

Clavicles, interclavicles, gastralia, and sternal ribs in sauropod dinosaurs: new reports from Diplodocidae and their morphological, functional and evolutionary implications

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Abstract

Ossified gastralia, clavicles and sternal ribs are known in a variety of reptilians, including dinosaurs. In sauropods, however, the identity of these bones is controversial. The peculiar shapes of these bones complicate their identification, which led to various differing interpretations in the past. Here we describe different elements from the chest region of diplodocids, found near Shell, Wyoming, USA. Five morphotypes are easily distinguishable: (A) elongated, relatively stout, curved elements with a spatulate and a bifurcate end resemble much the previously reported sauropod clavicles, but might actually represent interclavicles; (B) short, L-shaped elements, mostly preserved as a symmetrical pair, probably are the real clavicles, as indicated by new findings in diplodocids; (C) slender, rod-like bones with rugose ends are highly similar to elements identified as sauropod sternal ribs; (D) curved bones with wide, probably medial ends constitute the fourth morphotype, herein interpreted as gastralia; and (E) irregularly shaped elements, often with extended rugosities, are included into the fifth morphotype, tentatively identified as sternal ribs and/or intercostal elements. To our knowledge, the bones previously interpreted as sauropod clavicles were always found as single bones, which sheds doubt on the validity of their identification. Various lines of evidence presented herein suggest they might actually be interclavicles – which are single elements. This would be the first definitive evidence of interclavicles in dinosauromorphs. Previously supposed interclavicles in the early sauropodomorph *Massospondylus* or the theropods *Oviraptor* and *Velociraptor* were later reinterpreted as clavicles or furculae. Independent from their identification, the existence of the reported bones has both phylogenetic and functional significance. Their presence in non-neosauropod Eusauropoda and Flagellicaudata and probable absence in rebbachisaur and Titanosauriformes shows a clear character polarity. This implicates that the ossification of these bones can be considered plesiomorphic for Sauropoda. The proposed presence of interclavicles in sauropods may give further support to a recent study, which finds a homology of the avian furcula with the interclavicle to be equally parsimonious to the traditional theory that furcula were formed by the fusion of the clavicles. Functional implications are the stabilizing of the chest region, which coincides with the development of elongated cervical and caudal vertebral columns or the use of the tail as defensive weapon. The loss of ossified chest bones coincides with more widely spaced limbs, and the evolution of a wide-gauge locomotor style.

Key words: diplodocidae; furcula; interclavicle; pectoral girdle; sauropod dinosaurs.

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Introduction

The plesiomorphic composition of the chest region in early reptiles includes various elements of the pectoral girdle (scapula, suprascapula, pro- and metacoracoids, cleithrum, clavicle, and the interclavicle), the sternal apparatus (sternal plates and ribs) and other chest bones (gastrea; Romer, 1956; Vickaryous & Hall, 2006; see Table 1 for a summary of

Table 1 Bones present in the chest regions of tetrapods.

	General shape and distinction	Paired/single. Number	Embryological origin (dermal / endochondral)	Articulations	Previously identified in Sauropoda
Clavicles (Morphotype B)	Curved element	Paired, can fuse into one (furcula, questioned herein). One pair present	Dermal bone	Dorsal to coracoids (covering it sometimes), between cleithrum scapula, and interclavicle in basal reptiles. Attaches to the acromion	Yes
Interclavicles (Morphotype A)	Variable. Diamond shaped in early tetrapods, rod-like with or without transverse processes in crocodylians and lacertilians	Single (very rarely paired). Only one present	Dermal bone	Between the clavicles. Connects to the coracoid and/or sternal plates posteriorly. In rare cases (e.g. monotremes) attaching to acromion	No
Sternal Ribs (Morphotypes C and E)	Irregularly shaped, often rugose	Paired. Maximum one per dorsal rib, often less	Endochondral	Connects the sternal plates with the dorsal ribs or intercostal elements	Yes
Intercostal elements (Morphotype E?)	Irregularly shaped, often rugose	Paired. Maximum one per dorsal rib, often less	Endochondral	Connects sternal ribs with dorsal ribs	No
Gastralia (Morphotype D)	Slender, slightly curved bones. Medial elements with expanded medial end for articulation with corresponding gastralia. Anteriormost sometimes fused	Four elements per row (2 lateral, 2 medial). Up to 21 rows in large theropods	Dermal bone	Articulate among themselves and to dorsal ribs, as well as maybe the sternal apparatus	Yes
Cleithrum	Spoon-shaped	Paired. Only one pair present	Dermal bone	Capping scapulacoracoid, attaches to clavicles	No
Sternal plates	Shield-like: flat oval or reniform	Paired or single. One single or two mirrored elements	Endochondral	Articulate among themselves, sternal ribs attached to them sometimes touching the interclavicle anteriorly	Yes
Furcula	Wide V-shape	Single, rarely two paired elements	Dermal bone	With acromia laterally	No
Scapulacoracoid	Large, flat, subcircular acromion with a elongate, more narrow posterodorsal projection	Paired. One pair present	Endochondral	Dorsal and external to sternal apparatus, connected medially by cleithrum, clavicles, and interclavicle	Yes

pectoral and sternal elements in Reptilia). The term chest bones is here informally used to include gastralia, sternal plates and ribs, clavicles, and interclavicles based on the topographic position, and independent from their embryological or evolutionary origin.

In Diapsida, the cleithrum was lost, and pro- and metacoracoids fused to form a single element (Vickaryous & Hall, 2006; Remes, 2008). The interclavicle is generally interpreted to have been lost in Dinosauriformes (Nesbitt, 2011). A supposed absence of clavicles was often used as synapomorphy of Dinosauria or even more inclusive clades, and as reason against the ancestry of this clade to birds (see Sereno, 1991; Novas, 1996; Yates & Vasconcelos, 2005). However, numer-

ous reports of clavicles in various dinosaur clades imply that these elements are plesiomorphically present, and that it is mostly due to diagenetic or taphonomic reasons that they are not recovered (Yates & Vasconcelos, 2005; Remes, 2008). On the other hand, a recent study on the embryology of the avian furcula and the crocodylian interclavicle revealed that an interpretation of the furcula as derived interclavicle would be equally parsimonious as the traditional hypothesis, where the furcula represents the medially fused clavicles (Vickaryous & Hall, 2010). The suggestion of Vickaryous & Hall (2010) that all previously reported dinosaurian clavicles might actually be interclavicles would bring back the earlier stated hypothesis that the absence of clavicles would be

synapomorphic for Dinosauriformes, paralleled by extant crocodylians. However, the evidence remains ambiguous, and especially Sauropodomorpha appear to have both ossified clavicles and interclavicles (von Huene, 1926; Yates & Vasconcelos, 2005; this study).

In the Sauropodomorpha, pectoral girdles usually only preserve the scapula and the coracoid, which in sauropods generally fuse during ontogeny (Ikejiri et al. 2005; Schwarz et al. 2007a,b; Remes, 2008). Putative clavicles are predicted to connect the scapulae dorsal to the coracoids but, until recently, no articulated pair had been reported in sauropods (Remes, 2008; but see Galiano & Albersdörfer, 2010 for an articulated specimen). Unpaired rod-like structures interpreted as clavicles were found in a variety of sauropod taxa, sometimes associated with the pectoral girdle (Dong & Tang, 1984; He et al. 1988; Zhang, 1988; Hatcher, 1901, 1903; Sereno et al. 1999; Harris, 2007; Remes et al. 2009). However, most of these identifications rely solely on the similarity to previously reported 'clavicles' – which themselves are not beyond doubt.

The sauropod scapulacoracoid articulates posteroventrally with the sternal plates, which are connected with the dorsal ribs through usually cartilaginous sternal ribs (Schwarz et al. 2007a; Remes, 2008; Hohn-Schulte, 2010). As they remain mostly cartilaginous, sternal ribs are very rarely preserved in the fossil record. The only reports are from the *Apatosaurus excelsus* holotype YPM 1980 (Marsh, 1896), a set of ribs associated with the holotype of *A. louisae* (Holland, 1915), a sternal rib fused to a sternal plate in a probable early macronarian (Tschopp & Mateus, 2012), and maybe from the holotype of *Eobrontosaurus yahnahpin* (Filla & Redman, 1994; Claessens, 2004). Filla & Redman (1994) initially interpreted these structures as gastralia, based on superficial similarity to gastralia in theropods, non-sauropod sauropodomorphs, and other archosaurs like crocodylians or sphenodonts. Gastralia were also reported from *Gongxiansaurus shibeiensis* and *Jobaria tiguidensis* (He et al. 1998; Sereno et al. 1999), but Claessens (2004) and Fehner (pers. comm., 2011), based on a detailed comparison with theropod and non-sauropod sauropodomorph gastralia, recently questioned this identification, and suggested them to be ossified sternal ribs instead. In short, the evolutionary and developmental origin of these elements is hotly debated, and the sauropod chest bones other than the scapulacoracoid remain poorly understood.

Herein we describe five morphotypes of bones from the chest region, and state their most probable identifications. This classification helps identifying disarticulated elements. It yields important new information on the proper reconstruction of the sauropod pectoral girdle.

Locality

The new material described herein comes exclusively from the Howe Quarry in the Bighorn Basin of Wyoming, USA

(Fig. 1). Two periods of extensive excavation were conducted at this site. In 1934 Barnum Brown collected 3000–4000 bones at the Howe Quarry for the American Museum of Natural History, NY, USA (AMNH; Brown, 1935; Michelis, 2004), and in 1990 Hans-Jakob Siber reopened the site with a team of the Sauriermuseum Aathal, Switzerland (SMA) and excavated another 700–800 elements (Ayer, 2000; Michelis, 2004; Tschopp & Mateus, in press). Only one of the specimens found during these two periods has since been described in detail, and was identified as subadult specimen of a new diplodocine species (Tschopp & Mateus, in press). Brown (1935) tentatively identified the majority as Diplodocinae, except for some elements belonging to *Apatosaurus* or *Camarasaurus* (see also Michelis, 2004; Tschopp & Mateus, in press).

Both the AMNH and the SMA expeditions yielded various sets of bones resembling the gastralia or sternal ribs described from *Eobrontosaurus yahnahpin* (Filla & Redman, 1994). Furthermore, five single elements like the bones previously identified as sauropod clavicles, as well as two pairs of L-shaped, symmetrical elements were recovered, the identity of which is discussed below (Fig. 2; Table 2). Although such an accumulation of chest bones is unusual, none of these bones from the Howe Quarry has been reported to date. Given the predominance of Diplodocidae in the Howe Quarry, and the close association of some of the clusters of gastralia/sternal ribs and the clavicles to diplodocid cervical vertebrae, an attribution of these elements to this group can be considered highly probable.

Description and discussion

Morphotype A

Previous identification: clavicles, sternal ribs, os penis (baculum; Fig. 3; Table 3; Suppl. Figs 1–5)

Our interpretation: interclavicles.

General morphology

Morphotype A elements are relatively stout, elongated bones. They are usually bowed, and exhibit a spatulate and a bifurcate end. Interpreting that the concave side follows the curvature of the body, this side can be regarded as internal. The spatulate end bears more or less linear rugose striations for muscle or ligament attachment. The shafts are suboval in cross-section at mid-length, and achieve their greatest breadth at two-thirds to three-quarters of their total length, toward the spatulate end. The notch in the bifurcated end is usually only visible in internal or external view.

Morphotype A elements show some superficial similarities to dorsal ribs. They can be distinguished from ribs by the presence of the spatulate and bifid ends, the more circular cross-section at midlength, and the striated rugosities present on the spatulate end.

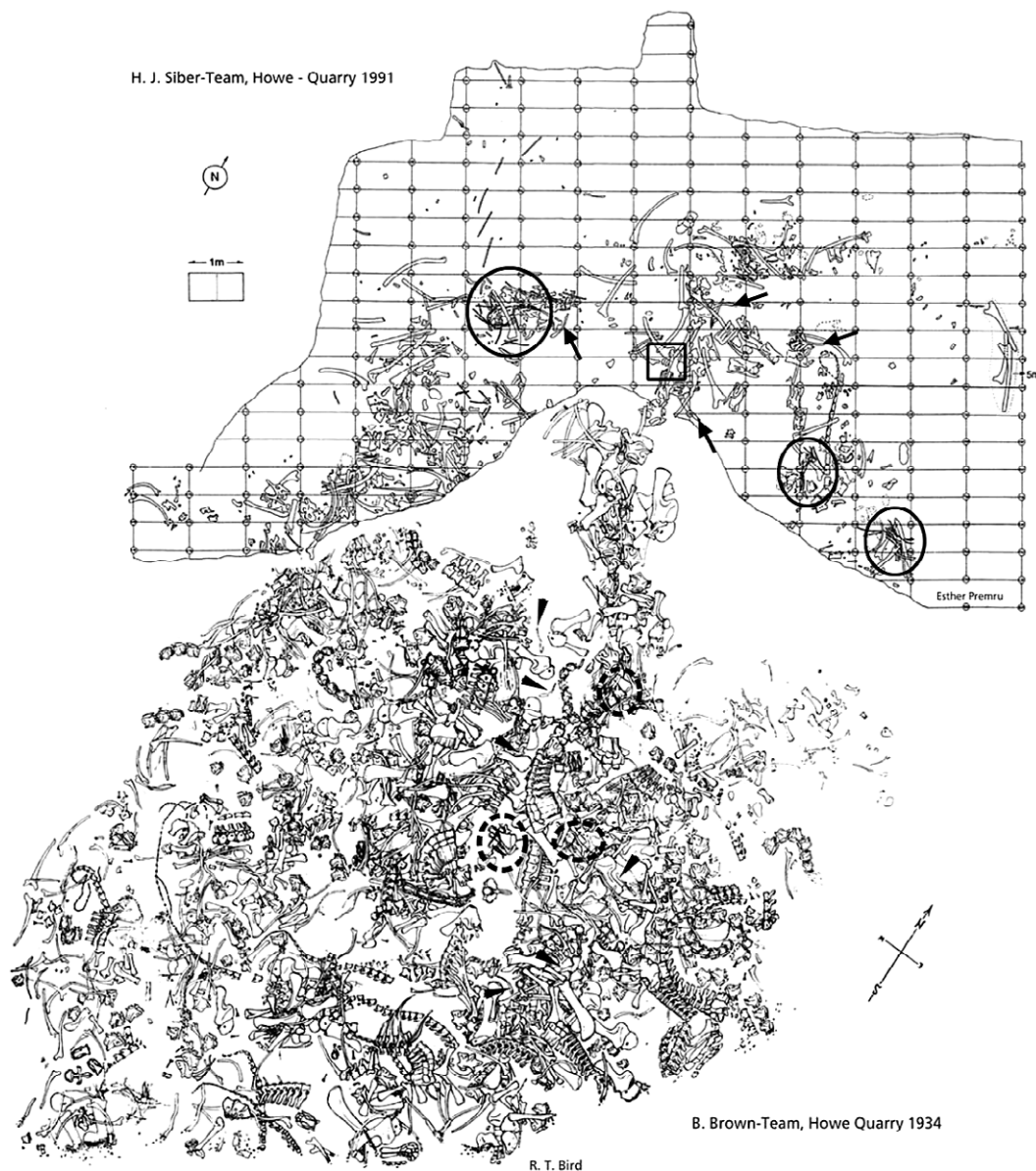


Fig. 1 Compiled quarry map of the two excavation periods at the Howe Quarry (AMNH map below; SMA map above). Arrows indicate supposed clavicles at SMA, arrowheads possible locations of the supposed clavicle at AMNH. Circles indicate gastral or sternal baskets (full circles: SMA; dashed circles: AMNH), rectangle marks the SMA pair of symmetrical bones. AMNH map modified from Bird (1985); SMA map drawn by Esther Premru.

Howe Quarry material

Five elements were located in the collections of the AMNH and the SMA (AMNH 30900; SMA field numbers I 24-4, L 22-3, L 27-7 and M 25-3; Fig. 3). Whereas the provenance and association of the AMNH element within the Howe Quarry is unclear, the SMA specimens were found close to dorsal ribs and an associated but disarticulated series of diplodocid cervical vertebrae (I 24-4); neck and skull remains of a new diplodocine sauropod (Tschopp & Mateus, in press), and a gastral/sternal rib cage (L 22-3); anterior cervical vertebrae, a dorsal rib, some skull remains and a metatarsal (L 27-7); as well as associated with dorsal ribs,

posterior diplodocid cervical vertebrae and an articulated series of midcaudal vertebrae (M 25-3). All these elements were found as single elements, which is consistent with the earlier findings of similar finds in other sauropod taxa.

Previous reports

Several bones belonging to morphotype A have been reported in the literature, and were usually identified as sauropod clavicles (Table 2). The species preserving morphotype A elements are the non-neosauropod Eusauropoda *Shunosaurus lji*, *Spinophorosaurus nigerensis*, *Omeisaurus junghsiensis*, *O. tianfuensis*, *Mamenchisaurus*

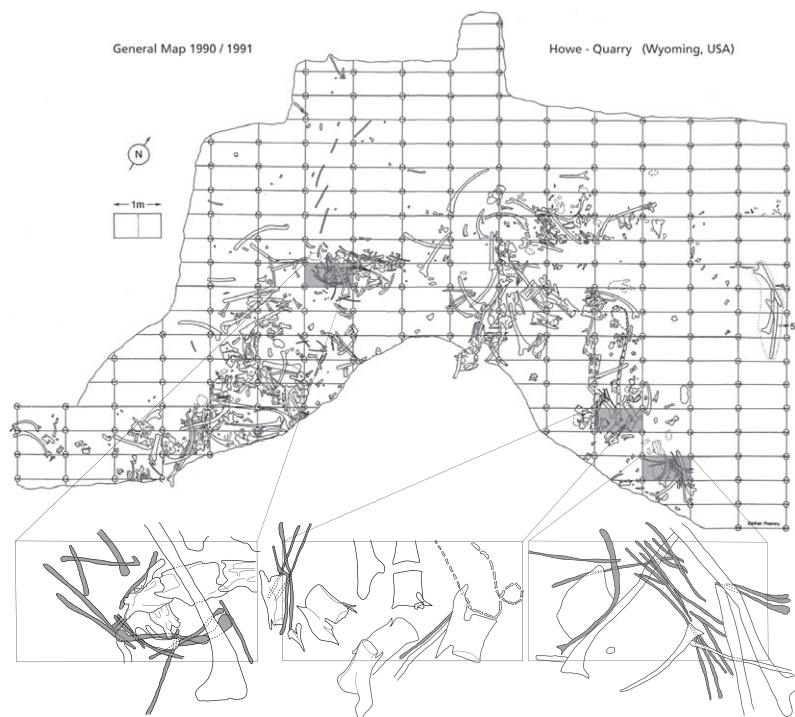


Fig. 2 Detail of the 1991 quarry map, with sections producing associated morphotype C–E elements enlarged (from left to right: clusters M 21, F 27 and D 28). The morphotype C–E elements are highlighted in grey in the enlarged sections.

sp. and *Datousaurus bashanensis*, as well as the Flagellicaudata *Diplodocus carnegii*, *D. hayi* and *Suuwassea emilieae* (Dong et al. 1983; Dong & Tang, 1984; He et al. 1988; Zhang, 1988; Hatcher, 1901, 1903; Harris, 2007; Remes et al. 2009). In none of these taxa, morphotype A elements were recovered in pairs, even though some of the specimens were reasonably complete and articulated.

Variation in morphology

Two different orientations of the spatulate end can be observed in the five elements from the Howe Quarry, as well as in previously reported bones belonging to morphotype A: perpendicular to the curvature of the bone, so that its thin edges face internally and externally (e.g. SMA L 22-3; Fig. 3d), or turned 90° (e.g. SMA I 24-4; Fig. 3b). The spatulate end can bear a deep slot-like concavity on its internal side (e.g. in SMA M 25-3 and L 22-3; Fig. 3c,d), giving the impression of a deeply bifurcated end on this side as well, in internal view. In other elements, the internal side of the spatulate end bears shallow (*Diplodocus hayi* HMNS 175 or *Spinophorosaurus nigerensis* NMB-1698-R) to distinct ridges (*Suuwassea emilieae* ANS 21122) with varying lengths (Hatcher, 1903; Harris, 2007; Remes et al. 2009). Differences in curvature (see the straight element SMA I 24-4 or the outwards curve in SMA L 27-7; Fig. 3b,e, respectively) are most probably of taphonomical origin.

Identification

The first reported element of morphotype A was found associated with the scapulacoracoid of *Diplodocus carnegii* CM 84 and was tentatively identified as clavicle (Hatcher, 1901). Although this interpretation has never been definitely confirmed, it has become generally accepted, and subsequent finds of similar bones continued to be identified as clavicles (Hatcher, 1903; Dong et al. 1983; Dong & Tang, 1984; He et al. 1988; Zhang, 1988; Harris, 2007; Remes et al. 2009). The suggestions of Nopcsa (1905) or Holland (1906) that morphotype A elements represent the os penis or sternal ribs, respectively, are improbable given the absence of bacula in extant reptiles, and because they are relatively much more massive compared with articulated sternal ribs of pterosaurs or crocodylians (Claessens et al. 2009; *Crocodylus niloticus*, NHM, unregistered display specimen, ET, pers. obs.).

The five elements recovered as single bones in the Howe Quarry, as well as the corresponding elements of *Diplodocus carnegii* (CM 84), *D. hayi* (HMNS 175), *Spinophorosaurus nigerensis* (NMB-1698-R) and *Suuwassea emilieae* (ANS 21122), are slightly asymmetrical (see also Hatcher, 1901, 1903; Holland, 1906), but have a longitudinal midline extending through the bifid end and dividing the expanded spatulate end in two halves. These bones could therefore also represent elements of the chest region that

Table 2 New and already reported chest bones of sauropods, ordered by morphotype and first mention. Reported chest bones of unknown morphotype are listed in the end.

	Specimen Number	Taxonomy	References	first identified as	Comments
Morphotype A	CM 84	<i>Diplodocus carnegii</i>	Hatcher, 1901, 1903; Nopcsa, 1905; Holland, 1906; McIntosh 1981	clavicle	
	HMNS 175 (= CM 662)	<i>Diplodocus hayi</i>	Hatcher, 1903; Nopcsa, 1905; Holland, 1906;	clavicle	stored at CM
	?	<i>Mamenchisaurus</i> sp.	Dong et al. 1983;	clavicle	three elements mentioned
	?	<i>Omeisaurus junghsiensis</i>	Dong et al. 1983;	clavicle	
	IVPP V7262	<i>Datousaurus bashanensis</i>	Dong & Tang, 1984;	clavicle	
	IVPP V7263	<i>Datousaurus bashanensis</i>	Dong & Tang, 1984;	clavicle	
	T5704	<i>Omeisaurus tianfuensis</i>	He et al. 1988;	clavicle	
	T5401	<i>Shunosaurus lii</i>	Zhang, 1988;	clavicle	
	ANS 21122	<i>Suuwassea emilieae</i>	Harris, 2007;	clavicle	
	NMB-1698-R	<i>Spinophorosaurus nigerensis</i>	Remes et al. 2009;	clavicle	
	AMNH 30900	?diploclodid	this study	interclavicle	
	SMA I 24-4	?diploclodid	this study	interclavicle	
	SMA L 22-3	?diploclodid	this study	interclavicle	
	SMA L 27-7	?diploclodid	this study	interclavicle	
	SMA M 25-3	?diploclodid	this study	interclavicle	
SMA 0009	non-somphospondyliian macronarian	Schwarz et al. 2007b; this study	possible furcula	pair recovered	
Morphotype B	GCP-CV 4229	<i>Spinophorosaurus nigerensis</i>	Remes et al. 2009;	tail spikes	two elements, possibly not symmetrical
	DQ-SB	Diplodocidae indet.	Galiano & Albersdörfer, 2010;	clavicle	pair recovered
	DQ-TY	Diplodocidae indet.	Galiano & Albersdörfer, 2010;	clavicle	
	KUVP 129716	<i>Camarasaurus</i> sp.	A. Maltese, pers. comm. 2012	–	articulated pair (Bader et al. 2009; Fig. 4B)
	SMA K 24-3 & 6	?diploclodid	this study	clavicle	pair recovered
	AMNH 30789	?diploclodid	this study	clavicle	pair recovered
	AMNH 5760/5761	<i>Camarasaurus supremus</i>	Osborn & Mook, 1921;	clavicle	single element
	Tate 001	<i>Eobrontosaurus yahnahpin</i>	Filla & Redman, 1994;	sternal/ventral rib	almost complete set including morphotype E as well
	AMNH 30901	?diploclodid	this study	gastralia	
	SMA ?	?diploclodid	this study	?sternal rib	various unnumbered elements
	SMA C 17-5	?diploclodid	this study	?sternal rib	
	SMA D 28-6 to 11	?diploclodid	this study	?sternal rib	part of D 28-cluster
	SMA D 28-18 to 19	?diploclodid	this study	?sternal rib	part of D 28-cluster
	SMA E 19-9	?diploclodid	this study	?sternal rib	
	SMA E 21-2 to 3	?diploclodid	this study	?sternal rib	
SMA F 19-10	?diploclodid	this study	?sternal rib		
SMA F 19-21	?diploclodid	this study	?sternal rib		
SMA F 20-9	?diploclodid	this study	?sternal rib		
SMA F 27-16 to 17	?diploclodid	this study	?sternal rib	part of F 27-cluster	
SMA F 27-33 to 35	?diploclodid	this study	?sternal rib	part of F 27-cluster	

Table 2. (continued)

Specimen Number	Taxonomy	References	first identified as	Comments
SMA G 21-2	?diplodocid	this study	?sternal rib	probably part of F 27-cluster
SMA G 27-3 to 4	?diplodocid	this study	?sternal rib	probably part of F 27-cluster
SMA G 27-22 to 23	?diplodocid	this study	?sternal rib	
SMA H 20-7	?diplodocid	this study	?sternal rib	
SMA H 21-2	?diplodocid	this study	?sternal rib	bears a foramen
SMA H 21-5	?diplodocid	this study	?sternal rib	
SMA H 21-9 to 10	?diplodocid	this study	?sternal rib	
SMA H 21-12	?diplodocid	this study	?sternal rib	
SMA L 21-3 to 5	?diplodocid	this study	?sternal rib	probably part of M 21-cluster
SMA M 21-4	?diplodocid	this study	?sternal rib	part of M 21-cluster
SMA M 21-6 to 7	?diplodocid	this study	?sternal rib	part of M 21-cluster
SMA M 21-11	?diplodocid	this study	?sternal rib	part of M 21-cluster
SMA M 21-13	?diplodocid	this study	?sternal rib	probably part of M 21-cluster
SMA N 22-2	?diplodocid	this study	?sternal rib	
SMA P 19-1	?diplodocid	this study	?sternal rib	
SMA P 21-1	?diplodocid	this study	?sternal rib	
SMA S 22-3	?diplodocid	this study	?sternal rib	
SMA V 21-1	?diplodocid	this study	?sternal rib	
SMA 0011	Diplodocidae indet.	this study	?sternal rib	
SMA D 28-5	?diplodocid	this study	gastralia	part of D 28-cluster
SMA D 28-14 to 15	?diplodocid	this study	gastralia	part of D 28-cluster
SMA F 19-11 to 12	?diplodocid	this study	gastralia	
SMA G 21-3	?diplodocid	this study	gastralia	part of M 21-cluster
SMA M 21-2	?diplodocid	this study	gastralia	part of M 21-cluster, fused element
SMA M 21-8	?diplodocid	this study	gastralia	part of M 21-cluster, fused element
SMA N 21-16	?diplodocid	this study	gastralia	probably part of M 21-cluster
SMA N 21-3	?diplodocid	this study	sternal ribs	several elements, 2 figured
YPM 1980	<i>Apatosaurus excelsus</i>	Marsh, 1883, 1896;	gastralia	almost complete set including
Tate 001	<i>Eobrontosaurus yahnahpin</i>	Filla & Redman, 1994;	gastralia	morphotype C as well
ML 684	?non-titanosauriform macronarian	Tschopp & Mateus, 2012;	sternal rib	fused with sternal plate
SMA H 21-1	?diplodocid	this study	sternal rib	associated with SMA H 21-3 and morphotype C elements
SMA H 21-3	?diplodocid	this study	sternal rib	associated with SMA H 21-1 and morphotype C elements
SMA M 21-15	?diplodocid	this study	sternal rib	part of M 21-cluster
SMA N 22-12	?diplodocid	this study	sternal rib	probably part of M 21-cluster
?CM 3018	? <i>Apatosaurus louisae</i>	Holland, 1915;	/ intercostal element sternal ribs	several elements, not described/figured

Table 2. (continued)

Specimen Number	Taxonomy	References	first identified as	Comments
GMNH-PV 101 ?	<i>Camarasaurus grandis</i> <i>Gongxianosaurus shibeiensis</i>	McIntosh et al. 1996; He et al. 1998;	gastralia gastralia	one element, figured but not described several elements, not described, inadequately figured
?	<i>Jobaria tiguidensis</i>	Sereno et al. 1999;	clavicle	not described, inadequately figured
?	<i>Jobaria tiguidensis</i>	Sereno et al. 1999;	gastralia	several elements, not described/figured
DNM ?	? <i>Camarasaurus</i>	Claessens, 2004;	sternal ribs	several elements in the wall, not described/figured, possibly the same as the ones mentioned by Holland, 1915
AODF 603	<i>Diamantinasaurus matildae</i>	Hocknull et al. 2009;	gastralia	fragmentary, not described/figured
DQ-TY	Diplodocidae indet.	Galiano & Albersdörfer, 2010;	sternal ribs	several elements, not described/figured
DQ-SB	Diplodocidae indet.	Galiano & Albersdörfer, 2010;	gastralia or sternal ribs	several elements, not described/figured
DQ-EN	Diplodocidae indet.	Galiano & Albersdörfer, 2010	sternal ribs	several elements, not described/figured
DMNS 59329	<i>Diplodocus carnegii</i>	Denver Museum Database	clavicle	not described/figured; probably morphotype A

lie on the body midline, and their continuous findings as single elements might have been no coincidence. The two areas abutting to the right and left of the ridges subdividing the spatulate end in the elements of *Suuwassea* and *Spinophorosaurus* resemble articulation surfaces, implying that the morphotype A elements covered two symmetrical elements externally, and medially. The absence of such a ridge in the other taxa might be of taxonomic significance.

The only median pectoral element in the non-avian shoulder girdle is the interclavicle. As the morphotype A elements, also *Alligator* interclavicles have slightly asymmetrical outlines (Vickaryous & Hall, 2010; R. Wilhite, pers. comm. 2012). Whereas early tetrapods had diamond-shaped interclavicles (Steyer et al. 2000), crocodylomorphs and some lepidosaurs developed rod-like shapes without lateral processes (Vickaryous & Hall, 2010), similar to the elements described herein. Following this interpretation, the bifurcated end probably represents the reduced lateral processes, and the spatulate end would articulate with either the coracoids or the sternal plates – covering them externally and anteromedially.

A bone found in the pectoral girdle of the early sauropodomorph *Massospondylus carinatus* shows a similar spatulate expansion on one end, and in fact has first been interpreted as interclavicle (Cooper, 1981). Sereno (1991) and Yates & Vasconcelos (2005) subsequently reinterpreted this element as a clavicle, based on its similarity to paired, articulated clavicles in both *Plateosaurus* and other specimens of *Massospondylus*. The articulated specimens connect to the acromion process of the scapulae, which is typical for clavicles, but almost never the case in interclavicles (Table 1; Romer, 1956). The only reported exception is the interclavicle in some monotreme mammals, where the transverse processes reach the acromion (Klima, 1973). The articulation of these elements with the acromia of the scapulae in both *Massospondylus* (Yates & Vasconcelos, 2005) and *Plateosaurus* (B. Pabst, pers. comm., 2011; ET, pers. obs.) thus make an interpretation as clavicles more probable. However, given that sauropods appear to have both clavicles and interclavicles, Cooper's (1981) interpretation of the single *Massospondylus* 'interclavicle' might have to be reconsidered.

An alternative hypothesis would be that morphotype A represents a neomorphic element, independently developed in Sauropoda. This would be the case if interclavicles would really have gotten lost in Dinosauriformes. However, given the incompleteness of the finds of early dinosauriforms and dinosaurs, it cannot be ruled out that the absence of an ossified interclavicle is due to taphonomy. Therefore, and since the presence of an interclavicle is plesiomorphic for tetrapods, an interpretation of the sauropod morphotype A elements as interclavicle seems more appropriate.

Table 3 Measurements of new and the two first reported finds of morphotype A elements (interclavicles; in mm).

Specimen	AMNH 30900	SMA M 25-3	SMA L 27-7	SMA I 24-4	SMA L 22-3	CM 84	HMNS 175
Length along curvature	455*	650	545	550	554		660
Length measured straight	437*	585	484	540	510		613
Length spatulate portion		185	173	200	206		225
Width compressed end	21*	25	6	31	24		77
Width bifurcated end	29	30	27	35	21	75	
Depth of bifurcation	17	30	17	19	41	50	40

*Indicate incomplete measurements due to fractures, empty cells were measurements impossible to obtain.

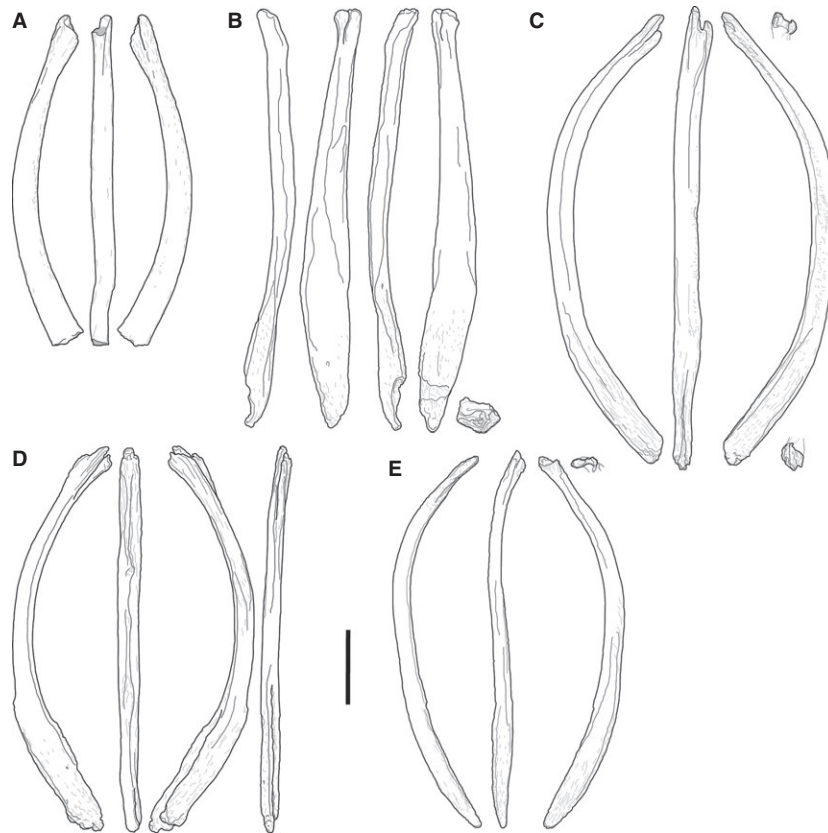


Fig. 3 Morphotype A elements, to scale. (a) AMNH 30900; (b) SMA I 24-4; (c) SMA M 25-3; (d) SMA L 22-3; (e) SMA L 27-7. Scale bar: 10 cm. Gray areas in (a) indicate broken surfaces. Note the bifurcate end on top and the spatulate end at the bottom.

Morphotype B

Not previously recognized (Figs 4 and 5; Suppl. Figs 6–9).

Our interpretation: clavicles.

General morphology

Morphotype B elements are L-shaped, and of similar thickness as morphotype A, but shorter. They are concave on one side, and convex on the opposite surface, and are usually found in pairs. Morphotype B elements have a D- to crescentic-shaped cross-section at midlength. The convex side is hereinafter interpreted as external, the flat

to slightly concave surface as internal. Towards the end of the longer leg of the L, a striated rugosity develops on both sides, and the bone expands slightly. This end is broken pre-burial in one of the SMA elements (K 24-6; Fig. 4), and post mortem in both AMNH elements, so that they appear shorter and stouter (Fig. 5). The shorter leg of the L is expanded 'backwards' as well, especially so in the SMA specimen, forming a somewhat heel-like, rounded flange (Figs 4 and 5). Towards the tip of the short leg, the bone curves externally. This portion shows a similar but stronger striated rugosity as in the longer leg of the L.

Morphotype B elements have a peculiar morphology. The most similar bones are the anterior- or posterior-most dorsal ribs, but neither capitulum nor tuberculum are present on the morphotype B. Furthermore, the striations marking soft tissue attachment do not occur on dorsal ribs.

Howe Quarry material

Two pairs of morphotype B elements were found at this site. The first specimen was found in 1934 by the AMNH (AMNH 30789), the other pair was recovered in the SMA excavation and bear the field numbers SMA K 24-3 and K 24-6. Whereas it is clear that the two bones of AMNH 30789 were found together (this collection number was given to all bones in a plaster jacket bearing the field number 151), their placement within the Howe Quarry is impossible to locate to date. AMNH 30789 also includes chevrons and pedal material. The SMA specimens were found closely together, below several dorsal ribs, and between posterior cervical and anterior dorsal diplodocid vertebrae.

Previous reports

Not much is known about the occurrence of morphotype B elements in sauropods. The only formal reports of similar

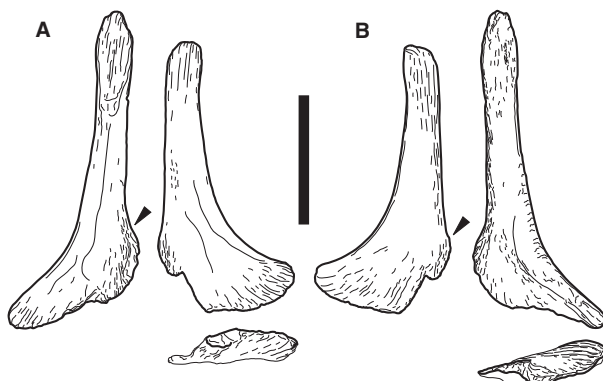


Fig. 4 Pair of Morphotype B elements SMA K 24-3 (outer bone) and SMA K 24-6 (inner bone) in internal (a) and external (b) view. Short leg of L-shaped bones shown in perpendicular view below. Note the considerable bend of this portion in respect to the main axis of the bone. Scale bar: 10 cm.

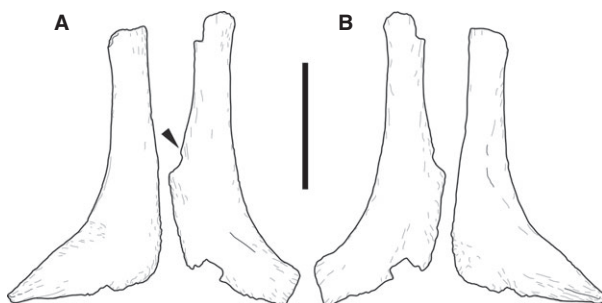


Fig. 5 Pair of Morphotype B elements AMNH 30789 in internal (a) and external (b) view. Scale bar: 10 cm.

elements concerns an element recovered with an early juvenile sauropod (Schwarz et al. 2007b), as well as two bones belonging to the holotype of *Spinophorosaurus nigerensis* (Remes et al. 2009). Due to superficial affinities to elements in *Shunosaurus lili*, Remes et al. (2009) tentatively identified the *Spinophorosaurus* elements as tail spikes. Recently, Galiano & Albersdörfer (2010) informally reported three elements (one pair and a single bone) found associated with indeterminate diplodocid sauropods.

Variation in morphology

One of the AMNH elements develops a conspicuous ridge towards the tip of the short leg of the L. In its counterpart, this end is broken off. Contrary to the state in the AMNH elements, the same end is transversely expanded in the single morphotype B bone reported by Galiano & Albersdörfer (2010; H. Galiano, pers. comm. 2011).

The SMA specimens bear a thickened portion resembling an articulation facet at about midlength of the shorter leg of the L. As the AMNH elements show broken edges in this region, this facet might also constitute to the general morphology.

Identification

The three morphotype B elements recently reported by Galiano & Albersdörfer (2010) include a set of paired bones articulated between the acromia of the scapulae of a diplodocid specimen (DQ-SB; Fig. 6), where clavicles are supposed to attach (Romer, 1956; Vickaryous & Hall, 2006). Similarly, detailed examination of the juvenile sauropod SMA 0009 revealed that a second, L-shaped element is actually present attached to the dorsal corner of the right coracoid (Fig. 7). Schwarz et al. (2007b), in their initial description of SMA 0009, described this bone as 'dorsally pointing tip' of the coracoid, but a thin layer of matrix



Fig. 6 Morphotype B elements of the diplodocid DQ-SB, articulated with the acromia (arrowheads) of the scapulae, as they were found. Co, coracoid; MB, morphotype B element; Sc, scapula. Picture courtesy of H. Galiano.

between the elements indicates that they are taphonomically pressed onto each other. A third pair of morphotype B elements, articulated between the scapulae, appears to be present in a *Camarasaurus* (KUVV 129716, Bader et al., 2009; A. Maltese, pers. comm. 2012).

The topology and paired appearance of these morphotype B elements strongly suggests that they fit an identification as clavicles better than morphotype A. Such an interpretation would also match previous findings of similarly shaped clavicles in ceratopsian dinosaurs (Chinnery & Weishampel, 1998: Fig. 6; Vickaryous & Hall, 2010: Fig. 5). On the other hand, paired finds of non-sauropod sauropodomorph clavicles appear to be more straight (von Huene, 1926; Yates & Vasconcelos, 2005; Martínez, 2009; B. Pabst, pers. comm., 2011), but without the bifurcated end – resembling the elements recovered from *Jobaria tiguidensis* (Sereno et al. 1999: Fig. 3e). However, other than the report of the presence of this bone in *J. tiguidensis*, no other information about which bones it was associated with, and no detailed description has been provided to date.

Another explanation would be that morphotype B comprises sternal ribs. However, a taphonomical shifting of sternal ribs into a position equal to the clavicular articulation typical for tetrapods (as is the case in the specimen DQ-5B) is highly improbable. Therefore, an interpretation of morphotype B elements as the true sauropod clavicles is the most convincing. This interpretation challenges Hatcher's (1901, 1903) identification of the morphotype A bones. As the gross morphology of the shoulder girdle remains similar in the majority of Sauropoda, a high diversity in the shape

of clavicles seems improbable. Therefore, an interpretation of the morphotype A elements as interclavicles is supported as well by the presence of morphotype B bones as the true clavicles.

Morphotype C

Previous identification: gastralia, ventral ribs, sternal ribs (Fig. 8; Suppl. Figs 10–11).

Our identification: sternal ribs.

General morphology

Morphotype C elements are elongated, rod-like bones with a suboval cross-section. The smooth shafts are generally slightly curved, in some elements (e.g. SMA D 28-6, D 28-7) in two directions forming a weak S-shape. Both ends are rugose and irregular. One end is flattened and often shows differing degrees of rugosity on the two sides of the flattened portion.

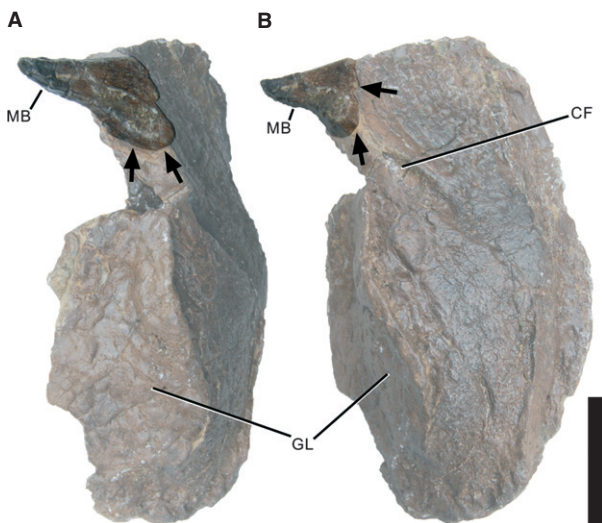


Fig. 7 Coracoid with taphonomically attached morphotype B element (MB) of the non-somphospondylan macronarian SMA 0009 in posteroventral (a) and lateral (b) view. Coracoid made semitransparent in order to visualize better the morphotype B element. Arrows indicate brightly coloured matrix present between the MB and the coracoid. CF, coracoid foramen; GL, glenoid surface. Scale bar: 2 cm.



Fig. 8 Morphotype C elements SMA H 20-7 (a) and L 21-5 (b). Both elements are incomplete, fracture surface at the top is indicated by the grey area. Scale bar: 10 cm.

The most similar bones to morphotype C elements would be cervical ribs or ossified tendons. However, cervical ribs are usually concave dorsally. Ossified tendons are often attached to other bones, or do not exhibit expanded ends, but if only a portion of the shaft of a morphotype C element is found, distinguishing between the two might be difficult.

Howe Quarry material

In the Howe Quarry sample, three clusters of gastral/steral ribs were found by the SMA (around field area D 28, F 27 and M 21; Fig. 2). All three clusters contain about 15 single elements. Within these clusters, morphotype C elements constitute the majority of the recovered bones. They (as well as elements belonging to morphotypes D and E) were always found in association with dorsal ribs. In the field area F 27, also two distal tail segments of different sizes as well as single posterior cervical vertebrae were recovered in the vicinity of the gastral/steral rib cage. The M 21 cluster was associated with the skull and neck of a diplodocine sauropod, as well as single (probably diplodocid) anterior chevrons. Additional morphotype C elements come from various areas within the Howe Quarry, and were found more scattered.

Previous reports

Such elements were usually described as sternal or gastral ribs, and are often associated with bones of morphotypes D and E. Taxa reported to preserve morphotype C elements include the non-neosauropod eusauropod *Jobaria tiguidensis*, the diplodocids *Apatosaurus louisae*, *Eobrontosaurus yahnahpin*, as well as the macronarian *Camarasaurus supremus* and *Diamantinasaurus matildae* (Holland, 1915; Osborn & Mook, 1921; Filla & Redman, 1994; Sereno et al. 1999; Hocknull et al. 2009).

Variation in morphology

Instead of being slightly curved, some morphotype C elements remain straight during their entire length. Toward the non-flattened ends, some of the elements remain straight, whereas others show a distinct bend.

Identification

Probable sauropod gastral/steral ribs have been reported more often than clavicles, and in a wider range of taxa (Table 2). As mentioned above, their interpretation as gastral/steral ribs has been challenged by Claessens (2004), pointing out their anatomical differences compared with non-sauropod sauropodomorph or theropod gastral/steral ribs. Claessens (2004) proposes that Marsh (1896) was right in identifying such elements as sternal ribs.

Sternal ribs are of endochondral origin, and present in both extant birds and crocodylians, but remain often cartilaginous (Claessens, 2004; Claessens et al. 2009; R. Fehner, pers. comm., 2011). They connect the distal tips of the anterior dorsal ribs with the sternum, either directly as in birds, or articulating with the dorsal ribs through generally carti-

laginous intercostal elements (Claessens et al. 2009; R. Fehner, pers. comm., 2011; pers. obs.). Within dinosaurs, only very few reports of sternal ribs exist besides the ones from Marsh (1883, 1896): they are described in hypsilophodont Ornithischia (e.g. Parks, 1926; Galton & Jensen, 1973; Weishampel & Heinrich, 1992), and Theropoda (e.g. Clark et al. 1999; Ruben et al. 2003).

Gastralia are dermal bones embedded in the abdominal musculature, and are usually thought to support the breathing apparatus and/or protect the belly (Claessens, 2004; Claessens et al. 2009). As sternal ribs, also gastral/steral ribs are present in both birds and crocodylians (Claessens, 2004). Unambiguous evidence for gastral/steral ribs in dinosaurs appears to exist only in Theropoda and early Sauropodomorpha ('prosauropods'; Claessens, 2004; R. Fehner, pers. comm., 2011). None of the bones of morphotype C exhibit the typical longitudinal articulation facets that occur between the medial and lateral elements of theropod or early sauropodomorph gastral/steral ribs (Claessens, 2004). On the other hand, for a bird-like sternal rib configuration, 15 elements are too many: in birds, distally expanded dorsal ribs usually connect to sternal segments through cartilage (Parks, 1926; Clark et al. 1999; Schwarz et al. 2007a), and straight or converging distal rib ends mark free ribs. Fully articulated ribcages of *Apatosaurus* and *Diplodocus* show transversely expanded ends only in the first five–seven dorsal ribs (Gilmore, 1936; Schwarz et al. 2007a) – which would allow a maximum number of 14 sternal ribs. However, the about 15 elements recovered per cluster include at least three morphotype D elements. Given that the latter most probably are not sternal ribs (see below), the maximum number of sternal ribs per individual would not be exceeded. An identification of morphotype C elements as sternal ribs is thus the most convincing.

Morphotype D

Not previously recognized (Fig. 9; Suppl. Figs 12–14).

Our identification: gastral/steral ribs.

General morphology

Morphotype D elements are more irregularly formed than morphotype C, shorter and thicker. They are curved bones with both ends expanded and rugose. The expansions are not equal on the two extremities, one of them being wider than the other. The wider end is flattened, very irregularly expanded, and with strong rugosities. On one side, this end is slightly convex, indicating that this side was not articulating with any other element. These bones all show some curvature at the opposite end, resulting in an outward pointing extremity.

Morphotype D elements can be very similar to bones belonging to morphotype C, and thus also to ossified tendons and cervical ribs. The wide, probably medial (see below) extremity is the best characteristic to define morphotype D. It is more irregular, wider and resembles

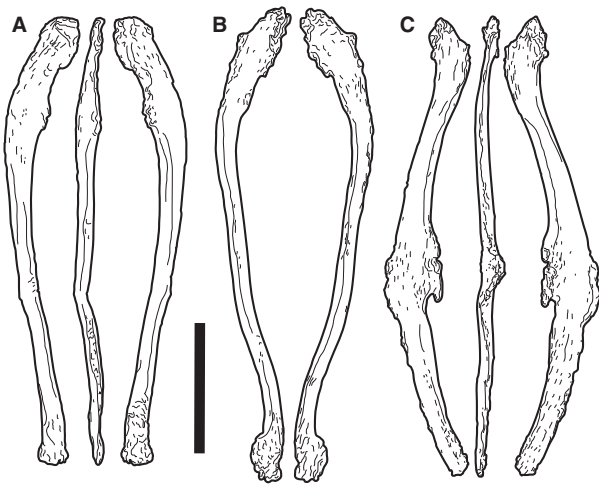


Fig. 9 Morphotype D elements SMA D 28-5 (a), M 21-2 (b) and M 21-8 (c). The bottom end of M 21-8 is broken. Scale bar: 10 cm.

more bony overgrowth than what is usually present in morphotype C.

Howe Quarry material

Morphotype D elements are less frequently found. However, all three gastral/sternal rib clusters in the SMA collection contain morphotype D elements. Two bones of the cluster D 28 are symmetrical, and can be nicely articulated at their wider ends (D 28-5 and 14; Fig. 10).

Previous reports

To our knowledge, elements of this morphotype are described for the first time in this paper. It is possible, however, that previously mentioned sets of 'gastralia' or 'sternal ribs' include morphotype D elements, but that these were not recognized as such and not figured (see Table 2).

Variation in morphology

Certain elements in the M 21-basket (e.g. SMA M 21-8; Fig. 9c) appear to be fused symmetric elements. They reproduce the slight upward curvature of two articulated opposing elements similar to the pair SMA D 28-5 and 14, and exhibit an outgrowth in the middle of the bone, which would come to lie on the body midline. This outgrowth resembles somewhat pathological bony overgrowth but also the shape of two unfused anterior or posterior gastralia with their enlarged medial ends. Towards the extremities the curvature of the bone becomes inverted in a way that the expanded ends are pointing somewhat downwards again (or probably straightly outwards when articulated). This results in a slightly sinuous curve, similar to tyrannosaur furculae described by Makovicky & Currie (1998).

Identification

Although associated with the probable sternal ribs belonging to morphotype C, bones like SMA M 21-8 (Fig. 9c),



Fig. 10 Proposed articulation between two morphotype D elements (left, SMA D 28-5; right, SMA D 28-14) in three views (internal/dorsal view in the centre, grey lines indicate the same morphological landmarks on the respective elements). Note the similarity to the central portion of the fused morphotype D element (Fig. 9c). Scale bar: 5 cm.

which seem to be composed of two fused elements like D 28-5 or M 21-2 (Fig. 9a or b, respectively), have no equivalent in previously described sternal ribs known to us. Sternal ribs sometimes connect to other, more anteriorly placed elements, instead of articulating directly with the sternal plates (Galton & Jensen, 1973; Clark et al. 1999; Claessens et al. 2009), but no specimen has been reported to date exhibiting fused left and right ribs.

Manual manipulation of the two corresponding elements SMA D 28-5 and 14 shows that the expanded ends would articulate relatively nicely in a way similar to the midline joint of two gastralia in non-sauropod sauropomorphs and theropods (Fig. 10). Median gastralia of the anterior-most row were previously shown to fuse in certain cases, thereby forming irregularly shaped and asymmetric sutures (e.g. Makovicky & Currie, 1998; Claessens, 2004). Such a development resembles much the herein described fused elements. Morphotype D is thus most convincingly interpreted as the anterior-most gastralia, close to the sternal apparatus.

Morphotype E

Previous identification: gastralia, sternal ribs (Fig. 11; Suppl. Figs 15–16).

Our identification: sternal ribs and/or intercostal elements.

General morphology

Bones belonging to morphotype E have irregular shapes that cannot be included in any of the above defined morphotypes. Peculiar morphologies include projections (e.g. SMA H 21-1; Fig. 11a), irregular expansions (SMA N 22-12; Fig. 11b), and bifurcated ends (SMA M 21-15; Fig. 11c). Due to their particular shapes, morphotype E elements do not resemble any other bone in the sauropod skeleton.

Howe Quarry material

Few of these elements were recovered at the Howe Quarry, always in association with bones of the morphotypes C and D. SMA H 21-1 and 3 form a symmetrical pair.

Previous reports

Similar elements include bones of *Apatosaurus excelsus*, identified as sternal ribs by Marsh (1883, 1896), and some of the elements of the gastral basket of *Eobrontosaurus yahnahpin* described by Filla & Redman (1994).

Variation in morphology

SMA H 21-1 and H 21-3 develop a projection approximately at one-third to two-fifths of their entire length, which appears to proceed at an acute angle to the longer portion of the bone (Fig. 11a). How long this projection is remains unclear, as their ends are broken in both elements. M 21-15 is a rather thick bone of medium length, compared with the usual gastral/steral ribs. Both ends are flattened, one of them is markedly and slightly asymmetrically bifurcated (Fig. 11c). On the edge running from the longer portion of

the bifurcation, somewhat inwards, a tubercle can be seen with fractured bone surface so that the original expansion of this feature can not be determined. The opposing end is irregular as well, exhibiting a very shallow notch. N 22-12 is a short and very thin bone, with one end greatly expanded in two dimensions, forming a spatulate shape with irregular margins, and a weak, radiating striation extending from the centre of the bone towards the outer margins on both sides (Fig. 11b). At the base of this expansion, both sides are marked by a well visible foramen that lie on the same level in regard to the long axis of the bone, and only very slightly displaced perpendicular to the long axis. Towards the other end, at about two-thirds of the entire length, there is a rugose tubercle. Further towards this end, the bone curves and becomes more rugose again.

Identification

Considering a crocodylian arrangement, morphotype E elements (like the particularly shaped SMA N 22-12, and maybe also the short elements described by Filla & Redman, 1994: Fig. 11h,i,q,r) might represent intercostal elements. Furthermore, the two SMA elements with the projection (H 21-1 and H 21-3), as well as the very irregularly shaped bone figured by Marsh (1896): Figs 12 and 13 resemble somewhat the posterior sternal ribs in the pterosaur *Rhamphorhynchus* (Claessens et al. 2009: Fig. 2d). The projections as well as the bifurcations might have articulated with more anterior sternal ribs.

As gastral and sternal ribs have differing developmental origins (Table 1), a histological analysis might yield more definitive results concerning the identity of morphotypes C–E, but should include elements of all of them. However, histological sections of dermal and endochondral bones are difficult to distinguish in a fully ossified state (T. Scheyer, pers. comm., 2009). Such a study has thus to await further analyses and comparisons of known gastral/steral ribs in extant animals, and lies outside the scope of this paper.

Morphological implications

The rarity of finds of ossified chest elements other than the scapulacoracoid or the sternal plates render proper identifications difficult, especially due to the fact that they are often recovered disarticulated from the corresponding pectoral girdle. This might imply that the soft tissue connection between them and the pectoral girdle or the sternal apparatus was not very strong during lifetime – and as a consequence, chest bones were possibly easily disarticulated if not lost entirely before burial. When preserved and found, the indistinct shape and consequential difficulties identifying these elements make them more likely to not be reported or not even collected, increasing such a taphonomic bias even more. Nonetheless, the herein reported bones indicate that additional elements like the clavicles,

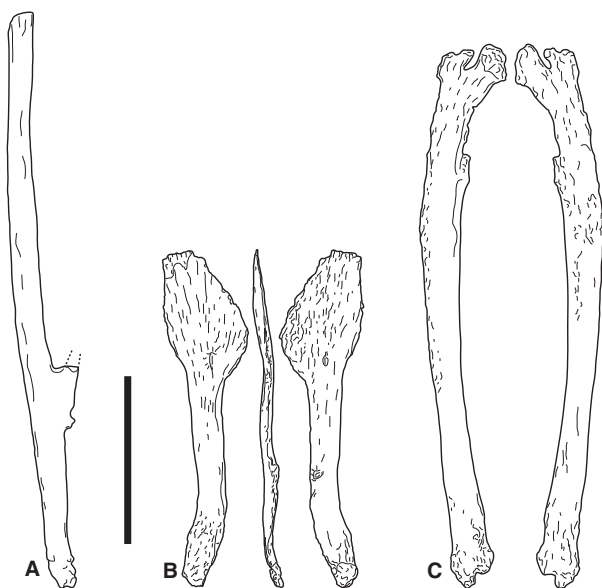


Fig. 11 Morphotype E elements SMA H 21-3 (a), N 22-12 (b) and M 21-15 (c). Note the irregular shapes that do not allow an assignment to any other morphotype. Dotted lines in (a) indicate direction of the broken hook-like projection. Scale bar: 10 cm.

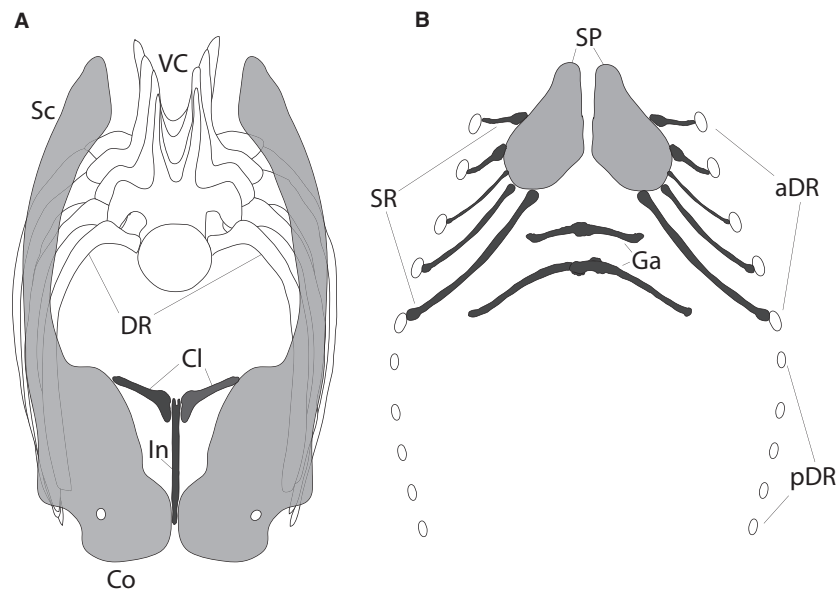


Fig. 12 Reconstruction of the pectoral girdle and the chest region of an indeterminate diplodocid sauropod, based on the finds reported. Light grey elements represent pectoral girdle elements not discussed in the paper, dark grey elements mark the bones identified as chest bone morphotypes in this paper. Anterior (a) and ventral (b) view. Abbreviations: aDR, anterior dorsal ribs; Cl, clavicle (morphotype B); Co, coracoid; DR, dorsal rib; Ga, gastralia (morphotype D); In, interclavicle (morphotype A); pDR, posterior dorsal ribs; Sc, scapula; SP, sternal plates; SR, sternal ribs (morphotypes C and E); VC, vertebral column. Modified from Schwarz et al. (2007a; a) and Filla & Redman (1994; b).

interclavicle, sternal ribs, gastralia, and possibly intercostal elements do ossify in some sauropod taxa. However, it must be noted that no articulated sauropod specimen has yet been found preserving both morphotype A (interclavicles) and B elements (clavicles). The finds, where clavicles were found articulated (DQ-SB, KUVV 129716) or associated (SMA 0009) with the scapulacoracoids, do not appear to preserve an interclavicle. In the Howe Quarry sample described herein, all the elements were found disarticulated in a bonebed. Nonetheless, the tight association with diplodocid material suggests that if not from the same individuals, they were at least from the same taxon. A novel reconstruction of the diplodocid pectoral girdle and sternal apparatus, taking these interpretations into account, is shown in Fig. 12.

The only species from which both types of bones are reported is *Spinophorosaurus nigerensis*, but they are from two different individuals (Remes et al. 2009). The somewhat L-shaped elements of the holotype of *Spinophorosaurus nigerensis* appear to be of considerably different sizes, which was one of the reasons leading to their identification as tail spikes (Remes et al. 2009; R. Kosma and A. Ritter, pers. comm., 2011). However, the *Spinophorosaurus* elements resemble much more the L-shaped bones found at the Howe Quarry than the supposed *Shunosaurus* tail spikes (Zhang, 1988). They do not bear the typical osteoderm surface rugosity as seen in thyreophorans and sauropods, neither shows the specimen any club-like distal extension as present in *Shunosaurus*. Compared with the Howe Quarry material, the base of the *Spinophorosaurus* elements (which

would correspond to the shorter leg of the L) is slightly broader, and the two legs curve gently into each other, giving the entire bone a rather triangular outline. Also, the obviously broken edges of the preserved elements shed some doubt on them being of considerably different size as described by Remes et al. (2009). Given that these elements were found below the scapula (Remes et al. 2009), an interpretation as clavicles seems possible for the *Spinophorosaurus* elements, and the original material should be reassessed under the light of the new findings.

Functional implications

An ossification of such a variety of chest elements creates anchor attachments for musculature and stabilizes the entire pectoral girdle, the sternal apparatus and in case of ossified gastralia also the rest of the trunk. A substitution of soft tissues (probably cartilage or ligaments in the case of the sauropod pectoral apparatus) by bone helps to cope with higher loads (Romer, 1956; Haines, 1969). The sauropod taxa exhibiting ossification of the various chest elements show some correlation with taxa usually interpreted to use their tail as laterally swinging defensive weapon, indicated by the presence of tail clubs (*Shunosaurus*, *Omeisaurus*, *Mamenchisaurus*; Zhang, 1988; Dong et al. 1989; Xing et al. 2009), possible tail spikes (*Shunosaurus*, *Spinophorosaurus*; Zhang, 1988; Remes et al. 2009; but see above) or whip-lash tails (*Suuwassea*, *Diplodocus*; Hatcher, 1901; Harris, 2006). Lateral movements of the tail might request a firm trunk in order to not disequilibrate the entire

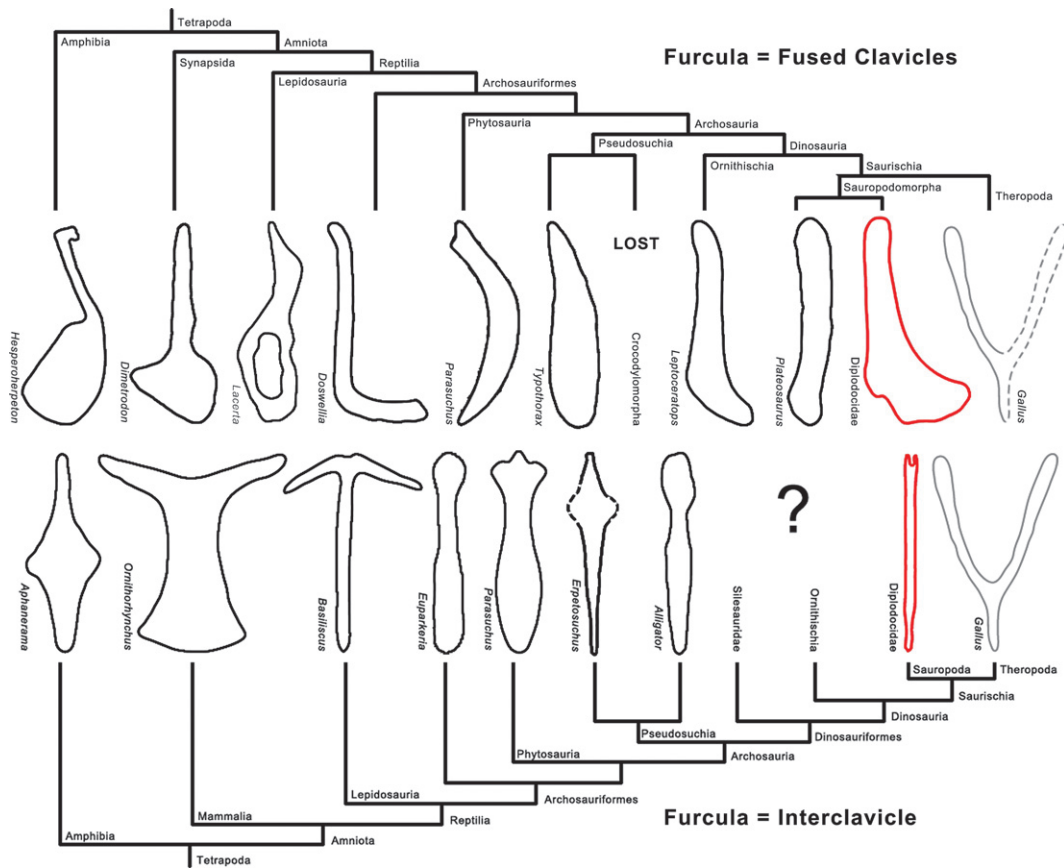


Fig. 13 Evolution of the furcula, comparison between the two hypotheses. Note the gap within Dinosauriformes in the furcula-interclavicle hypothesis. Line drawings scaled to same size. Eaton & Stewart (1960: *Hesperoherpeton*); Chatterjee (1978: *Parasuchus*); Klima (1987: *Ornithomorphus*); Rieppel (1992: *Lacerta*); Steyer et al. (2000: *Aphanerama*); Benton & Walker (2002: *Erpetosuchus*); Martz (2002: *Typothorax*); Vickaryous & Hall (2006: *Dimetrodon*; 2010: *Alligator*, *Basiliscus*, *Gallus*, *Leptoceratops*); Remes (2008: *Euparkeria*); Dilkes & Sues (2009: *Doswellia*).

animal. Since the pelvic girdle – in contrast to the shoulder girdle – is co-ossified with the vertebral column, reinforcements would be particularly essential in the pectoral girdle. Furthermore, a posteriorly located centre of mass, as present especially in diplococids, appears to induce important lateral stresses to the pectoral girdle during locomotion (Sander et al. 2011).

The loss of ossified chest elements coincides with the evolution of the particular wide-gauge locomotor style of titanosauriform sauropods (Wilson & Carrano, 1999; Carrano, 2005). The question remains, if the loss of ossified chest bones allowed the wider spacing of the legs, or if the latter enhanced stability enough to render the ossification useless. The presence of clavicles and/or interclavicles in *Datousaurus*, *Jobaria*, and *Camarasaurus* might just represent an example of retained plesiomorphies without strong functional significance.

Phylogenetical implications

The proposed presence of ossified elements in the chest region of some sauropods has also phylogenetical implica-

tions – even in case some of the above-stated interpretations would remain controversial. Although a taphonomical bias leading to the absence of chest bones in titanosauriforms and rebbachisaurids cannot be excluded to date, their distinctly taxonomically restricted appearance appears striking. As an ossification of additional chest elements in diplococids and early eusauropods does also make sense in a functional point of view (see above), their presence is herein interpreted as plesiomorphic for Sauropoda, whereas the loss of ossified clavicles, interclavicles, sternal and/or gastral ribs might result a synapomorphy for Titanosauriformes, and maybe Rebbachisauridae as well. The single findings of sternal ribs in the lithostrotian *Diamantinasaurus* Hocknull et al. 2009) remain doubtful, or might represent exceptions to the rule.

The presence of interclavicles in dinosaurs is herein stated for the first time with direct morphological evidence. The other reported possible dinosaurian interclavicles were reinterpreted as clavicles or furculae, and thus their identification remains ambiguous (Cooper, 1981; Yates & Vasconcelos, 2005). This supports Vickaryous & Hall’s (2010) statement that the theropod and avian furcula could also be

homologous to the interclavicle instead of representing the fused clavicles, as generally proposed (Yates & Vasconcelos, 2005; Nesbitt et al. 2009). The evolutionary gap between non-dinosauriform interclavicles and theropod furculae, for which we did not have conclusive data before, is shortened by the presence of interclavicles in sauropods. If the interclavicle-furcula homology would get confirmed by future studies, theropods would have reduced the stem-like central body of the interclavicle as seen in sauropods to the hypocleidium, and the transverse processes would have been enlarged, and would have substituted the clavicles, which would have gotten lost early in theropod evolution. However, because both clavicles and interclavicles are present in sauropods, conclusions have to await finds of articulated specimens of early dinosaurs, or dinosauriforms, which might shed more light on the evolution of the theropod pectoral girdle. The strongest evidence against the furcula-interclavicle homology are the topology of the furcula (it articulates with the acromion as clavicles do; see Nesbitt et al. 2009), and the pairs of bones found in *Massospondylus* and early theropods, which articulate with the scapular acromion laterally, and among themselves medially (Yates & Vasconcelos, 2005; Nesbitt et al., 2009). Since in articulation, they resemble much the theropod furcula, and Nesbitt et al. (2009) interpreted them as an intermediate evolutionary state between unfused clavicles and the furcula. The competing hypotheses are summarized in Fig. 13.

Conclusions

Several elements recovered at the Howe Quarry (Bighorn County, Wyoming, USA) resemble bones previously identified as sauropod clavicles, as well as gastralia and/or sternal ribs. The finding of pairs of symmetric bones associated with pectoral girdle elements sheds new light on these old interpretations. In fact, detailed investigations lead to the conclusion that the bones previously supposed to represent clavicles, most probably are interclavicles, with the symmetrical, L-shaped pairs being the true clavicae. This supports the result of developmental studies of Vickaryous & Hall (2010), which questions the loss of the interclavicle in Dinosauria – and proposes a homology between the avian furcula and the reptilian interclavicle. This would change the usual interpretation that the furcula represents the fused clavicles.

A review of the occurrence of such bones within Sauropoda implies that the tendency to ossify interclavicles, clavicles, and sternal and/or gastral ribs has a distinct taxonomic distribution, with non-neosauropod Eusauropoda and Flagellicaudata representing the plesiomorphic state, and Titanosauriformes as well as possibly Rebbachisauridae exhibiting the derived condition. Functional implications of retaining the ossified chest bones include the stabilization of the trunk in order to have a firm base for lateral movements of elongated necks and tails. On the other hand, the

loss of these osseous elements could have allowed the evolution of the wide-gauge locomotion in Macronaria.

Institutional abbreviations

AMNH, American Museum of Natural History, New York; ANS, Academy of Natural Sciences, Philadelphia, Pennsylvania; AODF, Australian Age of Dinosaurs Fossil; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; DMNS, Denver Museum of Nature and Science, Denver, Colorado; DNM, Dinosaur National Monument, Vernal, Utah; DQ, Dinosauria International (Dana Quarry collection), New York; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; KUVP, University of Kansas Natural History Museum, Kansas; NMB, Naturhistorisches Museum Braunschweig, Germany; SMA, Sauriermuseum Aathal, Switzerland; Tate, Tate Geological Museum, Casper, Wyoming; YPM, Yale Peabody Museum, New Haven, Connecticut.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Morphotype A element (interclavicle) AMNH 30900 in left lateral, internal and right lateral (from left to right). The left spur of the bifid anterior end as well as the distal posterior tip are lacking. Scale bar: 10 cm.

Fig. S2. Morphotype A element (interclavicle) SMA I 24-4 in right lateral, external, left lateral, internal (from left to right) and posterior view (bottom). Note the bifurcate anterior end towards the top of the picture. Scale bar: 10 cm.

Fig. S3. Morphotype A element (interclavicle) SMA L 22-3 in right lateral, external, left lateral and internal view (from left to right). Note the different orientation of the spatulate end compared with SMA I 24-4. Scale bar: 10 cm.

Fig. S4. Morphotype A element (interclavicle) SMA L 27-7 in left lateral, internal, right lateral (from left to right) and anterior view (top). Note the outwards curvature in the anterior half, probably due to taphonomy. Scale bar: 10 cm.

Fig. S5. Morphotype A element (interclavicle) SMA M 25-3 in left lateral, internal, right lateral (from left to right), anterior (top) and posterior view (bottom). Note the bifurcate anterior end. Scale bar: 10 cm.

Fig. S6. Morphotype B element (clavicle) SMA K 24-6 in internal, anterior, external, posterior (from left to right), lateral (top) and medial view (bottom). It is interpreted as left element of the SMA pair. Scale bar: 5 cm.

Fig. S7. Morphotype B element (clavicle) SMA K 24-3 in external (left), internal (right), lateral (top) and medial view (bottom). It is interpreted as right element of the SMA pair. Scale bar: 10 cm.

Fig. S8. Left morphotype B element (clavicle) of the pair included in AMNH 30789 in internal (left) and external view (right). The lateral-most end is lacking (top). Note the conspicuous ridge on the tip of the short leg of the L. Scale bar: 10 cm.

Fig. S9. Right morphotype B element (clavicle) of the pair included in AMNH 30789 in external (left) and internal view (right). Both the lateral-most end and the tip of the short leg of the L are lacking. Scale bar: 10 cm.

Fig. S10. Morphotype C element (sternal rib) SMA H 20-7. The end towards the top is broken. Scale bar: 10 cm.

Fig. S11. Morphotype C element (sternal rib) SMA L 21-5. The end towards the top is broken. Note the very slender and almost straight shaft. Scale bar: 10 cm.

Fig. S12. Morphotype D element (gastralia) SMA D 28-5. Note the irregular medial expansion (top) and the curved shaft. Scale bar: 10 cm.

Fig. S13. Morphotype D element (gastralia) SMA M 21-2. Note the irregular medial expansion (top) and the curved shaft. Scale bar: 10 cm.

Fig. S14. Two fused morphotype D elements (gastralia, SMA M 21-8). The lateral-most portion towards the bottom of the picture is broken, and would probably mirror the opposite end. Scale bar: 10 cm.

Fig. S15. Morphotype E element (sternal rib or intercostal element) SMA N 22-12. Scale bar: 10 cm.

Fig. S16. Morphotype E element (sternal rib or intercostal element) SMA M 21-15. Scale bar: 10 cm.