Journal of Vertebrate Paleontology 34(3):618–634, May 2014

ARTICLE

ZBY ATLANTICUS, A NEW TURIASAURIAN SAUROPOD (DINOSAURIA, EUSAUROPODA) FROM THE LATE JURASSIC OF PORTUGAL

OCTÁVIO MATEUS,*[,1,2] PHILIP D. MANNION,[3] and PAUL UPCHURCH[4]
[1]CICEGe, Faculdade de Ciências e Tecnologia, FCT, Universidade Nova de Lisboa, 2829-516 Caparica, Portugal, omateus@fct.unl.pt;
[2]Museu da Lourinhã, Rua João Luis de Moura, 2530-157 Lourinhã, Portugal;
[3]Department of Earth Science and Engineering, Imperial College London, South Kensington Campus, London SW7 2AZ, U.K., philipdmannion@gmail.com;
[4]Department of Earth Sciences, University College London (UCL), Gower Street, London WC1E 6BT, U.K., p.upchurch@ucl.ac.uk

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 lourinhanensis* (Bonaparte and Mateus, 1999; Mannion et al., 2012), *Lourinhasaurus alenquerensis* (Lapparent and Zbyszewski, 1957; Dantas et al., 1998), and *Lusotitan 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 *Lusotitan* 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; Mocho 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

---

*Corresponding author.

Member also includes the sauropod *Dinheirosaurus lourinhanensis*, the theropods *Lourinhanosaurus antunesi*, *Torvosaurus gurneyi*, and *Ceratosaurus* sp., as well as the ornithischians *Miragaia longicollum*, *Hypsilophodon* sp., '*Trimucrodon cuneatus*,' and indeterminate remains attributable to basal Iguanodontia (Bonaparte and Mateus, 1999; Antunes and Mateus, 2003; Mateus, 2006; Mateus et al., 2006, 2009). This geologic member has also produced dinosaur eggs and embryo remains (Mateus et al., 1998; Ricqlès et al., 2001), as well as several dinosaur tracks (Milàn et al., 2005; Mateus and Milàn, 2010).

Here we describe this new sauropod material and compare it with approximately contemporaneous sauropods from Iberia and elsewhere. In particular, we examine the proposal that it represents a turiasaurian sauropod, through detailed comparisons with *Turiasaurus*.

Institutional Abbreviations—**CPT**, Museo de la Fundación Conjunto Paleontológico de Teruel-Dinópolis, Aragón, Spain; **MG**, Museu Geológico, Lisbon, Portugal (formerly MIGM and SGP); **ML**, Museu da Lourinhã, Lourinhã, Portugal; **MPG**, Museo Paleontológico de Galve, Aragón, Spain.

SYSTEMATIC PALEONTOLOGY

SAUROPODA Marsh, 1878
EUSAUROPODA Upchurch, 1995
TURIASAURIA Royo-Torres, Cobos, and Alcalá, 2006
ZBY ATLANTICUS, n. gen. et sp.
(Figs. 1–11)

Etymology—*Zby* (zee-bee) after the Russian-French paleontologist Georges Zbyszewski (1909–1999), who devoted his career to the geology and paleontology of Portugal; *atlanticus* because the specimen was found in a scenic bay over the Atlantic Ocean.

Holotype—ML 368. Associated partial skeleton comprising a complete tooth with root, a fragment of cervical neural arch, an anterior chevron, and a right pectoral girdle and forelimb consisting of a distally incomplete scapula, coracoid, humerus, radius, ulna, metacarpals I, III, and IV, and manual phalanges I-1, I-2, and II(?)-1. Casts of the specimen (pectoral girdle and forelimb only) are on display at the Wills Memorial Building in Bristol (U.K.), and the Saurier Museum Aathal (Aathal, Switzerland).

Diagnosis—*Zby atlanticus* can be diagnosed by four autapomorphies: (1) posteroventral margin of the scapular acromial plate and the anteroventral margin of the blade meet at an abrupt angle (approximately 110°) following a change in slope; (2) humerus expands both anteriorly and posteriorly at the point of the distal half of the deltopectoral crest, as a result of a prominent posterior bulge; (3) laterodistal corner of humerus forms an anteroposteriorly thin flange of bone that does not expand as far anteriorly as the rest of the distal end of the humerus; and (4) manual ungual phalanx I-2 subrectangular in lateral view.

Locality and Horizon—Vale Pombas, municipality of Lourinhã, central west Portugal; coordinates 39°17′N, 9°20′W; top of the Amoreira–Porto Novo Member of the Lourinhã Formation, late Kimmeridgian, Upper Jurassic (Mateus, 2006; Schneider et al., 2009; Kullberg et al., 2012).

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 resorbtion 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.

TABLE 1. Measurements of the tooth of *Zby atlanticus* (ML 368).

Dimension	Measurement
Total apicobasal length of crown + root	106
Apicobasal length of crown	38
Maximum mesiodistal width of crown	28
Maximum labiolingual width of crown	14

All measurements are in millimeters.

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 *Oplosaurus*; 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, anastamosing 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), *Patagosaurus* (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

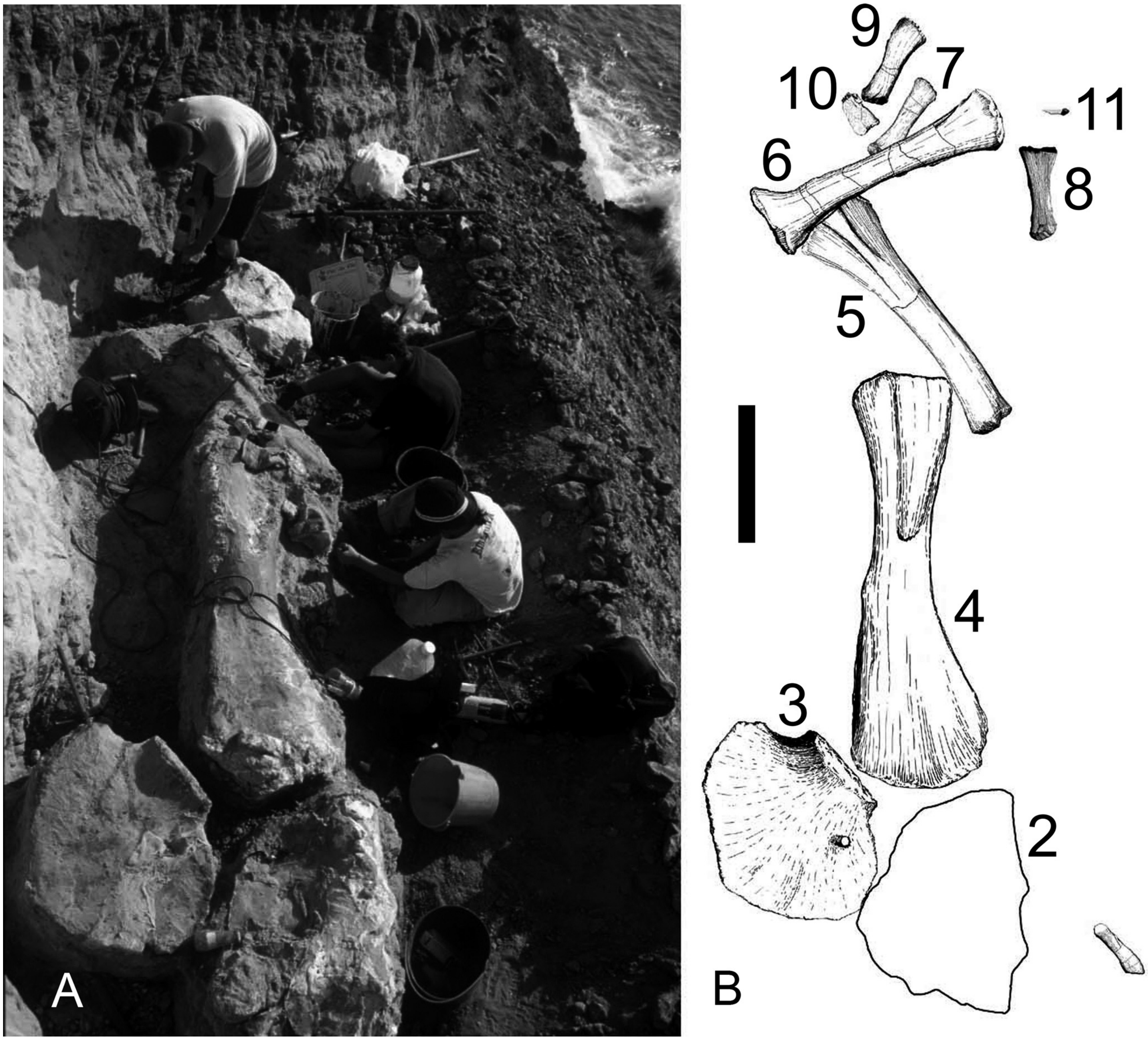

FIGURE 1. Locality of *Zby atlanticus*, n. gen. et sp. **A**, photograph of the elements in the ground; **B**, line drawing of the elements in the ground. Numbers refer to (1) chevron; (2) scapula; (3) coracoid; (4) humerus; (5) ulna; (6) radius; (7) metacarpal I; (8) metacarpal III; (9) metacarpal IV; (10) manual ungual phalanx I-2; (11) tooth. Note that the additional two manual phalanges are not visible in this view. Scale bar equals 500 mm.

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 Turiasauria (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

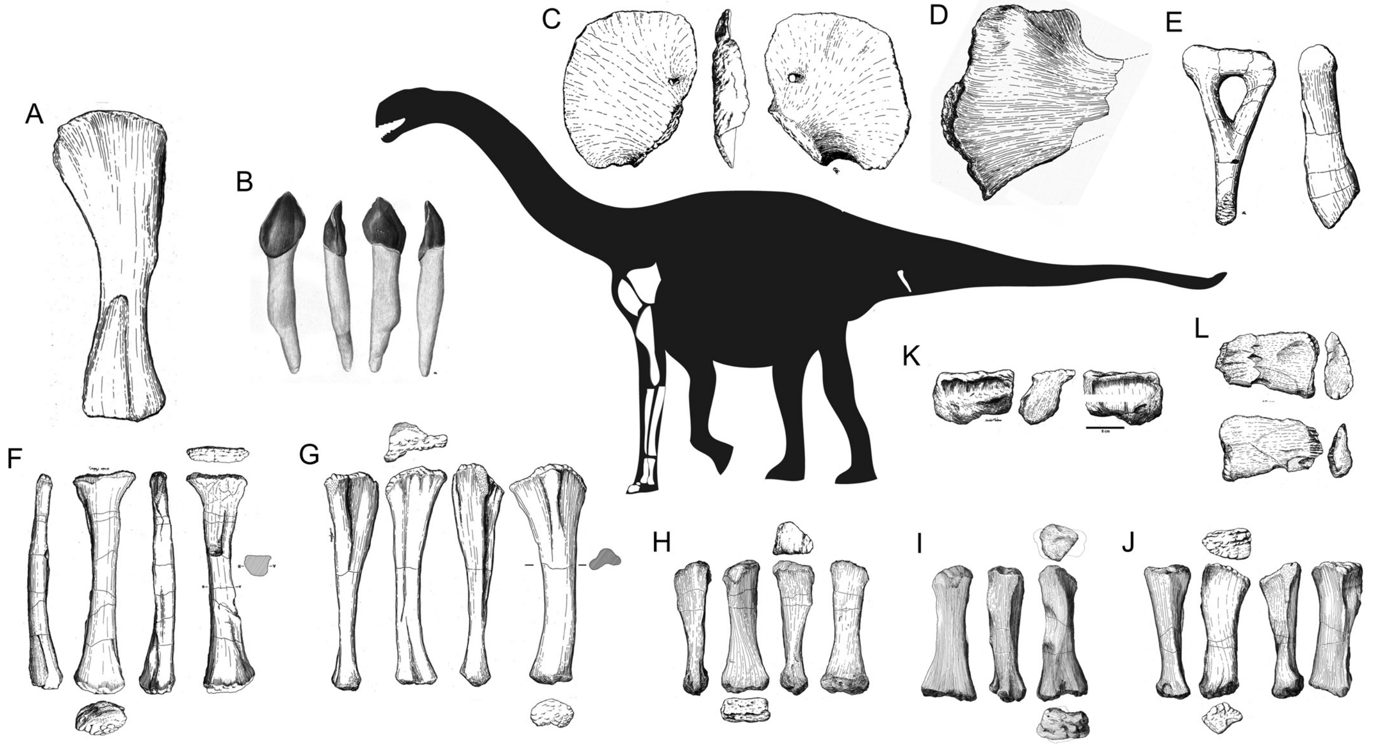

FIGURE 2. Silhouette outline and line drawings of *Zby atlanticus*, n. gen. et sp. **A**, humerus; **B**, tooth; **C**, coracoid; **D**, scapula; **E**, chevron; **F**, radius; **G**, ulna; **H**, metacarpal I; **I**, metacarpal III; **J**, metacarpal IV; **K**, manual phalanx I-1; **L**, manual ungual claw I-2. Figures not proportionally to scale to one another.

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 posteroventrally 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.'

TABLE 2. Measurements of the anterior chevron of *Zby atlanticus* (ML 368).

Dimension	Measurement
Dorsoventral height of chevron	217*
Mediolateral width across proximal end	110
Anteroposterior width of proximal ramus	40
Dorsoventral height of hemal canal	57
Maximum mediolateral width of hemal canal	26
Maximum anteroposterior width of distal blade	59*

All measurements are in millimeters. An asterisk indicates that a measurement is based on an incomplete element.

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

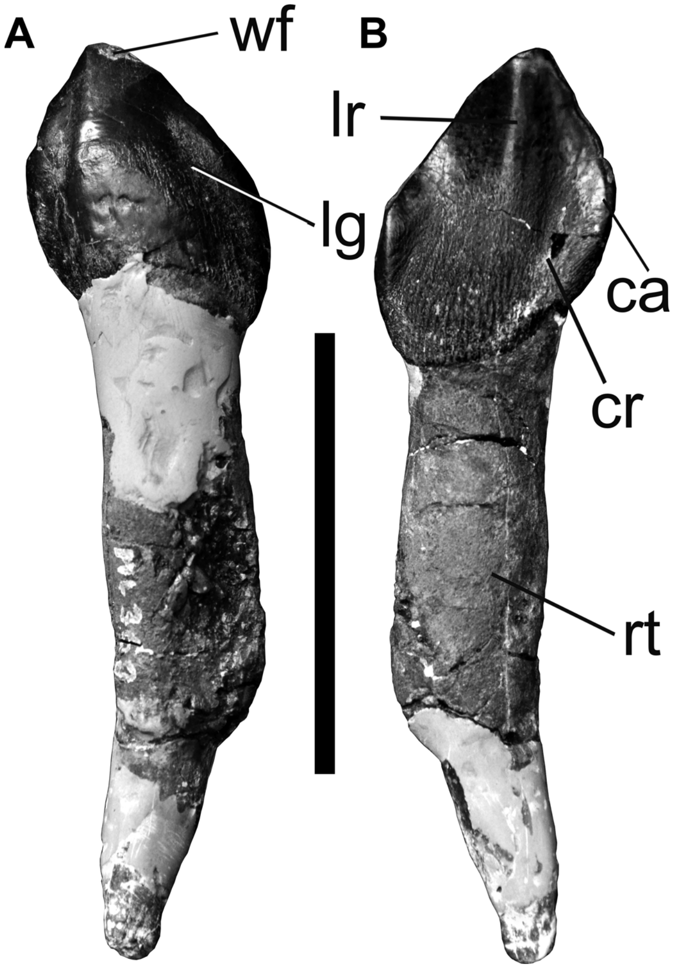

FIGURE 3. Tooth of *Zby atlanticus*, n. gen. et sp. (ML 368). **A**, labial and **B**, lingual views. **Abbreviations**: **ca**, carina; **cr**, crown; **lg**, labial groove; **lr**, lingual ridge; **rt**, root; **wf**, wear facet. Scale bar equals 50 mm.

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

Element	Dimension	Measurement
Scapula	Total preserved anteroposterior length	698
	Dorsoventral height of acromial plate (measured perpendicular to long axis of blade)	804
	Anteroposterior length of acromial plate	550
	Dorsoventral height of glenoid	277
	Maximum mediolateral width of glenoid	163
	Minimum dorsoventral height of scapular blade	232
Coracoid	Maximum anteroposterior length	569
	Maximum dorsoventral height	779
	Distance from dorsal margin of coracoid to dorsal margin of coracoid foramen	280
	Dorsoventral height of glenoid	249
	Maximum mediolateral width of glenoid	139

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.

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 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 diplodocoids 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 medially (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 margin forms an approximately continuous, steeply inclined (approximately 45°), posteroventrally facing surface that curves into the ventral margin of the scapular blade. However, in *Zby* 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* (Mateus et al., 2011).

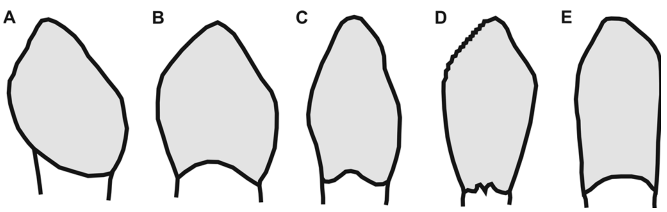

FIGURE 4. Comparative line drawings of representative eusauropod spatulate teeth in labial view. **A**, *Zby atlanticus*, n. gen. et sp. (ML 368); **B**, *Turiasaurus riodevensis* (Royo-Torres and Upchurch, 2012); **C**, *Barapasaurus tagorei* (Bandyopadhyay et al., 2010); **D**, *Omeisaurus tianfuensis* (He et al., 1988); **E**; *Camarasaurus grandis* (Ostrom and McIntosh, 1966). Teeth are not drawn to scale.

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 titanosaurs, 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

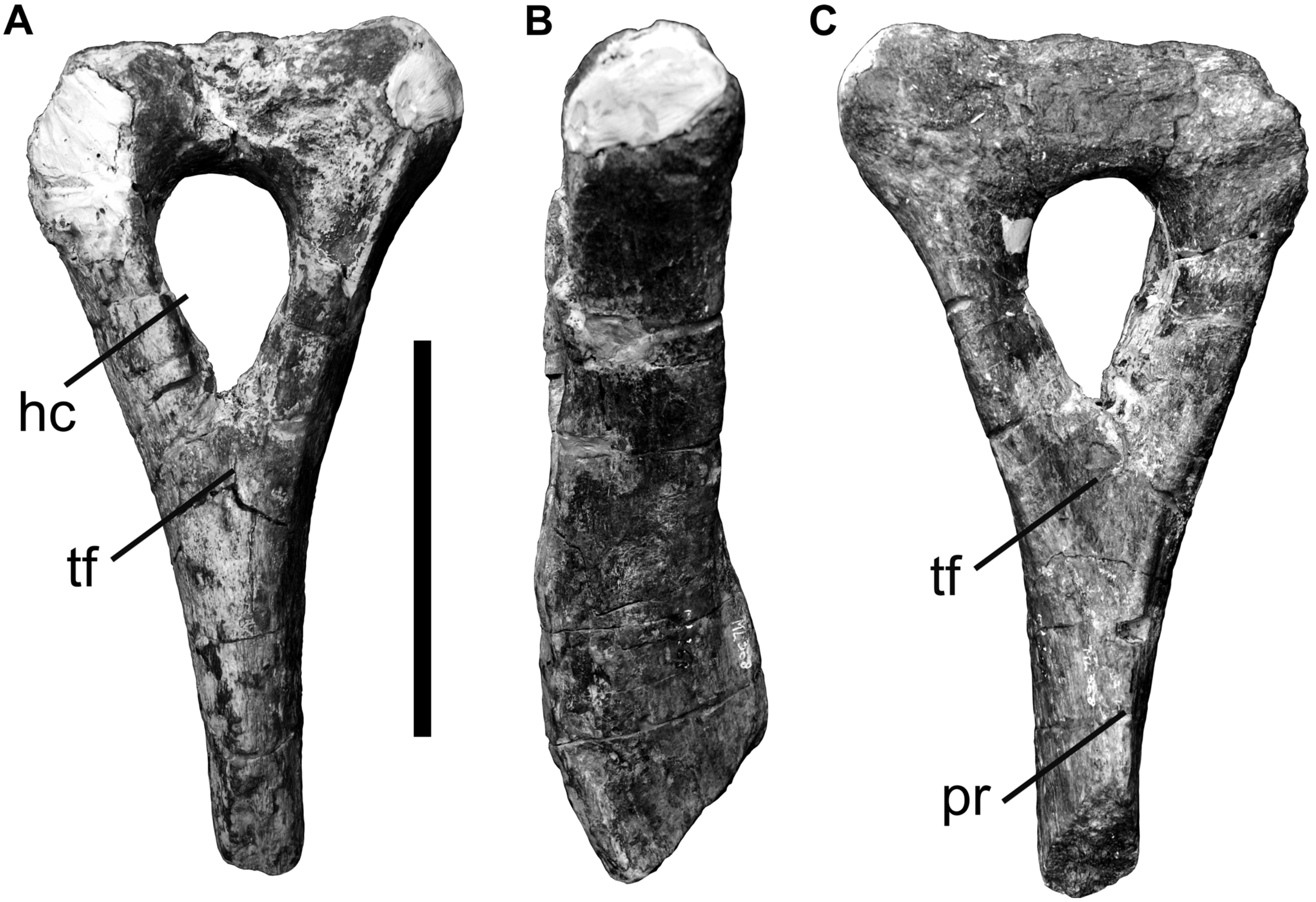

FIGURE 5. Anterior chevron of *Zby atlanticus*, n. gen. et sp. (ML 368). **A**, anterior; **B**, left lateral; and **C**, posterior views. **Abbreviations**: **hc**, hemal canal; **pr**, posterior ridge; **tf**, triangular fossa. Scale bar equals 100 mm.

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 posteroventral view, with a straight medial margin. This articular surface is mildly concave dorsoventrally

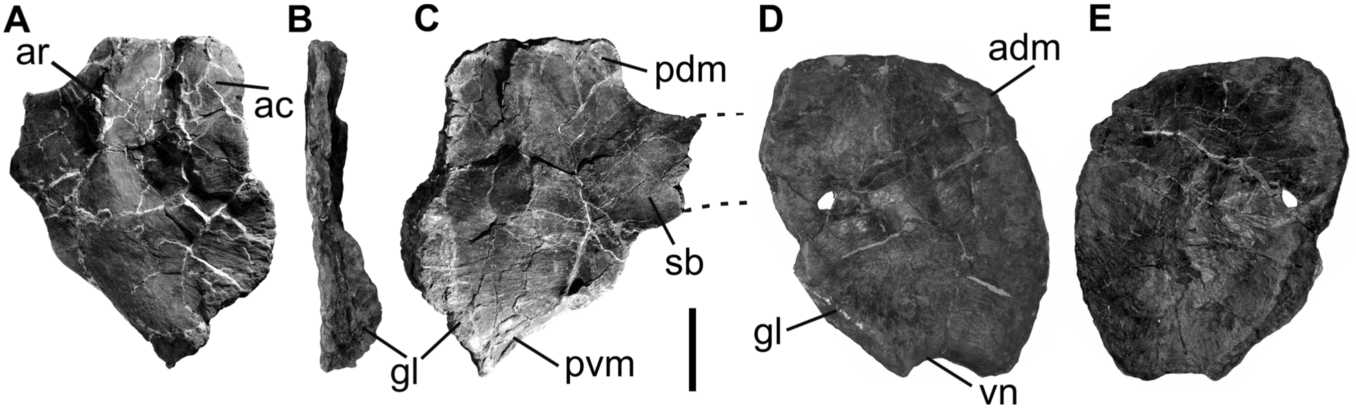

FIGURE 6. Right pectoral girdle of *Zby atlanticus*, n. gen. et sp. (ML 368). Scapula in **A**, lateral; **B**, anteroventral; and **C**, medial views; coracoid in **D**, lateral and **E**, medial views. **Abbreviations**: **ac**, acromion; **adm**, anterodorsal margin; **ar**, acromial ridge; **gl**, glenoid; **pdm**, posterodorsal margin; **pvm**, posteroventral margin; **sb**, scapular blade; **vn**, ventral notch. Dashed lines represent extrapolation of scapular blade. Scale bar equals 200 mm.

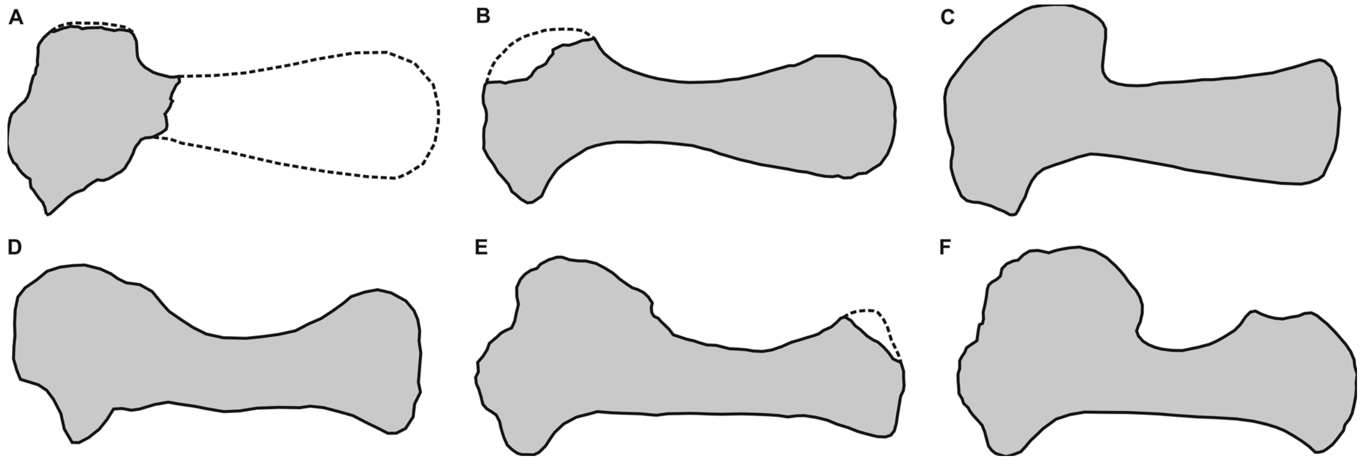

FIGURE 7. Comparative line drawings of representative eusauropod scapulae in lateral view. **A**, *Zby atlanticus*, n. gen. et sp. (ML 368); **B**, *Shunosaurus lii* (Zhang, 1988); **C**, *Omeisaurus tianfuensis* (He et al., 1988); **D**, *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003); **E**, *Patagosaurus fariasi* (Bonaparte, 1986); **F**, *Camarasaurus grandis* (Ostrom and McIntosh, 1966). Dashed lines represent extrapolation of incomplete scapula margins. Scapulae are not drawn to scale.

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.

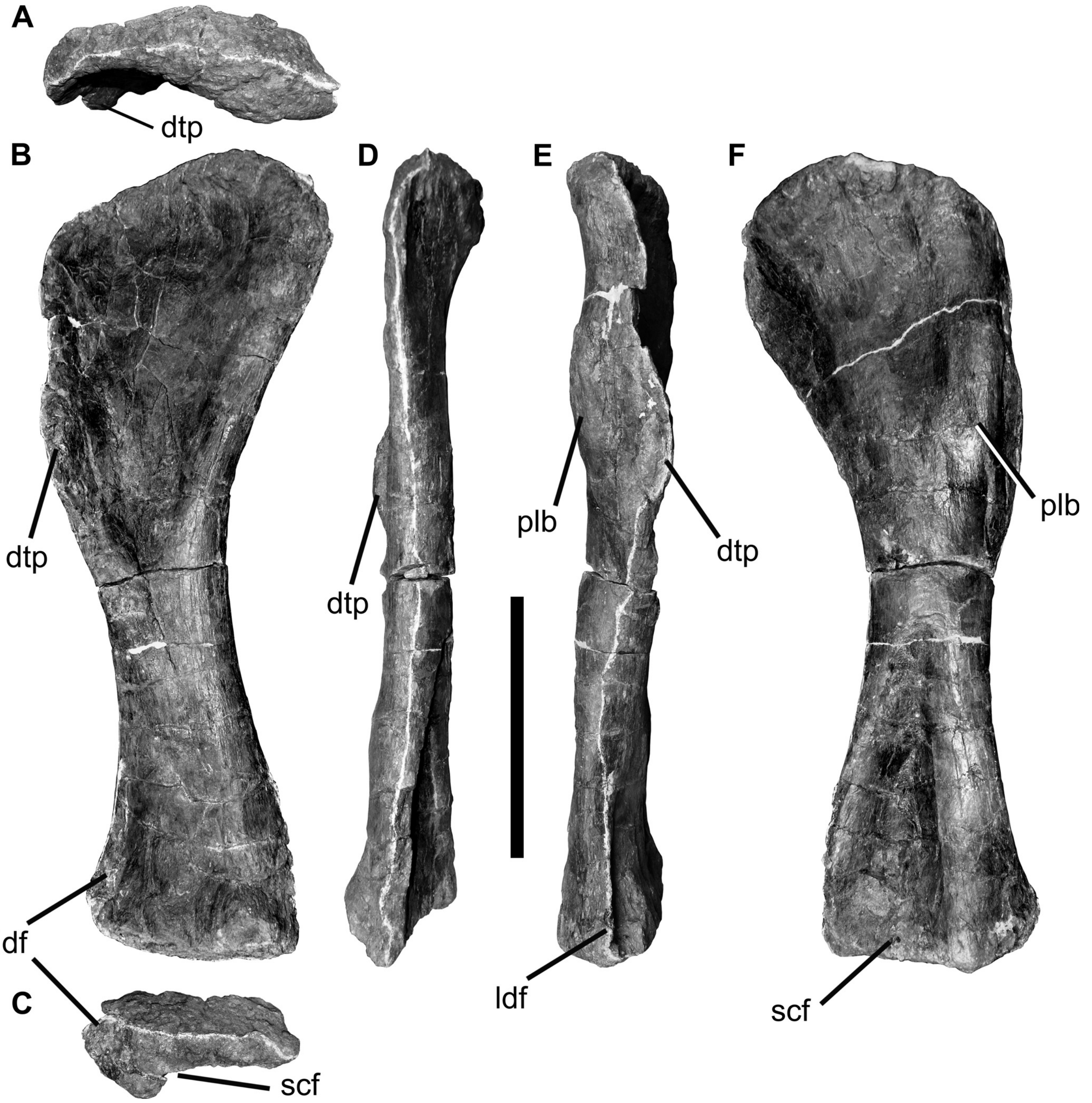

FIGURE 8. Right humerus of *Zby atlanticus*, n. gen. et sp. (ML 368). **A**, proximal; **B**, anterior; **C**, distal; **E**, medial; **F**, lateral, and **G**, posterior views. **Abbreviations**: **dtp**, deltopectoral crest; **ldf**, laterodistal flange; **plb**, posterolateral bulge; **scf**, supracondylar fossa. Scale bar equals 500 mm.

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 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 autapomorphic 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 posterolateral 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 *Aragosaurus* (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 beveled at an angle of approximately 35° (Fig. 9B). Although strongly beveled distal radii are generally regarded as a titanosaur feature (Wilson, 2002), there is some variation between taxa. For example, in some titanosaurs, almost the entire distal surface is laterally beveled (e.g., *Opisthocoelicaudia*; Borsuk-Bialynicka, 1977), whereas in others only the lateral half is upturned (e.g., *Malawisaurus*; Gomani, 2005). Furthermore, a number of non-titanosaurs show the second of these morphologies (e.g., *Apatosaurus*, Gilmore, 1936:fig. 12; *Ferganasaurus*, Alifanov and Averianov, 2003:fig. 8; and *Tehuelchesaurus*, 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; *Omeisaurus*, 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 titanosaurs, 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

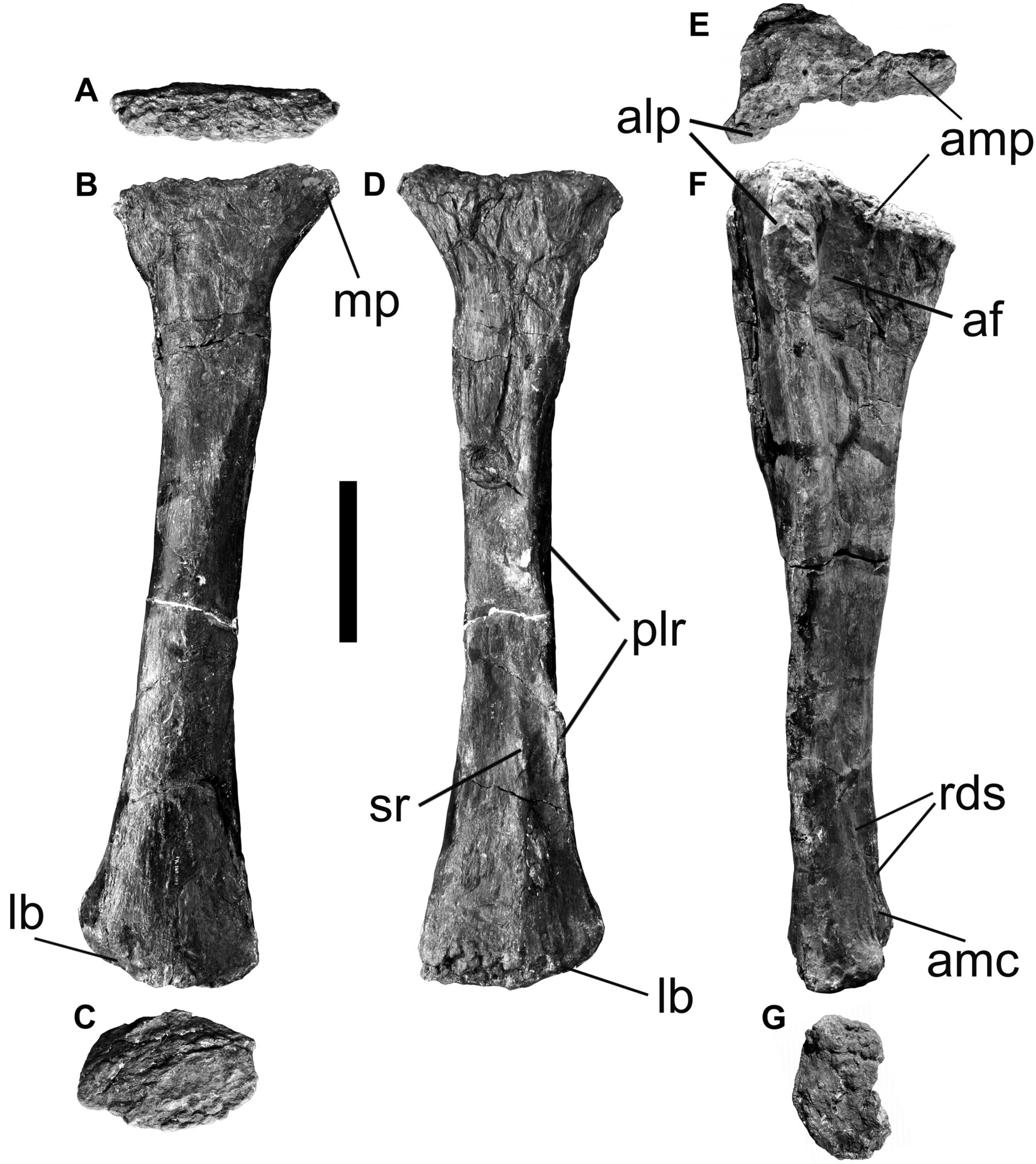

FIGURE 9. Right radius and ulna of *Zby atlanticus*, n. gen. et sp. (ML 368). Radius in **A**, proximal; **B**, anterior; **C**, distal; **D**, posterior views; ulna in **E**, proximal; **F**, anterior; **G**, distal views. **Abbreviations**: **af**, anterior fossa; **alp**, anterolateral process; **amc**, anteromedial concavity; **amp**, anteromedial process; **lb**, lateral beveling; **mp**, medial projection; **plr**, posterolateral ridge; **rds**, ridges; **sr**, second ridge. Scale bar equals 200 mm.

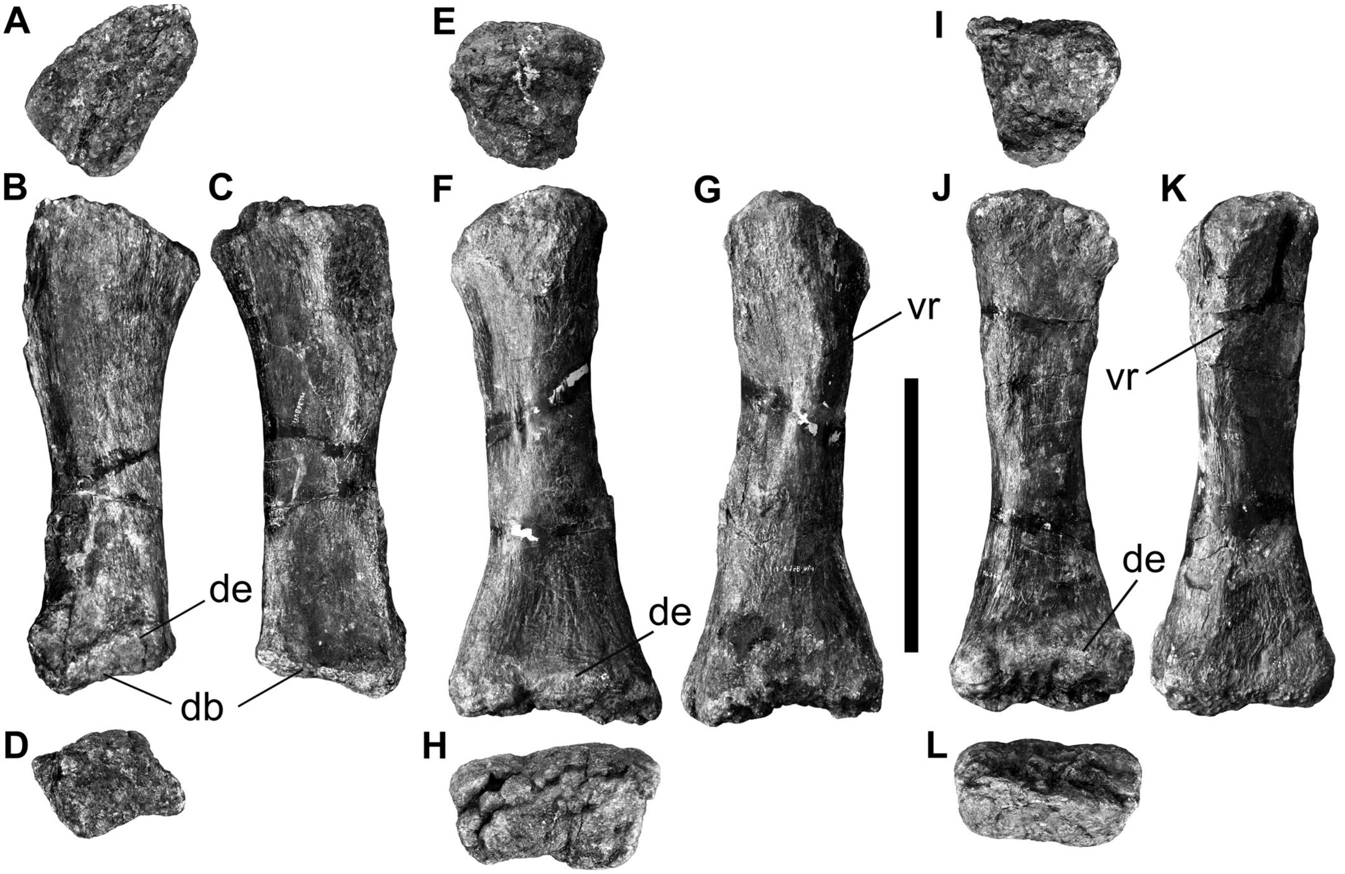

FIGURE 10. Right metacarpals of *Zby atlanticus*, n. gen. et sp. (ML 368). Metacarpal I in **A**, proximal; **B**, dorsal; **C**, ventral; **D**, distal views; metacarpal III in **E**, proximal; **F**, dorsal; **G**, ventral; **H**, distal views; metacarpal IV in **I**, proximal; **J**, dorsal; **K**, ventral; **L**, distal views. **Abbreviations**: **db**, distal beveling; **de**, dorsal extension of distal articular surface; **vr**, ventral 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 titanosaurs (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 5. Measurements of the metacarpus of *Zby atlanticus* (ML 368).

Dimension	Mc. I	Mc. III	Mc. IV	I-1	I-2	II-1
Maximum proximodistal length	365	398	382	82/65	172	47
Proximal end maximum mediolateral width	142	116	117	97	49	92
Proximal end maximum dorsoventral height	122	105	113	56	111	65
Midshaft maximum mediolateral width	79	90	71	—	—	—
Midshaft maximum dorsoventral height	68	90	62	—	—	—
Midshaft circumference	240	275	213	—	—	—
Distal end maximum mediolateral width	109	158	139	—	—	—
Distal end maximum dorsoventral height	88	98	76	47	—	49

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.

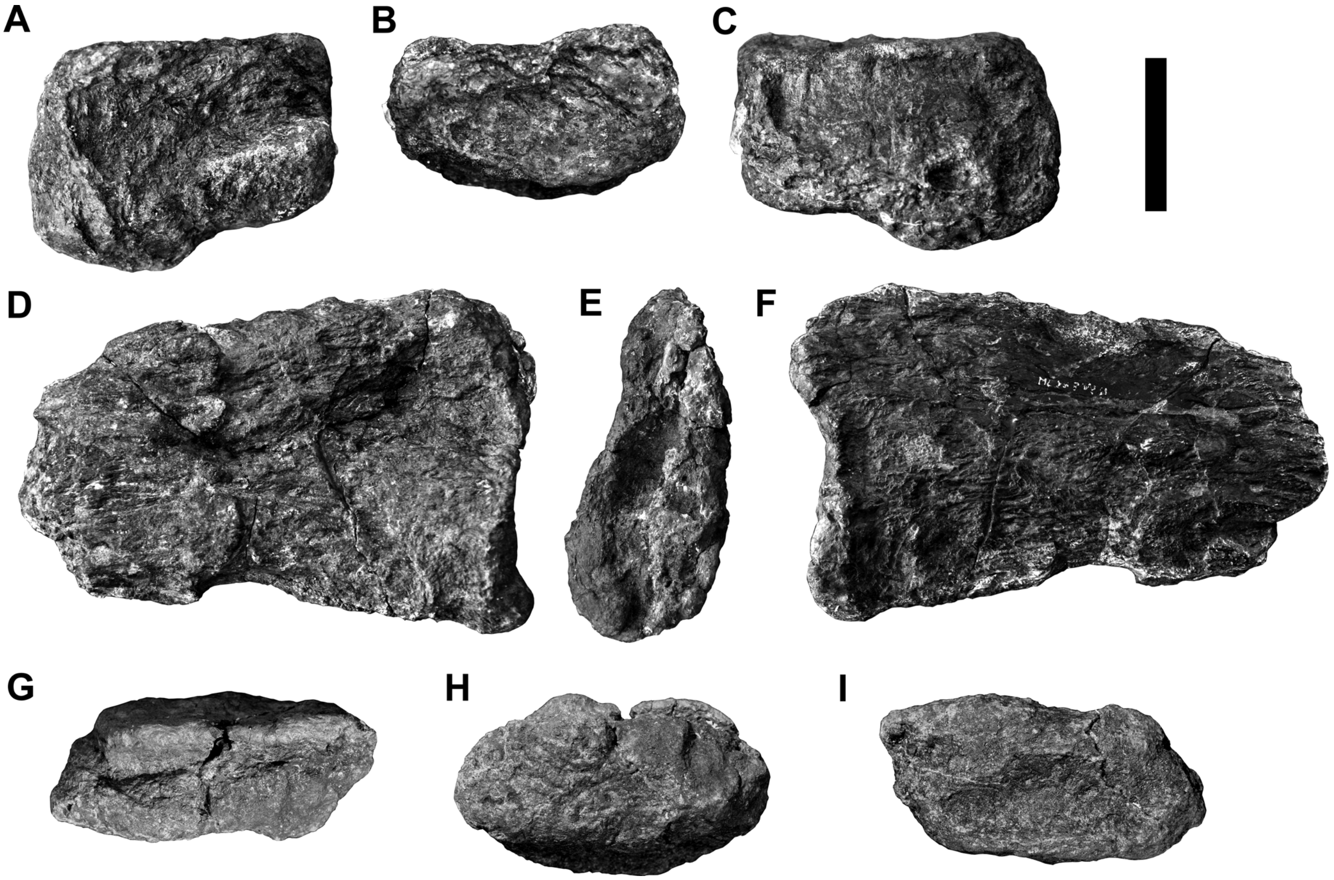

FIGURE 11. Right manual phalanges of *Zby atlanticus*, n. gen. et sp. (ML 368). Phalanx I-1 in **A**, dorsal (distal end at bottom of image); **B**, proximal; **C**, ventral views; ungual phalanx I-2 in **D**, medial; **E**, proximal; **F**, lateral views; phalanx II-1 (?) in **G**, dorsal (distal end at bottom of image); **H**, distal; **I**, ventral views. Scale bar equals 50 mm.

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 less developed than in the previously described metacarpals. The distal articular surface is rugose and strongly convex dorsoventrally. There is an extremely subtle midline concavity on the ventral margin of the distal end, but again there is no excavation of the ventral surface more proximally.

Phalanx I-1 (Fig. 11A–C) is wider mediolaterally than its proximodistal length, as in other eusauropods (Wilson and Sereno, 1998). The proximal articular surface is elliptical, with the long axis oriented mediolaterally, and is dorsoventrally taller along the lateral half. The proximal articular surface is mildly concave in both directions, mainly caused by the slight overhang of the dorsal margin. The lateral margin is proximodistally longer than the medial margin, with the lateral distal condyle projecting further distally than the medial one, whereas there is very little change in mediolateral width along the phalanx. In dorsal view, the phalanx has a trapezoidal outline, with the proximal, medial, and lateral margins meeting at right angles. This shape is typical of derived eusauropods (Wilson, 2002). The dorsal surface of the phalanx is proximodistally concave as a result of a raised area on the proximal-most part of the surface, as well as a dorsomedial projection of the medial distal condyle. The ventral surface is mediolaterally convex and gently concave proximodistally; the latter is a result of a slight ventral expansion of the proximal margin. The distal articular surface is convex both mediolaterally and dorsoventrally. There is a lateromedial curvature between the two distal condyles on the articular surface, although there is no ventral concavity separating them.

The complete ungual claw from manual digit I (Fig. 11D–F) is proximodistally long and mediolaterally narrow. The concave proximal articular surface is much broader dorsoventrally than transversely, and has a sigmoidal profile in lateral view. A shallow concavity is present at the proximodorsal corner, on the medial surface of the ungual. The lateral surface is convex and bears a shallow 'nail' groove. One of the most striking features of this ungual is the strongly developed rugosity of all surfaces. Consequently, the proximal parts of the lateral nail grooves have a 'bubbly' texture, whereas more distally the surface becomes striated. Towards the distal end, the ungual increases in mediolateral width, most noticeably as a result of expansion of the lateral face. This distal region has a different surface texture to the rest of the ungual: it is not clear whether this distal portion represents part of the ungual phalanx itself, or an additional portion of ossified cartilage. The distal end of this ungual is also unusual in terms of its dorsoventral height. In most sauropods, the ungual tapers to a distal point that is only a fraction of the dorsoventral height of the proximal articulation. In *Zby*, however, the distal end remains tall. Furthermore, the dorsal and ventral margins of the ungual are not strongly curved. As a result of this lack of curvature, as well as the abnormal dorsoventral height of the distal end, the ungual possesses a highly unusual and autapomorphic subrectangular outline in lateral view.

A second, smaller phalanx (possibly II-1) is complete (Fig. 11G–I) but has undergone some crushing. The irregular proximal articular surface is elliptical, with the long axis oriented mediolaterally. In dorsal view, the phalanx has a rhomboidal outline, with the medial and lateral margins both oriented distolaterally. There is little change in mediolateral width along the phalanx. The dorsal and ventral surfaces are proximodistally concave, as a result of dorsal and ventral expansions of the proximal margin. These surfaces are flat to mildly convex mediolaterally. There is no distinct separation of the distal end into lateral and medial condyles.

DISCUSSION

Zby and *Turiasaurus*

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 Turiasauria. 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 Turiasauria 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 Turiasauria is not universally accepted, and some studies have argued that at least one putative turiasaur (*Galveosaurus*) is a macronarian (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 Turiasauria. 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).

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) spatulate 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 extensor fossa on the distal part of the anterior surface 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 colonnade (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 (*Haplocanthosaurus* 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. The unusually low acromial expansion of the scapular in *Zby* would also be highly unusual for a neosauropod, but can be seen in several non-neosauropod eusauropods such as *Shunosaurus* (Zhang, 1988), *Patagosaurus* (Bonaparte, 1986), and *Barapasaurus* (Bandyopadyay et al., 2010).

Zby possesses a few character states that could potentially strengthen support for its placement within Macronaria or even Titanosauriformes, and some of these are also present in *Turiasaurus* (partly because of our reinterpreting of the orientation of the radius in the latter taxon). These character states include (1) a medially deflected scapular glenoid (cannot be assessed in currently available *Turiasaurus* specimens); (2) a deep humeral supracondylar fossa; (3) a proximally extensive interosseous ridge on the radius (absent in *Turiasaurus*); and (4) a strongly bevelled distal radius. The medial deflection of the scapular glenoid is a synapomorphy of Somphospondyli (Wilson and Sereno 1998), but this has also occurred convergently in *Apatosaurus* (Gilmore, 1936). The deep fossa on the distal part of the posterior humerus is present in many titanosauriforms, but unlike the situation in *Turiasaurus* and *Zby*, this fossa is normally bounded by somewhat sharper lateral and medial ridges (Upchurch et al., 2004). The well-developed ridge on the posterior surface of the radius is perhaps the most compelling piece of evidence that supports placement of *Zby* within Macronaria. This structure occurs in several macronarians (e.g., *Aragosaurus* [P.U. and P.D.M., pers. observ., 2009], *Rapetosaurus* [Curry Rogers, 2009], and several other titanosaurs (Curry Rogers, 2005]), although its precise distribution requires clarification. Finally, as noted above, strong beveling of the distal end of the radius has been proposed as a titanosaurian synapomorphy (Wilson, 2002). More detailed investigation, however, suggests that this character is more complex than previously realized (Mannion et al., 2013) and might benefit from being split into three states (i.e., beveling absent, beveling restricted to the lateral half of the distal end, and beveling occurs across the entire distal surface). The more extreme condition in which the entire distal end of the radius is set at an angle of 20° or more to the long axis of the shaft (sloping proximolaterally in anterior view) does indeed seem to characterize a restricted clade of derived titanosaurs, including *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977) and *Saltasaurus* (Powell, 2003). The condition observed in *Turiasaurus* and *Zby* (where beveling is limited to the lateral half of the radial distal end) is somewhat more widespread, because it occurs in several titanosauriforms (e.g., *Angolatitan*, Mateus et al., 2009; *Giraffatitan*, Janensch, 1961) and some non-titanosauriforms (e.g., *Apatosaurus* and *Ferganasaurus*; see Description, above). Thus, several of the character states that potentially support the placement of *Zby* within Macronaria (or Titanosauriformes) are actually more widespread and/or display evidence of homoplasy. More detailed evaluation of these and other relevant characters must await formal phylogenetic analyses that incorporate *Zby* and other putative turiasaurs.

Late Jurassic Portuguese Sauropod Diversity and Paleoecology

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*, *Lourinhasaurus*, 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 turiasaurs 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 'Dinoeggs PTDC/BIA-EVF/113222/2009.' P.D.M.'s research was supported by a 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

Alifanov, V. R., and A. O. Averianov. 2003. *Ferganasaurus verzilini*, gen. et sp. nov., a new neosauropod (Dinosauria, Saurischia, Sauropoda) from the Middle Jurassic of Fergana Valley, Kirghizia. Journal of Vertebrate Paleontology 23:358–372.

Antunes, M. T., and O. Mateus. 2003. Dinosaurs of Portugal. Comptes Rendus Palevol 2:77–95.

Bandyopadhyay, S., D. D. Gillette, S. Ray, and D. P. Sengupta. 2010. Osteology of *Barapasaurus tagorei* (Dinosauria: Sauropoda) from the Early Jurassic of India. Palaeontology 53:533–569.

Barco, J. L. 2009. Sistemática e implicaciones filogenéticas y paleobiogeográficas del saurópodo *Galvesaurus herreroi* (Formación Villar del Arzobispo, Galve, España). Unpublished thesis, Universidad de Zaragoza, Zaragoza, Spain, 389 pp.

Barco, J. L., J. I. Canudo, and G. Cuenca-Bescós. 2006. Descripción de las vértebras cervicales de *Galvesaurus herreroi* Barco, Canudo, Cuenca-Bescós & Ruiz-Omeñaca, 2005 (Dinosauria, Sauropoda) del tránsito Jurásico-Cretácico en Galve (Teruel, España). Revista Española de Paleontología 21:189–205.

Bonaparte, J. F. 1986. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétosauridés) du Jurassique Moyen de Cerro Cóndor (Chubut, Argentina). Annales de Paléontologie (Vert.-Invert.) 72:325–386.

Bonaparte, J. F., and O. Mateus. 1999. A new diplodocid, *Dinheirosaurus lourinhanensis* gen. et sp. nov., from the Late Jurassic beds of Portugal. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales, Paleontología 5:13–29.

Borsuk-Bialynicka, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii*, gen. n., sp. n. from the Upper Cretaceous of Mongolia. Palaeontologica Polonica 37:1–64.

Calvo, J. O. 1994. Jaw mechanics in sauropod dinosaurs. Gaia 10:183–193.

Calvo, J. O., and L. Salgado. 1995. *Rebbachisaurus tessonei* sp. nov. a new Sauropoda from the Albian-Cenomanian of Argentina; new evidence on the origin of the Diplodocidae. Gaia 11:13–33.

Carballido, J. L., and D. Pol. 2010. The dentition of *Amygdalodon patagonicus* (Dinosauria: Sauropoda) and the dental evolution in basal sauropods. Comptes Rendus Palevol 9:83–93.

Carballido, J. L., O. W. M. Rauhut, D. Pol, and L. Salgado. 2011. Osteology and phylogenetic relationships of *Tehuelchesaurus benitezii* (Dinosauria, Sauropoda) from the Upper Jurassic of Patagonia. Zoological Journal of the Linnean Society 163:605–662.

Carballido, J. L., L. Salgado, D. Pol, J. I. Canudo, and A. Garrido. 2012. A new basal rebbachisaurid (Sauropoda, Diplodocoidea) from the Early Cretaceous of the Neuquén Basin; evolution and biogeography of the group. Historical Biology 24:631–654.

Casanovas, M. L., J. V. Santafe, and J. L. Sanz. 2001. *Losillasaurus giganteus*, un nuevo sauropodo del transito Jurasico-Cretacico de la cuenca de "Los Serranos" (Valencia, España). Paleontologia i Evolucio 32–33:99–122.

Chure, D., B. B. Britt, J. A. Whitlock, and J. A. Wilson. 2010. First complete sauropod dinosaur skull from the Cretaceous of the Americas and the evolution of sauropod dentition. Naturwissenschaften 97:379–391.

Curry Rogers, K. A. 2005. Titanosauria: a phylogenetic overview; pp. 50–103 in K. A. Curry Rogers and J. A. Wilson (eds.), The Sauropods: Evolution and Paleobiology. University of California Press, Berkeley, California.

Curry Rogers, K. A. 2009. The postcranial osteology of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 29:1046–1086.

Curry Rogers, K. A., and C. A. Forster. 2001. The last of the dinosaur titans: a new sauropod from Madagascar. Nature 412:530–534.

Dantas, P. M., J. L. Sanz, C. M. Silva, F. Ortega, V. F. Santos, and M. Cachão, M. 1998. *Lourinhasaurus* nov. gen. Novo dinossauro saurópode do Jurássico superior (Kimmeridgiano superior–Titoniano inferior) de Portugal. Comunicações do Instituto Geológico e Mineiro 84:91–94.

D'Emic, M. D. 2012. The early evolution of titanosauriform sauropod dinosaurs. Zoological Journal of the Linnean Society 166:624–671.

Edmund, A. G. 1960. Tooth replacement phenomena in the lower vertebrates. Life Sciences Division Royal Ontario Museum Toronto, Contributions 52:1–190.

Gilmore, C. W. 1936. Osteology of *Apatosaurus* with special reference to specimens in the Carnegie Museum. Memoirs of the Carnegie Museum 11:175–300.

Gomani, E. M. 2005. Sauropod dinosaurs from the Early Cretaceous of Malawi. Palaeontologia Electronica 8(1):27A.

Haluza, A., J. I. Canale, A. Otero, L. M. Pérez, and C. A. Scanferla. 2012. Changes in vertebral laminae across the cervico-dorsal transition of a well-preserved rebbachisaurid (Dinosauria: Sauropoda) from the Cenomanian of Patagonia, Argentina. Journal of Vertebrate Paleontology 32:219–224.

Harris, J. D. 2006. The significance of *Suuwassea emilieae* (Dinosauria: Sauropoda) for flagellicaudatan intrarelationships and evolution. Journal of Systematic Palaeontology 4:185–198.

He, X.-L., K. Li, and K.-J. Cai. 1988. The Middle Jurassic Dinosaur Fauna from Dashanpu, Zigong, Sichuan. Volume IV. Sauropod Dinosaurs (2). Omeisaurus tianfuensis. Sichuan Publishing House of Science and Technology, Chengdu, China, 143 pp. [Chinese, English summary]

Janensch, W. 1961. Die gliedmaszen und gliedmaszengürtel der Sauropoden der Tendaguru-Schichten. Palaeontographica (Supplement 7) 3:177–235.

Kullberg, J. C., R. B. Rocha, A. F. Soares, J. Rey, P. Terrinha, A. C. Azerêdo, P. Callapez, L. V. Duarte, M. C. Kullberg, L. Martins, J. R. Miranda, C. Alves, J. Mata, J. Madeira, O. Mateus, M. Moreira, and C. R. Nogueira. 2012. A Bacia Lusitaniana: Estratigrafia, Paleogeografia e Tectónica; pp. 989–1141 in R. Dias, A. Araújo, P. Terrinha, and J. C. Kullberg (eds.), Geologia de Portugal no contexto da Ibéria. Escolar Editora, Lisbon.

Lapparent, A. F. de, and G. Zbyszewski. 1957. Les dinosauriens du Portugal. Mémoires des Services Géologiques du Portugal, nouvelle série 2:1–63.

Mannion, P. D. 2009. A rebbachisaurid sauropod from the Lower Cretaceous of the Isle of Wight, England. Cretaceous Research 30:521–526.

Mannion, P. D., and J. O. Calvo. 2011. Anatomy of the basal titanosaur (Dinosauria, Sauropoda) *Andesaurus delgadoi* from the mid-Cretaceous (Albian–early Cenomanian) Río Limay Formation, Neuquén Province, Argentina: implications for titanosaur systematics. Zoological Journal of the Linnean Society 163:155–181.

Mannion, P. D., and P. Upchurch. 2010. Completeness metrics and the quality of the sauropodomorph fossil record through geological and historical time. Paleobiology 36:283–302.

Mannion, P. D., P. Upchurch, R. N. Barnes, and O. Mateus. 2013. Osteology of the Late Jurassic Portuguese sauropod dinosaur *Lusotitan atalaiensis* (Macronaria) and the evolutionary history of basal titanosauriforms. Zoological Journal of the Linnean Society 168:98–206.

Mannion, P. D., P. Upchurch, M. T. Carrano, and P. M. Barrett. 2011. Testing the effect of the rock record on diversity: a multidisciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. Biological Reviews 86:157–181.

Mannion, P. D., P. Upchurch, O. Mateus, R. N. Barnes, and M. E. H. Jones. 2012. New information on the anatomy and systematic position of *Dinheirosaurus lourinhanensis* (Sauropoda: Diplodocoidea) from the Late Jurassic of Portugal, with a review of European diplodocoids. Journal of Systematic Palaeontology 10:521–551.

Marsh, O. C. 1878. Principal characters of American Jurassic dinosaurs. Part I. American Journal of Science, Series 3 16:411–416.

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

Mateus, O. 2009. The sauropod dinosaur *Turiasaurus riodevensis* in the Late Jurassic of Portugal. Journal of Vertebrate Paleontology, Program and Abstracts 2009:144A.

Mateus, O., and J. Milàn. 2010. A diverse Upper Jurassic dinosaur ichnofauna from central-west Portugal. Lethaia 43:245–257.

Mateus, O., S. C. R. Maidment, and N. A. Christiansen. 2009. A new long-necked 'sauropod-mimic' stegosaur and the evolution of the plated dinosaurs. Proceedings of the Royal Society B 276:1815–1821.

Mateus, O., A. Walen, and M. T. Antunes. 2006. The large theropod fauna of the Lourinhã Formation (Portugal) and its similarity to that of the Morrison Formation, with a description of new species of *Allosaurus*. New Mexico Museum of Natural History and Science Bulletin 36:123–129.

Mateus, I., H. Mateus, M. T. Antunes, O. Mateus, P. Taquet, V. Ribeiro, and G. Manuppella. 1998. Upper Jurassic theropod dinosaur embryos from Lourinhã (Portugal). Memórias da Academia das Ciências de Lisboa 37:101–110.

Mateus, O., L. L. Jacobs, A. S. Schulp, M. J. Polcyn, T. S. Tavares, A. B. Neto, M. L. Morais, and M. T. Antunes. 2011. *Angolatitan adamastor*, a new sauropod dinosaur and the first record from Angola. Anais da Academia Brasileira de Ciências 83:1–13.

Milàn, J., P. Christiansen, and O. Mateus. 2005. A three-dimensionally preserved sauropod manus impression from the Upper Jurassic of Portugal: implications for sauropod manus shape and locomotor mechanics. Kaupia 14:47–52.

Mocho, P., F. Ortega, and R. Royo-Torres. 2012. Morphological variation of Turiasauria-like teeth and their stratigraphic distribution in Portuguese Upper Jurassic. Annual Meeting of the European Association of Vertebrate Palaeontologists 10:159A–163A.

Myers, T. S., N. J. Tabor, L. L. Jacobs, and O. Mateus. 2012. Palaeoclimate of the Late Jurassic of Portugal: comparison with the Western United States. Sedimentology 59:1695–1717.

Ortega, F., R. Royo-Torres, F. Gascó, F. Escaso, and J. L. Sanz. 2010. New evidences of the sauropod *Turiasaurus* from the Portuguese Upper Jurassic. Annual Meeting of the European Association of Vertebrate Palaeontologists 8:62A.

Ostrom, J. H., and J. S. McIntosh. 1966. Marsh's Dinosaurs. Yale University Press, New Haven, Connecticut, 388 pp.

Otero, A. 2010. The appendicular skeleton of *Neuquensaurus*, a Late Cretaceous saltasaurine sauropod from Patagonia, Argentina. Acta Palaeontologica Polonica 55:399–426.

Otero, A., P. A. Gallina, J. I. Canale, and A. Haluza. 2012. Sauropod haemal arches: morphotypes, new classification and phylogenetic aspects. Historical Biology 24:243–256.

Powell, J. E. 2003. Revision of South American titanosaurid dinosaurs: palaeobiological, palaeobiogeographical and phylogenetic aspects. Records of the Queen Victoria Museum 111:1–173.

Rauhut, O. W. M., K. Remes, R. Fechner, G. Cladera, and P. Puerta. 2005. Discovery of a short-necked sauropod dinosaur from the Late Jurassic period of Patagonia. Nature 435:670–672.

Ricqlès, A. de, O. Mateus, M. T. Antunes, and P. Taquet. 2001. Histomorphogenesis of embryos of Upper Jurassic theropods from Lourinhã (Portugal). Comptes Rendus de l'Académie des Sciences, Series IIA, Earth and Planetary Science 332:647–656.

Royo-Torres, R., and A. Cobos. 2009. Turiasaur sauropods in the Tendaguru Beds of Tanzania. Journal of Vertebrate Paleontology, Program and Abstracts 2009:173A.

Royo-Torres, R., and P. Upchurch. 2012. The cranial anatomy of the sauropod *Turiasaurus riodevensis* and implications for its phylogenetic relationships. Journal of Systematic Palaeontology 10:553–583.

Royo-Torres, R., A. Cobos, and L. Alcalá. 2006. A giant European dinosaur and a new sauropod clade. Science 314:1925–1927.

Royo-Torres, R., A. Cobos, L. Luque, A. Aberasturi, E. Espílez, I. Fierro, A. N. A. González, L. Mampel, and L. Alcalá. 2009. High European sauropod dinosaur diversity during Jurassic–Cretaceous transition in Riodeva (Teruel, Spain). Palaeontology 52:1009–1027.

Sánchez-Hernández, B. 2005. *Galveosaurus herreroi*, a new sauropod dinosaur from Villar del Arzobispo Formation (Tithonian–Berriasian) of Spain. Zootaxa 1034:1–20.

Sanz, J. L., J. E. Powell, J. Le Loueff, R. Martinez, and X. Pereda Suberbiola. 1999. Sauropod remains from the Upper Cretaceous of Laño (northcentral Spain). Titanosaur phylogenetic relationships. Estudios del Museo de Ciencias Naturales de Alava 14:235–255.

Schneider, S., F. Fürsich, and W. Werner. 2009. Sr-isotope stratigraphy of the Upper Jurassic of central Portugal (Lusitanian Basin) based on oyster shells. International Journal of Earth Sciences 98:1949–1970.

Upchurch, P. 1995. The evolutionary history of sauropod dinosaurs. Philosophical Transactions of the Royal Society of London, Series B 349:365–390.

Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. Zoological Journal of the Linnean Society 124:43–103.

Upchurch, P. 1999. The phylogenetic relationships of the Nemegtosauridae (Saurischia, Sauropoda). Journal of Vertebrate Paleontology 19:106–125.

Upchurch, P., and P. M. Barrett. 2000. The evolution of sauropod feeding mechanisms; pp. 79–122 in H.-D. Sues (ed.), The Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record. Cambridge University Press, Cambridge, U.K.

Upchurch, P., and J. Martin. 2002. The Rutland *Cetiosaurus*: the anatomy and relationships of a Middle Jurassic British sauropod dinosaur. Palaeontology 45:1049–1074.

Upchurch, P., and J. Martin. 2003. The anatomy and taxonomy of *Cetiosaurus* (Saurischia: Sauropoda) from the Middle Jurassic of England. Journal of Vertebrate Paleontology 23:208–231.

Upchurch, P., P. M. Barrett, and P. Dodson. 2004. Sauropoda; pp. 259–324 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria, second edition. University of California Press, Berkeley, California.

Upchurch, P., P. M. Barrett, and P. M. Galton. 2007. The phylogenetic relationships of basal sauropodomorphs: implications for the origin of sauropods. Special Papers in Palaeontology 77:57–90.

Upchurch, P., P. D. Mannion, and P. M. Barrett. 2011a. Sauropod dinosaurs; pp. 476–525 in D. J. Batten (ed.), English Wealden Fossils. The Palaeontological Association Field Guide to Fossils Number 14. Wiley-Blackwell, London.

Upchurch, P., P. D. Mannion, R. J. Butler, R. B. J. Benson, and M. T. Carrano. 2011b. Geological and anthropogenic controls on the sampling of the terrestrial fossil record: a case study from the Dinosauria. Geological Society of London, Special Publications 358:209–240.

Wedel, M. J. 2003. The evolution of vertebral pneumaticity in sauropod dinosaurs. Journal of Vertebrate Paleontology 23:344–357.

Weishampel, D. B., P. M. Barrett, R. E. Coria, J. Le Loeuff, E. S. Gomani, Z. Zhao, X. Xu, A. Sahni, and C. Noto. 2004. Dinosaur distribution; pp. 517–606 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria, second edition. University of California Press, Berkeley, California.

Whitlock, J. A. 2011a. A phylogenetic analysis of Diplodocoidea (Saurischia: Sauropoda). Zoological Journal of the Linnean Society 161:872–915.

Whitlock, J. A. 2011b. Inferences of diplodocoid (Sauropoda: Dinosauria) feeding behavior from snout shape and microwear analyses. PLoS ONE 6:e18304.

Whitlock, J. A., M. D. D'Emic, and J. A. Wilson. 2011. Cretaceous diplodocids in Asia? Re-evaluating the phylogenetic affinities of a fragmentary specimen. Palaeontology 54:351–364.

Wilson, J. A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zoological Journal of the Linnean Society 136:217–276.

Wilson, J. A. 2005. Integrating ichnofossils and body fossil records to estimate locomotor posture and spatiotemporal distribution of early sauropod dinosaurs: a stratocladistic approach. Paleobiology 31:400–423.

Wilson, J. A., and P. C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Memoir of the Society of Vertebrate Paleontology 5:1–68.

Yates, A. M. 2007. The first complete skull of the Triassic dinosaur *Melanorosaurus* Haughton (Sauropodomorpha: Anchisauria). Special Papers in Palaeontology 77:9–55.

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]

Zhang, Y.-H. 1988. The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan. Sauropod dinosaurs. *Shunosaurus*. Sichuan Publishing House of Science and Technology, Chengdu, China, 106 pp. [Chinese, English summary]

Submitted December 6, 2012; revisions received June 4, 2013; accepted June 30, 2013.

Handling editor: Emily Rayfield.