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First rebbachisaurid dinosaur (Sauropoda, Diplodocoidea) from the early Cretaceous of Spain : palaeobiogeographical implications

XABIER PEREDA SUBERBIOLA[1], FIDEL TORCIDA[2], LUIS ANGEL IZQUIERDO[2], PEDRO HUERTA[2], DIEGO MONTERO[2] and GUSTAVO PÉREZ[2]

Key words. – Dinosauria, Sauropoda, Rebbachisauridae, Cretaceous, Burgos, Iberian Peninsula.

Abstract. – Sauropod remains from the early Cretaceous (late Barremian–early Aptian) of Salas de los Infantes (Burgos, Spain) are described. The material consists of several caudal vertebrae, chevrons, a pair of ischia and a femur that is presumed to belong to a single medium-sized individual. Based on the tall neural arches and broad neural spines of the anterior caudal vertebrae, the specimen is referred to the Diplodocoidea. Moreover, it shows affinities with the Rebbachisauridae, a basal clade of diplodocoids. Both the caudal vertebrae and ischium of the Burgos sauropod are similar in form to those of '*Rebbachisaurus' tessonei* from the Albian-Cenomanian of South America. However, there are some differences with regard to this taxon, so the Burgos sauropod is provisionally referred to as Rebbachisauridae indet. Rebbachisaurids are known in the Aptian-Cenomanian of the western Gondwanan landmasses (Africa and South America), although further remains have been reported from the Coniacian-Santonian of Argentina and the Hauterivian–Barremian of Croatia. The Burgos diplodocoid appears to be one of the earliest representative of the Rebbachisauridae. This discovery supports previous evidence of a land connection between Europe and Africa across the Tethys seaway sometime in the early Cretaceous.

Première découverte d'un dinosaure rebbachisauridé (Sauropoda, Diplodocoidea) dans le Crétacé inférieur d'Espagne : implications paléobiogéographiques

Mots-clés. – Dinosauria, Sauropoda, Rebbachisauridae, Crétacé, Burgos, Péninsule ibérique.

Résumé. – Des restes fossiles d'un sauropode provenant du Crétacé inférieur (Barrémien supérieur-Aptien inférieur) de Salas de los Infantes (Burgos, Espagne) sont décrits. Le matériel, qui comporte plusieurs vertèbres caudales, des chevrons, une paire d'ischions et un fémur, pourrait appartenir à un seul individu de taille moyenne. D'après la hauteur de l'arc neural et la largeur de l'épine neurale des vertèbres caudales antérieures, le spécimen est rapporté aux Diplodocoidea. De plus, il montre des affinités avec les Rebbachisauridae, un clade basal de diplodocoïdes. La forme des vertèbres caudales antérieures et de l'ischion du sauropode de Burgos est similaire à celle de '*Rebbachisaurus' tessonei* de l'Albien-Cénomanien d'Amérique du Sud. Néanmoins, il existe des différences par rapport à celui-ci, de sorte que le sauropode de Burgos est rapporté provisoirement à un Rebbachisauridae indéterminé. Les rebbachisauridés sont connus dans l'Aptien-Cénomanien des continents gondwaniens (Afrique et Amérique du Sud), même si du matériel provenant du Coniacien-Santonien d'Argentine et de l'Hauterivien-Barrémien de Croatie leur a été rapporté. Le diplodocoïde de Burgos semble être un des plus anciens représentants des Rebbachisauridae. Cette découverte appuie l'hypothèse déjà soutenue d'une connexion terrestre entre l'Europe et l'Afrique à travers la Téthys durant le Crétacé inférieur.

INTRODUCTION

The fossil record of dinosaurs from the early Cretaceous of the Cameros Basin, in northern Spain (provinces of Burgos, La Rioja and Soria) is mainly represented by footprints [see Sanz *et al.*, 1997 ; Lockley and Meyer, 2000 and references therein]. Additional dinosaur remains include theropods such as the spinosaurid *Baryonyx* [Viera and Torres, 1995 ; Fuentes *et al.*, 2001], ornithopods like *Iguanodon* [Maisch, 1991], hypsilophodontids and dryosaurids [Ruiz-Omeñaca, 2001 ; Fuentes and Meijide, 2001], and thyreophorans such as the ankylosaur *Polacanthus* [Sanz, 1983 ; Pereda Suberbiola *et al.*, 1999] and an indeterminate stegosaur [Pereda Suberbiola *et al.*, 2003]. Sauropods are represented by scarce remains, mostly of them still undescribed. Sanz *et al.* [1992] mentioned limb bones and vertebrae of an indeterminate sauropod from the late Jurassic-early Cretaceous near Lara (Burgos) and an isolated femur from Tera (Soria). Platt and Meyer [1991] listed sauropod remains (e.g., rib, vertebra, limb fragments) from the Berriasian Rupelo Formation of Mamolar (Burgos), Mambrillas de Lara (Burgos) and Espejón (Soria). Torcida [1996] noted the discovery of large brachiosaurid-like bones from Aldea del Pinar (Burgos) and of teeth, vertebrae and limb bones from sev-

[1] Universidad del País Vasco/EHU, Facultad de Ciencias, Departamento de Estratigrafía y Paleontología, Apdo. 644, 48080 Bilbao (Spain) gpppesuf@lg.ehu.es ; and Muséum National d'Histoire Naturelle, Département Histoire de la Terre, 8 rue Buffon, 75005 Paris (France).
[2] Museo de Dinosaurios, Colectivo Arqueológico-Paleontológico de Salas (C.A.S.), Plaza Jesús Aparicio, 9, 09600 Salas de los Infantes, Burgos (Spain) museodesalas@salasdelosinfantes.net
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eral localities of the Lower Wealden (Berriasian-Valanginian) of southeast Burgos, currently kept in the Museo de Dinosaurios de Salas de los Infantes, Burgos (MPS collection[1], unpublished). Some of these remains could belong to Titanosauriformes.

Recent field work in the early Cretaceous (Barremian-Aptian) rocks of the western Cameros Basin near Salas de los Infantes (Burgos) has yielded vertebrae, girdle and limb bones of a medium-sized diplodocoid. These remains are described below and referred to the Rebbachisauridae.

GEOLOGICAL SETTING

The dinosaur locality is Tenadas de los Vallejos II, situated near the villages of La Revilla and Ahedo at about 10 km southwest of Salas de los Infantes, province of Burgos, Spain (fig. 1). The site is located in the southern part of the Contreras anticline, western Cameros Basin. The fossiliferous beds are red clays intercalated with alluvial sandstones of the Castrillo de la Reina Formation, which correspond to the fifth sedimentary sequence of Mas *et al.* [1993] and Martín-Closas and Alonso [1998]. These are regarded as late Barremian to early Aptian in age (Salas Group ; Aptian [sensu Platt, 1989]).

The sauropod bones consist of caudal vertebrae, haemal arches, rib fragments, two ischia and one femur. These remains were found disarticulated in the same level and in close proximity to each other, so they presumably belong to the same individual. Other dinosaur remains found in the Tenadas de los Vallejos II locality include two cervical vertebra of a spinosaurid theropod (A.C. Milner, J. Le Lœuff, pers. comm.).

1. Abbreviation : MPS, Museo de Dinosaurios – Paleontología, Salas de los Infantes, Burgos, Spain.

SYSTEMATIC PALAEONTOLOGY

Sauropodomorpha Huene, 1932
Sauropoda Marsh, 1878
Diplodocoidea Upchurch, 1995
Rebbachisauridae Bonaparte, 1997
Gen. et sp. indet.
(figs. 2-3)

Referred material. MPS-RV II-2, 3, 4, 9, 10, 11, 12, 13, 15, 17, anterior and middle caudal vertebrae ; MPS-RV II-23, haemal arch ; MPS-RV II-14, rib fragment ; MPS-RV II-6, 7, 8, other vertebral remains ; MPS-RV II-18, 19, left and right ischium ; MPS-RV II-16, left femur ; MPS-RV II-22, indeterminate bone.

Locality and horizon. Tenadas de los Vallejos II (La Revilla-Ahedo), near Salas de los Infantes, province of Burgos, Spain ; Castrillo de la Reina Formation, western Cameros Basin, Lower Cretaceous, Barremian-Aptian [Platt, 1989 ; Mas *et al.*, 1993 ; Martín-Closas and Alonso, 1998].

Description

For measurements see table I.

Caudal vertebrae and haemal arches (fig. 2). Ten caudal vertebrae are known, including vertebrae from the anterior and middle regions of the tail. All the centra are amphiplatyan to slightly amphicoelous. In the anteriormost caudals, the anterior articulation surface is flat and the posterior articulation is slightly concave. Pleurocoels are absent. The centrum of the best preserved anterior caudal (MPS-RV II-15 ; figs. 2A-E) is anteroposteriorly shorter than high, and transversely higher than wide (anterior articulation) or as high as wide (posterior articulation).The lateral faces are concave. The ventral side has separate articulation surfaces for the haemal arches which are more marked distally than proximally. Between the anterior and

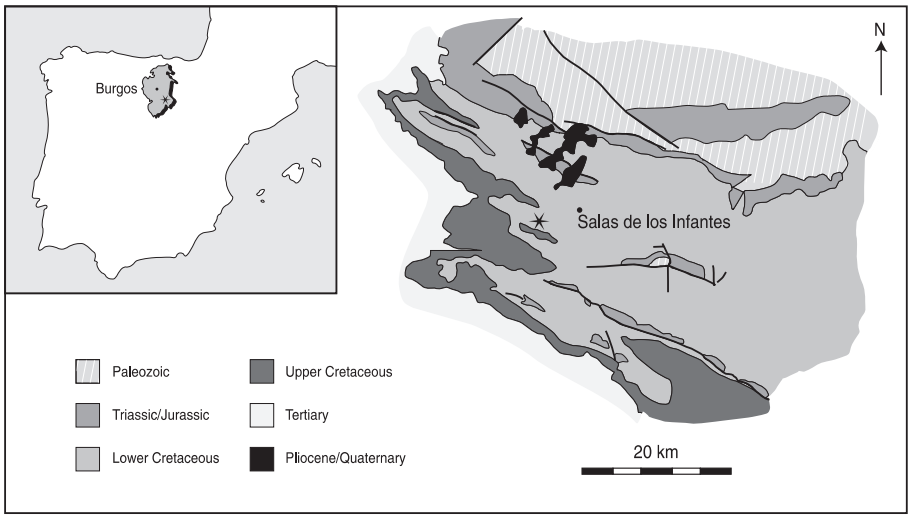

FIG. 1. – Synoptic map of the main geological units of western Cameros Basin, Burgos, Spain. The dinosaur locality is marked by an asterisk.
FIG. 1. – *Carte avec les principales unités géologiques de l'Ouest du bassin de Cameros, Burgos, Espagne. Le gisement à dinosaure est indiqué par un astérisque.*

TABLE I. – Measurements (in mm) of the rebbachisaurid dinosaur from the early Cretaceous of Burgos, Spain.
TABL. I. – *Mesures (en mm) du dinosaure rebbachisauridé du Crétacé inférieur de Burgos, Espagne.*

Caudal vertebrae	MPS-RV II-15	II-3	II-2	II-4	II-11
Total height	390				
Height of neural arch (from dorsal surface of centrum to top of neural spine)	250				
Height from postzygapophyses to top of neural spine	190				
Maximum width of neural spine (near the top)	85				
Anteroposterior length of neural spine	55				
Centrum length	98	150	155	150	130
Centrum height (anterior)	125		120		
(posterior)	135	135	125	95	115
Centrum width (anterior)	115		135		
(posterior)	135	135	135	130	135
Neural canal height	29	40	25		

Haemal arch	MPS-RV II-23
Height	135
Length	30

Ischium	MPS-RV II-18 (left)	MPS-RV II-19 (right)
Length (distance from proximal corner of pubic peduncle to distal end)	790	805
Maximal dimensions of iliac peduncle	117 x 82	
Maximal dimensions of pubic peduncle	115 x 63	
Minimal length of the neck of pubic peduncle	55	
Distance from the pubic peduncle to distal margin of the bone	160	
Dorsoventral length of the pubic peduncle	120	
Distal width		90
Distal thickness		25

Femur	MPS-RV II-16 (left)
Length	1080
Proximal length	230
Distal width	235

posterior chevron surfaces, there are prominent ridges that delimit a shallow and wide longitudinal groove. The transverse processes are broken, but they are well-developed, forming a deep projection that extends from the centrum to the neural arch. As preserved, they are not wing-like but appear to be formed by fusion of a dorsal and a ventral bar [see Calvo and Salgado, 1996]. The neural arch is dorsoventrally tall, about 1.9 higher than the centrum. The neural spine is cruciform-shaped, with four laminae at right angles, including a prespinal lamina, a postspinal lamina and two lateral laminae (suprapostzygapophyseal laminae [see Upchurch, 1998, fig. 10] ; spinopostzygapophyseal laminae [sensu Wilson 1999b : fig. 4]). The prespinal lamina is more marked at the basal part of the neural spine than towards the top. In dorsal view, the postspinal lamina is much more developed than the prespinal one. The lateral laminae have small wing-like projections near the top of the neural spine. Anterior caudal vertebrae located more posteriorly in the tail series (e.g., MPS-RV II-3 ; figs. 2G-H) show a longitudinal ridge (rudimentary transverse process ?) on the upper third of the lateral surface of the centrum. The centrum of MPS-RV II-3 is comparatively longer than that of anteriormost caudals. The neural canal is much higher than wide ; the ventral longitudinal groove is very shallow. The chevrons of the anterior caudals (MPS-RV II-23 ; fig. 2F) are V-shaped and open at their proximal ends.

The middle caudal vertebrae (MPS-RV II-2, 4 ; figs. 2I-J) have slightly amphicoelous centra that are longer than high or wide. They are characterised by two longitudinal ridges on the lateral side of the centra, the upper ridge being more prominent than the lower one. The neural arches are placed over the middle of the centra. The prezygapophyses slightly overhang the anterior margin of the centra. The neural spines are broken. Ventrally, the articulation surfaces for the haemal arches are visible on both anterior and posterior ends.

Additional remains from the axial skeleton consist of a rib fragment and indeterminate vertebral bones.

Ischium (figs. 3A-C). Both ischia are preserved, the left ischium is more complete than the rigth one (MPS-RV II-18, 19). The bones are approximately 80 cm long from the

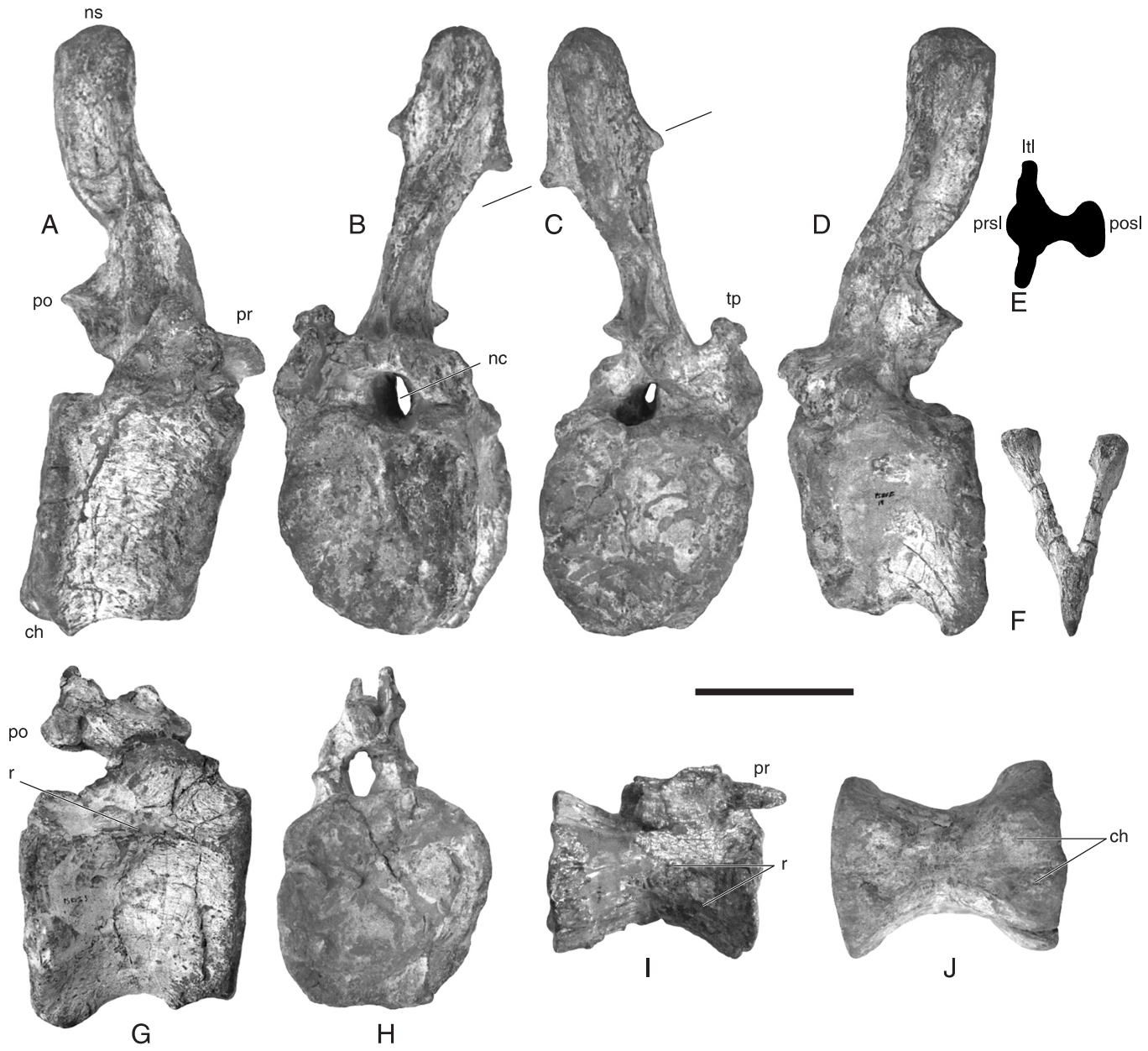

FIG. 2. – Rebbachisauridae indet., early Cretaceous (Barremian-Aptian), Burgos, Spain. A-E, anterior caudal vertebra MPS-RV II-15 in right lateral, anterior, posterior, left lateral and dorsal (cross-section at the level of the wing-like projections ; see fig. C) views ; F, anterior chevron MPS-RV II-23 in anterior view ; G-H, anterior to middle caudal vertebra MPS-RV II-3 in right lateral and posterior views ; I, middle caudal vertebra MPS-RV II-4 in right lateral view ; J, middle caudal vertebra MPS-RV II-2 in ventral view. Abbreviations : ch, chevron surface ; ltl, lateral lamina ; nc, neural canal ; ns, neural spine ; posl, postspinal lamina ; po, postzygapophysis ; prsl, prespinal lamina ; pr, prezygapophysis ; r, lateral ridge ; tp, transverse process. Scale bar = 10 cm.

FIG. 2. – *Rebbachisauridae indet., Crétacé inférieur (Barrémien-Aptien), Burgos, Espagne.* A-E*, vertèbre caudale antérieure MPS-RV II-15 en vues latérale droite, antérieure, postérieure, latérale gauche et dorsale (section transversale à la hauteur des projections en forme d'aile ; voir fig. C) ;* F*, chevron antérieur MPS-RV II-23 en vue antérieure ;* G-H*, vertèbre caudale antérieure à moyenne MPS-RV II-3 en vues latérale droite et postérieure ;* I*, vertèbre caudale moyenne MPS-RV II-4 en vue latérale droite ;* J*, vertèbre caudale moyenne MPS-RV II-2 en vue ventrale. Abréviations :* ch*, surface pour le chevron ;* ltl*, lame latérale ;* nc*, canal neural ;* ns*, épine neurale ;* posl*, lame postspinale ;* po*, postzygapophyse ;* prsl*, lame préspinale ;* pr*, prézygapophyse ;* r*, crête latérale ;* tp*, processus transverse. Barre d'échelle = 10 cm.*

proximal corner of the acetabular region to the distal end (see table I). The ischial shaft is very slender and almost straight. The iliac peduncle is more prominent than the pubic one, but the articular margin of the latter is comparatively longer. Medially, there is a concavity that forms part of the acetabulum. The distal end of the ischial shaft is bladelike and narrow, only slightly expanded relative to the rest of the shaft. The ischia are not coossified at their distal ends, but they show a very rugose symphyseal surface. The distal ends are almost horizontal and form a nearly coplanar structure in cross-section. Distally, the shaft is flattened dorsoventrally and has subequal medial and lateral depths ;

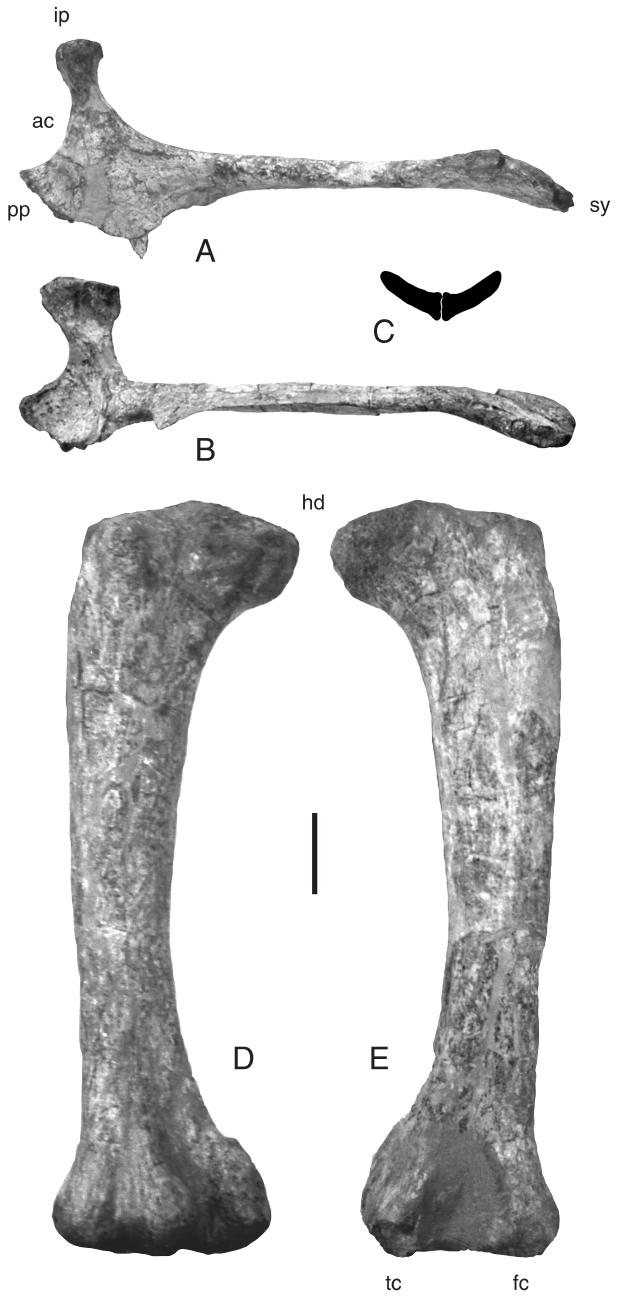

FIG. 3. – Rebbachisauridae indet., early Cretaceous (Barremian-Aptian), Burgos, Spain. A, left ischium MPS-RV II-18 in lateral view ; B, right ischium MPS-RV II-19 in medial view ; C, both ischia in distal view ; D-E, left femur MPS-RV II-16 in anterior and posterior views. Abbreviations : ac, acetabulum ; fc, fibular condyle ; hd, head ; ip, iliac peduncle ; pp, pubic peduncle ; tc, tibial condyle ; sy, symphysial surface. Scale bar = 10 cm.
FIG. 3. – *Rebbachisauridae indet., Crétacé inférieur (Barrémien-Aptien), Burgos, Espagne.* A, *ischium gauche MPS-RV II-18 en vue latérale ;* B, *ischium droit MPS-RV II-19 en vue médiale ;* C, *ischia en vue distale ;* D-E, *fémur gauche MPS-RV II-16 en vues antérieure et postérieure. Abréviations :* ac, *acetabulum ;* fc, *condyle fibulaire ;* hd, *tête ;* ip, *processus iliaque ;* pp, *processus pubien ;* tc, *condyle tibial ;* sy, *symphyse. Barre d'échelle = 10 cm.*

the maximum width is almost four times its minimal thickness.

Femur (figs. 3D-E). As reconstructed, the femur (MPS-RV II-16) is 108 cm long. The shaft is straight and relatively slender, with expanded proximal and distal ends. The femoral head is almost perpendicular to the shaft. It rises very slightly above the greater trochanter. The lesser trochanter is not developed. The lateral margin of the shaft is straight. There is no a prominent bulge on the proximal third of the lateral surface. The cross-sectional shape of the shaft is suboval, with the long axis oriented lateromedially. The fourth trochanter is reduced to a low ridge located above the midlength of the shaft, between the midline and the caudomedial margin. The distal condyles are prominent, the medial condyle larger than the lateral one, and separated from each other by a deep intercondylar groove.

Ontogenetic growth. The neural arches of the caudal vertebrae are firmly co-ossified to the centra, so the skeletal remains probably belong to a mature individual. The relative size of the bones suggests a medium-sized individual whose total length is approximately 10-12 m.

DISCUSSION

Affinities of the Burgos sauropod

The dinosaur remains from Tenadas de los Vallejos II (Burgos) are referred to Sauropoda on the basis of the bladelike distal shaft of the ischium ; elliptical (long axis oriented mediolaterally) cross-sectional shape of the femur ; and femoral fourth trochanter reduced to crest or ridge [see Wilson and Sereno, 1998 ; Wilson, 2002]. The material of Burgos also shows synapomorphies of Neosauropoda : anterior caudal neural arches with prespinal and postspinal laminae (also present in *Jobaria*) ; chevrons without a proximal "crus" bridging dorsal margin of haemal canal ; and ischial shaft flat, nearly coplanar (also in *Jobaria*) [Wilson, 1999a, 2002]. Moreover, the Burgos sauropod shares at least a synapomorphy with the Diplodocoidea sensu Upchurch, 1995 [senior synonym of Diplodocimorpha Calvo and Salgado, 1996] : tall neural arch in anterior caudal vertebrae. In diplodocoids, the neural arch is at least 1.5 higher than the centrum [Calvo and Salgado, 1996 ; 2.5 higher according to Wilson and Sereno, 1998]. In fact, the neural arch is at least two times higher than the centrum in the anterior caudals of '*Rebbachisaurus*' and the dicraeosaurid *Dicraeosaurus*, while it is between 1.5 and 2 in the diplodocoids *Diplodocus* and *Barosaurus* [see Calvo and Salgado, 1996]. In the Burgos sauropod, the neural arch of the single complete anterior caudal vertebra is about 1.9 higher than the centrum.

Diplodocoids consist of diplodocids, dicraeosaurids and rebbachisaurids [Sereno *et al.*, 1999 ; Wilson, 1999a, 2002]. Upchurch [1999] regarded nemegtosaurids as members of Diplodocoidea but they appear to be more closely related to titanosaurs within Titanosauriformes [Salgado and Calvo, 1997 ; Curry Rogers and Forster, 2001 ; Wilson, 2002]. The Burgos diplodocoid exhibits the following synapomorphy of the clade Rebbachisauridae + (Diplodocidae + Dicraeosauridae) : anterior caudal neural spines broad, i.e. transverse breadth approximately 50 % greater than the anteroposterior length [Wilson, 2002]. Moreover, it does not show synapomorphies of the clade formed by the Dicraeosauridae (*Dicraeosaurus*, *Amargasaurus*) and Diplodocidae (*Diplodocus*, *Apatosaurus*, *Barosaurus*, *Seismosaurus*, *Supersaurus*). For example, the anterior cau-

dal centra are not slightly procoelous ; the haemal canal of anterior caudal vertebrae is not closed proximally ; and the ischial shaft is neither expanded distally nor V-shaped, without a triangular cross-section [see Calvo and Salgado, 1996 ; Upchurch, 1998 ; Wilson and Sereno, 1998 ; Salgado, 1999 ; Wilson, 1999a, 2002].

Rebbachisaurids are basal diplodocoids outside the Diplodocidae-Dicraeosauridae clade. Bonaparte [1997] erected the Rebbachisauridae mainly on the basis of characters of the scapula and dorsal vertebrae. The Burgos specimen does not preserve synapomorphies of Rebbachisauridae listed by Wilson [2002] but it closely resembles rebbachisaurids in the form of both the anterior caudal vertebrae and ischium. The Spanish taxon exhibits a combination of primitive and derived characters that is only known in rebbachisaurids [see Calvo and Salgado, 1996 ; Upchurch, 1998 ; Wilson, 2002] : (1) 'petal'-shaped anterior caudal neural spines [Wilson, 2002 regarded the 'petal'-shaped posterior dorsal neural spines as synapomorphic for Rebbachisauridae (paralleled in dicraeosaurids), but this character is also present in the anteriormost caudals ; see Calvo and Salgado, 1996 : figs. 9-10] ; (2) transversely expanded, cruciform-like in dorsal view, anterior caudal neural spines (known in all diplodocoids but *Haplocanthosaurus*) ; 3) amphiplatyan or platycoelous anterior caudal centra, without pleurocoels (known in '*R.*' *tessonei*, *Haplocanthosaurus*, *Dicraeosaurus* and *Apatosaurus* within Diplodocoidea) ; 4) triangular-shaped, tapering distally anterior caudal transverse processes (only known in '*R.*' *tessonei* and *Haplocanthosaurus* among diplodocoids) ; 5) anterior caudal chevrons with open proximal articulation (only present in rebbachisaurids and *Haplocanthosaurus* among diplodocoids) ; 6) very slender ischium, with a narrow and flat distal end, nearly coplanar in cross-section (only '*Rebbachisaurus' tessonei* and *Haplocanthosaurus priscus* [Hatcher, 1903] have a similar morphology among diplodocoids).

It is difficult to compare the Burgos remains with those of *Rebbachisaurus garasbae* from the middle Cretaceous of Morocco as the latter has no homologue elements except caudal vertebrae [Lavocat, 1954]. Unfortunately, most of the remains of *R. garasabae* kept at the Museum National d'Histoire Naturelle of Paris is still unprepared (P. Taquet., pers. comm.). The Burgos diplodocoid is most similar to '*Rebbachisaurus' tessonei*, a rebbachisaurid from the middle Cretaceous of Argentina [Calvo and Salgado, 1996]. However, the incomplete nature of the Burgos remains does not allow us to recognize either the diagnostic characters of '*Rebbachisaurus' tessonei* as described by Calvo and Salgado [1996] or Wilson [2002] as *Rayososaurus*, with, perhaps, the exception of anterior caudal transverse processes composed of two lateral bars (while wing-like in most diplodocoids). A comparison of the Burgos sauropod with '*R.' tessonei* shows several minor differences : the neural arch of the anterior caudal is just 1.9 higher than the height of the centrum (versus 2.5 in '*R.' tessonei* [see Calvo and Salgado, 1996, fig. 10]) ; the postspinal lamina is greater than the prespinal lamina in anterior caudals (in contrast to '*R.' tessonei*) ; the lateral laminae have small wing-like projections towards the top of the neural spine (absent in '*R.' tessonei*), and the ischium is straighter and the dorsoventral length of the pubic articular surface is comparatively longer than in the South American specimen. The significance of these differences is unclear but they could represent taxonomic characters. Pending the discovery of new fossils, the Burgos sauropod is provisionally referred to the Rebbachisauridae as an indeterminate genus and species.

Rebbachisaurid distribution

Rebbachisaurids are known in the western Gondwanan landmasses (Africa and South America). They include the following taxa : *Rebbachisaurus garasbae* LAVOCAT, 1954 from the Albian-Cenomanian of Morocco ; *'Rebbachisaurus' tessonei* CALVO and SALGADO, 1996 from the Albian-Cenomanian of Argentina ; *Rayososaurus agrioensis* BONAPARTE, 1996 from the Aptian of Argentina ; and *Nigersaurus taqueti* SERENO *et al.*, 1999 from the Aptian-Albian of Niger.

The status of the rebbachisaurid remains from Argentina is currently under debate. The material from the Candeleros Member of the Rio Limay Formation of Neuquén in Patagonia has been referred to *Rebbachisaurus tessonei* [Calvo and Salgado, 1996 ; Calvo, 1999 and references] or to a different genus, listed either as *Limaysaurus* [Novas, 1997] or as *Rayososaurus* [Wilson and Sereno, 1998 ; Bonaparte, 1999a ; Wilson, 2002]. In contrast, Calvo and Salgado [1996] and, subsequently, Calvo [1999] referred the material of *Rayosaurus agrioensis* to as *Rebbachisaurus* sp. Moreover, Bonaparte [1999b] mentioned the presence of isolated rebbachisaurid remains in the Neocomian of Neuquén (Argentina), but no more information is given. The presence of additional diplodocoid bones in the upper member of the Bajo Barreal Formation (early late Cretaceous : Turonian- ?Coniacian) of Chubut, Argentina, has also been documented [Sciutto and Martínez, 1994 ; Lamanna *et al.*, 2001].

With regard to the African rebbachisaurid material, Lavocat [1954] described originally *Rebbachisaurus garasbae* from the "Continental intercalaire" of the Kem Kem, southern Morocco [see also Lavocat, 1952 ; Bonaparte, 1999b, fig. 39]. Later, Russell [1996] referred some isolated remains from the Albian-Cenomanian Red Sandstones ("Grès Rouges infracénomaniens") of the Tafilalt, southern Morocco, to *Rebbachisaurus garasbae* and cf. *Rebbachisaurus* sp. *Nigersaurus taqueti* is known from the Aptian-Albian Tegama Group (GAD 5, upper part of the Elrhaz Formation and lower part of the Echkar Formation [Sereno *et al.*, 1999]). The original material of *Rebbachisaurus tamesnensis* from the Hauterivian-Barremian Tiourarén Formation of Niger, first considered as camarasaurid by Lapparent [1960] and later as diplocodoid by McIntosh [1990], is not diagnostic ; the remains described by Lapparent [1960] could belong to the basal sauropod *Jobaria tiguidensis* [Sereno *et al.*, 1999]. Rebbachisaurid remains also occur in the Cenomanian Bahariya Formation of Egypt [Smith *et al.*, 2001] and, tentatively, in the Albian "Continental intercalaire" of Algeria and Tunisia [see Lapparent, 1960].

Additional rebbachisaurid remains have been reported from the late Cretaceous (Coniacian-Santonian [Novas, 1997] ; formerly considered as Campanian [see Powell, 1986] or Maastrichtian [see Weishampel, 1990]) of Argentina as '*Antarctosaurus wichmannianus'* Huene, 1929. The phylogenetic position of this taxon is unclear : the referred

dentary was originally attributed to the Titanosauridae [Huene, 1929]. Powell [1986] and Chiappe *et al.* [2001] have supported the titanosaurid affinities of this taxon [see also Salgado and Calvo, 1997]. In contrast, McIntosh [1990] regarded the dentary of *A. wichmannianus* as diplodocoid, and Jacobs *et al.* [1993] removed it from the Titanosauridae to the Diplodocidae. Wilson and Sereno [1998] and Upchurch [1999] interpreted the dentary of '*A. wichmannianus'* as that of a late diplodocoid, while Sereno *et al.* [1999] and Wilson [2002] referred it to the Rebbachisauridae. With regard to other possible late Cretaceous diplodocoids, there is poor evidence to support the occurrence of the diplodocid *Dyslocosaurus polyonychius* in the Maastrichtian Lance Formation of Wyoming, North America. Derivation of this specimen from the late Jurassic of the Morrison Formation is more likely [McIntosh *et al.*, 1992].

Rebbachisaurids have not been described in Europe, with the exception of *Histriasaurus boscarollii* from the early Cretaceous of Croatia [Dalla Vecchia, 1998]. This taxon is based on an isolated dorsal vertebra from the late Hauterivian-early Barremian of Istria [Dalla Vecchia, 1998, figs. 13D-E]. The specimen is similar to mid-posterior dorsal vertebrae of *Rebbachisaurus garasbae* from Morocco and '*Rebbachisaurus' tessonei* from Patagonia in having a 'petal'-shaped posterior dorsal neural spine, but differs in having a hyposphene-hypantrum complex. *Histriasaurus* is a member of the Diplodocoidea on the basis of the tall neural arch, which is three times higher than that of the centrum [sensu Calvo and Salgado, 1996], and the presence of a postspinal lamina on the neural spine [Upchurch, 1998]. It differs from dicraeosaurids in retaining pleurocoels, and is probably different from diplodocids in having the neural spine 75 per cent higher than the neural arch. The affinities of *Histriasaurus* with the Rebbachisauridae need to be confirmed but this taxon testifies of the presence of a basal diplodocoid in the early Cretaceous of Croatia [Dalla Vecchia, 1998].

Besides *Histriasaurus* and the Burgos rebbachisaurid, diplodocoids are rare in the Wealden succession of Europe as they are only represented by scarce remains. Charig [1980] described a sled-shaped diplodocid chevron from the Barremian Wessex Formation of the Isle of Wight (England), but the referral of this bone to the Diplodocoidea must be provisional [Naish and Martill, 2001]. Other possible diplodocoid material from the same area and horizon consists of isolated remains [see Upchurch, 1995 ; Naish and Martill, 2001]. *Cetiosauriscus stewartii* from the Middle Jurassic (Callovian) of England was referred to the Diplodocidae by McIntosh [1990], but it could be a basal neosauropod [Wilson et al., 1999]. In the Iberian Peninsula, the only known diplodocoids are *Dinheirosaurus lourinhanensis* from the late Jurassic (Kimmeridgian) Camadas de Alcobaça Formation of Lourinhã, Portugal [Bonaparte and Mateus, 1999] and *Losillasaurus giganteus* from the late Jurassic-early Cretaceous transition of Valencia, Spain [Casanovas *et al.*, 2001]. *Losillasaurus* lacks several diplodocid and dicraeosaurid synapomorphies, and differs from rebbachisaurids in having hyposphene-hypantrum complex on dorsal vertebrae, slightly opisthocoelous dorsal centra, and slightly procoelous anterior caudal centra. It has been regarded as sister-group to the clade (*Barosaurus* + *Diplodocus*) + *Dicraeosaurus* by Casanovas *et al.* [2001]. In other words, *Losillasaurus* is a diplodocoid, but it is probably not a rebbachisaurid. In Portugal, Bonaparte and Mateus [1999] considered *Dinheirosaurus* as a member of the Diplodocidae on the basis of features of the presacral vertebrae. Both *Losillasaurus* and *Dinheirosaurus* are regarded as members of the clade formed by dicraeosaurids and diplodocids by Wilson [2002]. Finally, Cuenca Bescós et al. [1997] referred tentatively an isolated tooth from the late Jurassic of the Villar del Arzobispo Formation of Teruel (Spain) to as Diplodocidae indet., and Martínez *et al.* [2000] described as diplodocid a tooth from the late Jurassic of the Lastres Formation of Asturias (Spain). This material seems too incomplete for an accurate identification.

PALAEOBIOGEOGRAPHICAL IMPLICATIONS

The discovery of a rebbachisaurid sauropod in the early Cretaceous (Barremian-Aptian) of Burgos demonstrates the presence of this basal clade of diplodocoids in the Iberian Peninsula. It confirms the presence of rebbachisaurids in Europe, and adds to previous reports of the Rebbachisauridae in Africa and South America.

From a biogeographical point of view, the occurrence of a rebbachisaurid in the Barremian-Aptian of Spain suggests a land connection between Europe and Africa during the early Cretaceous (although an alternative scenario involving an earlier dispersal episode cannot be excluded as basal diplodocoids are known as early as the late Jurassic). This hypothesis supports previous evidence based on the intercontinental distribution of dinosaurs across the Tethys seaway, such as the dryosaurid ornithopods [Galton and Taquet, 1982] and spinosaurid theropods [Sereno *et al.*, 1999].

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