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P. E. Ahlberg, *et al.*

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Comment on "The Early Evolution of the Tetrapod Humerus"

In their analysis of humeral evolution in early tetrapods (taken here as meaning vertebrates with limbs), Shubin *et al.* (*1*) described a suite of derived characters that represents a significant advance on previous analyses (*2*–*4*). This makes their negative assessment of GSM 104536, the humerus provisionally attributed to *Elginerpeton pancheni* (*2, 4, 6*), all the more surprising. The specimen (see Fig. 1, A to F) derives from the late Frasnian (mid-Late Devonian) locality of Scat Craig in Scotland, and is thus about 10 million years older than the Catskill Formation humerus ANSP 21350 that forms the centerpiece of the Shubin *et al.* study (*1, 7*). It is associated with tetrapod lower jaws, snout fragments, shoulder girdle fragments, ilia, a femur, a tibia, and a probable tetrapod neural arch (*2, 4, 6, 8*). The Scat Craig specimens form the earliest known group of postcranial tetrapod elements, and GSM 104536—if correctly interpreted—is the earliest known tetrapod humerus.

After presenting their list of derived humeral characters, Shubin *et al.* (*1*) state, in the caption of figure 2, that "[t]he putative humerus of *Elginerpeton* . . . becomes difficult to interpret in light of these observations, because it has none of the synapomorphies shown in Fig. 2. By lacking the shared characters present in the most basal node, the identification of *Elginerpeton* as a tetrapod humerus would require both the evolution of unique features and the loss of all the apomorphies shared by tetrapods and their successive two outgroups." They reference the provisional description of GSM 104536 from 1991 (*2*), but the full description from 1998 (*4*) is not cited. The Shubin *et al.* statement that GSM 104536 has no tetrapod characteristics whatsoever begs the question of why I ever identified it as a tetrapod, and their claim is a contradiction of the published descriptions of the specimen (*2, 4*).

The derived characters described by Shubin *et al.* for *Panderichthys* + tetrapods include a dorsoventrally flattened shaft; an enlarged and posteriorly inclined ectepicondylar ridge; a broad, shallow proximal depression for scapulohumeral muscle insertion; and an enlarged area for muscle insertion above the radial condyle. The characters described for tetrapods alone include a distally expanded ectepicondylar process, a distinct recess and incipient crest at the proximal union of ectepicondylar and entepicondylar processes, an enlarged and proximodistally expanded entepicondylar process, and a ventral crest confluent with the posteromedial rim of the entepicondylar process. Shubin *et al.* claim that all of these features are absent in GSM 104536.

My 1991 description (see Table 1) explicitly compared GSM 104536 with the humeri of *Eusthenopteron* and early tetrapods and identified equivalents of a number of these synapomorphies. The "thin, flat entepicondyle, continuous with flat body of humerus" and "sharp preaxial margin" in that description are collectively equivalent to the Shubin *et al.* "dorsoventrally flattened shaft" plus "enlarged and proximodistaly expanded entepicondylar process" [see figure 2 in (*1*)]. My "narrow, tall ectepicondyle" overlaps with their "enlarged and posteriorly inclined ectepicondylar ridge" and "distally expanded

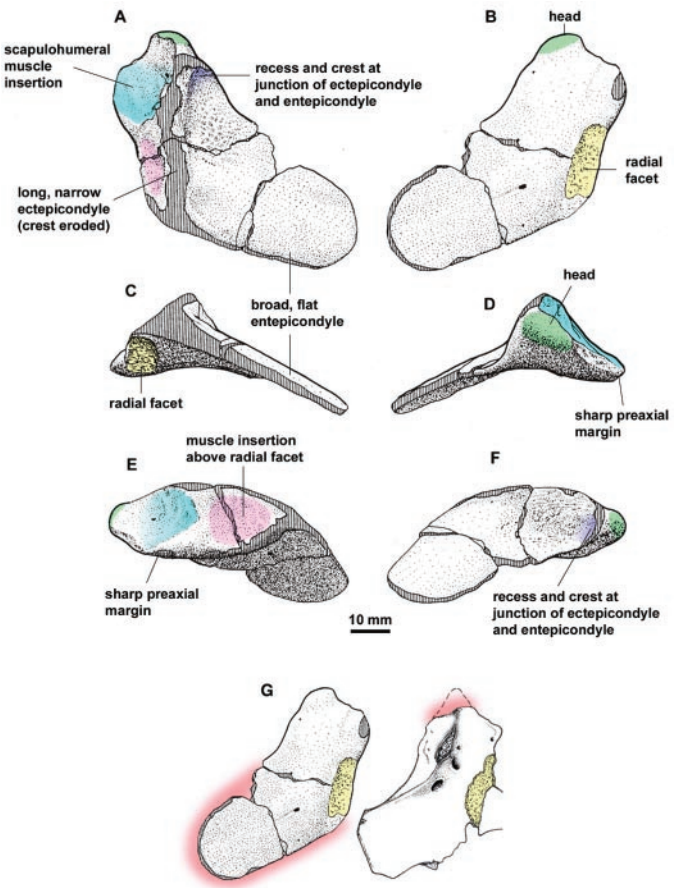


Fig. 1. GSM 104536, tetrapod humerus from the Late Devonian of Scotland. (**A**) Dorsal, (**B**) ventral, (**C**) distal, (**D**) proximal, (**E**) cranial, and (**F**) caudal views. Drawing from (*4*), highlighted with color. The same drawing was figured in (*2*), but at that time the radial facet (still partly obscured by matrix) was interpreted as a broken surface. GSM denotes British Geological Survey, Keyworth, UK. Thick outline indicates true edge, thin outline indicates broken edge, and vertical hatching indicates broken surface. The crest of the ectepicondyle and the distal margin of the bone have been eroded away, but most other surfaces and edges are perfectly preserved. Character numbers as in text: scapulohumeral muscle insertion (blue), muscle insertion above radial facet (pink), recess and crest at junction of ectepicondyle and entepicondyle (purple), articular head (green), radial facet (yellow). Note the flatness of the humeral shaft and entepicondyle in (C) and (D). (**G**) Comparison between GSM 104536 (left) and an immature *Ichthyostega* humerus collected in Greenland in 1998 (right, image courtesy of J. A. Clack), both in ventral view. Radial facet (yellow); incomplete margin (eroded in GSM 104536, covered by matrix in *Ichthyostega*) (red). Dashed outline in *Ichthyostega* indicates articular head reconstructed, from an associated specimen. Note that the radial facet is partly covered by the radius in *Ichthyostega*. Not to precise scale, but the specimens are of comparable size.

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Table 1. Comparison of humeral character states [a reproduction of table 1 in (*2*), the preliminary description of GSM 104536].

Humeral character state	*Eusthenopteron*	GSM 104536	Tetrapods
Entepicondyle	Thick, curved, rounded end; distinct from cylindrical body of humerus	**Thin, flat**, round end; **continuous with flat body of humerus**	**Thin, flat, rectangular**; **continuous with flat body of humerus**
Transverse humeral ridge	Present, strong	*Absent*	Present
Preaxial margin	Rounded	Sharp	**Sharp**
Pectoral process	Weak	**Strong**	**Strong**
Proximal region	Short	Short	**Long**
Ectepicondyle	Broad, low	**Narrow, tall**	**Narrow, tall**
Ectepicondylar foramen	Present	*Absent*	Present*
Supinator process	Close to ectepicondyle	Close to ectepicondyle	**On preaxial margin**
Size of caput	Large	*Small*	**Large**

The Scat Craig humerus GSM 104536 was compared with those of the osteolepiform *Eusthenopteron* and the early and primitive tetrapods *Ichthyostega*, *Acanthostega*, *Crassigyrinus*, *Proterogyrinus*, *Eoherpeton*, and *Greererpeton*. The tetrapod humeri agree with respect to all the characters compared in the table, except (*) that an ectepicondylar foramen is absent in *Proterogyrinus*, *Eoherpeton*, and *Greererpeton* (I regard this character state as derived within the Tetrapoda). The humerus of *Eusthenopteron* compares well with those of other osteolepiforms and rhizodonts, although there are minor differences in the shapes and positions of the processes; this humeral morphology is assumed to be primitive relative to that of tetrapods. 'Body' refers to the central core or shaft of the humerus, running from the caput to the radial and ulnar facets. The "proximal region" is that part of the body of the humerus which lies proximal to the entepicondyle and pectoral process. Bold typeface indicates shared derived character state; italics indicate unique character state.

ectepicondylar process." The narrow, linear, sharp-edged quality of the tetrapod ectepicondyle is not specifically mentioned by Shubin *et al*., but is shared by all Devonian representatives of the group and is clearly visible in figure 2 in (*1*).

The description of GSM 104536 cited by Shubin *et al*. thus directly contradicts their assertion that this specimen lacks tetrapod characteristics. No explanation for this anomaly is given in their report (*1, 2*). Furthermore, the specimen drawings in the 1991 description show several of the new derived characters defined by Shubin *et al.* The depression for scapulohumeral muscle insertion, the enlarged area for muscle insertion above the radial condyle, and the recess and crest at the junction of ectepicondyle and entepicondyle can all be easily identified (Fig. 1, A to F). Again, these similarities are not discussed in (*1*).

GSM 104536 is incomplete and has some unusual features for a tetrapod humerus. For example, it lacks a ventral crest and has a very short proximal shaft portion with a small head. However, the latter feature is shared with subadult individuals of *Ichthyostega* (*9*) and may be a juvenile feature (Fig. 1G). Given these points, it is unfortunate that Shubin *et al.* did not examine the specimen GSM 104536 itself before embarking on their analysis. It is also regrettable that they did not cite the full description (*4*), which shows that it has an elongate, anteroventrally positioned radial facet (Fig. 1)—a feature otherwise only known in *Ichthyostega* (*9, 10*). By denying the existence of the described and figured tetrapod characters of GSM 104536, rather than subjecting them to constructive criticism, Shubin *et al.* missed a valuable opportunity to investigate the affinities of what is still, probably, the earliest known tetrapod humerus. We now need to move on from assertion to explicit debate.

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