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

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Ossified chest bones (gastralia, sternal ribs, clavicles, and interclavicles) in diplodocid sauropods from the Late Jurassic of Wyoming and the evolutionary implications of interclavicles in dinosaurs

Running head: Ossified chest bones in Diplodocidae

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Abstract

Ossified gastralia, clavicles, and sternal ribs are known in a variety of reptilians, including dinosaurs. In sauropods, however, the identification of these bones remains debated: supposed gastralia were recently reinterpreted as sternal ribs, based on their different morphology from undoubted theropod and basal sauropodomorph gastralia. Bones previously interpreted as clavicles were thought to represent sternal ribs or an Os penis. The rareness and lack of articulation of such finds in sauropods complicates their identification and makes them less likely to be reported. However, accurate reconstructions of the pectoral girdle, forelimb movements, as well as the respiratory musculature can only be based on more complete skeletons, and reporting such bones as well as their proper identification thus remains crucial. Herein we describe different bones from the chest region of diplodocids, found near Shell, Wyoming. Five morphotypes are well distinguishable. Elongated, relatively stout, curved elements with a spatulate and a bifurcate end resemble much the previously reported sauropod clavicles, but might actually represent interclavicles. A second type is L-shaped, and mostly preserved as a symmetrical pair. Similar elements in *Spinophorosaurus* were identified as tail spikes, but new findings in diplodocids indicate that they are the true sauropod clavicles. Slender, rod-like bones with rugose ends are highly similar to elements identified as sauropod sternal ribs. Curved bones with wide, probably medial ends or expanded central parts constitute the fourth morphotype (herein interpreted as gastralia), and irregularly shaped elements, often with extended rugosities, are included into the fifth morphotype, tentatively identified as sternal ribs.

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 report of interclavicles in dinosaurs. Previously supposed interclavicles in the basal sauropodomorph *Massospondylus* were later reinterpreted as clavicles.

Independent from their identification, the existence of the reported bones bear both phylogenetic and functional significance. Their presence in flagellicaudatans and absence in rebbachisaurs implicates that the ossification of the chest bones can be considered synapomorphic of Flagellicaudata. As alternative hypothesis, the non-ossification appear only in Macronaria. A presence of interclavicles in sauropods gives further support to a recent hypothesis, which proposes the avian furcula to be homologous to the interclavicles, instead of being formed by the fused clavicles.

Functional implications are a stiffening 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. Lateral stresses due to tail swinging can then be absorbed better. The loss of ossified chest bones correlates with more widely spaced limbs, and the evolution of a wide-gauge locomotor style.

Keywords: Diplodocidae, Pectoral girdle, Interclavicle, Furcula

Introduction

The original pectoral girdle of early reptiles consisted of various elements: scapula, suprascapula, anterior and posterior coracoids, cleithrum, clavicle, and the interclavicle (Romer 1956). Whereas the suprascapula remains cartilaginous in all reptiles, the other pectoral bones were originally ossified, and were ventroposteriorly followed by the sternal plates and ribs (Romer 1956; Remes 2008; see Table 1 for a summary of pectoral and sternal elements in Reptilia). In the process of the evolution of dinosaurs, several changes occurred: the cleithrum was lost and anterior and posterior coracoids fused to form a single element shortly after the rise of Reptilia. The interclavicle is generally interpreted to have been reduced within Archosauria, after the separation of the pterosaurs, some of which still preserve this bone in a juvenile state (Romer 1956; Remes 2008; Nesbitt 2011). Furthermore, also the 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, numerous 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). Lately, also the loss of the interclavicle was doubted at least for Theropoda, where the furcula actually might not represent the fused clavicles as previously thought, but that it is actually homologous to the interclavicle (Vickaryous & Hall 2010). Vickaryous & Hall (2010) extended their hypothesis to all previously reported dinosaurian clavicles. As clavicles (but not interclavicles) are lost in extant pseudosuchians as well, this would imply that the loss of these pectoral elements happened early in the evolution of Archosauria, before pseudosuchians split from dinosauromorphs (Vickaryous & Hall 2010). 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). The orientation of the scapulacoracoid is still debated, but recent analyses suggest that the scapular blade was inclined at an angle of 60-65° to the horizontal, with the

coracoids almost touching anteriorly at the midline (Schwarz et al. 2007a; Remes 2008; Hohn-Schulte 2010). Such a reconstruction implies that the sternal plates are shifted backwards underneath the ribcage, with whom they are connected through usually cartilaginous sternal ribs (Schwarz et al. 2007pect; Remes 2008). This arrangement was corroborated by finite element structure synthesis analyses (Hohn-Schulte 2010). Supposed clavicles would connect the scapulae dorsal to the coracoids, but no articulated pair has yet been reported in sauropods (Remes 2008). Single rod-like structures interpreted as clavicles were found in a variety of sauropod taxa, sometimes associated with the pectoral girdle (Hatcher 1901, 1903; Dong & Tang 1984; He et al. 1988; Zhang 1988; Sereno et al. 1999; Harris 2007; Remes et al. 2009). However, most of these reports rely solely on the validity of previous identifications - which themselves are not beyond doubt. Sternal ribs are even less well known, the only references being from the *Apatosaurus excelsus* holotype YPM 1980 (Marsh 1896), a set of ribs associated with the holotype of *A. louisae* (Holland 1915), and maybe from the holotype of *Eobrontosaurus yahnahpin* (Filla & Redman 1994). Filla & Redman (1994) initially interpreted these structures as gastralia, based on their similarity to gastralia in theropods, basal sauropodomorphs, and other archosaurs like crocodiles or sphenodonts. Later, also *Gongxianosaurus shibeiensis* and *Jobaria tiguidensis* were reported to preserve gastralia (He et al. 1998; Sereno et al. 1999). However, Claessens (2004) and Fechner (pers. comm., 2011), based on comparison with theropod and basal sauropodomorph gastralia, recently questioned this identification, and suggested them to be ossified sternal ribs instead.

Herein we report both bones resembling the rod-like elements previously identified as clavicles, as well as bones resembling the gastralia or sternal ribs in *E. yahnahpin*. Furthermore, two pairs of symmetrical bones are described, yielding more information on the proper identification of all of these types of bones. A review of the previous reports suggests that their presence might be used as a valuable phylogenetic character: to date, almost only non-neosauropod eusauropods, members of the Flagellicaudata, and basal Macronaria were mentioned to preserve clavicles and/or ossified gastralia or sternal ribs. The single report of a gastral rib in the somphospondylian *Diamantinasaurus matildae* (Hocknull et al. 2009) probably represents an exception of the rule.

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, Dana Quarry, Tensleep, Wyoming; IVPP, Institute of

Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NMB: Naturhistorisches Museum Braunschweig, Germany; SMA, Sauriermuseum Aathal, Switzerland; Tate, Tate Geological Museum, Casper, Wyoming; YPM, Yale Peabody Museum, New Haven, Connecticut.

Material

The new material described herein comes exclusively from the Howe Quarry in the Bighorn Basin of Wyoming, USA (Fig. 1). Two excavation periods were conducted at this site: Barnum Brown recovered 3000 to 4000 bones at the Howe Quarry for the American Museum of Natural History (hereinafter reported as AMNH) in 1934 (Brown 1935; Michelis 2004), and Hans-Jakob Siber reopened the site with a team of the Sauriermuseum Aathal (hereinafter reported as SMA) in 1990 and excavated another 700 to 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, *Kaatedocus siberi* (Tschopp & Mateus, in press). Concerning the remaining sauropod specimens, 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 gastralia or sternal ribs, as well as single appearances of elements resembling the bones previously identified as sauropod clavicles. Furthermore, two pairs of L-shaped, symmetrical elements were recovered, the provenance of which is discussed below.

Given the predominance of Diplodocidae in the Howe Quarry, and 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. In the following, the elements to be described are grouped into five morphotypes. Their identification will be discussed in detail below, and elements belonging to these morphotypes are listed in Table 2.

Morphotype A (seen here as interclavicles, previously identified as clavicles)

Elements belonging to the morphotype A are relatively stout, rod-like elements. They are usually bowed, and exhibit a spatulate and a bifurcate end. To date, such bones were usually identified as sauropod clavicles. Five such 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). 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 the holotype of *Kaatedocus siberi* (SMA 0004; 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.

Morphotype B (seen here as clavicles)

Bones taken together as morphotype B have a L-shaped outline, are 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. Similar elements have previously been identified as tail spikes (Remes et al. 2009). Of the two pairs of morphotype B, one was found in 1934 by the AMNH (AMNH 30789), the other pair was recovered in the SMA excavation and bear the field numbers 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 bearing the field number 151), their placement within the Howe Quarry remains difficult to locate. 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.

Morphotype C (seen here as sternal ribs)

This morphotype includes elongated, slender bones. They are generally slightly curved, and have somewhat expanded, rugose ends. Such elements were usually described as sternal or gastral ribs, and are often associated with bones of morphotypes D and E (as e.g. in *Eobrontosaurus yahnahpin*, Filla & Redman 1994). In the Howe Quarry sample, three clusters of gastralia/sternal ribs were found by the SMA (around field area D 28, F 27, and M 21; Fig. 2). 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/sternal rib cage. The M 21 cluster was associated with the holotype of *Kaatedocus siberi* (SMA 0004), as well as single (probably diplodocid) anterior chevrons. Additional

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morphotype C elements come from various areas within the Howe Quarry, and were found more scattered.

Morphotype D (seen here as gastralia)

Elements described herein as morphotype D 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 gastral or sternal rib cluster D 28 in the SMA collection contains two such elements, which are mirrored, and can be nicely articulated at their wider end (D 28-5 and 14). Other bones exhibiting a morphology resembling two of these elements that got fused are included into morphotype D as well. To our knowledge, elements of this morphotype are described for the first time in this paper.

Morphotype E (seen here as sternal ribs)

Bones belonging to morphotype E have irregular shapes that cannot be included in any of the above defined morphotypes. Few of these elements were recovered at the Howe Quarry, always in association with bones of the morphotypes C and D. Similar elements include the bones identified as sternal ribs by Marsh (1883, 1896), or some of the elements of the gastral basket described by Filla & Redman (1994). SMA H 21-1 and 3 form a symmetrical pair.

Description & Discussion

Usually the pectoral girdle in sauropods is only represented by the scapulacoracoid and sometimes the sternal plates. However, both an extant phylogenetic bracket approach as well as comparisons with closely related extinct groups indicate that more elements – if not ossified – should at least be present as cartilaginous structures (Schwarz et al. 2007a). For a proper reconstruction of the pectoral girdle and functional studies of the forelimb it is therefore crucial to report any preserved possible indication of osseous or cartilaginous chest bones. Both in the early years of sauropod discoveries as well as in recent publications, clavicles, gastralia, and sternal elements have been reported every now and then (e.g. Marsh 1883, Hatcher 1901, Holland 1906, Osborn & Mook 1921, Dong et al. 1983; Dong & Tang 1984, Filla & Redman 1994, Sereno et al. 1999, Harris 2007; Hocknull et al. 2009; Galiano & Albersdörfer 2010; see Table 2). However, the rarity of such finds as of clavicles, gastralia, or sternal ribs render proper identifications difficult, especially due to the fact that they are often recovered disarticulated from the corresponding pectoral girdle. In the following, the new elements of the above described morphotypes will be described in detail. The occurrences of

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these bones will be reviewed separately, discussing the implications of the herein reported finds.

Morphotype A

Description. The five elements recovered at the Howe Quarry are elongated and relatively massive, curved bones (Fig. 3; Table 3). Assuming that the concave side follows the curvature of the body, this side can be regarded as internal. One end is slightly bifid, the other extremity is extended in a spatulate-like manner, usually having a flattened aspect in perpendicular view. This end is always exhibiting more or less linear rugose striations for muscle attachment. The shafts are suboval in cross-section at mid-length, and achieve their greatest breadth at 2/3 to 3/4 of their total length, toward the spatulate end. The notch in the bifurcated end is usually only visible in internal or external view. However, in two of these elements (AMNH 30900 and SMA I 24-4; Figs 3A and B), the notched end is twisted by 90°. Furthermore, SMA I 24-4 is not curved, but straight. In SMA L 27-7 the bifurcated end is not only curved along the long axis of the bone, but also curves outwards (Fig. 3E). However, the thinner and thus more fragile nature of this element and several fractures in its shaft indicate that it has suffered stronger post mortem deformation than the other three elements, so that this feature might also be of taphonomical reason.

Two SMA elements (M 25-3 and L 22-3; Figs 3C and D) exhibit a peculiar morphology of their spatulate end. It is oriented perpendicular to the curvature of the bone, so that its thin edges face internally and externally. Whereas the external face of the two bones is convex, the internal edge bears a deep slot-like concavity, giving the impression of a deeply bifurcated end on this side as well, when seen in this view.

Discussion. The first reported element of morphotype A was found associated with the scapulacoracoid of *Diplodocus carnegii* CM 84 and identified as probable clavicle (Hatcher 1901). Two years later, Hatcher (1903) described another similar bone in *Diplodocus hayi* HMNS 175, which reinforced his opinion that these bones were clavicles. However, partly based on the fact that they were not found in pairs, Nopcsa (1905) interpreted them as Os penis, which was shown to be very improbable shortly after by Holland (1906). Holland on the other hand reported several differences between the two questionable elements, and was thus also sceptical about Hatcher's (1901, 1903) interpretation that they are clavicles, proposing that they rather represent ossified sternal ribs (Holland 1906). In fact, personal observations showed that the two elements of CM 84 and HMNS 175 exhibit the two different orientations of the notched bifurcated ends as noted as well in the Howe Quarry specimens. Similar bones continued to be found as single elements, even though some of the

specimens were reasonably complete and articulated (Tab. 2). Of these, the element of *Suuwassea emilieae* ANS 21122 is notable as its spatulate end bears a very distinct, distally tapering ridge, which is marked by a strong striation. The ridge originates at the base of the spatulate expansion and terminates abruptly 85 mm before the end. It divides the spatulate portion into two oblique concavities (Harris 2007; pers. obs.). A similar condition can be seen in the element of HMNS 175, but here, the ridge is not more than a shallow convexity extending from the base of the expansion to about midlength of the spatulate end (Holland 1906; pers. obs.).

One of the reasons put forward to justify the identification as clavicle was a supposed asymmetry of the recovered elements. However, close examination of the five elements recovered as single bones in the Howe Quarry, and of the corresponding elements of *Diplodocus carnegii* (CM 84), *D. hayi* (HMNS 175), *Spinophorosaurus nigerensis* (NMB-1698-R), and *Suuwassea emilieae* (ANS 21122) revealed that their asymmetry might also be due to deformation. A symmetry plane can be imagined when looking at them from a point of view perpendicular to the curvature, running through the bifid end and dividing the expanded spatulate end in two symmetric halves. These bones could therefore also represent elements of the chest region that lie on the body midline - and their continuous findings as single elements might have been no coincidence. The ridge described above, subdividing the concave portion of the spatulate end would then mark the body midline as well. As the two areas abutting to the right and left of the ridge resemble articulation surfaces, this would imply that the morphotype A elements covered two symmetrical elements externally, and medially.

The only median pectoral element is the interclavicle. Whereas early tetrapods show diamond-shaped interclavicles, crocodylomorphs and some lepidosaurs develop rod-like shapes without lateral processes (Steyer et al. 2000; Vickaryous & Hall 2010), similar to the elements described herein. Following this interpretation, the bifurcated end could represent the reduced lateral processes, and the spatulate end would articulate with either the coracoids or the sternal plates - covering them externally and anteromedially as hypothesized above. A bone found in the pectoral girdle of the basal sauropodomorph *Massospondylus carinatus* shows a similar spatulate expansion on one end, and in fact has first been interpreted as interclavicle (Cooper 1981). Although Sereno (1991) and Yates & Vasconcelos (2005) mention its high similarity to the supposed clavicles in both *Plateosaurus* and other specimens of *Massospondylus*, Vickaryous & Hall (2010) point out that also interclavicles in some cases can consist of two single, but symmetrical elements. The two differing orientations of the spatulate end in some of the bones, as well as the deep slot-like concavity

in two SMA elements could then be explained as individual variation or taxonomic diversity. A high variability in the shape of this bone was already recognized by Kälin (1929).

Morphotype B

Description. The bones of morphotype B are L-shaped and have a D- to crescentic shaped outline in cross section at midlength (Figs 4 and 5). 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 (see Figs 4 and 5). Towards the tip of the short leg, the bone curves externally. In one of the AMNH elements, it develops a conspicuous ridge, and the tip is very rugose. In its counterpart, this end is broken off. This portion shows a similar but stronger striated rugosity as in the longer leg of the L. At about midlength of the shorter leg of the L there is a thickened portion resembling an articulation facet on the SMA specimens (the AMNH elements show broken edges in this region).

Discussion. Recently, Galiano & Albersdörfer (2010) reported a diplodocid specimen (DQ-SB) found near Tensleep, Wyoming, with two symmetric, paired bones articulated between the two scapulacoracoids, where clavicles are supposed to attach. These bones are very dissimilar from any of the previously described supposed clavicles (morphotype A). Infact, they are L-shaped and do not show any bifurcation on either end of the element and thus appear to belong to morphotype B. Also a second, probably juvenile, specimen reported by Galiano & Albersdörfer (2010; DQ-TY) exhibits a single bone of similar shape. Other morphotype B elements were recovered partly on top of the left scapula of the early juvenile sauropod SMA 0009 (Schwarz et al. 2007b), as well as on top of its right coracoid (Fig. 6). This was described as a “dorsally pointing tip” of the coracoid in Schwarz et al. (2007b), but close examination of the specimen indicates that it was taphonomically pressed onto the coracoid. Based on these findings, morphotype B fits an identification as clavicles better than morphotype A. Such an interpretation would also match previous findings in ceratopsian dinosaurs (Chinnery & Weishampel 1998: fig. 6, Vickaryous & Hall 2010: fig. 5). On the other hand, paired finds of basal sauropodomorph clavicles appear to be more straight (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. The presence of bones resembling both of these morphotypes in the holotype of *Spinophorosaurus nigerensis* provides more information on the validity of this assignment. The somewhat L-shaped elements appear to be of considerably different sizes, and were interpreted to represent tail spikes, due to some superficial alikeness to supposed *Shunosaurus* spikes found associated with the tail club (Remes et al. 2009; R. Kosma and A. Ritter, pers. comm., 2011). However, based on the pictures of the *Shunosaurus* tail spikes provided by Zhang (1988), the *Spinophorosaurus* elements resemble much more the L-shaped bones found at the Howe Quarry. Their base (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. The only adaptations seen in the tail to support the bearing of such spikes are specialized posterior chevrons that interconnect among themselves to build a ventral rod supporting the caudal column from below (Remes et al. 2009; pers. obs.). Given that these elements were found below the dislocated scapula, close to the pelvic region of the skeleton (Remes et al. 2009), an interpretation as sternal ribs (but also as clavicles) seems more probable.

Whereas an identification of the morphotype B elements as sternal ribs would not challenge Hatcher's (1901, 1903) interpretation of the morphotype A bones as clavicles, the herein purported case of morphotype B being the true clavicles does. 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. The question thus arises what the morphotype A elements are. Two possibilities seem reasonable: either these rod-like, curved bones are sternal ribs, as proposed by Holland (1906), or they represent interclavicles, as already stated above. For unknown reasons, Holland's (1906) interpretation that they might be sternal ribs has never been mentioned afterwards. In favor of this designation are the irregular shape of some of the morphotype A elements, and the fact that also the symmetrical bones exhibit some morphological differences (although these can probably in parts be explained by pre- or postburial taphonomic reasons). However, even though one of the proposed sternal ribs of *Apatosaurus excelsus* YPM 1980 is elongated and relatively stout, it is also straight, and bears various knob-like tuberosities along its entire length (Marsh 1896) - rather resembling morphotype E than the usually strongly curved, and smooth bones belonging to morphotype A. Furthermore, compared to articulated sternal ribs of pterosaurs or crocodiles, they seem too massive (Claessens et al. 2009; pers. obs.). Their association with the scapulacoracoid in

many of the specimens where they were found, would imply an anterior position within the sternal apparatus, but the elongated shape would rather fit to a more posterior assignment. An interpretation of the morphotype A elements as interclavicles seems thus the most probable.

Morphotypes C, D, and E

Description. The morphotype C elements are elongated, rod-like bones with a suboval cross section (Fig. 7). The smooth shafts are generally slightly curved, in some elements (e.g. D 28-6, D 28-7) in two directions forming a weak S-shape. Few bones remain straight during their entire length. Both ends are rugose and irregular. One end is flattened and in certain cases shows a differing degree of rugosity on the two sides of the flattened portion. Toward the opposite ends some of the elements remain straight, whereas others curve in a way that this end points more straightly outwards, rather than outwards and upwards.

Morphotype D elements are less frequent. They are more irregularly formed, shorter and thicker (Fig. 8). One end is similarly flattened as in the rod-like gastralia, but more irregularly expanded and shows better developed 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. Certain elements in the M 21-basket (e.g. M 21-8; Fig. 8C) appear to be fused symmetric elements. They reproduce the slight upward curvature of two articulated opposing elements similar to the pair 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).

Four elements in the SMA collection (field numbers H 21-1, H 21-3, M 21-15, N 22-12) do exhibit peculiar shapes and are included in morphotype E. H 21-1 and H 21-3 develop a projection approximately at one third to two fifth of their entire length, which appears to proceed at an acute angle to the longer portion of the bone (Fig. 9A). 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 to the usual gastralia/sternal ribs. Both ends are flattened, one of them is markedly and slightly asymmetrically bifurcated (Fig. 9C). 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 slight 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 center of the bone towards the outer margins on both sides (Fig. 10B). 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.

Discussion. Probable sauropod gastralia and/or sternal ribs have been reported more often than clavicles, and in a wider range of taxa (Tab. 2). As mentioned above, their interpretation as gastralia has been challenged by Claessens (2004) pointing out their anatomical differences compared to basal sauropodomorph or theropod gastralia. Claessens (2004) proposes that Marsh (1896) was right in identifying such elements as sternal ribs. These structures are present in both extant birds and crocodiles, but remain often cartilaginous (Claessens 2004; Claessens et al. 2009; R. Fechner, 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 cartilaginous intercostal elements (Claessens et al. 2009; R. Fechner, 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). The herein described elements provide more information for the proper identification of the morphotypes C to E. The relatively well-articulated clusters SMA D28 and M21 contain approximately 15 bones. For a bird-like sternal rib configuration, 15 elements appear 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 represent free ribs. Fully articulated ribcages of *Apatosaurus* and *Diplodocus* show transversely expanded ends only in the first 5 to 7 dorsal ribs (Gilmore 1936; Schwarz et al. 2007a) - which would allow a maximum number of 14 sternal ribs. Considering a crocodilian arrangement, morphotype E elements (like the particularly shaped SMA N 22-12, and maybe also the short elements described by Filla & Redman 1994: fig. 11 H, 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: fig. 12 and 13) resemble somewhat the posterior sternal ribs in the pterosaur *Rhamphorhynchus* (Claessens et al. 2009: fig. 2d).

None of the bones of any morphotype exhibit the typical longitudinal articulation facets that occur between the medial and lateral elements of theropod or sauropodomorph gastralia. Furthermore, given that a complete gastral basket consists of four elements per row, the recovered 15 elements seem too few (Claessens 2004 reports 8 to 21 rows, which would add up to 32 to 84 single gastralia). However, in particular the morphotype D elements fit an identification as gastralia more than as sternal ribs. Bones like M 21-8 (Fig. 8C), which seem to be composed of two fused elements like D 28-5 or M 21-2 (Figs 8A or B, respectively), have no equivalent in previously described sternal ribs known to us. Sternal ribs sometimes connect to other, more anteriorly placed bones (Galton & Jensen 1973; Clark et al. 1999; Claessens et al. 2009), but no specimen has been reported to date exhibiting fused left and right elements. Moreover, 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 basal sauropomorphs and theropods (Fig. 10). Median gastralia of the anteriormost 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 elements. Given this, a definitive assignment of morphotypes C to E remains difficult at the moment. The herein described bones indicate that both gastral and sternal ribs might be present in diplodocids, with morphotypes C and E rather representing sternal ribs (and/or intercostal elements), and morphotype D being gastralia. This would explain the number of elements, which is too high for being solely sternal ribs, as proposed by Claessens (2004). Morphotype D could then represent the anteriormost gastralia, which are close to the sternal apparatus, and more posterior bones, as well as the lateral gastral elements could have been retained cartilaginous. A novel reconstruction taking these interpretations into account is shown in figure 11.

As gastral and sternal ribs have differing developmental origins (see Table 1), a histological analysis might yield some more results, but should include elements of all the herein defined morphotypes. However, histologic sections of dermal and endochondral bones are difficult to distinguish (T. Scheyer, pers. comm., 2009). Such a study has thus to await further analyzes and comparisons of known gastralia and sternal ribs in extant animals, and lies outside the scope of this paper.

Phylogenetical and Functional Implications

Although the identification of these elements remains unclear, their presence has both phylogenetical and functional implications. Their almost exclusive presence in non-neosauropod Eusauropoda, and in Flagellicaudata indicates that these sauropod taxa might

retain a higher potential to ossify these structures. The single findings of a gastral or sternal rib in *Camarasaurus* and the lithostrotian *Diamantinasaurus* (Osborn & Mook 1921; Hocknull et al. 2009) remain doubtful, or might represent an exception to the rule. The DNM specimens mentioned by Claessens (2004; see Table 2) were never described nor figured properly, and it remains thus unclear if they really belong to *Camarasaurus*, especially since the DNM is a multi-taxon assemblage including various diplodocids as well. Therefore, the loss of ossified clavicles, interclavicles, sternal and/or gastral ribs might result a synapomorphy for Macronaria, and maybe Rebbachisauridae as well. The fact that Hocknull et al. (2009) only mention gastral rib fragments of *Diamantinasaurus*, but neither figure nor describe them, makes it difficult to interpret their presence in this taxon. Taking for granted that their interpretation is right, it might be a diagnostic character of the genus, distinguishing it from other titanosaurs. On the other hand, due to the fact that only one specimen of this taxon is known to science to date, intraspecific variation can not yet be excluded in this case. The presence of the rod-like, curved elements here identified as interclavicles in various taxa on the evolutionary lineage from basal archosaurs to the neosauropod taxon Diplodocidae, implies that neither interclavicle nor clavicles were lost during the evolution of dinosaurs (contra Sereno 1991; Novas 1996; Remes 2008). Instead, they might have been retained cartilaginous in some taxa (see Vickaryous & Hall 2010 as well).

The herein purported identification of the morphotype A elements as interclavicles would be the first report of this bone in dinosaurs. It thus gives further support to Vickaryous and Hall's (2010) hypothesis that the theropod and avian furcula might actually be homologous to the interclavicle, and not represent fused clavicles as generally suggested (Yates & Vasconcelos 2005; Nesbitt et al. 2009). As stated by Vickaryous and Hall (2010), both the furcula and the interclavicle are dermal elements developing from two ossification centers, lie on the body midline, do not coexist in any organism, and share common ancestry (see also Kälin 1929; Rieppel 1993). Furthermore, both the reptilian interclavicula, as well as the avian furcula usually have a triradiate shape: the interclavicula has an elongate, central main body, and on the anterior end laterally expanding transverse processes (reduced in the sauropod interclavicles described herein), the furcula shows two transversely expanding epicleidia, and a ventroposteriorly projecting hypocleidium of varying lengths at its center, on the body midline. However, the interclavicle of crocodyles appears to initiate its ossification medially and fuse rapidly (Kälin 1929), while the furcula, as well as clavicles in marsupial mammals, begin to ossify at their lateral ends, proceeding medially (Hall 1986; Klima 1987). Even though this might indicate a clavicular rather than an interclavicular origin for the furcula, no

embryological studies have been published to date showing a definitive correlation between the spacing of the ossification centers and their embryological origin (M. Vickaryous, pers. comm., 2012). On the contrary, the homology of mammalian clavicles and the avian furcula has recently been questioned: unlike the furcula, mammalian clavicles develop from two ossification centers per element, and show a combination of endochondral and intramembraneous bone formation (Hall 2001). The interclavicle of monotreme mammals, on the other hand, develops from two dermal ossification centers close to the body midline, which finally unites with a third, singular, chondral element (Klima 1987). Furthermore, some researchers reported a membranous structure in both birds and crocodiles, at the position where mammals or more basal reptiles ossify their clavicles (Götte 1877; Hoffmann 1879; Kälin 1929). Kälin (1929) rejected an interpretation of these structures as reduced clavicles based on the assumption that the furcula represents the fused clavicles, and because therefore, the same element can not be present two times in the same individual. However, the presence of this membrane can also be taken as additional evidence that the furcula actually derives from the reptilian interclavicle.

The strongest evidence against this hypothesis is the pair of chest elements found in *Massospondylus* (Yates & Vasconcelos 2005). In this taxon, Yates & Vasconcelos (2005) report two symmetrical bones that articulate with the scapular acromion laterally, and with themselves medially. In articulation they resemble much the theropod furcula, and therefore Nesbitt et al. (2009) interpreted them as an intermediate evolutionary state between unfused reptilian clavicles and the theropod furcula. However, as Vickaryous & Hall (2010) state, unfused furculae are also present in some extant birds, whereas no case of fused clavicles is reported by any embryological study on mammalian or reptilian pectoral girdles. In order to satisfactorily confirm a clavicular derivation of the furcula, detailed embryological studies on reptilian claviculae are needed, which should show a differential development compared to mammalian clavicles (one ossification center per bone, no inclusion of chondral portions). If, on the contrary, the results would concur with the mammalian clavicular development, the herein supported hypothesis of Vickaryous & Hall (2010) that the furcula derives from the reptilian interclavicle would be definitely confirmed. The evolutionary pathway in the formation of the furcula would then go from the diamond-shaped interclavicles of early tetrapods, to elongated forms with transverse processes, which would get better developed in theropods, while the stem-like central body becomes reduced to the hypocleidium. In sauropods and crocodilians, on the other hand, the transverse processes got reduced to small bifid ends, or were even lost (Fig. 12). A more detailed assessment of morphological changes from the archosaur interclavicle to the theropod furcula is hampered due to the rare and

incomplete finds of basal dinosaurs, and especially saurischians (Nesbitt et al. 2009; Vickaryous & Hall 2010).

In any case, contrary to recent phylogenetic analyses that recovered the absence of interclavicles as synapomorphy for Dinosauria (e.g. Sereno 1991; Nesbitt 2011), both interclavicles and clavicles appear to be present plesiomorphically in the Dinosauria. Interclavicles would then have gotten lost in Ornithischia, and clavicles in Theropoda. However, the fact that sauropodomorphs preserve both clavicles and interclavicles, delimits conclusive implications on the homology of the furcula. In any respect, if the interclavicular origin of the furcula is confirmed in opposition to a fused clavicle origin, this will change the anatomy textbooks of theropod evolution and the origin of birds in which furculae (fused clavicles) have been seen as one of the keystones of the theropodian origin of birds.

An ossification of such a variety of chest elements does obviously also have functional implications. It stabilizes the entire pectoral girdle, the sternal apparatus, and in case of ossified gastralia also the rest of the trunk. Movements become thus more restricted. So has the presence of furculae in theropods already been interpreted as inhibiting quadrupedal locomotion (Hohn-Schulte 2010). The taxa exhibiting such an extended ossification usually have either an elongated cervical (e.g. mamenchisaurs) or caudal vertebral series (e.g. dicraeosaurs), or even both (diplodocids). Lateral movements of such long appendages might request a firm trunk in order to not disequilibrate the entire 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. As the ossification of otherwise cartilaginous elements and the development of dermal bones often follows such areas of higher stress (Haines 1969; Schwarz et al. 2007a), the presence of osseous interclavicles, clavicles, and gastralia and/or sternal ribs might be explained like this. Furthermore, a posteriorly located center of mass, as present especially in diplodocids, appears to induce important lateral stresses to the pectoral girdle during locomotion (Sander et al. 2011). A greater degree of ossification would thus also help to cope with these loads. However, some taxa do not entirely fit this interpretation: *Shunosaurus*, *Jobaria*, *Spinophorosaurus*, as well as *Gongxianosaurus* probably do not exhibit considerably elongated necks or tails (Zhang 1988; He et al. 1998; Sereno et al. 1999; Remes et al. 2009). Whereas *Gongxianosaurus* as very basal sauropod might simply have retained the basal sauropodomorph gastralia (neither clavicles nor interclavicles were reported from this taxon, and the description and figures in He et al. 1998 do not suffice to attribute them to the either basal sauropodomorph or advanced sauropod morphotypes), *Shunosaurus* bore a distal tail club, which probably served as weapon (Zhang 1988). This implies that this taxon used its tail often for lateral swinging,

and *Shunosaurus* might therefore have experienced the same evolutionary pressure as the long-tailed Flagellicaudata. If the identification by Remes et al. (2009) of the L-shaped bones as tail spikes in *Spinophorosaurus* holds, the same reasoning for ossified chest bones might apply in this taxon (although in this case, only an interclavicle would appear to have been present). However, the alleged tail-spikes in *Spinophorosaurus* are slender and do not bear the typical osteoderm surface rugosity as seen in thyreophorans and sauropods, neither the spike-shape or club expected to be found as a defensive tail structure. Furthermore, obviously broken edges of the preserved elements shed some doubt on them being of considerably different size as described by Remes et al. (2009). Therefore, these bones are also seen here as clavicles. As a detailed description of the remains of *Jobaria* is still missing, an evaluation of the functional implications of an ossification of the herein reviewed elements remains difficult.

The occurrence of ossified chest bones also coincides with the evolution of the particular wide-gauge locomotor style of macronarian sauropods, which probably initiates with *Camarasaurus* (Wilson & Carrano 1999; Carrano 2005; Tschopp & Brinkmann, in review). The loss of these elements might thus have allowed a wider spacing of the pectoral girdle, thereby allowing the development of this particular locomotion pattern.

Conclusions

Several elements recovered at the Howe Quarry (Bighorn County, Wyoming) 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, might actually be interclavicles, with the new, L-shaped pairs being the true claviculae. 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 Macronaria as well as 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.

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Tables

Table 1: Bones present in the chest regions of tetrapods.

	Embryological origin (dermal / endochondral)	Phylogenetic bracket	Bone connection	Previously identified in Sauropoda	General shape and distinction	Paired/single. Number
Clavicles	Dermal bone	Basal Sauropodomorpha: present Birds/Theropoda: fused to form furcula (?) Crocodylia: absent Basal Archosauria: present	Dorsal to coracoids (covering it sometimes), between cleithrum, scapula, and interclavicle in basal reptiles	Yes	Curved element	Paired, can fuse into one (furcula, questioned herein). One pair present
Interclavicles	Dermal bone	Basal Sauropodomorpha: ? Birds/Theropoda: = furcula? Crocodylia: present Basal Archosauria: present	Between the clavicles. Connects to the coracoid and/or sternal plates posteriorly	No	Variable. Diamond shaped in early tetrapods, rod-like with or without transverse processes in crocodylians and lacertilians	Single (very rarely paired). Only one present
Sternal Ribs	Endochondral	Basal Sauropodomorpha: absent? Birds/Theropoda: present Crocodylia: present Basal Archosauria: present	Connects the sternal plates with the dorsal ribs or intercostal elements	Yes	Irregularly shaped, often rugose	Paired. Maximum one per dorsal rib, often less
Intercostal elements	Endochondral	Basal Sauropodomorpha: absent Birds/Theropoda: absent Crocodylia: present: Basal Archosauria: present	Connects sternal ribs with dorsal ribs	No	Irregularly shaped, often rugose	Paired. Maximum one per dorsal rib, often less
Gastralium	Dermal bone	Basal Sauropodomorphs: present Birds/Theropoda: present Crocodylia: present Basal Archosauria: present	Articulate among themselves and through cartilage to dorsal ribs, as well as maybe the sternal apparatus	Yes	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
Cleithrum	Dermal bone	Basal Sauropodomorphs: absent Birds/Theropoda: absent Crocodylia: absent Basal Archosauria: absent	Capping scapulacoracoid, attaches to clavicles	No	Spoon-shaped	Paired. Only one pair present
Sternal plates	Endochondral	Basal Sauropodomorphs: present Birds/Theropoda: present Crocodylia: present Basal Archosauria: present	Articulate among themselves, sternal ribs attached to them, sometimes touching the interclavicle anteriorly	Yes	Shield-like: flat oval or reniform	Paired or single. One single or two mirrored elements
Scapulacoracoid	Endochondral	Basal Sauropodomorphs: present Birds/Theropoda: present Crocodylia: present Basal Archosauria: present	Dorsal and external to sternal apparatus, connected medially by cleithrum, clavicles, and interclavicle	Yes	Large, flat, subcircular acromion with a elongate, more narrow posterodorsal projection	Paired. One pair present

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	*Diplodocus carnegii*	Hatcher 1901, 1903; Nopsca 1905; Holland 1906; McIntosh 1981	clavicle	
	HMNS 175 (= CM 662)	*Diplodocus hayi*	Hatcher 1903; Nopsca 1905; Holland 1906	clavicle	stored at CM
	?	*Mamenchisaurus sp.*	Dong et al. 1983	clavicle	
	?	*Omeisaurus junghsiensis*	Dong et al. 1983	clavicle	three elements mentioned
	IVPP V7262	*Datousaurus bashanensis*	Dong & Tang 1984	clavicle	
	IVPP V7263	*Datousaurus bashanensis*	Dong & Tang 1984	clavicle	
	T5704	*Omeisaurus tianfuensis*	He et al. 1988	clavicle	
	T5401	*Shunosaurus lii*	Zhang 1988	clavicle	
	ANS 21122	*Suuwassea emilieae*	Harris 2007	clavicle	
	NMB-1698-R	*Spinophorosaurus nigerensis*	Remes et al. 2009	clavicle	
	AMNH 30900	?diplodocid	this study	interclavicle	
	SMA I 24-4	?diplodocid	this study	interclavicle	
	SMA L 22-3	?diplodocid	this study	interclavicle	
	SMA L 27-7	?diplodocid	this study	interclavicle	
	SMA M 25-3	?diplodocid	this study	interclavicle	
Morphotype B	SMA 0009	?brachiosaurid	Schwarz et al. 2007b, this study	possible furcula	pair recovered
	GCP-CV 4229	*Spinophorosaurus nigerensis*	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	
	SMA K 24-3 & 6	?diplodocid	this study	clavicle	pair recovered
	AMNH 30789	?diplodocid	this study	clavicle	pair recovered
Morphotype C	AMNH 5760/5761	*Camarasaurus supremus*	Osborn & Mook 1921	sternal/ventral rib	single element
	Tate 001	*Eobrontosaurus yahnahpin*	Filla & Redman 1994	gastralia	almost complete set including morphotype E as well
	AMNH 30901	?diplodocid	this study	?sternal rib	
	SMA ?	?diplodocid	this study	?sternal rib	various unnumbered elements
	SMA C 17-5	?diplodocid	this study	?sternal rib	
	SMA D 28-6 to 11	?diplodocid	this study	?sternal rib	part of D 28-cluster
	SMA D 28-18 to 19	?diplodocid	this study	?sternal rib	part of D 28-cluster
	SMA E 19-9	?diplodocid	this study	?sternal rib	
	SMA E 21-2 to 3	?diplodocid	this study	?sternal rib	
	SMA F 19-10	?diplodocid	this study	?sternal rib	
	SMA F 19-21	?diplodocid	this study	?sternal rib	
	SMA F 20-9	?diplodocid	this study	?sternal rib	
	SMA F 27-16 to 17	?diplodocid	this study	?sternal rib	part of F 27-cluster
	SMA F 27-33 to 35	?diplodocid	this study	?sternal rib	part of F 27-cluster
	SMA G 21-2	?diplodocid	this study	?sternal rib	
	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	probably part of F 27-cluster
	SMA H 20-7	?diplodocid	this study	?sternal rib	
	SMA H 21-2	?diplodocid	this study	?sternal rib	
	SMA H 21-5	?diplodocid	this study	?sternal rib	bears a foramen
	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	part of M 21-cluster
	SMA N 22-2	?diplodocid	this study	?sternal rib	probably part of M 21-cluster
	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	
Morphotype D	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	
	SMA M 21-2	?diplodocid	this study	gastralia	part of M 21-cluster
	SMA M 21-8	?diplodocid	this study	gastralia	part of M 21-cluster, fused element
	SMA M 21-16	?diplodocid	this study	gastralia	part of M 21-cluster, fused element
	SMA N 21-3	?diplodocid	this study	gastralia	probably part of M 21-cluster
Morphotype E	YPM 1980	*Apatosaurus excelsus*	Marsh 1883, 1896	sternal ribs	several elements
	Tate 001	*Eobrontosaurus yahnahpin*	Filla & Redman 1994	gastralia	almost complete set including morphotype C as well
	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
unknown	?CM 3018	*?Apatosaurus louisae*	Holland 1915	sternal ribs	several elements, not described/figured
	?	*Gongxianosaurus shibeiensis*	He et al. 1998	gastralia	several elements, not described, inadequately figured
	?	*Jobaria tiguidensis*	Sereno et al. 1999	clavicle	not described, inadequately figured
	?	*Jobaria tiguidensis*	Sereno et al. 1999	gastralia	several elements, not described/figured
	DNM ?	*?Camarasaurus*	Claessens 2004	sternal ribs	several elements in the wall, not described/figured, possibly the same as the ones mentioned by Holland 1915?
	AODF 603	*Diamantinasaurus matildae*	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	*Diplodocus carnegii*	Denver Museum Database	clavicle	not described/figured; probably morphotype A

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

Specimen	AMNH fd226	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

Asterices indicate incomplete measurements due to fractures, empty cells were measurements impossible to obtain.

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Figure captions

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.

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

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.

Fig. 4: 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: Morphotype B elements AMNH 30789 in internal (A) and external (B) view. Scale bar = 10 cm.

Fig. 6: Coracoid with taphonomically attached morphotype B element (MB) of the possible diplodocid SMA 0009 in posteroventral (A) and lateral (B) view. Arrows indicate brightly colored matrix present between the MB and the coracoid. GL, glenoid surface; CF, coracoid foramen. Scale bar = 2 cm.

Fig. 7: 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.

Fig. 8: 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.

Fig. 9: 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 assignation to any other morphotype. Dotted lines in A indicate direction of the broken hook-like projection. Scale bar = 10 cm.

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 center, 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.

Fig. 11: Reconstruction of the pectoral girdle and the chest region of an indeterminate diplodocid sauropod, based on the finds reported. **Light grey elements represent pectoral**

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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).

Fig. 12: Evolution of the furcular shape, based on an interclavicular origin. Note the basically triradiate shape of the elements within Amniota. Line drawings scaled to same size. Sources: Temnospondylia, *Aphanerama* (Steyer et al. 2000); Monotremata, *Ornithorhynchus* (Klima 1987); Lepidosauria, *Basiliscus* (Vickaryous & Hall 2010); Crocodylomorpha, *Alligator* (Vickaryous & Hall 2010); Sauropoda, Diplodocinae indet. (this study); Aves, *Gallus* (Vickaryous & Hall 2010).

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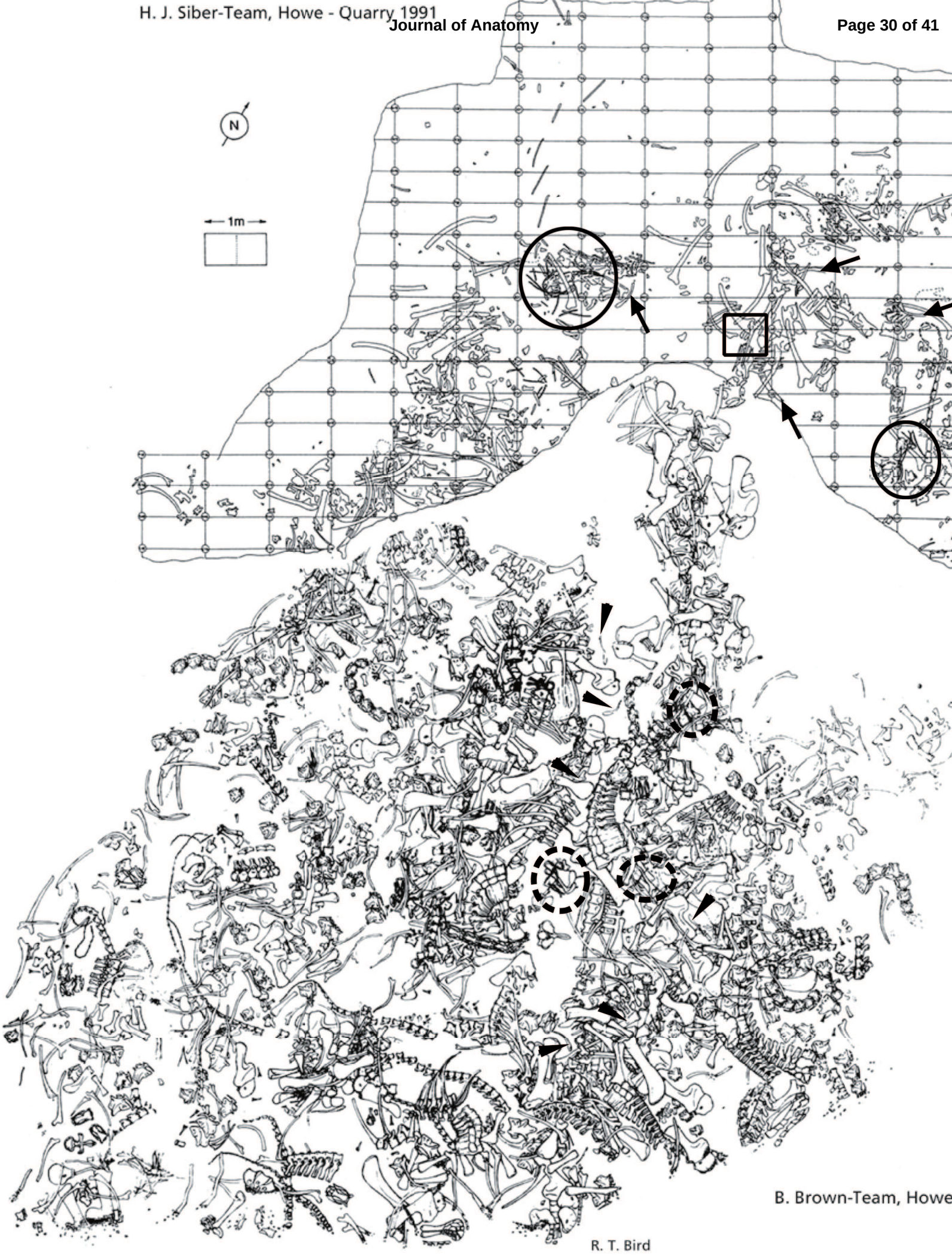
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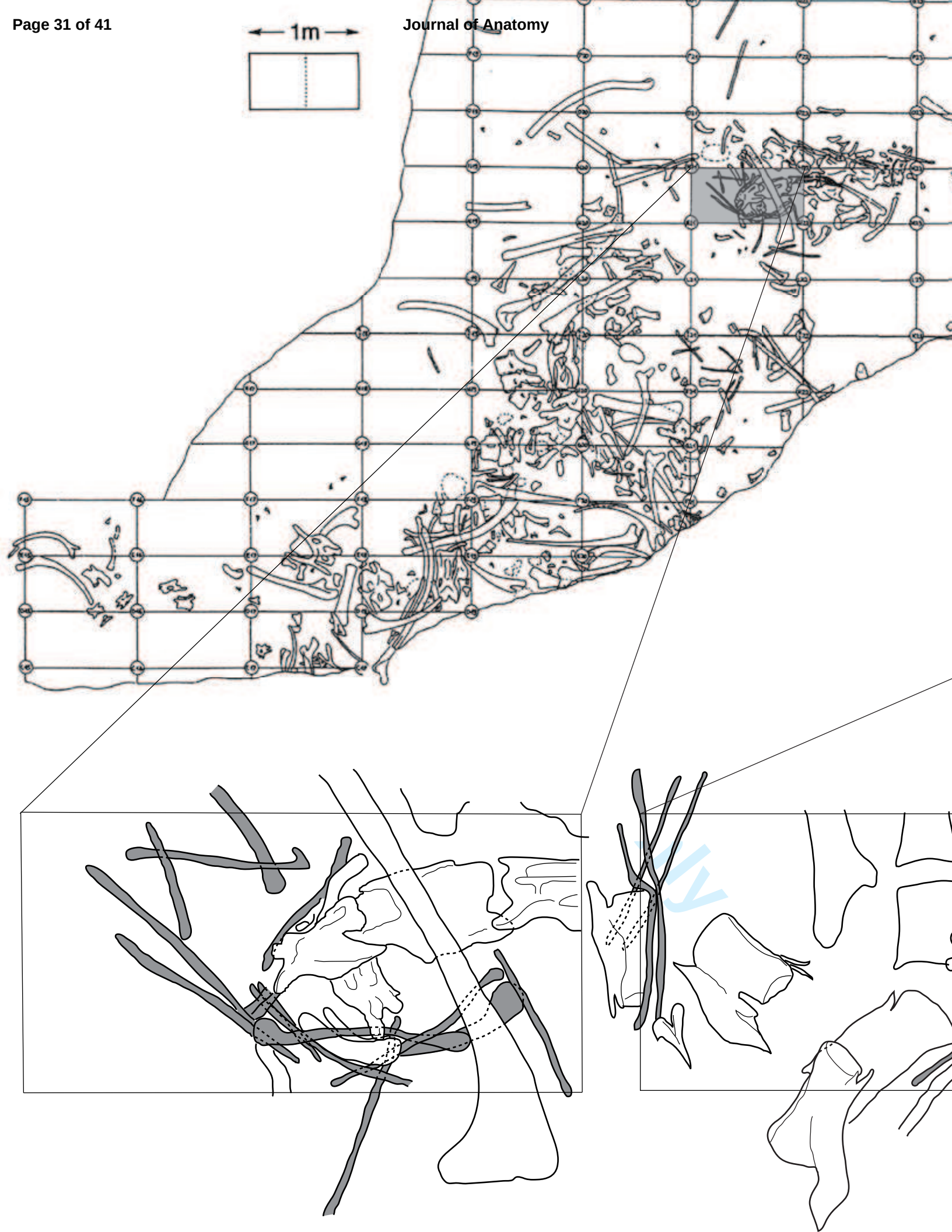
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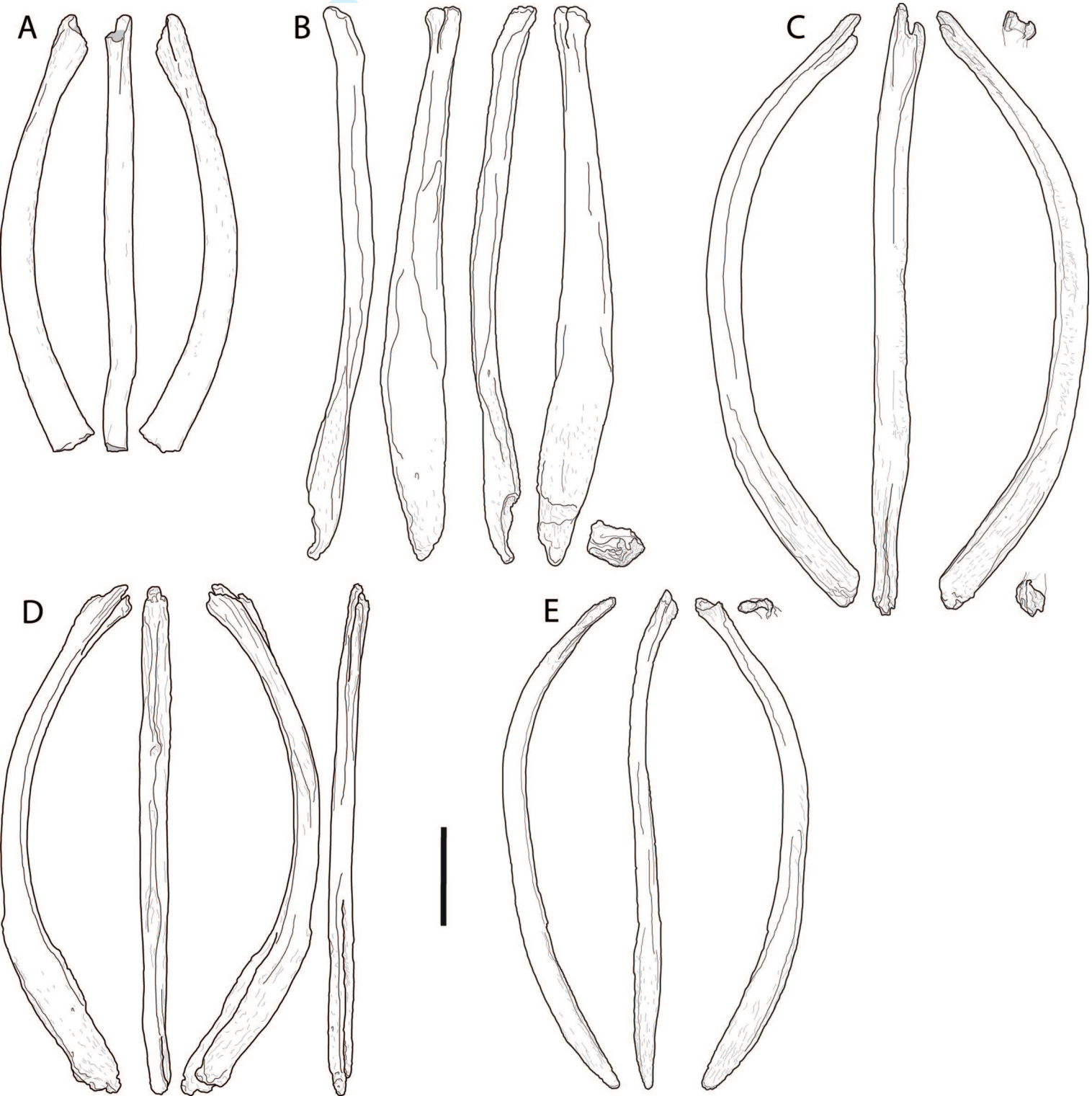
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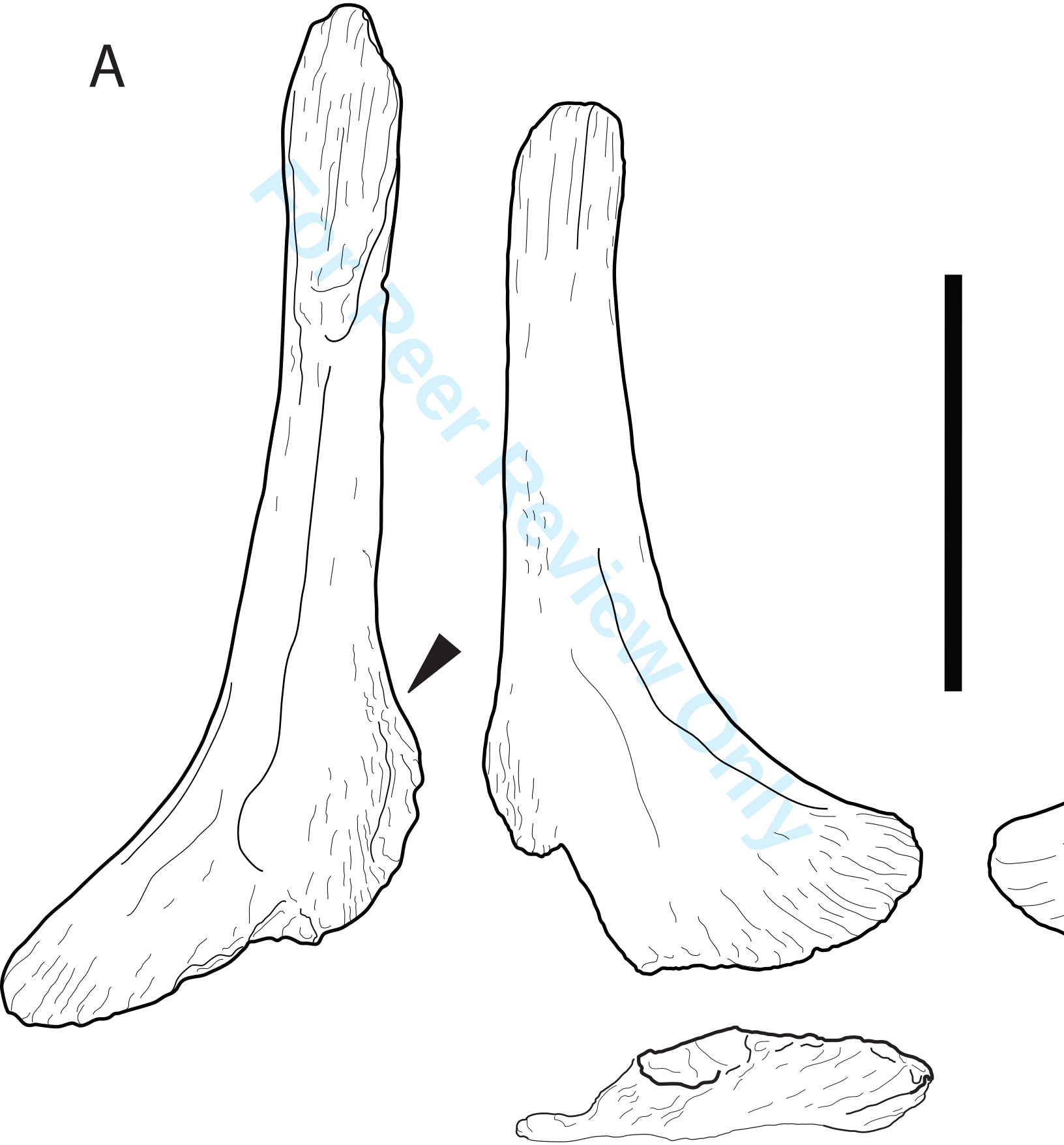

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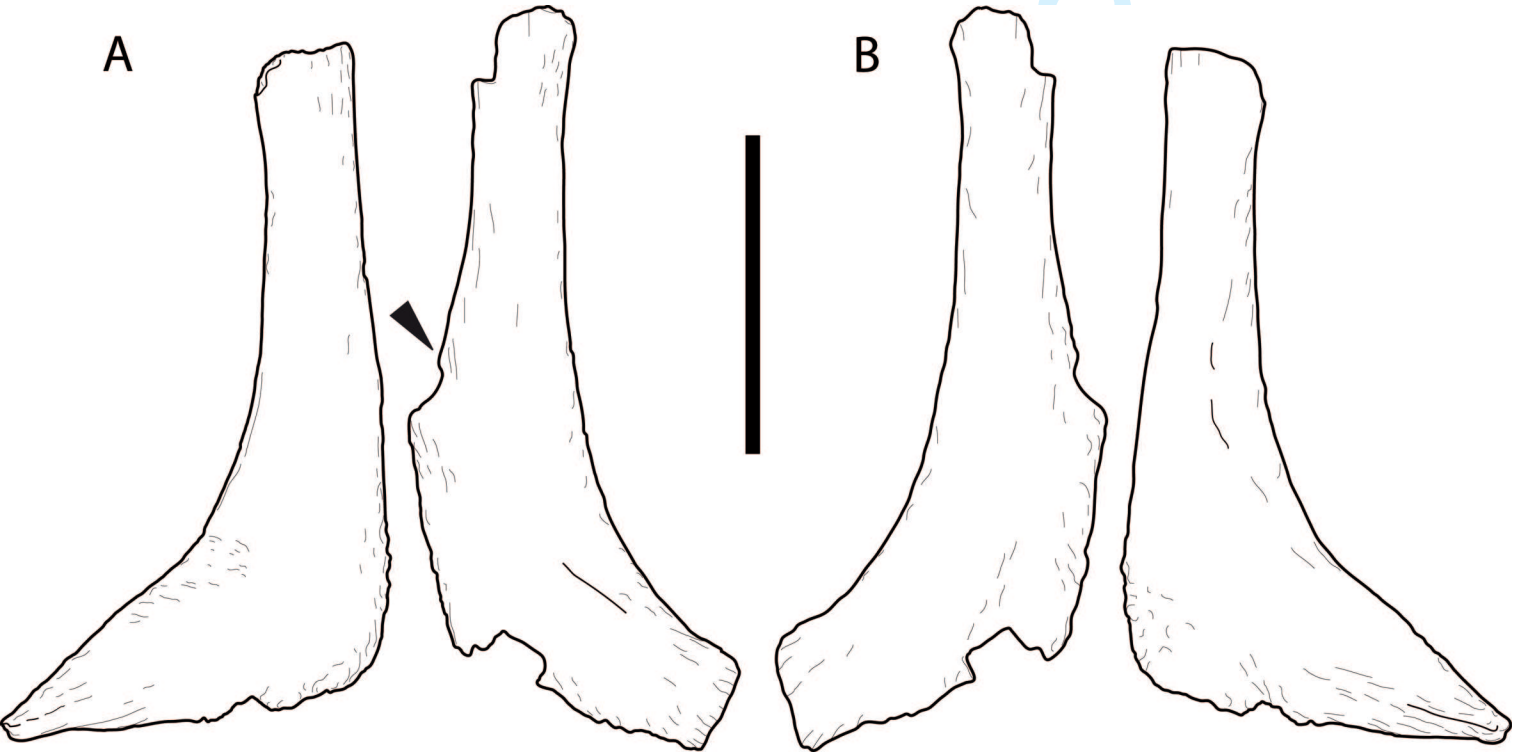

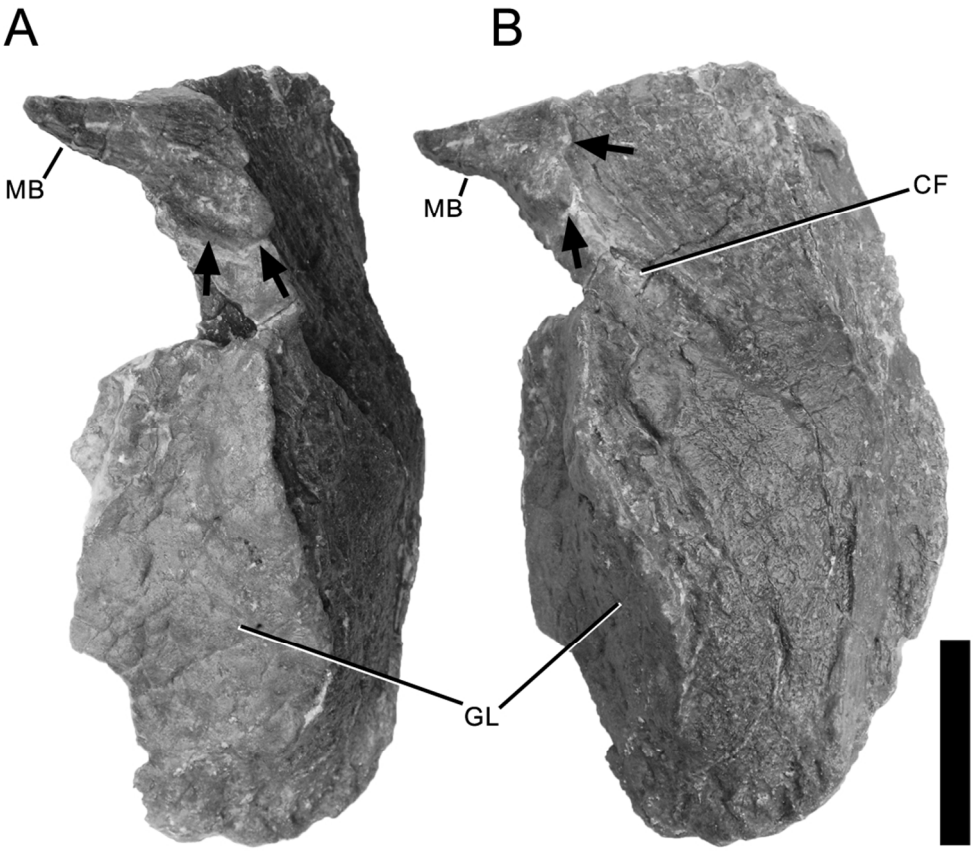

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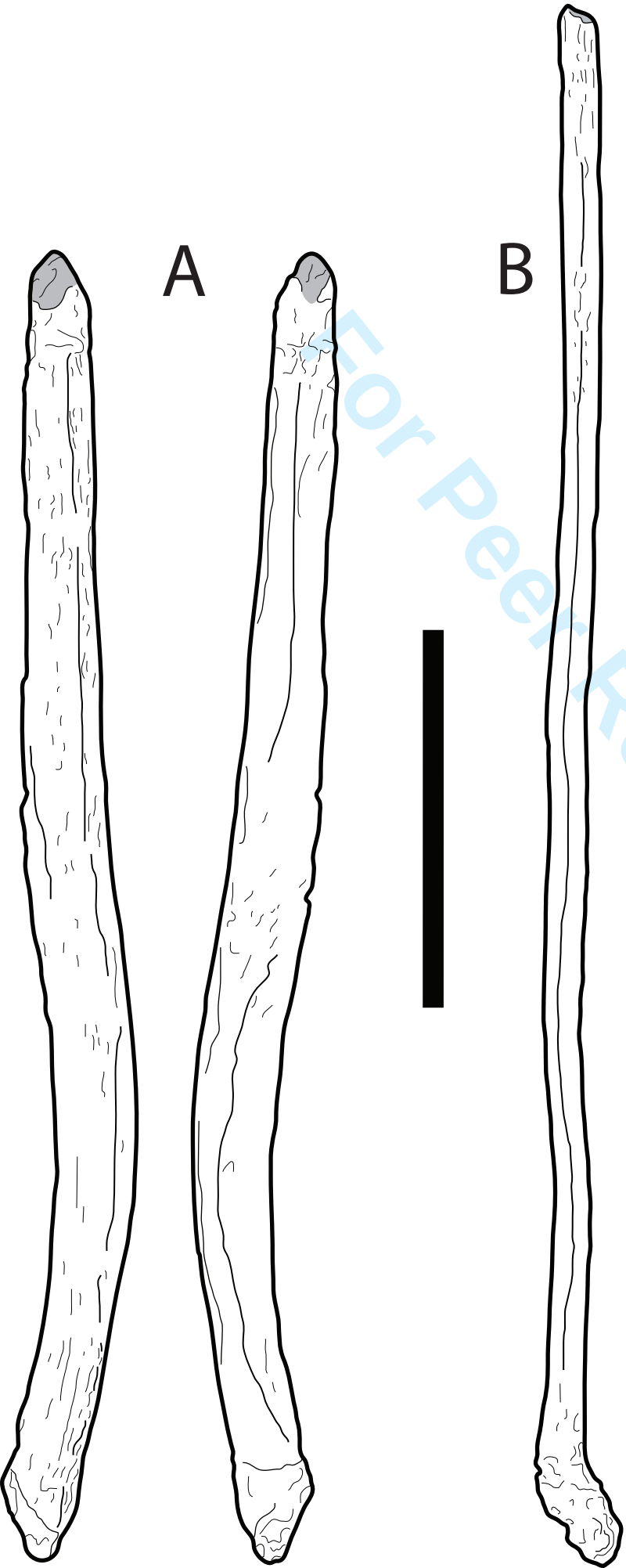

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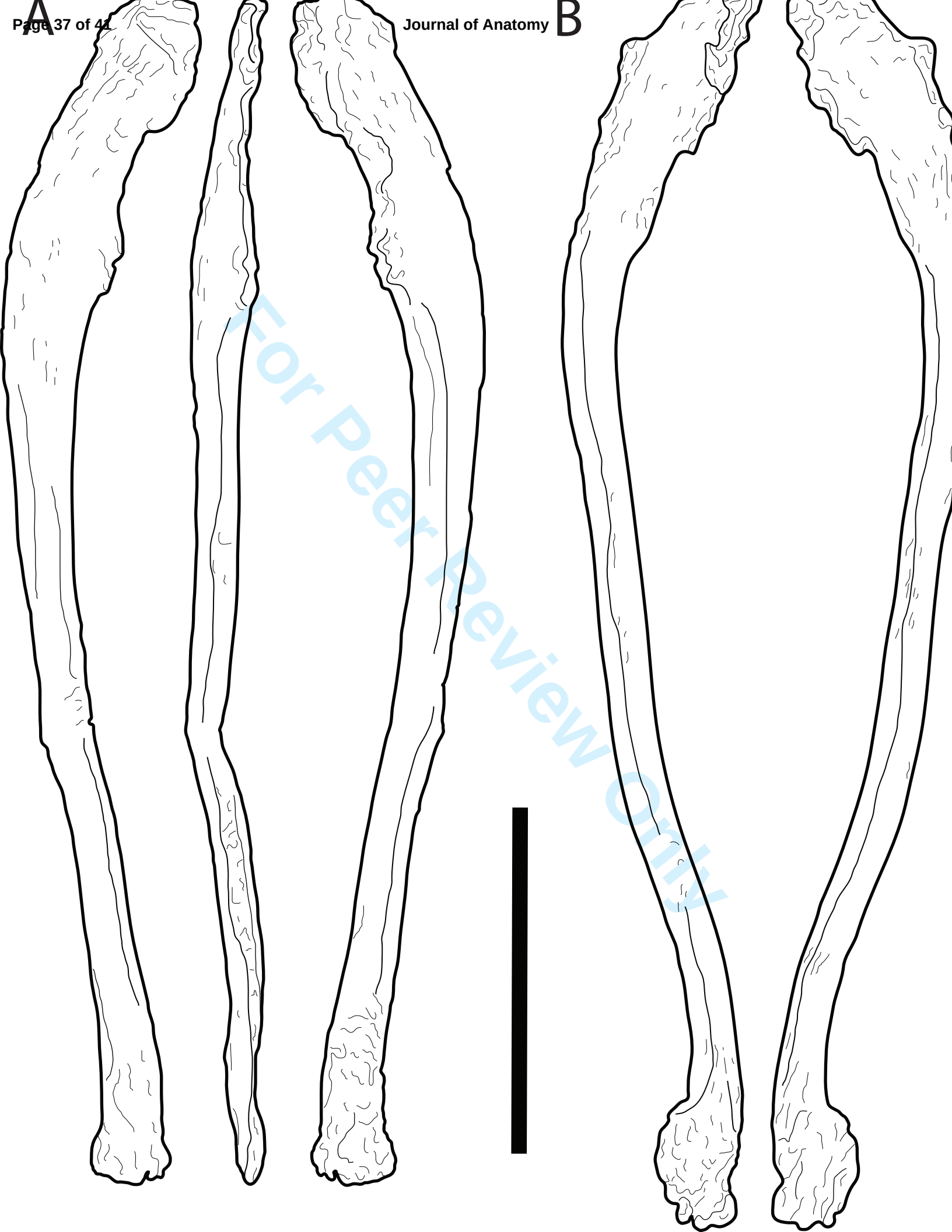

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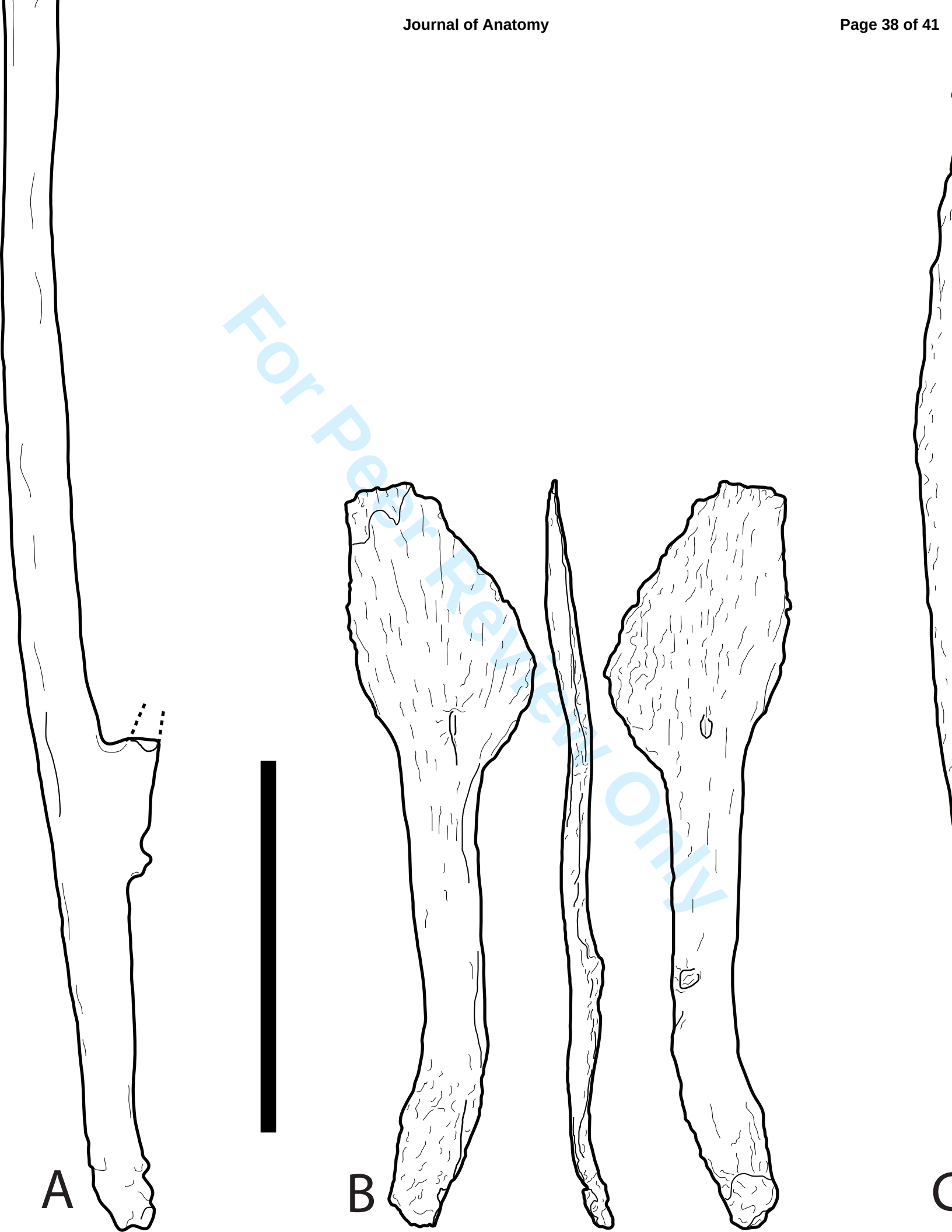

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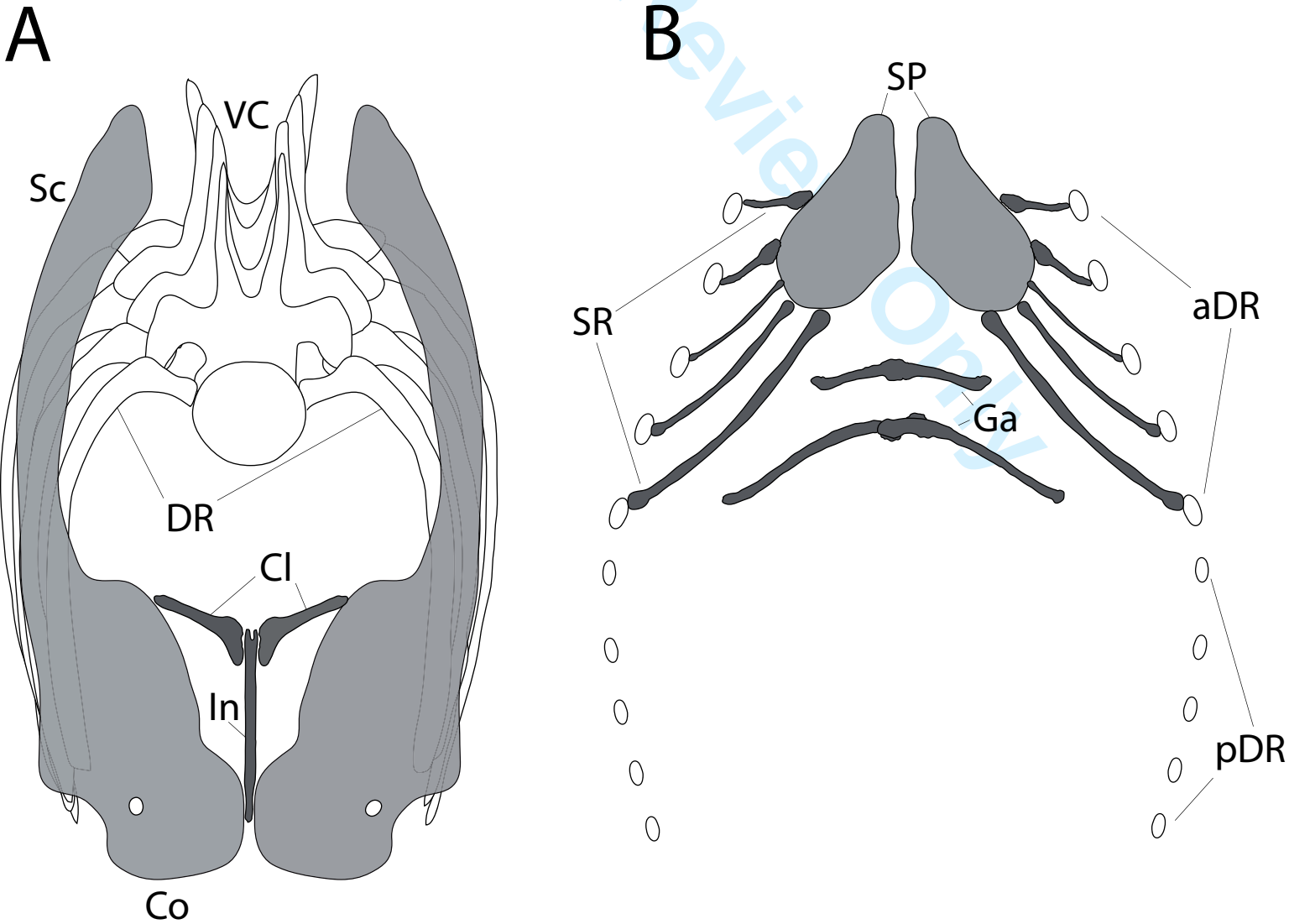

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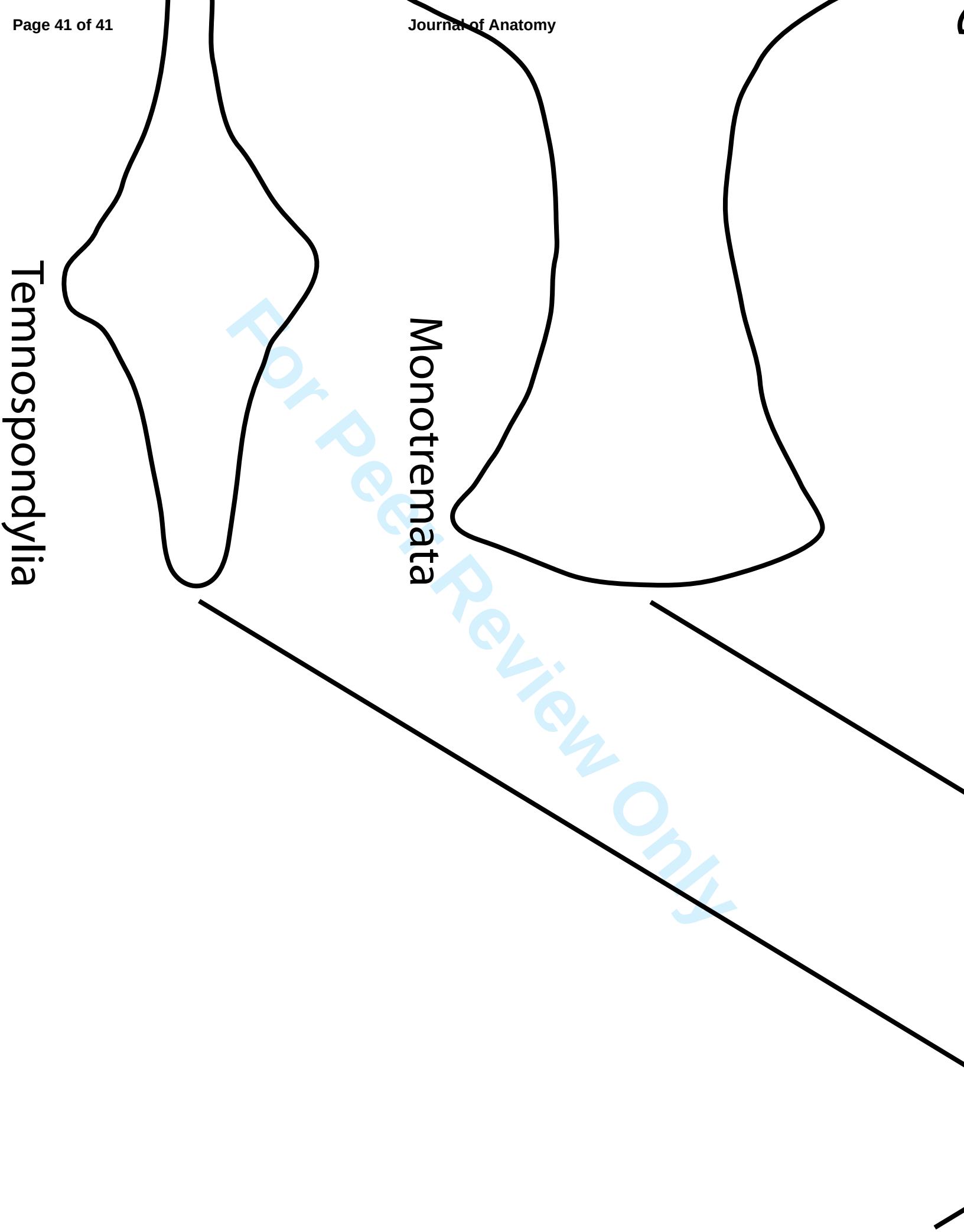

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