ABSTRACT—Here we describe a new partial sauropod skeleton from the late Kimmeridgian (Late Jurassic) of the Lourinhã Formation, central west Portugal. The closely associated specimen comprises a complete tooth (with root), a fragment of cervical neural arch, an anterior chevron, and an almost complete right pectoral girdle and forelimb. The new sauropod, Zby atlanticus, n. gen. et sp., can be diagnosed on the basis of four autapomorphies, including a prominent posteriorly projecting ridge on the humerus at the level of the deltopectoral crest. Nearly all anatomical features indicate that Zby is a non-neosauropod eusauropod. On the basis of several characters, including tooth morphology, extreme anteroposterior compression of the proximal end of the radius, and strong beveling of the lateral half of the distal end of the radius, Zby appears to be closely related to Turiasaurus riodevensis from approximately contemporaneous deposits in eastern Spain. However, these two genera can be distinguished from each other by a number of features pertaining to the forelimb. Whereas previously described Late Jurassic Portuguese sauropods show close relationships with taxa from the contemporaneous Morrison Formation of North America, it appears that turiasaurians were restricted to Europe. All adult sauropods recovered in the Late Jurassic of Portugal thus far are very large individuals: it is possible that the apparent absence of small- or medium-sized adult sauropods might be related to the occupation of lower-browsing niches by non-sauropods such as the long-necked stegosaur Miragaia longicollum.

INTRODUCTION

Sauropod dinosaurs were an important and diverse component of Mesozoic terrestrial ecosystems (Wilson, 2002; Upchurch et al., 2004). More than 180 valid or potentially valid species are known, with the zenith in their observed diversity occurring in the Late Jurassic (Mannion and Upchurch, 2010; Mannion et al., 2011; Upchurch et al., 2011b). Late Jurassic sauropods are known from each of the present day continents, with the exception of Antarctica and Australasia (both absences most likely relating to lack of suitably dated outcrops; Weishampel et al., 2004), and particularly diverse faunas are known in the Morrison Formation of the United States and the Tendaguru Formation of Tanzania (Upchurch et al., 2004). The Iberian Peninsula also preserves a diverse record of Late Jurassic or earliest Cretaceous (Kimmeridgian–middle Berriasian) sauropods, with valid genera consisting of Dinheirosaurus lourinhansensis (Bona-parte and Mateus, 1999; Mannion et al., 2012), Lourinhasaurus alenquerensis (Lapparent and Zbyszewski, 1957; Dantas et al., 1998), and Lasotitan atalaiensis (Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003; Mannion et al., 2013) from Portugal, and Galveosaurus herreroi (Sánchez-Hernández, 2005; Barco et al., 2006; Barco, 2009), Losillasaurus giganteus (Casanovas et al., 2001), and Turiasaurus riodevensis (Royo-Torres et al., 2006; Royo-Torres and Upchurch, 2012) from Spain. Whereas Dinheirosaurus and Lasotitan are representatives of the neosauropod clades Diplodocidae and Macronaria, respectively (Antunes and Mateus, 2003; Upchurch et al., 2004; Whitlock, 2011a; Mannion et al., 2012, 2013), the phylogenetic positions of the remaining Iberian taxa are less clear, and it has been proposed that the three Spanish taxa constitute a clade of non-neosauropod eusauropods, the Turiasauria (Royo-Torres et al., 2006, 2009; Royo-Torres and Upchurch, 2012), with further indeterminate occurrences referred to this group from Portugal (Ortega et al., 2010; Mochó et al., 2012). However, other authors have questioned the monophyly and/or phylogenetic position of this clade (e.g., Barco et al., 2006; Carballido et al., 2011).

The Lourinhã Formation, located in the central sector of the Lusitanian Basin on the west coast of Portugal, is early Kimmeridgian–late Tithonian in age (Schneider et al., 2009; Kullberg et al., 2012). The paleoclimate was arid, with temperatures between 27 and 34 °C and mean annual precipitation ranging from 766 to 1394 mm/year, but with a marked seasonality, resulting in conditions similar to those inferred for the North American Morrison Formation (Mateus, 2006; Kullberg et al., 2012; Myers et al., 2012).

On 7 September 1996, one of us (O.M.) discovered new sauropod material in the late Kimmeridgian Amoreira–Porto Novo Member of the Lourinhã Formation at Vale Pombas, Lourinhã. This material was excavated during field seasons in 1996, 2000, and 2002 and consists of a closely associated partial skeleton comprising a tooth, a fragment of cervical neural arch, a chevron, and a well-preserved partial right pectoral girdle and forelimb (Figs. 1, 2). A preliminary study indicated possible turiasaurian affinities and tentatively referred it to Turiasaurus riodevensis (Mateus, 2009). Other material found at this locality includes indeterminate pterosaur fragments, possible pleurosternid chelonian carapace fragments, and two cf. Lepidotes scales. The vertebrate faunal assemblage of the Amoreira–Porto Novo...
TABLE 1. Measurements of the tooth of Zby atlanticus (ML 368).

<table>
<thead>
<tr>
<th>Dimension</th>
<th>Measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total apicobasal length of crown + root</td>
<td>106</td>
</tr>
<tr>
<td>Apicobasal length of crown</td>
<td>38</td>
</tr>
<tr>
<td>Maximum mesiodistal width of crown</td>
<td>28</td>
</tr>
<tr>
<td>Maximum labiolingual width of crown</td>
<td>14</td>
</tr>
</tbody>
</table>

All measurements are in millimeters.

Description and Comparisons

Tooth

Only one tooth was recovered from the holotype specimen, but consists of a well-preserved and complete tooth crown and root (Figs. 2–4; see Table 1 for measurements). Sauropod teeth shed during an animal’s life usually consist only of the crown, possibly as a result of resorption of the root (Edmund, 1960). Thus, the presence of a long unresorbed root in *Zby* suggests that it was most likely separated from the skull postmortem.

The crown has a spatulate morphology, strongly narrowing mesiodistally towards its apex. In horizontal cross-section the crown is ‘D’-shaped. The labial surface is convex mesiodistally and apicobasally, and possesses moderately developed labial grooves where this convexity meets the mesial and distal carinae (Fig. 3A). The lingual surface is concave mesiodistally, partly because of the lingual curvature of the mesial and distal carinae. As occurs in almost all spatulate sauropod teeth (with the exception of the Early Cretaceous U.K. taxon *Optosaurus*; Upchurch et al., 2004, 2011a), there is a mesiodistally broad, rounded ridge that extends apicobasally along the midline of the lingual concavity (Fig. 3B), narrowing towards the crown apex.

The enamel surface of the crown bears apicobasally oriented, anastomosing wrinkles. These wrinkles are coarser on the lingual surface of the crown, and are concentrated on its basal half. They are generally absent on the apical half of the crown and also near the mesial and distal margins: this absence might reflect greater wear along the tooth margins and at the apex. A ‘V’-shaped wear facet is present (Fig. 3), which is much more strongly developed on the distal margin, with some of the mesial margin remaining unworn. This shoulder-like mesial and distal wear is comparable to that seen in *Camarasaurus* and several non-neosauropods (Calvo, 1994; Wilson and Sereno, 1998; Upchurch and Barrett, 2000; Upchurch et al., 2004). Tooth wear also seems to continue onto the distal half of the labial surface of the crown apex. The crown-root junction slopes slightly apically as it approaches the mesial margin; if the crown projected perpendicular to the jaw margin, this suggests that the root extended slightly backwards through the body of the jaw element that supported it. The root is distorted but is a slightly labiolingually compressed cone that has a narrower mesiodistal diameter than the crown.

The presence of wrinkled enamel covering most of the crown, the spatulate crown shape, the deep lingual concavity and ridge, the presence of prominent labial grooves, and the ‘V’-shaped wear represent a suite of derived character states that occur only in basal sauropods or eusauropods (Upchurch, 1995, 1998; Wilson and Sereno, 1998; Wilson, 2002; Carballido and Pol, 2010). Moreover, although the presence/absence of denticles seems to be relatively ‘plastic’ in phylogenetic terms (e.g., Upchurch, 1998), the fact that *Zby* lacks serrations is consistent with it belonging to a derived eusauropod, although it is possible that any serrations have been lost through wear. In general, this tooth resembles those seen in non-neosauropod eusauropods, such as *Barapasaurus* (Bandyopadhyay et al., 2010), *Omeisaurus* (He et al., 1988), *Putagosaurus* (Bonaparte, 1986), and especially *Turiasaurus* (Royo-Torres et al., 2006; Royo-Torres and Upchurch, 2012) (Fig. 4). In particular, the slenderness index (SI) (apicobasal crown length divided by the maximum mesiodistal crown width; see Upchurch, 1998) of the *Zby* tooth is 1.38, which is relatively low for a eusauropod (Chure et al., 2010), but similar to the SI values of 1.36 in *Jobaria* (Chure et al., 2010) and 1.45–1.53 observed in *Turiasaurus* (Royo-Torres and Upchurch, 2012). Although caution should be exercised when identifying the affinities of sauropod teeth on the basis of crown proportions alone, this SI value suggests that it is unlikely that *Zby* belonged to a
titanosauriform or diplodocoid, in which SI values typically range from 2.3 to 6.0 (Chure et al., 2010). Lastly, the tooth most closely matches the ‘heart’-shaped teeth of *Turiasaurus* (Royo-Torres et al., 2006) (Fig. 4) and numerous isolated teeth tentatively referred to *Turiasaurus* (Royo-Torres et al., 2009; Royo-Torres and Upchurch, 2012), in which the broad crown narrows mesiodistally along its apical half. In other sauropods with spatulate teeth, this mesiodistal narrowing is restricted to the apical third of the crown (e.g., *Omeisaurus*; He et al., 1988:fig.16; see Fig. 4).

### Axial Remains

Only two elements of the axial column are preserved: a fragment of cervical neural arch and a chevron. The first of these comprises a right postzygapophysis and spinopostzygapophyseal lamina of a probable middle–posterior cervical vertebra. An epipophysis is present on the dorsal surface of the postzygapophysis and extends slightly beyond the posterior margin of the postzygapophysis. Little further anatomical information can be gleaned from the specimen, other than that the internal tissue structure is fine and spongy, lacking the camellate structure observed in the presacral vertebrae of titanosauriforms (Wilson and Sereno, 1998; Wedel, 2003).

The chevron is nearly complete (Figs. 2, 5; see Table 2 for measurements), missing only the distal tip of the blade, and comes from the anterior to anterior–middle region of the tail. The proximal end of the chevron is ‘closed’: that is, a portion of bone links the left and right rami above the hemal canal (Fig. 5). Closed chevrons represent the plesiomorphic state, occurring in basal sauropodomorphs such as *Plateosaurus* and *Lufengosaurus*, as well as most basal eusauropods such as *Cetiosaurus* (Upchurch and Martin, 2002, 2003), *Omeisaurus* (He et al., 1988), and...
**Mamenchisaurus** (Young and Zhao, 1972) (see also Upchurch et al., 2007). By contrast, most neosauropods (except flagellicaudatans and a small number of macronarians) typically possess ‘open’ anterior chevrons (i.e., there is no portion of bone between the rami above the hemal canal) (Upchurch, 1998; Wilson, 2002; Upchurch et al., 2004; Mannion and Calvo, 2011; Otero et al., 2012). The proximal articular surface is anteroposteriorly convex, although does not form a mediolaterally oriented ridge separating the surface into distinct anterior and posterior facets. The hemal canal has an inverted ‘teardrop’-shaped outline in anterior view (Fig. 5) and is slightly taller than wide (see Table 2). The height of the hemal canal is relatively small when compared with total chevron length (approximately 30%). Again, this represents the plesiomorphic state seen in most eusauropods and diplodocoids, and contrasts with the derived state (hemal canal height divided by total chevron length = 0.4–0.5) that occurs in most titanosauriforms (Curry Rogers and Forster, 2001; Wilson, 2002). The anterior and posterior surfaces of the chevron, below the hemal canal, form weakly developed triangular fossae (Fig. 5), with the broader and deeper posterior one extending further distally. The distal end of the chevron forms a blade-like structure that curves posterodorsally in lateral view. There is no evidence for ridges on the anterior or lateral surfaces of the blade, but a rounded ridge is present along the posterior surface, beneath the triangular fossa. The anteroposterior width of the blade is approximately three times that of the mediolateral width; this morphology is typical for most sauropods, but contrasts with the autapomorphic chevrons of the Middle Jurassic U.K. eusauropod *Cetiosaurus*, which are subcircular in horizontal cross-section at their distal ends (Upchurch and Martin, 2002, 2003). Although incomplete distally, the blade clearly curves posteriorly. Following the scheme of Otero et al. (2012), the chevron morphology is ‘curved closed ‘Y’-shaped.’

**Scapula**

The right scapula is here described with the long axis of the blade oriented horizontally, although in life this axis would slope posterodorsally. Only the acromion (proximal plate) and base of the scapular blade is preserved (Figs. 6A–C, 7; see Table 3 for measurements). Although only the base of the scapular blade is preserved, this is sufficient to indicate the probable orientation of the blade, and thus the articular surface for the coracoid is oriented approximately perpendicular to the long axis of the scapular blade. Although the dorsal margin is not entirely complete along its full length, there appears to be little dorsal expansion of the acromion relative to the scapular blade, contrasting with the morphology of most eusauropods (Upchurch, 1998), including the sympatric eusauropod *Lourinhasaurus* (Lapparent and Zbyszewski, 1957). Instead, this dorsally low acromion more
closely resembles that of the non-neosauropod eusauropods Cetiosaurus (Upchurch and Martin, 2003) and Patagosaurus (Bonaparte, 1986) (Fig. 7). The lateral surface of the acromion is relatively flat to slightly irregular, but is concave anterior to the acromial ridge (Fig. 6A). The latter begins as a very weakly developed, posterodorsally curving ridge at about one-third of the height of the acromion. As it develops in prominence, thickening both anteroposteriorly and as well as laterally, it becomes mainly dorsally oriented, directed at an angle of approximately 100° to the long axis of the scapular blade. The area posterior to the acromial ridge is flat, and there is no excavated area unlike the condition seen in some neosauropods (e.g., Camarasaurus, some diplodocids, and several titanosauriforms; Upchurch et al., 2004). The posterior margin of the dorsal part of the acromion is approximately vertical and does not overhang the dorsal surface of the scapular blade (Fig. 6A), differing from the concave posterior margins seen in many diplodocids and some titanosauriforms (Rauhut et al., 2005; Mannion, 2009). The anteroventrally facing glenoid surface is strongly concave dorsoventrally and mediolaterally, forming an almost lip-like margin. Despite this concave surface, the glenoid is clearly beveled mediolaterally (Fig. 6B, C). This medial deflection is a synapomorphy of somphospondylan titanosauriforms (Wilson, 2002), but is also present in the scapulae of Apatosaurus (Wilson, 2002) and an unnamed Argentinean rebbachisaurid (Haluza et al., 2012). The posteroventral margin of the acromion has an autapomorphic morphology: in other sauropods (Fig. 7), this surface is more shallowly inclined, and there is a notable change of slope just anterior to the blade, such that the posteroventral margin of the acromion and the anteroventral margin of the blade meet at an abrupt angle of approximately 110° (Fig. 6A, C). No subtriangular posteroventral process is present, differing from that observed in Lourinhasaurus (MG 5780) and several titanosauriforms (Carballido et al., 2011), e.g., Angolatitan (Mathews et al., 2011).

As noted above, only the base (proximal end) of the scapular blade is preserved. The lateral surface is mildly convex dorsoventrally, whereas the medial surface is gently concave, resulting in a weakly developed ‘D’-shaped cross-section. Ventrally, the scapular blade is much thicker mediolaterally than at the dorsal margin. No ridges are present along the dorsal or ventral margins of the medial surface, unlike several derived titanosauruses, such as Lirainosaurus (Sanz et al., 1999).

**Coracoid**

The right coracoid is well preserved and nearly complete (Figs. 2, 6D, E; see Table 3 for measurements). In articulation, the dorsal margin of the coracoid lies below the level of the

**TABLE 3. Measurements of the right pectoral girdle of Zby atlanticus (ML 368).**

<table>
<thead>
<tr>
<th>Element</th>
<th>Dimension</th>
<th>Measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scapula</td>
<td>Total preserved anteroposterior length</td>
<td>698</td>
</tr>
<tr>
<td></td>
<td>Dorsoventral height of acromial plate (measured perpendicular to long axis of blade)</td>
<td>550</td>
</tr>
<tr>
<td></td>
<td>Anteroposterior length of acromial plate</td>
<td>804</td>
</tr>
<tr>
<td></td>
<td>Dorsoventral height of glenoid</td>
<td>277</td>
</tr>
<tr>
<td></td>
<td>Maximum mediolateral width of glenoid</td>
<td>232</td>
</tr>
<tr>
<td>Coracoid</td>
<td>Maximum anteroposterior length</td>
<td>569</td>
</tr>
<tr>
<td></td>
<td>Maximum dorsoventral height</td>
<td>779</td>
</tr>
<tr>
<td></td>
<td>Distance from dorsal margin of coracoid to dorsal margin of coracoid foramen</td>
<td>280</td>
</tr>
<tr>
<td></td>
<td>Dorsoventral height of glenoid</td>
<td>249</td>
</tr>
<tr>
<td></td>
<td>Maximum mediolateral width of glenoid</td>
<td>139</td>
</tr>
</tbody>
</table>

All measurements are in millimeters. Note that the scapula and coracoid are described as if the long axis of the scapular blade was oriented horizontally.
scapular acromion plate (Fig. 2), and is separated from the latter by a ‘V’-shaped notch, as is the case in all sauropods, with the exception of some derived somphospondylans (Upchurch, 1995, 1998). In lateral view, the anterior and dorsal margins of the coracoid meet at an angle of approximately 120°, although this corner is strongly rounded (Fig. 6D), in contrast to the more ‘squared’ corner observed in the coracoids of some titanosauriforms and Apatosaurus (Wilson, 2002; Upchurch et al., 2004). The lateral surface is somewhat irregular, although it is mostly mildly convex, whereas the medial surface is concave. The glenoid surface has a ‘D’-shaped outline in posteroverentral view, with a straight medial margin. This articular surface is mildly concave dorsoventrally...
and flat mediolaterally; however, towards its lateral edge it becomes mediolaterally convex, such that this portion of the glenoid is visible in lateral view. Anterior to the glenoid, the ventral margin of the coracoid forms a smoothly concave notch (Fig. 6D). The coracoid foramen is situated slightly above midheight, close to the scapular articular surface.

**Humerus**

The right humerus is a little damaged distally, but is otherwise complete and well preserved (Figs. 2, 8; see Table 4 for measurements). In anterior view, the proximal end is strongly convex mediolaterally, such that the proximomedial and proximolateral corners of the humerus are rounded and do not extend as far dorsally as the rest of the proximal end of the humerus (Fig. 8A, B). This contrasts with the humeri of somphospondylans, in which the proximolateral corner forms a ‘squared’ shape (Upchurch, 1999; Wilson, 2002). The proximal articular surface is strongly rugose and overhangs both the anterior and, particularly, posterior surfaces of the humerus at the anteroposteriorly widest point of the proximal end (at approximately one-third of the width from the medial margin of the humerus) (Fig. 8D, E). The posterior expansion does not extend distally as a ridge. The anterior surface of the proximal third is mediolaterally concave, and also becomes dorsoventrally concave at its proximal-most part as a result of the overhanging proximal end. At approximately an equal distance from the lateral and medial margins, there is a low, rounded, striated muscle scar within this anterior fossa, situated about 300 mm from the proximal end of the humerus. The posterior surface of the proximal two-thirds of the humerus is flat to mildly convex mediolaterally, becoming more strongly convex towards the lateral and medial margins (Fig. 8F). The exception to this is the proximomedial corner of the humerus, which is deflected slightly posteriorly, and thus creates a mediolaterally curved, shallow concavity on the posterior surface in this region.

The anteriorly projecting deltopectoral crest extends along the proximal 40% of the humerus (Fig. 8B). Along its proximal half, the deltopectoral crest is mediolaterally narrow and is deflected slightly laterally, whereas it thickens mediolaterally distally. There is no medial expansion of this crest across the anterior surface of the humerus, contrasting with that seen in many titanosauriforms (Wilson, 2002; Upchurch et al., 2004; Mannion and Calvo, 2011; Mannion et al., 2013). The lateral surface of the deltopectoral crest lacks rugosities. The humerus expands anteriorly, but also the same amount posteriorly, at the point of the thickened distal half of the deltopectoral crest, giving the humerus a sinuous outline in lateral view (Fig. 8E). This posterior expansion is the result of a dorsoventrally elongate, raised bulge along the lateral margin of the posterior surface of the humerus (Fig. 8E, F). Although a bulge or tuberosity, interpreted as the attachment site for M. latissimus dorsi, is present in a similar

| Table 4. Measurements of the right humerus, radius, and ulna of Zby atlanticus (ML 368). |
|-----------------------------------------------|-----------------------------------------------|-----------------------------|
| Element                                      | Dimension                                         | Measurement                |
| Humerus                                      | Proximodistal length                             | 1530                       |
|                                              | Proximal end maximum mediolateral width         | 540                        |
|                                              | Proximal end maximum anteroposterior width      | 190                        |
|                                              | Distance from proximal end of humerus to distal end of deltopectoral crest | 660                        |
|                                              | Midshaft mediolateral width                      | 238                        |
|                                              | Midshaft anteroposterior width                   | 130                        |
|                                              | Minimum circumference of shaft (approximately midshaft) | 620                        |
|                                              | Distal end maximum mediolateral width            | 405                        |
|                                              | Distal end maximum anteroposterior width (measured on lateral condyle) | 183                        |
|                                              | Distal end maximum anteroposterior width (measured on medial condyle) | 135                        |
| Radius                                       | Proximodistal length                             | 1040                       |
|                                              | Proximal end mediolateral width                  | 283                        |
|                                              | Proximal end maximum anteroposterior width      | 67                         |
|                                              | Midshaft mediolateral width                      | 102                        |
|                                              | Midshaft anteroposterior width                   | 96                         |
|                                              | Midshaft circumference                           | 350                        |
|                                              | Distal end mediolateral width                    | 212                        |
|                                              | Distal end anteroposterior width                 | 148                        |
| Ulna                                         | Proximodistal length                             | 1060                       |
|                                              | Proximal end mediolateral width (equivalent to anteromedial arm length) | 328                        |
|                                              | Proximal end anteroposterior width (equivalent to anterolateral arm length) | 255                        |
|                                              | Distal end maximum mediolateral width            | 157                        |
|                                              | Distal end maximum anteroposterior width         | 215                        |

All measurements are in millimeters.
position in some latest Cretaceous saltasaurids (Borsuk-Bialynicka, 1977; Otero, 2010), this is a considerably smaller structure than in Zby and does not produce the posterior expansion seen in that taxon. A bulge of this prominence is not seen in any other sauropod, and as such this morphology is considered an autapomorphy of Zby.

In anterior view, the lateral margin of the diaphysis (approximately the middle third of the humerus) is concave (Fig. 8B), differing from the straight margin seen in some somphospondylans (Curry Rogers, 2005; Mannion et al., 2013). At midshaft, the humerus is mediolaterally wide and anteroposteriorly compressed (ratio = 1.83), comparable to the higher end of the range of values observed in most sauropods (Mannion et al., 2012). There is little torsion between the proximal and distal halves of the humerus.

As already mentioned, the distal end is not as well preserved as the rest of the humerus and the anterior surface appears to have undergone some erosion. There is a shallow, mediolaterally oriented concavity between the lateral and medial condyles on the distal-most part of the anterior surface, but these condyles are weakly developed (Fig. 8B). A deep, subtriangular supracondylar fossa is present on the medial two-thirds of the posterior surface.

FIGURE 8. Right humerus of Zby atlanticus, n. gen. et sp. (ML 368). A, proximal; B, anterior; C, distal; E, medial; F, lateral, and G, posterior views. Abbreviations: dtp, deltopectoral crest; ldf, laterodistal flange; plb, posterolateral bulge; scf, supracondylar fossa. Scale bar equals 500 mm.
of the distal end (Fig. 8C, F), although its depth has been partly accentuated by crushing. This fossa is demarcated by rounded, rather than sharp, ridges, in contrast to the condition in many titanosaurs (Upchurch et al., 2004). The undivided distal articular surface is rugose and anteroposteriorly convex (Fig. 8C), although this articular surface does not extend onto the anterior and posterior surfaces of the humerus; however, this surface is slightly deflected, such that the distal surface is partly visible in anterior view. There is some posterior expansion of the humerus along the lateral distal condyle, but in general the distal end is not strongly expanded anteroposteriorly relative to the shaft. Markedly anteroposteriorly expanded distal humeral condyles are regarded as an autapomorphy of Turiasaurus (Royo-Torres et al., 2006); however, their apparent expansion in that taxon is more the result of moderately deep anterior and posterior fossae than actual anteroposterior expansion relative to the shaft (CPT-1195-1210). In Zby, the laterodistal corner of the humerus displays an unusual and probably autopomorphic morphology: it does not expand as far anteriorly as the rest of the distal end of the humerus, instead forming an anteroposteriorly thin flange of bone (Fig. 8B, C, E).

### Radius

The flat, rugose proximal end of the complete right radius (Figs. 2, 9A, B; see Table 4 for measurements) is extremely compressed anteroposteriorly and very prominently expanded mediolaterally, with prominent lateral and, particularly, medial projections that narrow anteroposteriorly towards their tips. The anteroposterior dimension of the proximal end is less than half that of the distal end (Fig. 9A, C; Table 4). In most sauropods, these two diameters are subequal, with the proximal end usually slightly broader anteroposteriorly than the distal end. Zby shares this unusual morphology of the proximal radius with Turiasaurus (CPT-1195-1210; P.U. and P.D.M., pers. observ., 2009).

In anterior view, the lateral margin of the diaphysis is fairly straight, whereas the medial margin is gently sinuous (Fig. 9B). The anterior surface of the radius is flat along the proximal and distal thirds, and mediolaterally convex along the midshaft. At approximately one-third of the length from the proximal end, a ridge runs along the anteroposterior margin for the remainder of the radius length (Fig. 9D). Similarly extensive ridges are present in a number of titanosaurs (Curry Rogers, 2005), as well as more basal macronarians, e.g., the Early Cretaceous Spanish taxon Losillasaurus (MPG specimen; P.U. and P.D.M., pers. observ., 2009). A second, parallel ridge is present on the posterior surface of the distal third, directed ventrolaterally (Fig. 9D). In anterior view, the medial half of the distal end is relatively flat, whereas laterally it is strongly bevelled at an angle of approximately 35° (Fig. 9B). Although strongly bevelled distal radii are generally regarded as a titanosaur feature (Wilson, 2002), there is some variation between taxa. For example, in some titanosaurids, almost the entire distal surface is laterally beveled (e.g., Opisthocoelicauda; Borsuk-Bialynicka, 1977), whereas in others only the lateral half is upturned (e.g., Malawisaurus; Gomani, 2005).

Furthermore, a number of non-titanosaurids show the second of these morphologies (e.g., Apatosaurus, Gilmore, 1936:fig. 12; Ferugnasaurus, Alfanov and Averianov, 2003:fig. 8; and Tehuelchisauros, Carballido et al., 2011:fig. 17), although the beveling in these taxa is closer to 20° (Mannion et al., 2013). Zby shares this extreme, laterally biased beveling with Turiasaurus (Royo-Torres et al., 2006:fig. 1e; note that the radius is figured upside down). The distal end is mediolaterally and anteroposteriorly expanded, with the latter expansion mainly restricted to the posterior margin, for articulation with the anteromedial fossa on the distal end of the ulna. The distal articular surface is rugose and mildly convex, and has an elliptical or ‘D’-shaped outline, with the flatter (mildly convex) margin of this ‘D’ facing posteriorly (Fig. 9C).

### Ulna

The right ulna is a relatively slender element that is approximately the same length as the radius (Figs. 2, 9E–G; see Table 4 for measurements). In proximal end view, the anteromedial and anterolateral processes meet each other at approximately 110° (Fig. 9E). The anteromedial process is longer than the anterolateral one (ratio = 1.29), which is similar to the condition in most sauropods (e.g., Camarasaurus, Ostrom and McIntosh, 1966:pl. 53; Omelouaris, He et al., 1988), but differs from the subequal proximal processes seen in some diplodocoids and titanosauriforms (Wilson, 2002). These processes define a deep anterior fossa that receives the proximal end of the radius (Fig. 9F), as in other eusauropods (Wilson and Sereno, 1998). Short, dorsoventrally oriented ridges for muscle attachment are present within this anterior fossa. The convex olecranon region, where the anteromedial and anterolateral proximal processes meet, is low and poorly defined. Thus, Zby has the derived reduced olecranon that occurs in most sauropods except for some titanosaurids, where a more prominent olecranon is reacquired (Upchurch, 1995, 1998; Wilson, 2002). Passing distally along the shaft of the ulna, the anteromedial and anterolateral processes and radial fossa gradually decrease in prominence, disappearing at around midheight. The posterior surface of the proximal half of the ulna is strongly concave mediolaterally (Fig. 2), although this has been accentuated by crushing. This concavity is bounded by the distal extension of the anteromedial process and a ridge formed along the proximal half of the posterolateral margin. The posterior surface of the distal half of the ulna lacks the deep vertical groove seen in Turiasaurus (CPT-1195-1210; P.U. and P.D.M., pers. observ., 2009) and Losillasaurus (MCNV Lo-8; P.U. and P.D.M., pers. observ., 2009). Along approximately the distal quarter of the ulna, the anteromedial surface is marked by a shallow concavity for articulation with the radius (Fig. 9F). This concavity is bounded anteriorly and posteriorly by dorsoventrally elongate ridges (Fig. 9F). The anterior of these two ridges appears to extend slightly further proximally than the concavity, and is deflected posteriorly. In distal view (Fig. 9G), the ulna has an approximately ‘D’-shaped outline, with its long axis oriented anteroposteriorly (as a result of the posterior expansion of the distal end), and an anteroposteriorly convex lateral margin and concave medial margin. Zby lacks the extreme mediolateral compression of the distal end seen in Turiasaurus (Royo-Torres et al., 2006) (anteroposterior to mediolateral ratio of distal end = 1.85 in Turiasaurus and 1.37 in Zby). As in the humerus and radius, the articular ends of the ulna are rugose.

### Manus

No carpal bones were found, but three right metacarpals and three right phalanges were recovered and are identified as metacarpals I, III, and IV, and phalanges I-1, I-2, and II-1 (Figs. 2, 10, 11; see Table 5 for measurements). Although the manus is incomplete, the three preserved metacarpals suggest that the metacarpus formed the vertically oriented ‘colonnade’ arrangement that occurs in most eusauropods, with the five original metacarpals forming a ‘horseshoe’-shaped structure in proximal view (Upchurch, 1995, 1998; Wilson and Sereno, 1998; Wilson, 2002, 2005). Evidence for the presence of this derived manus structure in Zby includes the subtriangular outline of the proximal ends of metacarpals III and IV (Fig. 10), and the long striated attachment areas along the proximal halves of the metacarpal shafts (Wilson, 2002; Upchurch et al., 2004). The longest of the metacarpals is metacarpal III, followed by metacarpal IV, and then metacarpal I. The ratio of the length of the longest metacarpal to radius length is 0.38; this demonstrates...
FIGURE 9. Right radius and ulna of *Zby atlanticus*, n. gen. et sp. (ML 368). Radius in A, proximal; B, anterior; C, distal; D, posterior views; ulna in E, proximal; F, anterior; G, distal views. **Abbreviations**: af, anterior fossa; alp, anterolateral process; amc, anteromedial concavity; amp, anteromedial process; lb, lateral beveling; mp, medial projection; plr, posterolateral ridge; rds, ridges; sr, second ridge. Scale bar equals 200 mm.
that Zby retained the plesiomorphic short metacarpals observed in basal eusauropods and diplodocoids, rather than possessing the derived macronarian condition in which this ratio is 0.45 or higher (Wilson and Sereno, 1998). The ratios of the lengths of metacarpals I to III and IV are 0.92 and 0.96, respectively, comparable to most derived eusauropods, with the exception of some titanosaurans (Upchurch, 1998; Wilson and Sereno, 1998). All manual elements are described as if they were held in a horizontal position, rather than the in vivo vertical position. Metacarpals are also described with the long axis of the distal end oriented mediolaterally, which removes the difficulty of describing the in vivo orientation of metacarpal I.

Metacarpal I (Fig. 10A–D) has a ‘D’-shaped outline in proximal view, as in most sauropods (Upchurch et al., 2004), with the flattened margin of this shape facing laterally and slightly ventrally. The proximal articular surface is rugose and irregular. The lateral surface of the proximal half forms a striated triangular region that is dorsoventrally (and slightly proximodistally) concave, with the ‘D’-shaped cross-section also extending along the proximal half. Prominent ridges demarcate the dorsal and ventral margins of this triangular region. The distal half of the metacarpal is twisted in relation to the proximal half. The lateral surface of the distal third also forms distinct ridges at the dorsal and ventral margins, with a striated surface in between. There is some

<table>
<thead>
<tr>
<th>Dimension</th>
<th>Mc. I</th>
<th>Mc. III</th>
<th>Mc. IV</th>
<th>I-1</th>
<th>I-2</th>
<th>II-1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum proximodistal length</td>
<td>365</td>
<td>398</td>
<td>382</td>
<td>82/65</td>
<td>172</td>
<td>47</td>
</tr>
<tr>
<td>Proximal end maximum mediolateral width</td>
<td>142</td>
<td>116</td>
<td>117</td>
<td>97</td>
<td>49</td>
<td>65</td>
</tr>
<tr>
<td>Proximal end maximum dorsoventral height</td>
<td>122</td>
<td>105</td>
<td>113</td>
<td>56</td>
<td>111</td>
<td>65</td>
</tr>
<tr>
<td>Midshaft maximum mediolateral width</td>
<td>79</td>
<td>90</td>
<td>71</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Midshaft maximum dorsoventral height</td>
<td>68</td>
<td>90</td>
<td>62</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Midshaft circumference</td>
<td>240</td>
<td>275</td>
<td>213</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Distal end maximum mediolateral width</td>
<td>109</td>
<td>158</td>
<td>139</td>
<td>47</td>
<td>—</td>
<td>49</td>
</tr>
<tr>
<td>Distal end maximum dorsoventral height</td>
<td>88</td>
<td>98</td>
<td>76</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

All measurements are in millimeters. Note that for the proximodistal length of phalanx I-1, the lengths along the lateral, followed by the medial, margin are provided.
evidence for a shallow subcircular fossa on the medial surface of the distal end, but this might be a preservational artifact. The distal end has dorsolateral and ventromedial projections, giving metacarpal I a rhomboidal outline in distal end view. The lateral half of the distal end extends more distally than that of the medial half, giving the distal end a beveled appearance in dorsal view, as is the case in *Shunosaurus* and a number of titanosauriforms (Wilson, 2002). The dorsolateral margin, close to the distal end, lacks the two rounded bulges present in metacarpal I of *Turiasaurus* (CPT-1195-1210; O.M., pers. observ., 2011). Although the ventral margin of the distal end is mildly concave, this does not continue further proximally along the ventral surface, and distinct medial and lateral distal condyles are absent. The distal articular surface extends up onto the dorsal surface, with this extension most prominent on the medial half. This dorsal extension differs from the condition in most titanosauriforms, whereby this articular surface is restricted to the distal end (D’Emic, 2012). The distal articular surface is very mildly concave mediolaterally and convex dorsoventrally.

Metacarpal III (Fig. 10E–H) is missing a small amount of material from the margins of its proximal end, but clearly had a subtriangular outline in proximal view, with the apex of this triangle pointing ventrally. Its proximal articular surface is convex in all directions. The proximal triangular cross-section is maintained along the proximal half of the metacarpal, formed by a mediolaterally convex dorsal surface, and ventrolaterally and ventromedially facing striated surfaces that meet to form a rounded but prominent ventral midline ridge. A sharp ridge is also formed where the dorsal and lateral margins meet. Along the distal half, the cross-section of the metacarpal is more elliptical. At the distal end, the lateral and medial surfaces are closer to vertical, although the medial surface is slightly ventrally deflected. The medial half of the distal end extends slightly further distally than that of the lateral half, and is also dorsoventrally taller. As in metacarpal I, the distal articular surface extends onto the dorsal surface of the metacarpal, and is again medially biased in its dorsal extension. The distal articular surface is strongly rugose, dorsoventrally convex, and saddle-shaped mediolaterally, where it becomes centrally concave. The ventral margin of the distal end is gently concave, but this concavity does not extend proximally along the ventral surface.

Although missing a small amount of material from the ventral margin, the proximal end of metacarpal IV (Fig. 10I–L) has a triangular outline, with the apex of this triangle pointing ventrally and continuing along the proximal half of the shaft as a ventromedially projecting ridge, eventually merging into the ventromedial margin. The proximal articular surface is rugose and irregularly convex. The proximal half of the medial surface faces almost entirely medially, and is flat to very mildly concave, as well as striated. Similarly, the proximal half of the lateral surface is also flat to mildly concave and striated, but faces ventrolaterally. Along the distal half, the metacarpal is elliptical, with the long axis oriented mediolaterally. The dorsal surface at the distal end overhangs the medial and, particularly, the lateral surfaces. As in metacarpals I and III, the distal articular surface extends onto the dorsal surface of the metacarpal, although the medial bias is
The teeth and forelimbs of Zby and Turiasaurus are morphologically very similar and share several potentially derived states. For example, the teeth possess the same ‘heart’-shaped crown morphology that might characterize a turiasaur clade (Royo-Torres et al., 2006; Royo-Torres and Upchurch, 2012), and the proximal end of the radius is unusual in its extreme anteroposterior compression. There are other character states shared by Zby and Turiasaurus, such as the low SI values for tooth crowns, the deep intercondylar fossa bounded by rounded ridges on the distal part of the posterior surface of the humerus, and the beveling of the lateral half of the distal articular surface of the radius, but these features also occur in several other sauropod taxa (see below). Given that Zby and Turiasaurus are approximately contemporaneous and both occur in the Iberian Peninsula, a prima facie case could be made that these taxa are congeneric or even conspecific. Indeed, Zby was first reported as a specimen assigned to Turiasaurus riodevensis (Mateus, 2009). However, the more detailed comparisons presented here indicate that there are some significant differences between Zby and Turiasaurus that justify a genus level distinction between these two taxa. In particular, Turiasaurus possesses the following character states that are absent in Zby (an asterisk indicates an autapomorphy of Turiasaurus): (1) the distal half of the posterior surface of the ulna possesses a well-developed vertical groove; (2) strong mediolateral compression of the distal end of the ulna; and (3) dorsolateral bulges near the distal end of metacarpal I* (Royo-Torres et al., 2006, 2009; Royo-Torres and Upchurch, 2012). Similarly, Zby possesses the following character states that are absent in Turiasaurus (an asterisk indicates an autapomorphy of Zby): (1) a prominent vertical ridge on the posterior surface of the humerus, level with the deltopectoral crest*; (2) an anteroposteriorly thin flange of bone projecting from the lateral margin of the distal end of the humerus*; (3) a well-developed interosseous ridge extending vertically on the posterior surface of the radius; and (4) the subrectangular outline of the ungual of manual digit I in lateral view*. Given that Turiasaurus and Zby can currently be compared only via their teeth and forelimb elements, there would seem to be a relatively large number of differences between them. We therefore provisionally conclude that Zby and Turiasaurus are closely related, but generically distinct, taxa that potentially represent members of a Late Jurassic radiation of turiasaurs (see below).

The Wider Phylogenetic Affinities of Zby and Other Turiasaurs

The placement of Zby within the wider context of sauropod phylogeny inevitably requires some consideration of the content and relationships of Turiasaurus. The latter clade was named by Royo-Torres et al. (2006) and is defined as all taxa that are more closely related to Turiasaurus than to Saltasaurus. One view is that the Turiasaurus is a clade that is closely related to, but lies outside of, the Neosauropoda (Royo-Torres et al., 2006, 2009; Royo-Torres and Upchurch, 2012). This clade is potentially represented by the Late Jurassic Iberian forms Turiasaurus, Losillasaurus, Galveosaurus, and Zby, some isolated teeth from the Middle and Late Jurassic of England and France, and perhaps some material from Tendaguru in Tanzania (see review in Royo-Torres and Upchurch, 2012). However, the monophyly of the Turiasaurus is not universally accepted, and some studies have argued that at least one putative turiasaur (Galveosaurus) is a macroranian (Barco et al., 2006; Carballido et al., 2011; D’Emic, 2012; Mannion et al., 2013).

Turiasaurus, as the clade specifier, is automatically a member of the Turiasaurus. This genus has been placed outside of Neosauropoda in all cladistic analyses that have included it (Royo-Torres et al., 2006; Carballido et al., 2012; Royo-Torres and Upchurch, 2012). Losillasaurus was initially regarded as a flagellicaudatan diplodocoid (Casanovas et al., 2001), but all subsequent analyses have agreed that this taxon lies outside of Neosauropoda (Rauhut et al., 2005; Harris, 2006; Whitlock, 2011a; Mannion et al., 2012; Royo-Torres and Upchurch, 2012).

DISCUSSION

Zby and Turiasaurus

The teeth and forelimbs of Zby and Turiasaurus are morphologically very similar and share several potentially derived states.
The relationships of *Galveosaurus* are perhaps the most controversial. Barco et al. (2006; see also Carballido et al., 2011; Mannion et al., 2013) suggested that *Galveosaurus* is actually a basal macronarian and noted five synapomorphies that support this placement. In contrast, Royo-Torres and Upchurch (2012) pointed out that four of these synapomorphies are more widespread among eusauropod taxa and found that addition of new data on the skull of *Turiasaurus* strengthened the support for the placement of *Galveosaurus* within the Turiasauria (the latter being recovered as the sister taxon to Neosauropoda). Nevertheless, the cervical vertebrae of *Galveosaurus* possess the camellate tissue structure that is generally indicative of titanosauriform affinities, and the taxon also shares anteriorly placed neural arches in middle caudal vertebrae with other titanosauriforms (Calvo and Salgado, 1995; Upchurch, 1998; Wilson and Sereno, 1998; Upchurch et al., 2004; see also D’Emic [2012] for proposed titanosauriform affinities of *Galveosaurus*).

These current uncertainties reflect both disagreements over the scoring of key phylogenetic characters, and the fact that no single study has included all four of the potential turiasaurian taxa. Although it would be preferable here to test this potential close relationship between *Turiasaurus* and *Zby*, as well as their placement within Eusauropoda, through cladistic analysis, existing matrices are poorly suited to such a task. All recent examinations of non-neosauropod relationships are based on largely unrevised (or only partially revised) reanalyses of the data matrices of Wilson (2002) and Upchurch et al. (2004), with little in the way of character modification or addition (Whitlock et al., 2011). A full and much needed revision of available data sets is beyond the scope of this work; instead, below we briefly review the character states present in *Zby* that we believe will play an important role in resolving its relationships in future analyses and that are likely to influence the placement of some of the other turiasaurian taxa.

Most of the character states that can be observed in *Zby* support the view that it represents a non-neosauropod eusauropod. For example, *Zby* possesses the following synapomorphies of the Eusauropoda (or slightly more or less inclusive clades within Sauropoda): (1) spathulate tooth crowns with a concave lingual surface and mesial and distal grooves on the labial surface (Upchurch, 1995, 1998); (2) the dorsal margin of the coracoid does not project as far dorsally as the proximal expansion of the scapula, and the dorsal margins of these two elements are separated from each other by a ‘V’-shaped notch in lateral view (Upchurch, 1998; Harris, 2006); (3) absence of the posterior proximal humerus on the distal part of the humerus (Yates, 2007); (4) the proximal end of the ulna is triradiate and has a poorly developed olecranon (Wilson and Sereno, 1998); (5) reduced carpus with two or fewer ossified carpal elements (Upchurch, 1998); (6) metacarpals held vertically and form a ‘U’-shaped colonnae (Upchurch, 1995, 1998); and (7) proximal manual phalanges are wider mediolaterally than long anteroposteriorly (Wilson, 2002; Yates, 2007). *Zby* also displays a number of relatively plesiomorphic states that are consistent with its placement outside of Neosauropoda or Macronaria, although inferences based on such plesiomorphies should be treated with caution because they indicate an absence of evidence for a given phylogenetic relationship rather than evidence against that relationship. For example, it seems probable that proximally unbridged anterior chevrons represents a synapomorphy of Neosauropoda, based on their presence in basal diplodocoids (*Haplocaentosaurus* and rebbachisaurids; Whitlock, 2011a; Mannion et al., 2012) and virtually all macronarians (Upchurch, 1998; Upchurch et al., 2004; Mannion and Calvo, 2011). Thus, the presence of a proximally bridged anterior chevron in *Zby* is consistent with its placement outside of Neosauropoda.

Late Jurassic Portuguese Sauropod Diversity and Paleoeology

The description of *Zby atlanticus* adds a fourth valid sauropod taxon to the Late Jurassic of Portugal. This fauna is often considered extremely similar to that of the contemporaneous Morrison Formation of North America (see Mateus, 2006; Mannion et al., 2012, and references therein), with the previously described Portuguese sauropods *Dinheirosaurus*, *Lourinhhasaurus*, and *Lusotitan* regarded as closely related to the North American taxa *Supersaurus*, *Camarasaurus*, and *Brachiosaurus*, respectively. However, there is no evidence yet for a Morrison sauropod closely related to *Zby*, suggesting that this may be a genuine difference between the two faunas, with sauropods potentially absent from North America and restricted to Europe (and possibly Africa; Royo-Torres and Cobos, 2009).

One interesting and potentially unusual aspect of the Late Jurassic of Portugal is the preponderance of large-bodied sauropods, with no small- or medium-sized adult sauropods
known (Mateus et al., 2009). Whereas in contemporaneous faunas, such as the Morrison, Tendaguru, and Cañadón Calcáreo formations, low-to-medium-browsing niches might have been occupied by smaller-bodied sauropods (e.g., dicraeosaurids) (though see Whitlock [2011b] for a more complex pattern regarding feeding heights among sauropods), it is possible that ornithischian dinosaurs, such as the long-necked stegosaur Miragaia longicollum, instead filled such niches in the Late Jurassic of Portugal (Mateus et al., 2009). However, a taphonomic bias cannot yet be entirely ruled out as an explanation, because currently no juvenile sauropod remains are known from the Late Jurassic of Portugal, and thus there may be some preservational bias against small-bodied sauropods.

ACKNOWLEDGMENTS

We would like to express our gratitude firstly to N. Christiansen, H. Mateus, V. Ribeiro, A. Sarzedas, and all volunteers that helped to excavate the skeleton of Zby, as well as to S. Mateus for his illustrations. The staff and volunteers at the Museu da Lourinhã are also thanked for their help and hospitality. We wish to thank all those who allowed us to study specimens in their care, in particular R. Royo-Torres and L. Alcalá for discussion and access to Turiasaurus. J. L. Carballido is thanked for providing additional photographs of Turiasaurus. Reviews by J. L. Carballido and J. A. Wilson greatly improved the quality of this work. English translations of many of the foreign-language papers used in this study are available at The Polyglot Paleontologist Web site (www.paleoglot.org). O.M.’s work was funded by the Portuguese ‘Fundação para a Ciência e Tecnologia,’ project ‘Dinoeigs PTDC/BIA-EVF/113222/2009.’ P.D.M.’s research was supported by an Imperial College London Junior Research Fellowship, and P.U. would like to acknowledge funding from The Palaeontological Association and the Abbey International Collaboration scheme, enabling study of sauropod specimens in Portugal and Spain.

LITERATURE CITED


Mateus, O. 2006. Late Jurassic dinosaurs from the Morrison Formation (USA), the Lourinhã and Alcoaça formations (Portugal), and the Tendaguru Beds (Tanzania): a comparison. New Mexico Museum of Natural History and Science Bulletin 36:223–231.


Young, C.-C., and X.-J. Zhao. 1972. Mamenchisaurus hochuanensis sp. nov. Institute of Vertebrate Paleontology and Paleoanthropology Monographs (Series A) 8:1–30. [Chinese]