Redescription of the wrist and manus of ?*Bothriospondylus madagascariensis*: new data on carpus morphology in Sauropoda

Émilie LÄNG
Florent GOUSSARD
Muséum national d'Histoire naturelle, Département Histoire de la Terre,
USM 0208-UMR 5143 CNRS "Paléobiodiversité et Paléoenvironnements",
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
lang@mnhn.fr
goussard@mnhn.fr

Läng É. & Goussard F. 2007. — Redescription of the wrist and manus of ?*Bothriospondylus madagascariensis*: new data on carpus morphology in Sauropoda. *Geodiversitas* 29 (4): 549-560.

ABSTRACT
Except for some rare exceptions, the arrangement of the carpus remains poorly understood among sauropodomorphs, mainly because of a bad preservation in the fossil record. When preserved, it is difficult to identify the carpal elements, which are rarely found in articulation. Whereas the carpus of Prosauropoda is relatively well known by the remains of *Massospondylus* and *Plateosaurus*, the structure of the sauropod carpus is still unknown and subject to many interpretations so far. Here, we redescribe the manus and the wrist of ?*Bothriospondylus madagascariensis*, a Bathonian (Middle Jurassic) sauropod from the Majunga Basin in Madagascar, previously described by Lavocat in 1955. The wrist consists of five carpal elements, an unusual disposal among sauropods, which typically preserves most of the time three or fewer carpal bones. Moreover, these five carpal elements are arranged in three carpal rows, another unexpected feature regarding to other sauropods. The comparison of the Malagasy carpus with that of an hypothetical basal archosaur leads us to propose a new hypothesis of homology for the carpus of ?*Bothriospondylus*. Therefore, this specimen would consist in: a radiale, the fused distal carpal 1 with the intermedium and one or two centrales, and three distal elements (distal carpal 2, distal carpal 3, and distal carpal 4 or distal carpal 4 + ulnare).

KEY WORDS
Dinosauria,
Sauropoda,
carpus,
manus,
homology.

RÉSUMÉ
*Redescription du poignet et de la main de ?*Bothriospondylus madagascariensis*: nouvelles données sur la morphologie du carpe des Sauropoda.*
Hormis quelques rares exceptions, l'arrangement du carpe est très mal connu au sein des sauropodomorphes, principalement en raison de la rareté des restes connus dans le registre fossile. Lorsqu'ils sont connus, un second problème repose sur la difficulté à identifier les éléments du carpe, rarement trouvés en articulation. Alors que le poignet des prosauropodes est relativement bien documenté chez *Massospondylus* et *Plateosaurus*, la structure du carpe des sauropodes est toujours débattue et a été jusqu'à présent l'objet de nombreuses interprétations. Ici, nous redécrivons la main et le poignet de ?*Bothriospondylus madagascariensis*, un sauropode du Bathonien (Jurassique moyen) du bassin de Majunga sur l'île de Madagascar, précédemment décrits par Lavocat en 1955. Constituée de cinq éléments, la structure du carpe est inédite au sein des sauropodes qui présentent habituellement trois éléments au moins. Ces cinq carpiens sont de plus organisés en trois rangées, une autre caractéristique intéressante au regard des autres carpes connus de sauropodes. La comparaison avec le modèle d'un poignet d'archosaure primitif hypothétique permet de proposer des hypothèses d'homologie pour les éléments du carpe de ?*Bothriospondylus*. Ainsi, le poignet de ce spécimen consisterait en un radial, en un élément fusionné composé du carpien distal 1 avec l'intermédiaire et un ou deux centraux, et de trois autres carpiens distaux (carpien distal 2, carpien distal 3 et carpien distal 4 ou carpien distal 4 + ulnaire).

MOTS CLÉS
Dinosauria,
Sauropoda,
carpe,
main,
homologie.

INTRODUCTION

In 1954, Lavocat prospected in the southwest of the Majunga Basin, near Tsinjorano, where many sauropod remains were already reported by Collignon (1954). One site received Lavocat's attention, Manary-Abo, located near the site that later yielded many juvenile sauropod remains attributed to *Lapparentosaurus madagascariensis* (Ogier 1975; Bonaparte 1986). The Manary-Abo site from the Bathonian (Middle Jurassic; Lavocat 1955b) yielded a nearly complete skeleton of ?*Bothriospondylus madagascariensis* Lydekker, 1895 that included a complete forelimb in articulation including the carpal bones (Lavocat 1955a-c, 1957; Fig. 1). Although it is clearly a eusauropod, ?*Bothriospondylus madagascariensis* is a *nomen dubium* (Upchurch *et al.* 2004). The wrist displays five carpal bones arranged in three rows, an unexpected feature among sauropods.

MATERIALS AND METHODS

A cast of the articulated manus that was made *in situ* at the time of Lavocat's discovery allows us to propose a faithful 3D reconstruction of the manus of ?*Bothriospondylus* (Fig. 2). The CT analysis of the original specimen was performed at the Villeneuve-St-Georges Hospital, and the reconstruction was produced with the MIMICS software (MATERIALISE 2007). The assumptions of homology here proposed are based on an hypothetical primitive reptile condition, following Romer (1956: 379, fig. 179B). Due to the anterior position of the radius to the ulna, we consider the manus positioned in a traditional orientation according to Wilson & Sereno (1998, with the McI placed anteriorly) *contra* Bonnan (2003, with the McI placed medially). Due to the tubular arrangement of the manus, the carpals are organized according to an angle about 270°, but for convenience the description of the

TABLE 1. — Measurements (in cm) of the manus of ?*Bothriospondylus madagascariensis*. Abbreviations: **L**, length; **H**, height; **øA-P**, anteroposterior diameter; **øA-P prox**, proximal anteroposterior diameter; **øT prox**, proximal transverse diameter; **øA-P mid**, middle anteroposterior diameter; **øT**, transerve diameter; **øT mid**, middle transverse diameter; **øA-P dist**, distal anteroposterior diameter; **øT dist**, distal transverse diameter.

Element		**Specimen number**	**H**		**øA-P**			**øT**	
Carpals	radiale	MNHN MAJ 289-2	4.66		-			14.85	
	dc1 + c + i	MNHN MAJ 289-8	15.15		15.78			21.63	
	dc2	MNHN MAJ 289-5e	6.13		8.51			6.78	
	dc3	MNHN MAJ 289-11	5.25		7.68			5.09	
	dc4	MNHN MAJ 289-7	8.07		10.90			13.21	
Element		**Specimen number**	**L**	**øA-P prox**	**øA-P mid**	**øA-P dist**	**øT prox**	**øT mid**	**øT dist**
Metacarpals	McI	MNHN MAJ 289-5a,c	31.10	13.33	5.76	7.98	12.52	6.69	10.08
	McII	MNHN MAJ 289-5b	36.50	11.14	6.22	7.92	11.45	6.51	12.30
	McIII	MNHN MAJ 289-6	38.50	9.90	6.04	7.65	12.30	5.58	12.97
	McIV	MNHN MAJ 289-9a	36.80	12.40	6.78	8.67	10.48	5.70	-
	McV	MNHN MAJ 289-9b	-	7.25	4.53	-	10.17	5.89	-
Phalanges	I-1	MNHN MAJ 289-5d	12.46	7.75	-	6.78	10.84	-	8.88
	I-2 (pollex)	MNHN MAJ 289-10	17.24	9.02	-	-	7.78	-	-
	II-1	MNHN MAJ 289-4a	10.19	7.56	-	4.62	11.13	-	9.39
	II-2	MNHN MAJ 289-4b	3.89	2.50	-	3.11	4.81	-	6.34
	III-1	MNHN MAJ 289-1	8.67	7.29	-	4.11	10.70	-	8.50

dislocated manus follows the orientation given in Figures 3 and 4. The measurements of the different elements (carpals, metacarpals and phalanges) are given in Table 1.

The material is deposited in the Majunga basin collections in the Muséum national d'Histoire naturelle, Paris (MNHN MAJ).

DESCRIPTION

CARPUS

The carpus of ?*Bothriospondylus madagascariensis* preserves five elements arranged in three rows (Fig. 2C). The five elements display a rugose surface, suggesting the presence of cartilage in life.

Proximal carpals

There are two proximal carpal elements.

The first (MNHN MAJ 289-2; Fig. 3A-C) has a crescent-like shape (the "torus-like element" of Lavocat 1955b, c). The height is regular, but the element becomes thick medially. The distal surface is more flattened medially to contact the proximal surface of the larger element of the carpus (the "main bone" of Lavocat 1955b, c). It is placed antero-medially on this element (Fig. 2D). This bone is tentatively interpreted as the radiale (r), because of its contact with the radius.

The second proximal carpal (MNHN MAJ 289-8; Fig. 3D, E, G) is subcylindrical. It is inclined dorsolaterally. Its distal end is firmly fused with the posterior part of the proximal surface of the "main bone" (Fig. 3E; see below "distal carpals"). The suture between the two elements is only visible in posterior view of the "main bone". This element is tentatively identified as the intermedium (i), because of contact with the radius and its posterolateral position to the radiale (Fig. 2D).

Distal carpals

There are four distal carpal elements.

Fig. 1. — Photograph of field works in 1954, Manary-Abo (Majunga Basin, Madagascar). Here, one of the planters who helped Lavocat to realize excavations, with the radius and complete manus on the left (after Lavocat 1955a).

The larger element of the carpus represents what Lavocat named the "main bone" (Lavocat 1955b, c). This bone (MNHN MAJ 289-8; Fig. 3D-G) has an elliptical outline in proximal view. It is taller proximodistally than any other carpal. The proximal surface is slightly convex if we except the fused intermedium (see above "proximal carpals"), and the distal surface bears two unequal shallow concavities (the medial being the largest) separated by a low osseous ridge. The anterolateral and posterior surfaces are pierced by foramina. The element is also pierced right through from the distal edge of the lateral surface to the lateral edge of the distal surface; this opening is of uncertain interpretation. In articulation, the distal surface of this "main bone" covers the proximal end of the first metacarpal (mcI) medially and the two adjacent distal carpals of smaller size laterally (which overlap the second and third metacarpals; Fig. 2C, D). This bone is identified as the distal carpal one (dc1) considering its position above the mcI. Its position relative to the two distal carpals suggests it is a composite element that is fused with one or two centrale(s) (dc1 + c), as already suggested by Lavocat (1955b, c). These two hypothetical centrales could thus represent a "centrale" row fused with the first distal carpal. According to this hypothesis, the "main bone" would represent a fusion between three different levels: the intermedium (proximal row, see above), the two centrale ("middle" row) and the first distal carpal (distal row). The "main bone" is thus identified here as "dc1 + c + i".

The second distal carpal (MNHN MAJ 289-5e; Fig. 3H, I) has a 8-shaped proximal outline that is oriented anteroposteriorly, with the anterior part smaller than the posterior one. This second distal element is placed on the posterior part of the proximal end of the second metacarpal (mcII)

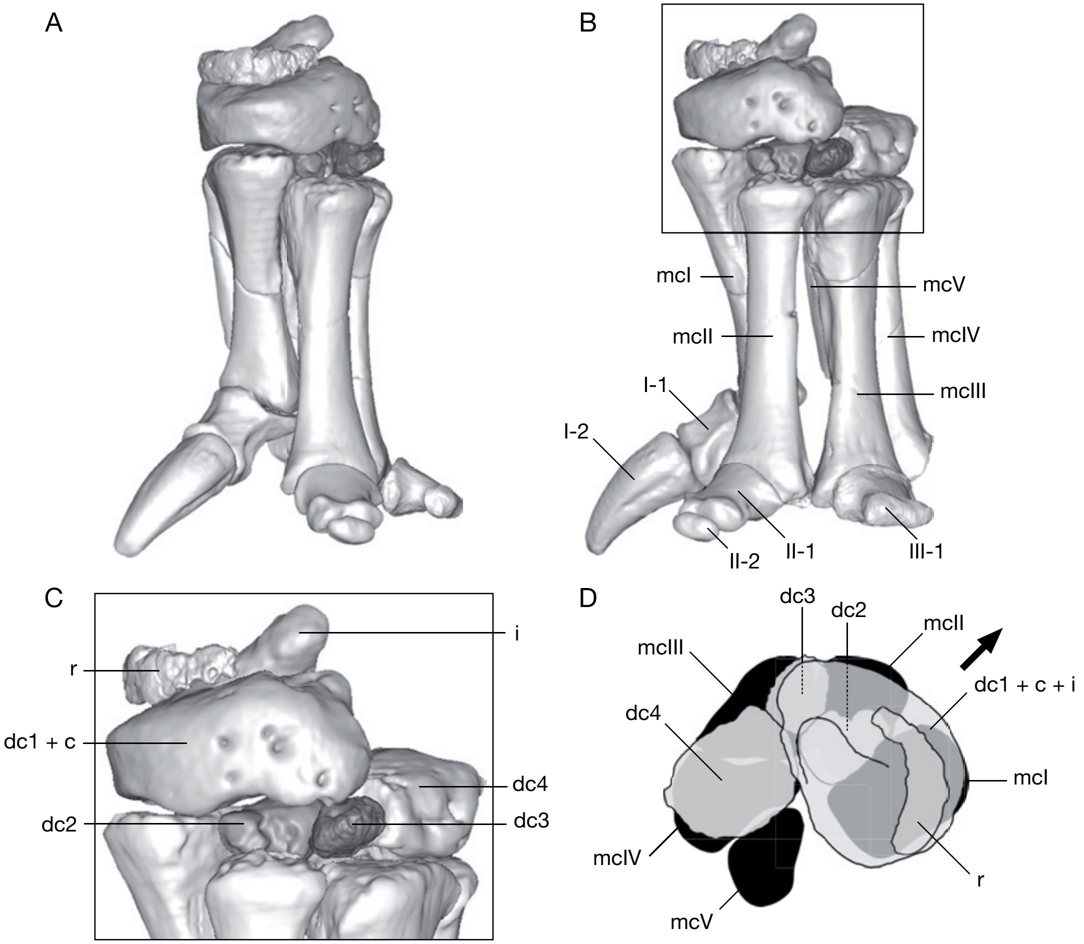

FIG. 2. — 3D reconstruction of the manus of ?*Bothriospondylus madagascariensis*: **A**, anterior view; **B**, lateral view; **C**, detail of the carpus in lateral view; **D**, arrangement of the carpus in proximal view. Abbreviations: **dc1 + c**, distal carpal 1 fused with one (or two) centrale; **dc1 + c + i**, distal carpal 1 fused with one (or two) centrale and intermedium; **dc2**, distal carpal 2; **dc3**, distal carpal 3; **dc4**, distal carpal 4 (possibly fused with distal carpal 5); **i**, intermedium; **I-1**, phalanx I-1; **I-2**, phalanx I-2 (pollex); **II-1**, phalanx II-1; **II-2**, phalanx II-2; **III-1**, phalanx III-1; **mcI**, metacarpal 1; **mcII**, metacarpal 2; **mcIII**, metacarpal 3; **mcIV**, metacarpal 4; **mcV**, metacarpal 5; **r**, radiale. The arrow indicates the anterior part of the manus in D.

(Fig. 2D). It contacts the mcI laterally and extends its proximal surface laterally. Although it is unclear on the original specimen, the CT study of the manus reveals the absence of fusion between this element and the two first metacarpals. It is identified as the distal carpal 2 (dc2) according to its position.

The third distal element (MNHN MAJ 289-11; Fig. 3J-M) is ovoid. Its medial surface is flattened to contact the dc2, and the distal one is slightly bevelled proximolaterally. The posterior surface is slightly convex and corresponds to the presumed contact with the fourth distal element (Figs 2D; 3K). In proximal view, a shallow groove extends anteroposteriorly on the posterior two thirds of the bone, while the anterior third displays a large depression which corresponds to the opening on the distal part of the anterolateral surface of the dc1 + c + i. This third distal element is located laterally to the dc2 and recovers the anteromedial part of the

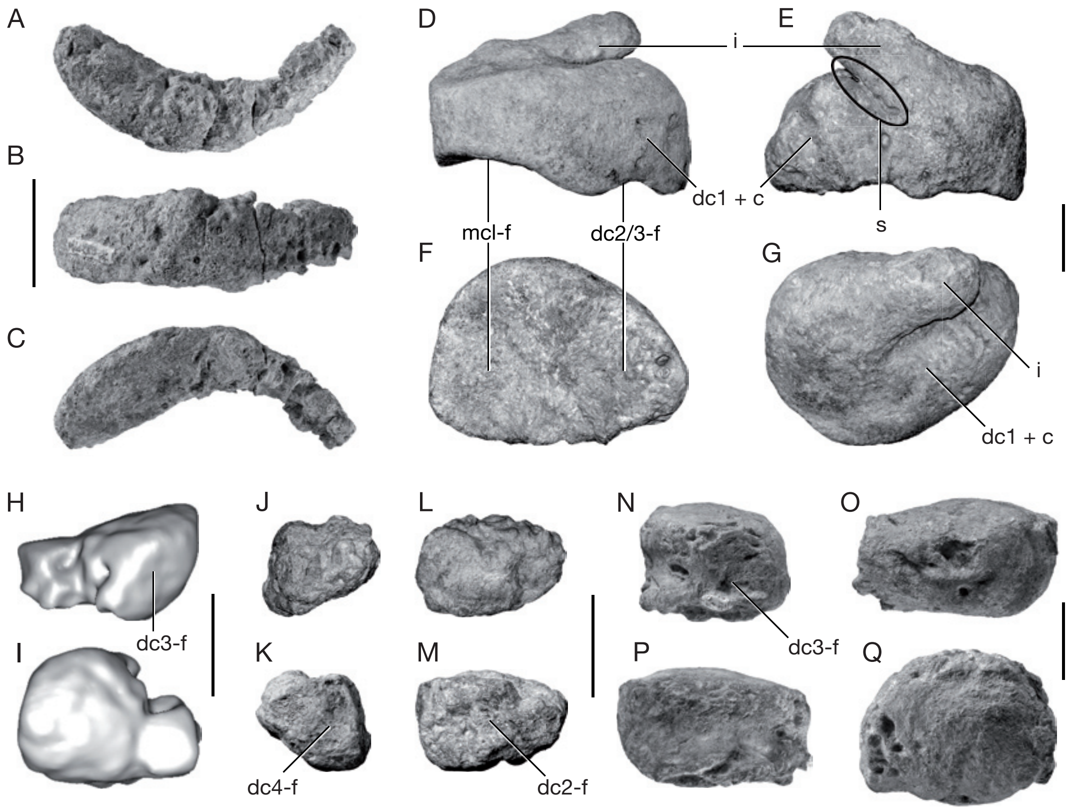

FIG. 3. — Carpal elements of ?*Bothriospondylus madagascariensis*: **A**-**C**, radiale (MNHN MAJ 289-2) in proximal (**A**), anterior (**B**) and distal (**C**) views; **D**-**G**, "main bone" dc1 + c + i (MNHN MAJ 289-8) in anterior (**D**), posterior (**E**), distal (**F**) and proximal (**G**) views; **H**, **I**, distal carpal 2 (MNHN MAJ 289-5e) in lateral (**H**) and proximal (**I**) views; **J**-**M**, distal carpal 3 (MNHN MAJ 289-11) in anterior (**J**), posterior (**K**), proximal (**L**) and medial (**M**) views; **N**-**Q**, distal carpal 4 (MNHN MAJ 289-7) in medial (**N**), anterior (**O**), posterior (**P**) and proximal (**Q**) views. Abbreviations: **dc1 + c**, distal carpal 1 fused with one (or two) centrale; **dc2/3-f**, contact facet with distal carpals 2 and 3; **dc3-f**, contact facet with distal carpal 3; **dc4-f**, contact facet with distal carpal 4; **mcI-f**, contact facet with metacarpal 1; **i**, intermedium; **s**, suture of the fusion between dc1+c and i. Scale bars: 5 cm.

proximal end of the metacarpal III (mcIII) (Fig. 2D). It is identified as the distal carpal 3 (dc3).

Because it was not found in articulation, the position of the fourth element (MNHN MAJ 289-7; Fig. 3N-Q) is unclear and subject to interpretation. Here, we postulate this element is astride the lateral part of the proximal end of the mcIII and the entire proximal surface of the metacarpal IV (mcIV) (Fig. 2D). This assumption is supported by a planar and circular surface on the medial surface of the bone, which could represent a contact with the posterior surface of the dc3 according to our interpretation (Figs 2D; 3N). So, we consider this element as the distal carpal 4 (dc4), even if it is also possible to consider it as the ulnare or a fusion between dc4 and ulnare. This bone is the second larger after the dc1 + c + i. It has a D-like outline in proximal view, with a plane anterior surface in our hypothesis. The proximal surface is convex while the distal one is plane to contact the proximal end of the mcIII and mcIV according to this orientation. It is pierced by a large foramen on the anterior surface.

METACARPALS

The mcI-III (mcI: MNHN MAJ 289-5a,c; mcII: MNHN MAJ 289-5b; mcIII: MNHN MAJ 289-6;

FIG. 4. — Metacarpals and phalanges of ?*Bothriospondylus madagascariensis*: **A**, **B**, metacarpals I-III (mcI: MNHN MAJ 289-5a,c; mcII: MNHN MAJ 289-5b; mcIII: MNHN MAJ 289-6), distal carpal 2 (MNHN MAJ 289-5e) and phalanges I-1 (MNHN MAJ 289-5d) and II-1 (MNHN MAJ 289-4a) in connexion in anterolateral (**A**) and anteromedial (**B**) views; **C**, metacarpal IV (mcVI: MNHN MAJ 289-9a) in anterior view; **D**, metacarpal V (mcV: MNHN MAJ 289-9b) in anterior view; **E**, proximal view of the metacarpals with the distal carpal 2 in connexion; **F**, **G**, phalanx I-2 (pollex, MNHN MAJ 289-10) in lateral (**F**) and proximal (**G**) views; **H**, phalanx I-1 (MNHN MAJ 289-5d) in dorsal view; **I**, phalanges II-1 (MNHN MAJ 289-4a) and II-2 (MNHN MAJ 289-4b) in dorsal view; **J**, phalanx III-1 (MNHN MAJ 289-1) in dorsal view. Abbreviations: **dc2**, distal carpal 2; **mcI**, metacarpal 1; **mcII**, metacarpal 2; **mcIII**, metacarpal 3; **mcIV**, metacarpal 4; **mcV**, metacarpal 5; **I-1**, phalanx I-1; **II-1**, phalanx II-1. Scale bars: 5 cm.

Fig. 4A, B) were found in articulation. Although the mcIV-V (mcIV: MNHN MAJ 289-9a; mcV: MNHN MAJ 289-9b; Fig. 4C, D) were found separated from the first three, there is no doubt about the tubular arrangement of the manus. McII is heightened relative to the mcIII, but in natural position the proximal articular surfaces of these two bones should be on the same level while the shift between the two first metacarpals is natural according to the position of the dc2 (Figs 2A, B; 4A). The metacarpals are gracile and present a subvertical orientation in a digitigrade posture, as observable in many neosauropods and *Mamenchisaurus youngi* Pi, Ouyang & Ye, 1996 or *Lapparentosaurus* Bonaparte, 1986 (Ogier 1975; Ouyang & Ye 2002). They contact each other proximally and distally with small articular surfaces (Fig. 2A, B), as usually observed in sauropods (Apesteguía 2005). McI-IV are of equivalent size, nevertheless the first is slightly smaller as in all non macronarian sauropods (Wilson 2002) and *Camarasaurus lewisi* Jensen, 1988 (McIntosh *et al.* 1996a). The distal part of the fifth metacarpal is broken, and it is thus impossible to determine if this element is really smaller than the mcIV as in *Ferganasaurus* Alifanov & Averianov, 2003. The proximal articular surface of the first metacarpal is subrectangular but those of other metacarpals are subtriangular (Fig. 4E). The distal surfaces of metacarpals I-IV are subrectangular and divided in two condyles. Both the proximal and distal articular surfaces are perpendicular to the longitudinal axis of diaphyses. The articular surfaces for the phalanges extend on the anterior face of the distal end of the metacarpals, in contrast to *Brachiosaurus* Riggs, 1903, in which these surfaces become restricted to distal surface (Janensch 1922, 1961). Like in *Shunosaurus* Dong, Zhou & Zhang, 1983 (Zhang 1988), *Lapparentosaurus* (Ogier 1975), and *Camarasaurus* Cope, 1877 (Osborn 1904), this peculiar morphology allows the phalanges to articulate at approximately 90° (Fig. 2A, B). This suggests a highest mobility with a possibility of flexor movements contrary to the single, rigid, block-like structure postulated by Bonnan (2003).

Phalanges

Only five phalanges belonging to the digits I to III have been collected (Fig. 4F-J). The first phalanx of the digit I (I-1; MNHN MAJ 289-5d; Fig. 4H) is longer proximodistally than transversely and of rectangular shape, contrary to the first phalanx broader transversely than proximodistally in other sauropods (Upchurch 1998; Wilson & Sereno 1998; Wilson 2002; Upchurch *et al.* 2004). The proximal articular surface is twisted laterally relatively to the whole phalanx. This morphology confers to the phalanx a laterally inclined position relatively to the shaft of the first metacarpal, and a divergent arrangement to other phalanges (Fig. 2A). Although there is no collateral fossa, this phalanx I-1 displays a strong concavity on the lateral surface of the distal end. In distal view, the articular surface is rectangular, contrary to *Lapparentosaurus* and some other sauropods where this surface is trapezoid. The first phalanges of digit II and III (II-1, MNHN MAJ 289-4a and III-1, MNHN MAJ 289-1; respectively Fig. 4I and Fig. 4J) are wider than long and their distal articular surfaces extend dorsally and ventrally. The ungual of digit I (I-2 or pollex, MNHN MAJ 289-10; Fig. 4F, G) is relatively conical and slightly curved ventrally in lateral view. It only displays a slight longitudinal groove on its lateral surface. Its proximal surface is transversely slightly compressed and presents two articular facets (the medial one is the larger). Following the twist of phalanx I-1, the pollex is also slightly inclined laterally, leading its lateroventral edge to contact the ground (Fig. 2A). The ungual of digit II (II-2, MNHN MAJ 289-4b; Fig. 4I) is very reduced, wider than longer, and nail-like. As in sauropods, digit II (and probably digit III) has two phalanges (Upchurch 1998; Wilson & Sereno 1998; Wilson 2002; Upchurch *et al.* 2004). This lead us to consider the following phalangeal formula: 2-2-2?-?-?.

DISCUSSION

Comparisons with other sauropods

The carpus of ?*Bothriospondylus* presented in this study displays some unusual features such as the number, the shape, and the arrangement of the carpal elements. It thus prevents any interpretation with the traditional characters proposed in most recent phylogenetic analyses, which usually consider in Sauropoda three or fewer carpals, rounded or block-shaped (Upchurch 1998; Wilson & Sereno 1998; Wilson 2002; Upchurch *et al.* 2004). However, some comparisons on metacarpals and phalanges lead us to determine more precise phylogenetic relationships of this specimen of ?*Bothriospondylus*.

Therefore, this manus displays some classical features of Sauropoda as the distal articular surface of the McI perpendicular to the long axis of the shaft (except in *Omeisaurus* Young, 1939,

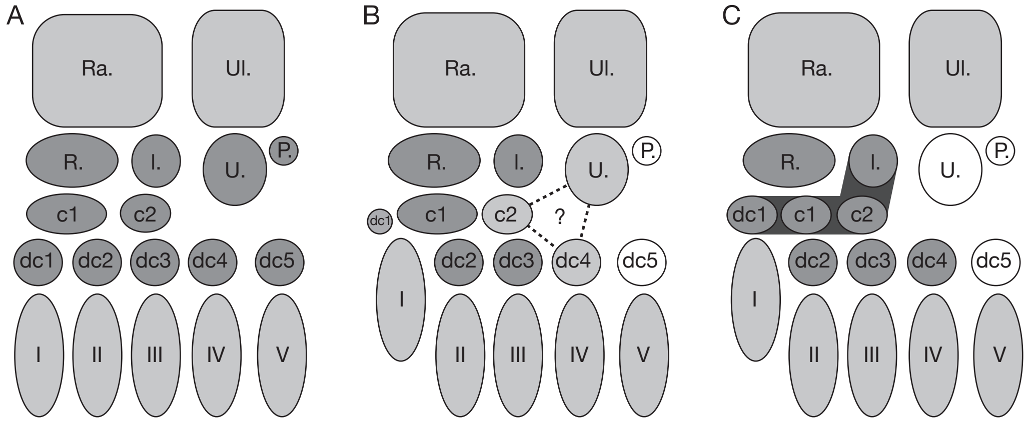

FIG. 5. — Schematic reconstitution of carpus: **A**, hypothetical primitive reptile condition after Romer (1956); **B**, *Massospondylus carinatus* after Broom (1911); **C**, ?*Bothriospondylus madagascariensis*. Absent or unpreserved elements are figured in white; present or preserved elements are figured in grey; doted lines indicate element of uncertain position; fused elements are linked with dark grey lines. Abbreviations: **c**, centrale; **dc**, distal carpal; **I**, intermedium; **P.**, pisiform; **R.**, radiale; **Ra.**, radius; **U.**, ulnare; **Ul.**, ulna.

Mamenchisaurus youngi, *Ferganasaurus*, *Jobaria* Sereno *et al.*, 1999 and diplodocids) and the digit II with two phalanges (except in *Opisthocoelicaudia* Borsuk-Bialynicka, 1977). The tubular arrangement of subparallel metacarpals in a U-shaped manus, subtending an angle of 270° (Fig. 4E), is characteristic of nearly all neosauropods, just as the first phalanges of digits II and III wider than long. In the same way, the gracile metacarpals could refer ?*Bothriospondylus* to macronarian sauropods like *Brachiosaurus*, *Camarasaurus* and *Malawisaurus* Haughton, 1928, but this character is also observable in eusauropods like *Lapparentosaurus*, *Atlasaurus* Monbaron, Russell & Taquet, 1999 and *Jobaria*. Interestingly, ?*Bothriospondylus* presents a phalanx I-1 longer than wider (Fig. 4H) contrary to other known sauropods and its rectangular shape is different to the wedge-shaped phalanx I-1 of *Jobaria* and diplodocids. Finally, the mcI is shorter than the mcIV and displays a divided distal articular surface contrary to *Lapparentosaurus*, *Ferganasaurus* and some titanosauriforms (*Brachiosaurus*, *Malawisaurus*, *Opisthocoelicaudia*).

Using only the manus, it is thus difficult to determine the phylogenetic relationships of this specimen of ?*Bothriospondylus*. This sauropod does not correspond to *Lapparentosaurus madagascariensis* discovered at proximity and thus accents the diversity of the Bathonian sauropods in the Majunga Basin (Madagascar). However, this specimen of ?*Bothriospondylus* can be excluded from basal eusauropods, diplodocoids and titanosauriform sauropods. Therefore, it could be closer to derived eusauropods or basal macronarian sauropods. The study of the remaining part of the skeleton would allow to clarify its phylogenetic position in the future.

CARPAL PATTERN IN ?*BOTHRIOSPONDYLUS*

Regarding to their odd shape nature, the articulation and orientation of the sauropod carpal bones are problematic, as well as their identitification (Bonnan 2003), and the problem of carpus homology among sauropods has been debated for a long time (Osborn & Granger 1901; Hatcher 1902; Osborn 1904; Gilmore 1936; McIntosh 1990; Wilson & Sereno 1998; Upchurch 1998; Bonnan 2003; Upchurch *et al.* 2004; Apesteguía 2005). Therefore, it remains uncertain whether the three or fewer carpals generally preserved in sauropods (McIntosh 1990; Wilson & Sereno 1998) represent proximal or distal elements (Apesteguía 2005).

The Figure 5 details the hypotheses of homology proposed for ?*Bothriospondylus madagascariensis* (Fig. 5C), assumptions based on an hypothetical basal archosaur (Fig. 5A) and the well known carpus of *Massospondylus* (Fig. 5B).

Interestingly, Osborn (1904) postulated the larger carpal of *Camarasaurus*, then considered as the radiale, would rather represent the coalescence of the distal elements as suggested by the articular facets for the metacarpals I-III on its distal end (McIntosh *et al.* 1996a, b). Lavocat (1955b, c) confirmed this assumption of the distal position of the larger carpal element thanks to its distal articular facets (Fig. 3D, F) and the position of the "torus-like" or crescent element (here considered as a radiale) above it (Fig. 2C, D). As previously suggested by Lavocat (1955b, c) and according to our hypotheses of carpus homology, we consider that the "main bone" of Lavocat could be assigned to the fusion of the dc1, one or two centrale(s) and the intermedium.

Concerning the proximal row, the radiale is reduced while the ulnare seems to be absent or unossified in this specimen, except if the hypothetical dc4 is considered as the ulnare (as considered in *Argyrosaurus*; Apesteguía 2005) or a fusion between dc4 and ulnare. Although fused to dc1 + c (the "main bone"), the intermedium seems to be a distinct element in regard of the "main bone" shape, contrary to the block-like carpals previously found in other sauropods like *Apatosaurus* Marsh, 1877, *Camarasaurus* or *Diplodocus* Marsh, 1878.

The arrangement of the distal elements is strongly correlated to the shift of the mcI relative to the mcII (Fig. 2C). Indeed, consequently to this shift, we can observe a fusion between three elements of three different levels: the intermedium (proximal row), one or two centrale ("middle" row) and the distal carpal 1 (distal row). ?*Bothriospondylus* could thus represent the first evidence of the presence of three carpal rows in a sauropod carpus (Fig. 5C). Another consequence is the overlapping of the "dc1 + c + i" on the two adjacent distal elements (dc2 and dc3; Fig. 2C, D). The same metacarpal and carpal arrangement is observed in prosauropods where the dc1 (+ c?) overlaps the dc2, like in *Massospondylus* Owen, 1854 (Cooper 1981: 737, fig. 32, 740, fig. 38; Broom 1911: pl. XV, figs 7, 8; Fig. 5B) and *Plateosaurus* von Meyer, 1837 (Huene 1932: pl. XI, fig. 1A, B). Interestingly, this shift between mcI and II is also present in the sauropods *Tazoudasaurus* Allain *et al.*, 2004 (Allain & Aquesbi in press), *Atlasaurus* (Monbaron *et al.* 1999), *Brachiosaurus* (Läng pers. obs.) and possibly in *Apatosaurus* (Hatcher 1902: pls 19, 20; Bonnan 2003: 604, fig. 7C, D). In *Tazoudasaurus*, a possibly dc1 (+ c?) is placed above the two first metacarpals and leaves a gap between its distal end and the proximal surface of the mcII, possibly occupied by a dc2 unfortunately unpreserved or unossified (it is a juvenile specimen, Allain & Aquesbi in press). In *Atlasaurus*, the larger carpal also overlaps the two first metacarpals with the dc2 possibly fused to the dc1 (+ c?), while the dc3 is free (Monbaron *et al.* 1999).

The number of carpal bones is a character commonly used in phylogenetic studies of Sauropoda. Basal sauropods have usually three carpal elements (McIntosh 1990) and the presence of two or fewer elements being characteristic of Neosauropoda (McIntosh 1990; Upchurch 1998; Wilson & Sereno 1998; Wilson 2002). Therefore, the five carpals preserved in the wrist of ?*Bothriospondylus* and the fewer elements in other sauropods can be interpreted in three ways:

– 1) ontogenetic hypothesis – a better ossification in ?*Bothriospondylus*: the number of carpal elements (five or more) is plesiomorphic and inherits from prosauropods. In regard of the ossification sequence in some extant taxa (Chelonia, Crocodylia; Burke & Alberch 1985; Müller & Alberch 1990), the distal row seems to be the first to ossify, the proximal elements representing the last one. Therefore, the highest number of carpals in ?*Bothriospondylus*, although possibly autapomorphic, could represent an older individual with an extremely advanced ossification and fusion of the carpal elements and the first occurrence of an ossified proximal row;

– 2) phylogenetic hypothesis – a more advanced fusion in other derived sauropods: correlated with the high development of the graviportality in most derived neosauropods, a reduced carpus could represent a more advanced fusion of the carpal elements, in relation with an hypothetical loss of mobility due to the columnar support of the body-mass. According to this hypothesis, the carpus of basal sauropods could be plesiomorphically constituted of five carpals or more, while a reduction would occur in most derived neosauropod which would reduce to two or fewer elements, even absent in

Titanosauria (except *Argyrosaurus*; Apesteguía 2005). In this assumption, ?*Bothriospondylus* would thus represent the primitive condition of numerous carpals in macronarian neosauropods;
– 3) taphonomic hypothesis: the same pattern of carpal arrangements could be found in other sauropods (especially closely related ones), but it has not been found them yet because preservation of these elements in articulation is rare.

CONCLUSION

The wrist of ?*Bothriospondylus* represents the first evidence of the presence of three carpal rows in a sauropod, as previously suggested by Lavocat (1955b, c). Likewise, the presence of five carpals constitutes an unusual feature among sauropods, which commonly display only three or fewer elements as classically considered. Therefore we propose to reconsider the systematic importance accorded to carpals in the most recent phylogenetic studies (McIntosh 1990; Upchurch 1998; Wilson & Sereno 1998; Wilson 2002).

If the interpretation of this particular arrangement is always uncertain relatively to the other sauropods where carpals are preserved, three scenarios can be proposed to date: a better ossification of the carpus in a possibly older individual (ontogenetic hypothesis), a possible reduction of the carpus in more derived neosauropods in relation with a highly-developed graviportality (phylogenetic hypothesis), and a bad preservation (taphonomic hypothesis) of the carpus in other sauropods. A combination of these three hypotheses could also be considered.

Acknowledgements
We want to dedicate this article to late René Lavocat, for his helpful informations, reprints and comments about the discovery of this specimen, and above all for his kindness. We also thank Dr. Jouan and the staff of the Villeneuve-St-Georges Hospital for their invaluable assistance and their hospitality during the CTScan analysis of the manus; Philippe Richir, Renaud Vacant and Batz Le Dimet, for the preparation of the specimen housed in the Muséum national d'Histoire naturelle de Paris; The SOGESERDIS company for the prototype of the manus realized with the CTScan data prepared with Materialise MIMICS software; Ronan Allain for his advice and remarks on previous versions of this manuscript; Didier Geffard-Kuriyama for his help for the Figure 1. Suggestions and remarks by Jeff Wilson and an other anonymous referee were especially instructive.

REFERENCES

ALLAIN R. & AQUESBI N. in press. — Anatomy and phylogenetic relationships of *Tazoudasaurus naimi* (Dinosauria, Sauropoda) from the late Early Jurassic of Morocco. *Geodiversitas*.

APESTEGUÍA S. 2005. — Evolution of the titanosaur metacarpus, *in* TIDWELL V. & CARPENTER K. (eds), *Thunderlizards*. Indiana University Press, Bloomington and Indianapolis: 321-345.

BONAPARTE J. F. 1986. — The early radiation and phylogenetic relationships of the Jurassic sauropod dinosaurs, based on vertebral anatomy, *in* PADIAN K. (ed.), *The Beginning of the Age of Dinosaurs*. Cambridge University Press, Cambridge: 247-258.

BONNAN M. F. 2003. — The evolution of manus shape in sauropod dinosaurs: implications for functional morphology, forelimb orientation and phylogeny. *Journal of Vertebrate Paleontology* 23: 595-613.

BROOM R. 1911. — On the dinosaurs of the Stormberg, South Africa. *Annals of the South African Museum* (series 7): 291-308.

BURKE A. C. & ALBERCH P. 1985. — The development and homology of the chelonian carpus and tarsus. *Journal of Morphology* 186: 119-131.

COLLIGNON M. 1954. — Découverte de dinosauriens à Tsinjorano, district d'Ambato-Boeni. *Bulletin de l'Académie malgache* 31: 59-61.

COOPER M. R. 1981. — The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occasional Papers of the National Museums and Monuments, Rhodesia* (Series B, Natural Sciences) 6: 689-840.

GILMORE C. W. 1936. — Osteology of *Apatosaurus* with special reference to specimens in the Carnegie Museum. *Memoirs of the Carnegie Museum* 11: 175-300.

HATCHER J. B. 1902. — Structure of the forelimb and manus of *Brontosaurus*. *Annals of Carnegie Museum* 1: 356-376.

HUENE F. VON 1932. — Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Palaeontologie* (serie 1) 4: 1-361.

JANENSCH W. 1922. — Das Handskelett von Gigantosaurus robustus und Brachiosaurus brancai aus den Tendaguru-Schichten Deutsch-Ostafrikas. *Centralblatt für Mineralogie, Geologie und Paläontologie* 15: 464-480.

JANENSCH W. 1961. — Die Gliedmaszen und Gliedmaszengürtel der Sauropoden der Tendaguru-Schichten. *Palaeontographica* suppl. VII: 177-235.

LAVOCAT R. 1955a. — Les recherches de reptiles fossiles à Madagascar. *Le Naturaliste malgache* VII: 203-207.

LAVOCAT R. 1955b. — Étude des gisements de dinosauriens de la région de Majunga (Madagascar). *Travaux du Bureau géologique, Service géologique de Tananarive* 69: 1-19.

LAVOCAT R. 1955c. — Sur un membre antérieur du dinosaurien sauropode *Bothriospondylus* Owen, recueilli à Madagascar. *Comptes Rendus de l'Académie des Sciences de Paris* 240: 1795-1796.

LAVOCAT R. 1957. — Sur les couches à dinosauriens de Madagascar. *Comptes-Rendus du Service géologique de Madagascar* 2: 363-364.

MATERIALISE 2007. — *Mimics*®, version 10.1, X64. Supplied by the UMR 5143 CNRS, Paris.

MCINTOSH J. S. 1990. — Sauropoda, *in* WEISHAMPEL D. B., DODSON P. & OSMOLSKA H. (eds), *The Dinosauria*. University of California Press, Berkeley: 345-401.

MCINTOSH J. S., MILLER W. E., STADTMAN K. L. & GILLETTE D. D. 1996a. — The osteology of *Camarasaurus lewisi* (Jensen, 1988). *Brigham Young University Geology Studies* 41: 73-115.

MCINTOSH J. S., MILES C. A., CLOWARD K. C. & PARKER J. R. 1996b. — A new nearly complete skeleton of Camarasaurus. *Bulletin of the Gunma Museum of Natural History* 1: 1-87.

MONBARON M., RUSSELL D. A. & TAQUET P. 1999. — *Atlasaurus imelakei* n.g., n.sp., a brachiosaurid-like sauropod from the Middle Jurassic of Morocco. *Comptes-Rendus de l'Académie des Sciences de Paris, Sciences de la Terre et des Planètes* 329: 519-526.

MÜLLER G. B. & ALBERCH P. 1990. — Ontogeny of the limb skeleton in *Alligator mississippiensis*: developmental invariance and change in the evolution of archosaur limbs. *Journal of Morphology* 203: 151-164.

OGIER A. 1975. — *Étude de nouveaux ossements de* Bothriospondylus *(Sauropode) d'un gisement du Bathonien de Madagascar*. Thèse, Université de Paris VI, France, 111 p.

OSBORN H. F. 1904. — Manus, sacrum, and caudals of Sauropoda. *Bulletin of the American Museum of Natural History* 20: 181-190.

OSBORN H. F. & GRANGER W. 1901. — Fore and hind limbs of Sauropoda from the Bone Cabin Quarry. *Bulletin of the American Museum of Natural History* 14: 199-208.

OUYANG H. & YE Y. 2002. — [*The First Mamenchisaurian Skeleton with Complete Skull,* Mamenchisaurus youngi]. Sichuan Science and Technology Publishing House, Chengdu, 111 p. (in Chinese with extended English abstract).

ROMER A. S. 1956. — *Osteology of the Reptiles*. University of Chicago Press, Chicago, 772 p.

UPCHURCH P. 1998. — The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society* 124: 43-103.

UPCHURCH P., BARRETT P. M. & DODSON P. 2004. — Sauropoda, *in* WEISHAMPEL D. B., DODSON P. & OSMOLKA H. (eds), *The Dinosauria*, 2nd ed. University California Press, Berkeley: 259-322.

WILSON J. A. 2002. — Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society* 136: 217-276.

WILSON J. A. & SERENO P. C. 1998. — Early evolution and higher-level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology* 18: 1-68.

ZHANG Y. 1988. — *The Middle Jurassic Dinosaur Fauna from Dashanpu, Zigong, China.* Volume III. *Sauropod Dinosaur* (I). *Shunosaurus*. Sichuan Publishing House of Science and Technology, Chengdu, 89 p. (in Chinese with extended English summary).

Submitted on 3 July 2007;
accepted on 27 September 2007.