are confidently attributable to Theropoda, but the possibility that some of this material belongs to distant taxa such as crocodylomorphs or squamates cannot be categorically excluded so far (some serrated teeth from Anoual were considered as pertaining to unknown ziphodont crocodylomorphs and therefore excluded from this study).

Binocular and scanning electron microscopy techniques were employed to study the material. For most of the specimens, measurements were taken with an eyepiece with a graduated ruler connected to an Olympus SZH stereomicroscope. For the largest specimens, a digital caliper was also used. Measurements for each specimen are presented in Table 1. When possible, these are the crown height (CH), the basal width (BW), the fore–aft basal length (FABL), the crown height ratio (CHR), the lateral compression ratio (LCR), the denticle density for the distal and mesial carinae (DDD, DDM) and the denticle size density index (DSDI). Details regarding the measurement of these parameters are provided in Grigorescu (1984), Currie, Rigby & Sloan (1990), Farlow *et al.* (1991), Rauhut & Werner (1995), Sankey *et al.* (2002) and Smith, Vann & Dodson (2005). The tooth orientation terminology used herein follows the proposal of Smith & Dodson (2003).

3. Systematic palaeontology

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Theropoda Marsh, 1881
Theropoda indet.

SA mcm 167. This specimen is reduced to a distal fragment of a crown (Fig. 2a). In distal view, it is slightly curved laterally (?lingually) and the carina appears relatively central. The lateral sides are smooth, especially at the base. The carina bears very fine serrations (see Table 1) on the basalmost two-thirds of the crown. The break reveals a centrally located inner groove that extends from the base of the crown fragment toward the apex, but that progressively disappears before reaching it.

SA 2004/2A. It is a small fragment of carina with five relatively coarse, chisel-like serrations (Fig. 2b).

SA 2004/2D. It is also a small fragment of carina with five relatively coarse, chisel-like serrations (Fig. 2c).

SA 2004/2C. This specimen is a fragment of a serrated distal carina (Fig. 2d). As far as we can assess them, the lateral sides of the crown appear smooth. The serrations (Fig. 2e) are much finer than in SA 2004/2A (Fig. 2b) and do not reach the base. They are relatively even and oriented perpendicular to the longest axis of the tooth. The interdenticle pits are oval in labial and lingual views, giving to the denticle a waisted, axe-like morphology in lateral view. This compares well with some of the denticles of *Nuthetes* teeth as figured by Milner (2002, fig. 2). Incidentally, the DDD is similar to that of some teeth attributed to *Fukuiraptor* (Currie & Azuma, 2006, table 1).

SA 2004/2E. It is a narrow fragment of mesial carina bearing 14 medium-sized, chisel-like serrations oriented roughly perpendicular to the long axis of the crown, except for the smaller ones at one extremity (?apical) which are slightly tilted (Fig. 2f, g).

SA 2004/2F. This is a fragment of a relatively straight (?distal) carina with 15 rounded or chisel-like serrations oriented perpendicular to the edge of the crown (Fig. 2h).

SA 2004/2G. It is a small crown sagittally broken and lacking the apex (Fig. 2i). The preserved lateral side is relatively flat and smooth. The mesial edge is not well preserved. The distal edge bears a series of fine serrations extending nearly down to the base.

SA 2004/3B. It is a fragment of serrated distal carina (Fig. 2j), which describes a slight sigmoid curve in labial or

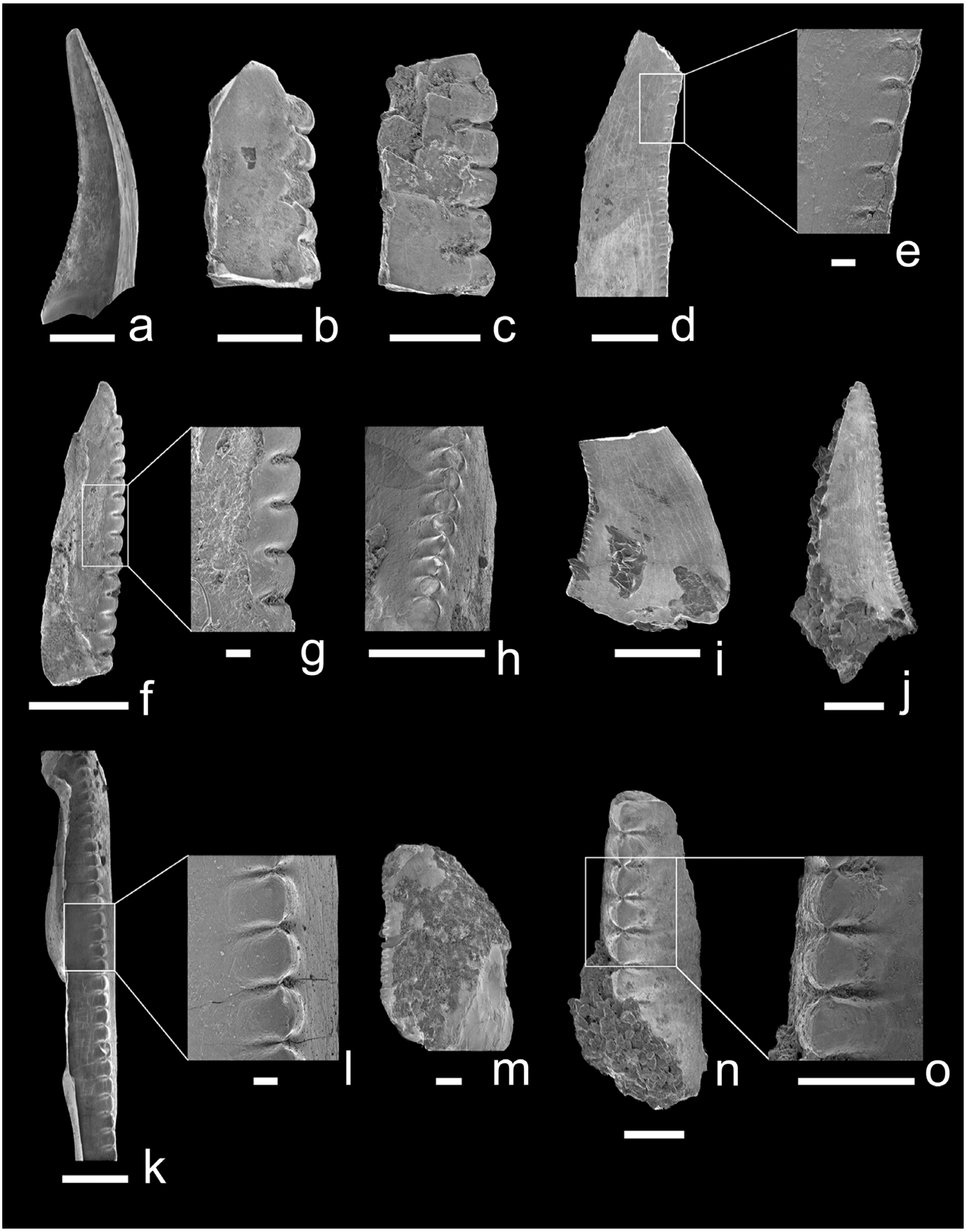

Figure 2. Theropod teeth from the Berriasian of Anoual (Theropoda indet.). (a) SA mcm 167 (lateral view); (b) SA 2004/2A (lateral view); (c) SA 2004/2D (lateral view); (d) SA 2004/2C (lateral view); (e) SA 2004/2C (detail of serrations); (f) SA 2004/2E (lateral view); (g) SA 2004/2E (detail of serrations); (h) SA 2004/2F (detail of serrations); (i) SA 2004/2G (lateral view); (j) SA 2004/3B (lateral view); (k) SA 2004/4A (?distal view); (l) SA 2004/4A (detail of serrations); (m) SA 2004/5C (lateral view); (n) SA 2004/5D (?distal view); (o) SA 2004/5D (detail of serrations). Scale bars = 1 mm (a–d, f, h–k, m–o) and 0.1 mm (e, g, l).

lingual view, as in *Carcharodontosaurus* (Sereno *et al.* 1996), for example. The lateral sides of the crown seem to have been smooth. The distal curvature of the crown was insignificant.

The series of medium-sized serrations extends all along the height of the crown, those in the middle part of the crown being the largest and the most distinct. The serration density

Table 1. Measurements of the theropod teeth from Anoual (see Section 2 for abbreviations)

<table>
<tr><th>Identification</th><th>Specimen no. SA</th><th>CH (mm)</th><th>BW (mm)</th><th>FABL (mm)</th><th>CHR</th><th>LCR</th><th>DDD (mm^{-1})</th><th>DDM (mm^{-1})</th><th>DSDI</th></tr>
<tr><td>Theropoda indet.</td><td>mcm 167</td><td>4.00</td><td>1.16</td><td>(1.20)</td><td>(3.33)</td><td>(0.97)</td><td>11.36(m)
14.29(b)</td><td>?</td><td>?</td></tr>
<tr><td></td><td>2004/2A</td><td>(3.40)</td><td>?</td><td>?</td><td>?</td><td>?</td><td colspan="2">2.00</td><td>?</td></tr>
<tr><td></td><td>2004/2D</td><td>(3.20)</td><td>?</td><td>?</td><td>?</td><td>?</td><td colspan="2">2.00</td><td>?</td></tr>
<tr><td></td><td>2004/2C</td><td>(5.60)</td><td>?</td><td>?</td><td>?</td><td>?</td><td>?</td><td>5.33(m)
6.25(b)</td><td>?</td></tr>
<tr><td></td><td>2004/2E</td><td>(3.30)</td><td>?</td><td>?</td><td>?</td><td>?</td><td colspan="2">5.00</td><td>?</td></tr>
<tr><td></td><td>2004/2F</td><td>(4.00)</td><td>?</td><td>?</td><td>?</td><td>?</td><td colspan="2">4.44</td><td>?</td></tr>
<tr><td></td><td>2004/2G</td><td>(2.60)</td><td>(0.60)</td><td>(2.16)</td><td>(1.20)</td><td>(0.28)</td><td>10.29(m)
10.71(b)</td><td>?</td><td>?</td></tr>
<tr><td></td><td>2004/3B</td><td>4.90</td><td>1.60</td><td>(2.10)</td><td>(2.33)</td><td>(0.76)</td><td>6.00(m)
8.00(b)</td><td>?</td><td>?</td></tr>
<tr><td></td><td>2004/4A</td><td>(7.20)</td><td>?</td><td>?</td><td>?</td><td>?</td><td colspan="2">4.03</td><td>?</td></tr>
<tr><td></td><td>2004/5C</td><td>(11.00)</td><td>(3.00)</td><td>(6.50)</td><td>(1.69)</td><td>(0.46)</td><td>3.13(a)
3.52(m)
3.91(b)</td><td>2.86(a)
2.93(m)
3.00(b)</td><td>0.91(a)
0.83(m)
0.77(b)</td></tr>
<tr><td></td><td>2004/5D</td><td>(5.80)</td><td>?</td><td>?</td><td>?</td><td>?</td><td colspan="2">1.65</td><td>?</td></tr>
<tr><td>Maniraptoriformes indet.</td><td>A0</td><td>1.68</td><td>0.56</td><td>0.88</td><td>1.91</td><td>0.64</td><td>0</td><td>0</td><td>–</td></tr>
<tr><td></td><td>2004/2B</td><td>2.60</td><td>0.88</td><td>1.40</td><td>1.86</td><td>0.63</td><td>0</td><td>0</td><td>–</td></tr>
<tr><td></td><td>2004/4C</td><td>3.68</td><td>1.08</td><td>2.28</td><td>1.61</td><td>0.47</td><td>0</td><td>0</td><td>–</td></tr>
<tr><td>Maniraptora indet.</td><td>2004/1</td><td>(13.99)</td><td>4.00</td><td>8.20</td><td>(1.69)</td><td>0.49</td><td>4.44(a)
4.45(m)
5.00(b)</td><td>0</td><td>–</td></tr>
<tr><td></td><td>mcm 153</td><td>(2.20)</td><td>1.00</td><td>1.92</td><td>(1.15)</td><td>0.52</td><td>12.00</td><td>?</td><td>?</td></tr>
<tr><td></td><td>mcm 162</td><td>1.48</td><td>0.52</td><td>1.08</td><td>1.37</td><td>0.48</td><td>12.50(m)
10.71(b)</td><td>0</td><td>–</td></tr>
<tr><td></td><td>mcm 166</td><td>1.52</td><td>0.56</td><td>(1.00)</td><td>(1.52)</td><td>(0.56)</td><td>13.64(m)
11.54(b)</td><td>0</td><td>–</td></tr>
<tr><td></td><td>2004/3E</td><td>3.44</td><td>0.80</td><td>1.88</td><td>1.82</td><td>0.43</td><td>9.09(a)
7.50(b)</td><td>0</td><td>–</td></tr>
<tr><td></td><td>2004/3F</td><td>(2.24)</td><td>0.64</td><td>(1.40)</td><td>(1.61)</td><td>(0.46)</td><td>10.00</td><td>0</td><td>–</td></tr>
<tr><td></td><td>2004/4B</td><td>1.48</td><td>0.40</td><td>1.08</td><td>1.37</td><td>0.37</td><td>11.93</td><td>0</td><td>–</td></tr>
<tr><td></td><td>2004/4D</td><td>2.28</td><td>0.88</td><td>1.52</td><td>1.49</td><td>0.58</td><td>10.29</td><td>0</td><td>–</td></tr>
<tr><td></td><td>2004/3C</td><td>2.76</td><td>0.68</td><td>1.80</td><td>1.54</td><td>0.38</td><td>8.88</td><td>0</td><td>–</td></tr>
<tr><td></td><td>2004/5A</td><td>(4.72)</td><td>1.32</td><td>2.60</td><td>1.82</td><td>0.51</td><td>11.49</td><td>0</td><td>–</td></tr>
<tr><td></td><td>2004/4E</td><td>(1.60)</td><td>0.72</td><td>1.60</td><td>(1.00)</td><td>0.45</td><td>8.33</td><td>?</td><td>?</td></tr>
<tr><td>Velociraporinae indet.</td><td>mcm 168</td><td>1.28</td><td>0.56</td><td>1.20</td><td>1.06</td><td>0.47</td><td>13.89(a)
10.66(m)
7.14(b)</td><td>15.00(a)
12.47(m)
10.00(b)</td><td>1.08(a)
1.17(m)
1.40(b)</td></tr>
<tr><td></td><td>2004/3A</td><td>3.20</td><td>0.80</td><td>2.20</td><td>1.45</td><td>0.36</td><td>8.75</td><td>10.85</td><td>1.24</td></tr>
<tr><td></td><td>2004/5B</td><td>(6.80)</td><td>1.40</td><td>(2.80)</td><td>(2.44)</td><td>(0.50)</td><td>7.52</td><td>8.33</td><td>1.11</td></tr>
<tr><td></td><td>mcm 158</td><td>4.32</td><td>0.76</td><td>(2.00)</td><td>(2.17)</td><td>(0.38)</td><td>8.20</td><td>11.90</td><td>1.45</td></tr>
</table>

(a), (m) and (b) indicate that the measurement has been taken in the apical, middle, and basal part of the carina, respectively. Bracketed values are based on deficient data and are indicative of the state of preservation of the specimen only.

is close, for example, to that of the maxillary and dentary teeth of *Huaxiagnathus* (Hwang *et al.* 2004) and to that of a number of isolated teeth attributed to *Saurornitholestes* (Sankey, Standhardt & Schiebout, 2005, table 7.2).

SA 2004/4A. It is a narrow fragment of carina with 28 chisel-like serrations (Fig. 2k, l).

SA 2004/5C. Despite being an imperfectly preserved tooth (Fig. 2m), this specimen is interesting in being one of the largest recovered at Anoual. One side appears to have been flatter than the other. The distal carina is not strongly curved. Both the mesial and distal carinae bear medium-sized, plesiomorphic, chisel-like serrations. As far as can be determined, their density is similar to that of the tetanuran *Condorraptor* (Rauhut, 2005), the Tyrannosauridae (Currie, Rigby & Sloan, 1990), and a tooth from the Maastrichtian of Cassagnau (France) identified by Laurent, Bilotte & Le Loeuff (2002, pl. 2C) as from an undetermined Dromaeosauridae, to cite but a few examples. This corroborates the hypothesis that denticle density alone is not determinant for systematic allocation (Farlow *et al.* 1991). The DSDI is similar to the mean DSDI of *Ceratosaurus* (Smith, 2005, fig. 17C) and to that of a tooth referred to *Eocarcharia* (Sereno & Brusatte, 2008, p. 30). The LCR of SA 2004/5C may also have been similar to that of *Eocarcharia* (Sereno & Brusatte, 2008, p. 30).

SA 2004/5D. This specimen is a fragment of carina with eight chisel-like serrations (Fig. 2n, o). It could be interpreted as evidence for the presence of a theropod of a larger size than that from which SA 2004/1 (see below) comes (or, alternatively, a theropod with proportionally larger teeth).

Tetanurae Gauthier, 1986
Coelurosauria Huene, 1914
Maniraptoriformes Holtz, 1995
Maniraptoriformes indet.

SA A0. This is a crown devoid of serrations or denticulations (Fig. 3a). The mesial edge lacks a well-marked carina. The distal edge bears a discrete carina, which is strongly eccentric (offset from the centre in distal view) and absent on the basalmost third of the crown. Assuming that this deflection is toward the lingual side, SA A0 would be a tooth from the right dentary or left maxilla, possibly from the rostral part. The crown is slightly curved ?labially. The ?labial side is relatively smooth except for a faint baso-apical ridge

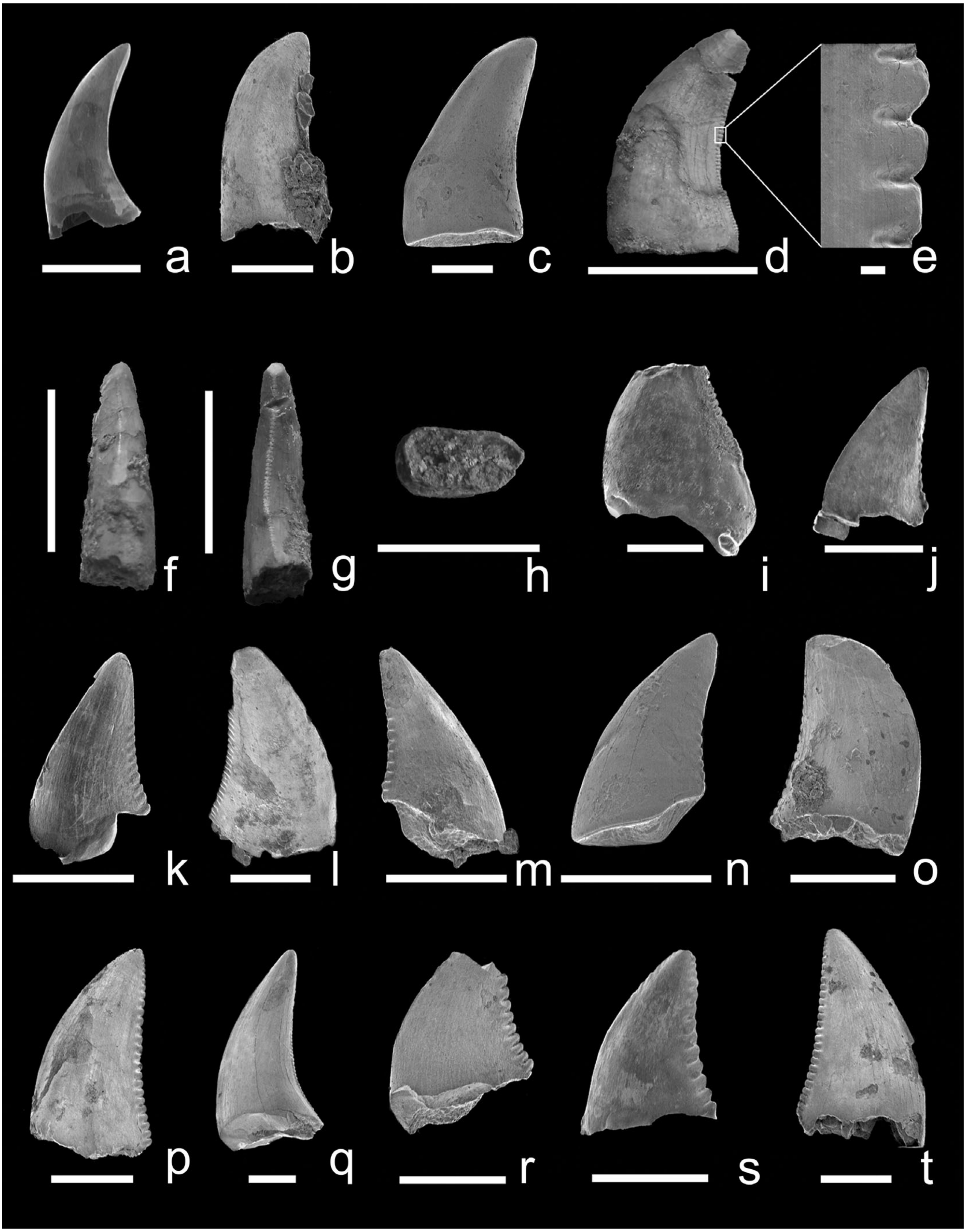

Figure 3. Theropod teeth from the Berriasian of Anoual (Maniraptoriformes indet., Maniraptora indet. Morphotype I to III, Velociraptorinae indet. Morphotype I). (a) SA A0 (?lingual view); (b) SA 2004/2B (lateral view); (c) SA 2004/4C (lateral view); (d) SA 2004/1 (?lingual view); (e) SA 2004/1 (detail of serrations); (f) SA 2004/1 (mesial view); (g) SA 2004/1 (distal view); (h) SA 2004/1(basal view); (i) SA mcm 153 (lateral view); (j) SA mcm 162 (lateral view); (k) SA mcm 166 (lateral view); (l) SA 2004/3E (lateral view); (m) SA 2004/3F (lateral view); (n) SA 2004/4B (lateral view); (o) SA 2004/4D (lateral view); (p) SA 2004/3C (lateral view); (q) SA 2004/5A (lateral view); (r) SA 2004/4E (lateral view); (s) SA mcm 168 (lateral view); (t) SA 2004/3A (lateral view). Scale bars = 10 mm (d, f–h), 1 mm (a–c, i–t) and 0.1 mm (e).

that possibly originates from a labial migration of a mesial carina. The ?lingual side is uniformly smooth.

SA A0 is superficially similar to isolated teeth from the Barremian of Castellote (Spain) assigned by Ruiz-Omeñaca, Canudo & Cuenca-Bescós (1996, fig. 13) to Coelurosauria indet., and also evokes a tooth from the Maastrichtian of Romania that Codrea *et al.* (2002, fig. 4N) referred to the *Euronychodon* morphotype.

SA 2004/2B. This is a crown with both lateral sides smooth and only slightly and relatively homogeneously convex (Fig. 3b). The apex is blunt. The crown is only very slightly curved distalward as the distal carina is almost straight. The mesial edge bears a discrete, but acute, carina that originates from the apex and vanishes at about mid-height of the crown. Interestingly, this carina is centrally positioned apically, but diverges laterally (?lingually) toward the base. The distal carina follows a straighter, though still eccentric, course and extends much further basally, nearly reaching the base of the crown. Neither carina bears serrations.

A lingually diverging mesial carina has been considered as diagnostic of *Dromaeosaurus* (Currie, Rigby & Sloan, 1990; Currie, 1995, p. 577; Baszio, 1997, p. 35) and as characteristic of dromaeosaurine Dromaeosauridae (Currie, 1995, p. 589; Rauhut, 2000, 2002). Nevertheless, in *Dromaeosaurus* this character concerns lateral teeth, whereas the 'rounded' appearance of SA 2004/2B suggests that it is an exemplar from the premaxilla (see e.g. Baszio, 1997, pl. 1 fig. 5; Zinke, 1998, fig. 3A). Assuming that SA 2004/2B is indeed a premaxillary tooth, the presence of carinae on both the mesial and distal edges argues against close affinity with a number of Coelurosauria, notably Compsognathidae (Currie & Chen, 2001, p. 1711). Interestingly, the mesial carina of the premaxillary teeth of *Richardoestesia* (= *Ricardoestesia*) *gilmorei* curves toward the lingual surface, according to Baszio (1997, p. 39). He has figured such a tentatively identified tooth (Baszio, 1997, pl. 4, fig. 49), which does resemble SA 2004/2B, although the former is finely serrated. The LCR is similar to that of a tooth from the Berriasian of Denmark pertaining to a Dromaeosauridae, according to Lindgren *et al.* (2008, p. 258). All in all, SA 2004/2B appears to represent a derived member of Maniraptoriformes, although that assertion is not supported by any synapomorphy.

SA 2004/4C. This is a shed crown with both lateral sides smooth and slightly flattened (Fig. 3c). The mesial edge is uniformly curved except for the basal fifth, which is straight. It bears a sharper carina than does the distal edge. Both carinae are slightly eccentric and their deflections are not toward the same side. There is no evidence of any serrations on either carina. The basal surface of the crown shows a central aperture.

The specimen is closely similar to the theropod teeth from the Maastrichtian of Aveiro and Taveiro (Portugal) identified as 'Famille aff. Coeluridae' by Antunes & Sigogneau (1992, pl. 2; also Antunes & Sigogneau-Russell, 1996, table 1), '?Coeluridae' by Galton (1996), Theropoda indet. by Pereda Suberbiola (1999) and Coelurosauria indet. by Weishampel *et al.* (2004, p. 592).

Maniraptora Gauthier, 1986
Maniraptora indet. Morphotype I

SA 2004/1. This is the largest complete theropod tooth recovered to date at Anoual (Fig. 3d–h). The labial and lingual sides are smooth and flat (Fig. 3d). The mesial edge shows no obvious serrations, but possesses a discrete, acute carina that disappears toward the base of the crown (Fig. 3f). The distal carina shows an eccentricity (Fig. 3g) that suggests that this tooth comes from the rostral part of the right dentary or left maxilla. In addition, this carina describes a slightly sigmoid line, even though the crown is itself fairly straight in mesial and distal views (Fig. 3f, g). The serrations are small, rounded or chisel-like and are oriented perpendicular to the longest axis of the crown (Fig. 3d, e). They are of relatively uniform size, except for the basal ones, which are smaller. The root is resorbed (Fig. 3h).

Except for bearing comparatively finer (but morphologically similar) denticles, SA 2004/1 resembles, for instance, a specimen from the Barremian of Galve (Spain) identified as Dromaeosauridae indet. 'type C' (Ruiz-Omeñaca *et al.* 1998; Barco *et al.* 2004, fig. 4.15), an isolated tooth from the Maastrichtian of Vitrolles (France) also identified as Dromaeosauridae indet. (Garcia *et al.* 1999, pl. fig. 2), as well as the seventh maxillary crown of *Tsaagan* figured by Norell *et al.* (2006, fig. 16). Incidentally, the distal carinae of the complete velociraptorine crowns studied by Sweetman (2004) are somewhat sinusoidal in distal view, recalling SA 2004/1. Finally, the DSDI of SA 2004/1 is close to the mean DSDI of *Dromaeosaurus*, according to Baszio (1997, p. 35) and, incidentally, the DDD of this tooth is similar to that of *Velociraptor*, according to Barsbold & Osmólska (1999). An assignment of SA 2004/1 to the Dromaeosauridae would therefore have some support.

SA mcm 153. This specimen is a fragmentary tooth lacking the apex (Fig. 3i). The labial and lingual sides are smooth and uniformly convex. The mesial edge of the crown possesses a discrete sharp carina. The distal edge bears medium-sized serrations. These carinae are slightly eccentric. Naturally, the preserved part of the root shows no acute carina and no serrations on the edges. There is no evidence of a constriction between the crown and the root.

SA mcm 162. This crown (Fig. 3j) shows some affinities with SA mcm 153 (Fig. 3i). It is relatively straight in mesial and distal views. Both lateral sides are smooth and homogeneously bulging. The mesial edge is unserrated. The distal edge bears serrations that disappear well before the apex. The carinae are relatively centrally positioned. Although not identical, SA mcm 162 presents some similarities with a tooth from the Barremian of Castellote identified by Ruiz-Omeñaca, Canudo & Cuenca-Bescós (1996, fig. 19) as Dromaeosauridae indet.

SA mcm 166. It is a small specimen (Fig. 3k) that shows some similarities to SA mcm 162 (Fig. 3j). Both lateral sides are smooth. The mesial edge is devoid of serrations. The distal edge bears relatively obliquely oriented (~ 45° with respect to the central axis of the crown) serrations, except for at the apex. The carinae are relatively centrally positioned. The systematic importance of obliquely oriented serrations should not be overestimated. They are present in a variety of theropods and, as suggested by Ostrom (1969, p. 40), could have varied (that is, become more horizontally oriented) during ontogeny.

SA 2004/3E. This is a crown that resembles SA 2004/1 (Fig. 3d–h), but is much smaller (Fig. 3l). It is rather straight in mesial and distal views. Both lateral sides are fairly smooth and flattened. In mesial and distal views, both carinae appear eccentric, but straight. The mesial edge possesses a carina that is devoid of serrations and that extends from the apex to nearly reach the base of the tooth. The distal carina is serrated. SA 2004/3E resembles a tooth from the Maastrichtian of the northwestern USA identified as cf. *Saurornitholestes* sp. (Sankey, 2008, fig. 2.12).

SA 2004/3F. This is a small tooth with fairly smooth sides (Fig. 3m). Both carinae are relatively centrally positioned and follow the very slight lateral curvature of the crown. The mesial edge bears an acute carina that extends from the apex to nearly reach the base. The basal surface of the tooth is oval in outline. The serrations, which are restricted to the distal edge, are oriented perpendicular to the longest axis of the crown.

SA 2004/4B. This small tooth is generally similar to those of dromaeosaurids (Fig. 3n). The lateral sides are smooth. The distal edge is serrated, except for its apical third. The height of this tooth is similar to that of SA mcm 162 (Fig. 3j).

Apart from its wider interdenticle spaces, SA 2004/4B shows characters recalling those of isolated teeth from the Barremian of Castellote identified by Ruiz-Omeñaca, Canudo & Cuenca-Bescós (1996, figs 17, 18), Canudo, Cuenca-Bescós & Ruiz-Omeñaca (1997, fig. 2a) and Ruiz-Omeñaca & Canudo (2001, fig. 7) as Dromaeosauridae indet. The LCR is similar to that of a tooth from the Berriasian of Denmark pertaining to a Dromaeosauridae according to Lindgren *et al.* (2008, p. 257).

SA 2004/4D. Although the apex is lacking, this specimen (Fig. 3o) is reminiscent of SA 2004/4B (Fig. 3n). The lateral sides are fairly smooth. The mesial carina lacks serrations. This carina is sharpest in the middle part of the crown. The distal edge bears relatively faint serrations that disappear toward the apex. The root is completely resorbed. The LCR is similar to that of a tooth from the Berriasian of Denmark pertaining to a Dromaeosauridae, according to Lindgren *et al.* (2008, p. 258).

SA 2004/3C. This is another tooth of the same overall morphology (Fig. 3p). Both lateral sides are smooth and only moderately convex. There are no obvious serrations on the mesial edge, but a discrete, acute carina extends from the apex to nearly reach the base. The distal carina bears serrations that are oriented perpendicular to the axis of the crown from the apex to the base. In mesial and distal views, both carinae appear straight and relatively centrally located. The basal side shows a central, elongate aperture that presumably extends inside the crown toward the apex.

Maniraptora indet. Morphotype II

SA 2004/5A. This is a relatively strongly recurved crown (Fig. 3q). The lateral sides are smooth and flattened. The mesial carina lacks serrations, but is rather sharp. The distal carina bears a series of minute, shallow, chisel-like serrations that disappear before reaching the apex. The carinae are not opposite, but strongly deflected toward one another, similar to those figured by Bakker, Williams & Currie (1988, fig. 12) in a tooth of Tyrannosauridae. The basal side presents a slit-like central aperture.

SA 2004/5A recalls a theropod tooth from the Middle Jurassic of Great Britain figured by Evans & Milner (1994, fig. 18.7D, E) and considered by these authors as pertaining to a relative of Late Cretaceous maniraptorans. It also shows some similarity to another Middle Jurassic theropod tooth figured by Alifanov & Sennikov (2001, fig. 1b) that these workers classified as from a member of Coelurosauria. It also bears some resemblances to the distally serrated premaxillary teeth of the possible basal maniraptoran *Juravenator* (Göhlich & Chiappe, 2006, fig. 1). Its CHR and LCR are very close to those of a possible velociraptorine tooth from the Late Cretaceous of Madagascar studied by Fanti & Therrien (2007, supplementary data, MSNM V 5349).

Maniraptora indet. Morphotype III

SA 2004/4E. It is a tooth (Fig. 3r) with smooth and uniformly convex (one being more strongly bulged than the other) lateral sides. As far as can be ascertained, the mesial carina is devoid of serrations. Nevertheless, this carina is somewhat jagged toward the apex, which renders the absence of mesial serrations in the complete tooth uncertain. The distal edge bears deep serrations separated by relatively large interdenticle slits. Their size and precise shape vary along the crown, but most are pointed apically rather than chisel-like. The tooth has an almond-shaped outline in basal view.

The pattern of denticulation of this crown can be considered as a derived character. It distinguishes this tooth from those of a wide array of theropods including *Dromaeosaurus* (Currie, Rigby & Sloan, 1990). The possibility that SA 2004/4E pertains to Troodontidae is worth considering because members of this taxon generally have teeth with proportionally large and apically hooked denticles (Makovicky & Norell, 2004). However, although the incomplete state of the specimen makes a definitive identification impossible, we judge this option unlikely in view of the description of *Troodon* teeth in Currie, Rigby & Sloan (1990) and of teeth that were confidently referred to this taxon by Baszio (1997). In fact, SA 2004/4E is most reminiscent of a probable tooth of *Saurornitholestes* figured by Currie, Rigby & Sloan (1990, fig. 8.2S) and considered by Sankey *et al.* (2002, p. 755) as being from a very young individual. SA 2004/4E would also fit perfectly well in the collection of probable *Saurornitholestes* teeth figured by Baszio (1997, pl. 2). SA 2004/4E also evokes some *Microraptor* teeth (Hwang *et al.* 2002, fig. 5), both in denticle morphology and DDD. Finally, the distal denticle morphology of SA 2004/4E recalls to some extent that of the lateral teeth of *Atrociraptor* (Currie & Varricchio, 2004, fig. 4.4B–D). Therefore, this morphotype probably pertains to a dromaeosaurid, and judging from its ‘stoutness’ may come from a young individual (e.g. Norell *et al.* 1994).

Dromaeosauridae Matthew & Brown, 1922
Velociraptorinae Barsbold, 1983
Velociraptorinae indet. Morphotype I

SA mcm 168. This well-preserved, small and short crown (Fig. 3s) is straight in mesial and distal views and its lateral sides are smooth. On the mesial edge, only some faint, apically inclined serrations are visible on the apical third of the crown. The distal edge is marked by large and deep serrations that are especially prominent on the basal half; their shape changes apically from pointed to chisel-like, and this cannot be accounted for by differential tooth wear. Both carinae are slightly eccentric. The extremely small size of this specimen together with the deepness of its serrations may suggest that it comes from a juvenile individual.

Because of the non-uniform curvature of the mesial carina in lateral view and its central prominence, SA mcm 168 is reminiscent of a tooth crown from the Campanian of the Spanish Pyrenees identified as Dromaeosauridae indet. by Torices Hernández (2002, pl. 1, fig. 4; 2003, fig. 3D). Nevertheless, the latter crown completely lacks mesial serrations. The DSDI of SA mcm 168 is close to the mean DSDI of *Velociraptor*, according to Smith (2005, fig. 17C) and *Dromaeosaurus*, according to Fanti & Therrien (2007, supplementary data) and identical to two teeth of a possible dromaeosaurid from the Maastrichtian of northern Madagascar (Fanti & Therrien, 2007, supplementary data).

SA 2004/3A. This is an only moderately bulging crown (Fig. 3t). The lateral sides are fairly smooth, being marked only by a series of extremely fine baso-apically trending enamel cracks that possibly indicate that this tooth endured a phase of subaerial exposure before its subsequent subaqueous transport and burial. The carinae are relatively straight and centrally positioned. Serrations are present on both. Mesially,

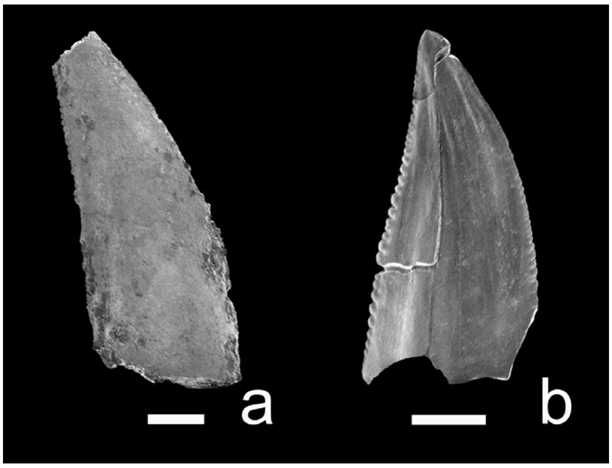

Figure 4. Theropod teeth from the Berriasian of Anoual (Velociraptorinae indet. Morphotype II and III). (a) SA 2004/5B (lateral view); (b) SA mcm 158 (lateral view). Scale bars = 1 mm.

serrations extend up to the apex, but not down to the base. There is no clear evidence of a constriction at the base of the crown.

Numerous teeth with a similar overall shape to that of SA 2004/3A (Fig. 3t) have been previously described from Cretaceous strata. To cite just three instances, this specimen resembles a lateral tooth of *Deinonychus antirrhopus* that Ostrom (1969, fig. 23A) figured together with the type specimen of this species, an isolated tooth from the Maastrichtian of Quintanilla del Coco (Spain) that Pol *et al.* (1992, fig. 5.3) identified as belonging to a possible dromaeosaurid, and a crown from the Barremian of the Isle of Wight (Great Britain) that Sweetman (2004, fig. 3C) determined to be from a velociraptorine. In addition, a close match of the DSDI of SA 2004/3A is found in a tooth from the Barremian of Castellote that Ruiz-Omeñaca, Canudo & Cuenca-Bescós (1996, fig. 23) identified as being from an indeterminate dromaeosaurid, as well as a tooth from the Campanian of the Tremp Syncline (Spain) that Torices Hernández (2002, 2003) and Torices *et al.* (2004) determined as Dromaeosauridae indet. and cf. Dromaeosauridae indet., respectively. Finally, the DSDI of SA 2004/3A is close to the mean DSDI of *Velociraptor* (Smith, 2005, fig. 17C).

Velociraptorinae indet. Morphotype II

SA 2004/5B. This is an imperfectly preserved, elongate tooth (Fig. 4a). The lateral sides are flattened and apparently were originally smooth. The crown is not strongly carinated. It bears chisel-like serrations on both edges, but those on the distal one are much better marked. The straightness of the distal edge possibly suggests a location near the rostral or caudal end of the toothrow. However, it is difficult to ascertain the original position of SA 2004/5B in the jaw, because the degree of distal curvature varies considerably between (and within) taxa. For example, in *Compsognathus* (Stromer, 1934, fig. 1; Ostrom, 1978, p. 86; Rauhut, 2000, fig. 11.7), the distal curvature increases rostrally. The inverse tendency is supposed to occur in velociraptorines (e.g. Sankey *et al.* 2002).

SA 2004/5B resembles, to some extent, specimens such as the isolated tooth from the Barremian of Castellote identified by Ruiz-Omeñaca, Canudo & Cuenca-Bescós (1996, fig. 16) as Dromaeosauridae indet. However, the LCR of the former appears to have been significantly lower, to cite just one difference. SA 2004/5B bears a stronger resemblance to the assortment of teeth from the Kimmeridgian of Guimarota (Portugal) and the Barremian of Uña (Spain) identified as cf. *Richardoestesia* sp., except possibly for the presence of a longitudinal groove on both the labial and lingual sides in these latter (Rauhut & Zinke, 1995; Zinke, 1998; Rauhut, 2000, 2002). The overall shape and DSDI are closely similar between SA 2004/5B and these Iberian cf. *Richardoestesia* teeth. Incidentally, the DDD of SA 2004/5B is also comparable to the average DDD of *Richardoestesia*, according to Baszio (1997, pp. 39–40). In overall morphology, LCR and DDD, SA 2004/5B is also strongly reminiscent of the tooth from the Campanian of L'Abeller (Spain) identified as being from a *Richardoestesia*-like theropod (Prieto-Márquez *et al.* 2000). Furthermore, in some aspects, SA 2004/5B matches the teeth of *Richardoestesia isosceles* as described by Sankey *et al.* (2002, pp. 757–8), although this taxon could in fact be a basal tetanuran such as a spinosaurid (Sankey, 2008) or even a crocodyliform (Company *et al.* 2005, p. 351) rather than a maniraptoran theropod. These resemblances indicate that the allocation of SA 2004/5B to Velociraptorinae is not certain. Incidentally, the DSDI of SA 2004/5B is also close to the mean DSDI of *Troodon* (Smith, 2005, fig. 17C).

Velociraptorinae indet. Morphotype III

SA mcm 158. This is a weakly recurved tooth (Fig. 4b). The crown is labiolingually flattened. The lateral sides are not smooth, but are instead marked by apicobasally oriented ridges. One side (Fig. 4b) shows numerous low ridges that become less distinct mesially; however, two much stronger ridges appear near the mesial carina. These two ridges extend from the apex to the middle of the crown, where they end abruptly. In addition, this side of the crown is not homogeneously bulging; instead it is somewhat corrugated. The opposite side of the crown is simpler, in that a limited number of medium-sized apico-basal ridges cover the surface and disappear toward the base of the tooth. Both edges exhibit a centrally placed, serrated carina. The mesial serrations are clearly finer than the distal ones, except toward the base. They nearly reach the apex, although they become very indistinct apically. The distal serrations also extend high on the crown. They point slightly apically.

This tooth resembles those of 'paronychodontids' due to the presence of baso-apically oriented ridges that extend along the height of the crown. Nevertheless, according to Currie, Rigby & Sloan (1990, p. 117), '*Paronychodon*' teeth are flattened and ridged on one side and convex on the other. These authors identify serrated teeth of this kind as *Troodon*, *Saurornitholestes*, and possibly *Dromaeosaurus*, depending on serration morphology. The teeth of *Troodon* are generally distinct in showing a peculiar denticle morphology (Currie, Rigby & Sloan, 1990) that eliminates close affinities with SA mcm 158. In contrast, Currie, Rigby & Sloan (1990, fig. 8.5A) figured a tooth reminiscent of SA mcm 158 as ''*Paronychodon*' (*Saurornitholestes*)'. More recently, Sankey *et al.* (2002, p. 754) described, as '?*Dromaeosaurus* Morphotype A', teeth of seemingly greater affinity to SA mcm 158 because ridges are present on both sides but are better developed on the convex one. Interestingly, SA mcm 158 also fits relatively well with teeth from the caudal half of the dentary of the abelisauroid *Masiakasaurus*, as described by Carrano, Sampson & Forster (2002, p. 514, fig. 5E), but has a higher DSDI. The DSDI of SA mcm 158 is, in contrast, similar to that of the isolated holotypic teeth of *Saurornitholestes langstoni* (Sues, 1978, pp. 390–1, pl. 4A), to that of a tooth from the Barremian of Castellote identified by Ruiz-Omeñaca, Canudo & Cuenca-Bescós (1996) as

Dromaeosauridae indet., to that of the maxillary teeth of *Bambiraptor* (Burnham *et al.* 2000, p. 2), to the mean DSDI of some teeth from the Bathonian of the Mahajanga Basin (Madagascar) comparable to those of velociraptorines (Maganuco, Cau & Pasini, 2005, fig. 9), and it also falls within the error bar for the DSDI of *Deinonychus*, according to Smith (2005, fig. 17C). All characters considered, the identification of the intriguing specimen SA mcm 158 as a velociraptorine is thus reasonable, but only tentative. In fact, the presence of a flat or concave area along each carina in the lateral teeth has been considered to be a ceratosaurian synapomorphy (Rauhut, 2004).

Incidentally, Zinke (1998, p. 185) highlighted the occurrence of '*Paronychodon*'-like teeth in the Iberian Peninsula, in the Upper Jurassic and Lower Cretaceous (but see Rauhut, 2000, p. 78). Currie, Rigby & Sloan (1990) clarified the systematic position of the serrated teeth found in North American Upper Cretaceous beds and identified as 'paronycodontid'. Nevertheless, there remain significant uncertainties regarding 'true', unserrated '*Paronychodon*' teeth, although they may also be from maniraptoriform theropods.

4. Discussion

Our knowledge of the diversity of Mesozoic theropods has increased tremendously in the last fifteen years or so, together with that of nonavian dinosaurs as a whole (Wang & Dodson, 2006). Nevertheless, a broadly accepted phylogenetic hypothesis for Theropoda has yet to be arrived at. This constitutes a critical shortcoming in referring isolated teeth to clades within Theropoda. Additional obstacles to the study of the theropods from Anoual are our very poor knowledge of the morphological changes experienced by theropod teeth during ontogeny, and of Berriasian theropod diversity worldwide.

The dental and skeletal record of theropods of well-constrained Berriasian age is extremely poor on a global scale (Weishampel *et al.* 2004). This is particularly so for Gondwana, where there is simply no theropod-producing site of definitive Berriasian age apart from Anoual. With respect to the Gondwanan ichnological record, the Antenor Navarro Formation tracksites (Brazil: Leonardi & Carvalho, 2002, 2007 and references therein) may be essentially of this age (Valença, Neumann & Mabesoone, 2003), but this is not yet well substantiated. In Africa, the closest sites to Anoual stratigraphically are possibly those of the Jema River (Ethiopia; Fig. 1), although they are likely to be Tithonian (uppermost Jurassic) in age (Goodwin *et al.* 1999). However, these localities have so far yielded only a small handful of indeterminate theropod specimens, some of which were compared to allosaurid and dromaeosaurid teeth (Werner, 1995; Goodwin *et al.* 1999). The two indeterminate theropod teeth (at least one of them probably being from a maniraptoran) described by Mateer (1987) and believed to come from the Enon Formation (South Africa) are possibly of earliest Cretaceous age, but this remains uncertain. Sites in the Galve area (Spain; Fig. 1), although outside Gondwana, are especially close to Anoual from both a stratigraphic and palaeogeographic point of view. In fact, a stratum of probable Berriasian age there has yielded a fragment of crown of maniraptoriform (Barco & Ruiz-Omeñaca, 2001*a*). A slightly older (but possibly still Berriasian in age) centrum from the same formation has been identified as being from an indeterminate theropod (Barco & Ruiz-Omeñaca, 2001*b*). A relatively large tooth from the same area and formation was recently formally described and identified as from a possible allosauroid by Canudo *et al.* (2006). Finally, the same formation has yielded two teeth of indeterminate theropods (Royo-Torres *et al.* 2003) near Riodeva (Spain) and a fragmentary tooth of a possible maniraptoran (Suñer, Santisteban & Galobart, 2005) near Alpuente (Spain).

As detailed above, of the 29 isolated theropod teeth recovered at Anoual, 11 specimens (~ 38 %) could not be identified beyond Theropoda, 3 (~ 10 %) were identified as Maniraptoriformes indet., 11 (~ 38 %) as Maniraptora indet. (3 morphotypes), and 4 (~ 14 %) as Velociraptorinae indet. (3 morphotypes). There is thus no incontrovertible evidence of the presence of Ceratosauria or of basal clades of Tetanurae such as Spinosauridae and derived Carcharodontosauridae, the teeth of which are often considered readily identifiable (even in juvenile form) and are so commonly found at a number of Moroccan sites of middle Cretaceous age (Weishampel *et al.* 2004, pp. 571, 604).

In fact, Velociraptorinae may well be represented in the majority of the specimens identified only as Maniraptora indet. (notably SA 2004/1, SA 2004/3E, SA 2004/3C and SA 2004/4E), even though the presence of Compsognathidae and/or Troodontidae in this sample cannot be ruled out (the character 'teeth with distal serrations but lacking mesial ones' having arisen in parallel in Compsognathidae and Deinonychosauria, according to the supplementary data of Hwang *et al.* 2004). Other theropods that cannot definitively be excluded from this sample are non-velociraptorine Dromaeosauridae like the microraptorines *Graciliraptor* and *Sinornithosaurus* (whose teeth have distal serrations that are significantly larger than the mesial ones: Xu & Wu, 2001; Xu & Wang, 2004). In fact, the presence of serrations and their extent on the mesial dental carina have been considered to be variable characters in velociraptorines, depending principally on position within the dental arcade and the ontogenetic stage of the individual (Currie, Rigby & Sloan, 1990; Norell *et al.* 1994; Sankey *et al.* 2002). Besides, the lack of serrations on the mesial edge has been reported in some teeth of the putative velociraptorine *Nuthetes* from the Berriasian of the United Kingdom (Milner, 2002), as well as in *Velociraptor* by Osborn (1924, pp. 1, 2). This character state is also known in the microraptorine *Microraptor* and the questionable unenlagiine *Shanag*, which also show unserrated teeth (Xu, Zhou & Wang, 2000; Hwang *et al.* 2002; Turner, Hwang & Norell, 2007), as does the unenlagiine *Buitreraptor* (Makovicky, Apesteguía & Agnolín, 2005). Hence, even the teeth identified here as Maniraptoriformes indet. could well be from species of the clade Dromaeosauridae.

The presence and relative abundance of teeth pertaining to Dromaeosauridae at Anoual should be highlighted in view of the earliest Cretaceous age of the site. Admittedly, a coeval possible dromaeosaurid is known in Europe (Milner, 2002), Kimmeridgian members of this clade may well have been found in Portugal (Zinke, 1998), and even the existence of a stem-lineage representative of Dromaeosauridae has been hypothesized in the Callovian of Kyrgyzstan (Averianov, Martin & Bakirov, 2005). However, all other Berriasian or earlier reported occurrences of dromaeosaurids remain unsubstantiated. Increasing theoretical data suggest that Dromaeosauridae were globally distributed by the Late Jurassic Epoch (Makovicky, Apesteguía & Agnolín, 2005). Nevertheless, the subclade of dromaeosaurids comprising velociraptorines and dromaeosaurines is still generally thought to have diversified in Laurasia during the Cretaceous Period (Novas & Pol, 2005).

The occurrence, in the Berriasian of northern Morocco, of low level taxa of possibly derived position within the maniraptoran clade (Velociraptorinae and perhaps Dromaeosaurinae, *Richardoestesia* and '*Paronychodon*') that are also present in the Lower Cretaceous and even Upper Jurassic of the Iberian Peninsula has interesting palaeobiogeographic implications. The issue is compounded by the complex nature, particular location and palaeogeographic history of the European region, which is considered to have been an archipelago for much of Jurassic and Cretaceous times (Fig. 1). However, in view of some temporally calibrated phylogenetic hypotheses of maniraptoran theropods (e.g. Novas & Pol, 2005; Turner *et al.* 2007; but see also Hartman, Lovelace & Wahl, 2005; Makovicky, Apesteguía & Agnolín, 2005), the rifting of the Iberian plate from Gondwana early in the Mesozoic (around the Triassic–Jurassic boundary), and the subsequent palaeogeographic history of the former during Jurassic and Cretaceous times (Dercourt, Ricou & Vrielynck, 1993; Dercourt *et al.* 2000) make it unlikely that these faunal similarities originated from vicariant events. A geodispersal explanation is therefore favoured and provides additional support for the existence of one or more trans-Tethyan passages allowing terrestrial faunal interchanges between Europe and North Africa during Late Jurassic–Early Cretaceous times. It should be noted that, besides theropods, other elements of the tetrapod fauna from Anoual show Laurasian affinities (e.g. Hahn & Hahn, 2003; Sigogneau-Russell, 2003; Gheerbrant & Rage, 2006).

Another interesting characteristic of the Anoual theropod fauna is the extremely small size of the specimens (which are mostly isolated tooth crowns, suggesting they are shed teeth). In fact, the largest well-preserved dinosaur tooth crown found at Anoual, which lacks only the very tip, is less than 14 mm tall (SA 2004/1, Maniraptora indet. Morphotype I; Fig. 3d–h). The size of this specimen is commensurate with the shed dromaeosaurid teeth mentioned by Barsbold & Osmólska (1999) at the type locality of *Velociraptor* (Campanian; Bayn Dzak, Mongolia). SA mcm 158 (Velociraptorinae indet. Morphotype III; Fig. 4b) is 4.32 mm tall, about the size of the largest crown in the juvenile and only known specimen of *Scipionyx* (Dal Sasso & Signore, 1998). SA mcm 168 (Velociraptorinae indet. Morphotype I; Fig. 3s) is a complete tooth crown only 1.28 mm tall. Small teeth do not necessarily imply small body size, because even within Dromaeosauridae there are some taxa with proportionally tiny teeth (e.g. *Buitreraptor*: Makovicky, Apesteguía & Agnolín, 2005), but if the same body proportions as *Deinonychus antirrhopus* (Ostrom, 1969, 1990; Paul, 1988*a*, *b*; Farlow *et al.* 1991; Brinkman, Cifelli & Czaplewski, 1998; Smith, Vann & Dodson, 2005) are assumed for the individual animal that yielded SA mcm 168, then the latter possibly reached less than 50 cm in total length.

Sweetman (2004, p. 362) invoked possible remote breeding sites to explain the absence of juvenile specimens in his material. Although the overwhelming prevalence of small elements at Anoual could indicate that this site represents one of Sweetman's (2004) hypothesized 'breeding grounds', it could also well be explained by environmental factors or/and taphonomic processes (sorting during transport from upstream ecosystems), such as has been proposed for the localities of Uña and Guimarota (Rauhut, 2001, 2002). This is especially plausible in view of the palaeoenvironmental data of the Ksar Metlili Formation that suggest this unit essentially represents a deltaic plain deposit (Haddoumi *et al.* 1998).

The problem rests on knowing whether these small teeth are from immature animals (like frogs from the same site: Jones, Evans & Sigogneau-Russell, 2003), from minute-toothed but 'standard' sized theropod taxa, or from dwarf species (or, as the case may be, from a combination of these possibilities). At the moment, the evidence for one hypothesis over the others is very poor and somewhat conflicting. In any case, the significance of the Anoual fauna is further highlighted.

5. Conclusions

The theropod fauna from the Anoual locality is important for our knowledge of the diversity of this group immediately after the J–K boundary. From both a palaeogeographic and a stratigraphic point of view, the closest theropod sites to Anoual are situated outside Gondwana, in the Iberian Peninsula. Nevertheless, only a very few theropodan specimens have been recorded there to date, and they are far from being suitable for precise systematic identification (Barco & Ruiz-Omeñaca, 2001*a*, *b*; Royo-Torres *et al.* 2003; Suñer, Santisteban & Galobart, 2005; Canudo *et al.* 2006).

Theropod remains from Anoual encompass a relatively wide morphological variety, suggesting that, in earliest Cretaceous times, northern Morocco was inhabited by diverse species. Only small to minuscule teeth have been recovered to date. Although this cannot be demonstrated with certainty so far, most of these species could prove referable to Dromaeosauridae. The probable presence of velociraptorine dromaeosaurids at Anoual suggests Laurasian affinities for the theropod fauna of this site and, on the whole, provides support for the existence of at least one trans-Tethyan passage allowing terrestrial faunal interchanges during Late Jurassic and/or earliest Cretaceous times.

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