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Response to Comment on "The Early Evolution of the Tetrapod Humerus"

The two issues at the heart of this dialogue are the particular problem of uncovering the character combination that defines a limb-bearing humerus, and the more general challenge of interpreting isolated and fragmentary fossil material. Fossils do not come readily labeled (*1*), and the contextual framework for analyzing the material has changed significantly in recent years. The early evolution of tetrapod humeri can now be explored as never before, with new descriptions and discoveries of taxa surrounding the origin of limbed tetrapods (*2*–*5*). We do not challenge Ahlberg's depictions (*6*–*8*) of GSM 104536, but think that his interpretation of this bone deserves re-examination. On the basis of the present and emerging data set, the identification of GSM 104536 as a humerus no longer seems plausible, but rather demands multiple ad hoc hypotheses to explain morphological specializations and functional peculiarities.

Figure 1 depicts relevant published material, including GSM 104536. If we accept Ahlberg's diagnosis of GSM 104536, the following discrepancies become apparent. The humeral head (caput) is ovoid, whereas those of all early limb-bearing humeri and the nearest fin-bearing examples are characteristically strap-shaped. The shaft of GSM 104536 is unusually deep, with a unique area projecting below the level of the humeral head [see figure 1D in (*6*)], unlike the dorsoventrally flattened, subrectangular shafts of comparable humeri. The full extent of the ectepicondylar crest is unknown; it cannot be described as narrow and tall, enlarged and posteriorly inclined, or projecting distally (*6*). However, the broken base runs from proximal to distal extremities of the bone and is unlike the broken base of any known early ectepicondyle. The posterior limit of the shaft in GSM 104536 is difficult to identify, and this has consequences for the determination of the entepicondyle. Besides being a sheet of bone (and thus consistent with Ahlberg's interpretation of GSM 104536), an entepicondyle is characterized by a suite of distinctive foramina and processes (Fig. 1). In GSM 104536, these characters are either absent, or were obliterated by post mortem damage. The large notch in the bony flange might thus represent the former site of the entepicondylar foramen. If so, this foramen was either uniquely remote from the posterior edge of the humeral shaft (against which it lies in other examples; see Fig. 1), or else the shaft of GSM 104536 extended far behind the ectepicondylar base. Ahlberg (*6*) identifies regions for scapulohumeral muscle insertion and muscle insertion above the radial facet, which are plausible interpretations if this bone is a humerus. However, identification of the recess and crest at the junction of the ectepicondyle and entepicondyle depends upon an appropriate restoration of the dam-

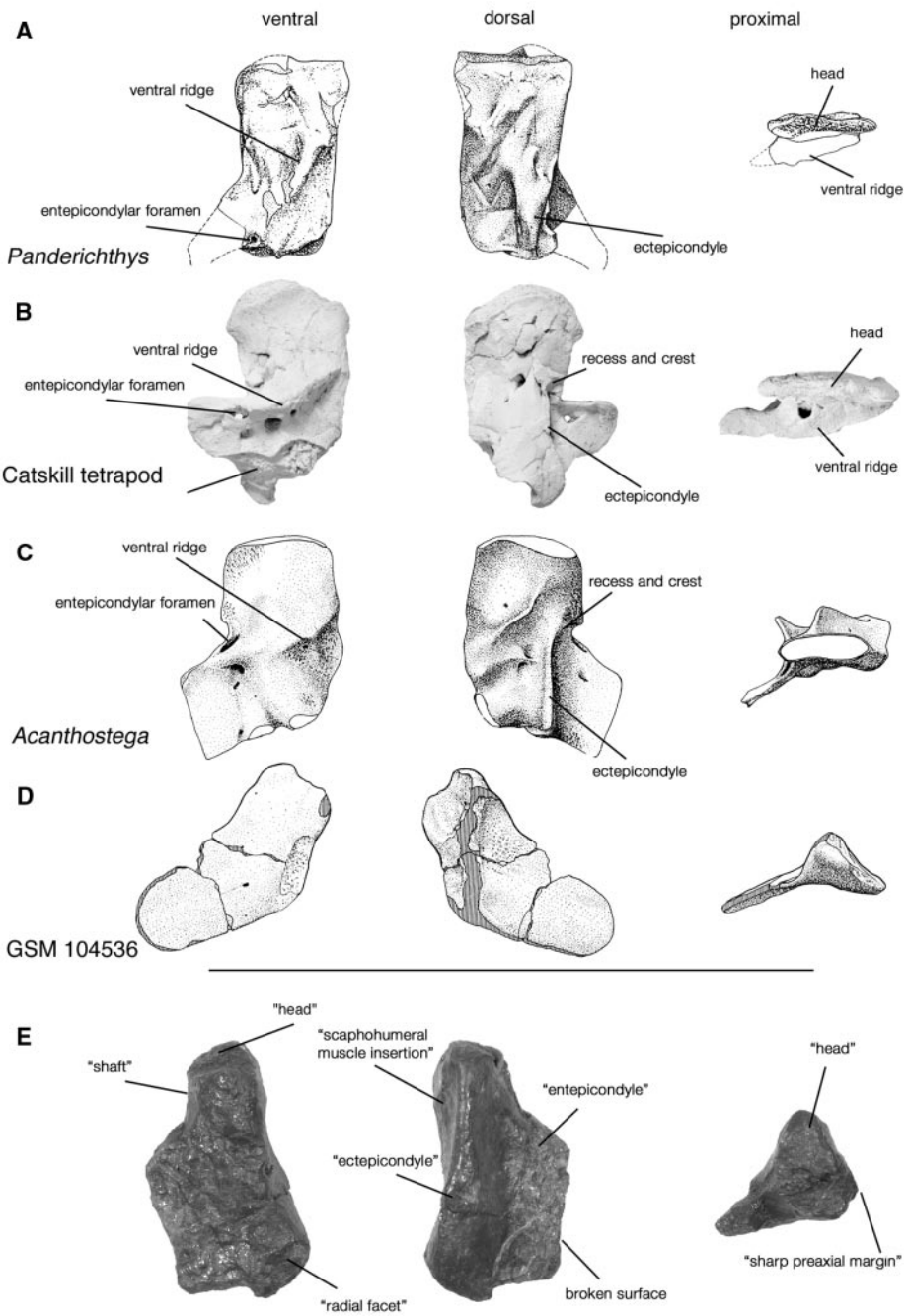


Fig. 1. Tetrapodomorph humeri in three views from (**A**) *Panderichthys* (*4*), (**B**) Catskill tetrapod (*5*), and (**C**) *Acanthostega* (*3*). (**D**) GSM 104536 (*7*). (**E**) Undescribed hypobranchial of porolepiform sarcopterygian from the Frasnian of Arctic Canada.

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aged surfaces (cross-hatched areas in the illustration of GSM 104536; Fig. 1). More importantly, we note that on the opposite surface of this specimen, there is no trace of a ventral crest or ridge, or remains of the canals, channels, and processes associated with it. This suite of features otherwise dominates the ventral/flexor surface of fin- and limb-bearing humeri distributed throughout tetrapod stem taxa (*2*–*5*). Even when absent, vestiges of these features remain. The entire ventral surface of GSM 104536 is curiously featureless. Thus, it is also difficult to make sense of the anteriorly directed flange interpreted as a pectoral process. In all other examples, the pectoral process projects ventrally and is formed from the anterior portion of the ventral ridge.

What are the functional implications of these morphological differences? Absence of the ventral ridge indicates weak development of elbow flexor musculature (*7*). It is therefore difficult to understand how this limb could be weight-bearing if it has lost processes for the major muscles that would allow this function, especially in conjunction with the interpretation of a ventrally facing radial facet. The undiscussed lack of an ulnar facet on GSM 104536 is of further concern in this regard.

GSM 104536 was first identified as a humerus before the mid-1990s, when the comparative data set was far more limited. Since then, the interpretive framework has changed, and GSM 104536 is no longer "approximately intermediate in shape between those of osteolepiforms and later stem tetrapods" (*8*). The nearest comparators—humeri of *Panderichthys* and *Acanthostega*—were known in only rudimentary and/or misinterpreted detail, and the Catskill specimen was unknown. In addition, it now appears that the peculiar radial facet of the *Ichthyostega* humerus (*2, 9*), identified as being especially like that of GSM 104536 (*8*), is an artifact of specimen reconstruction (*10*). Consequently, the humerus attributed to *Elginerpeton* [an undoubtedly tetrapod-like lower jaw (*7, 8, 11*)] has emerged as morphologically incongruent, whether placed in a "high" position (near-*Ichthyostega*) or "low" position (near-*Panderichthys*) in the tetrapod evolutionary tree. Table 1 in (*6*) is insufficient for the comparative task because the *Eusthenopteron* humerus is no longer the appropriate outgroup for comparison, and the tetrapod entries fail to reflect the detail and diversity of relevant character states now known (Fig. 1).

We argue that GSM 104536 needs more cautious treatment in the context of the reworked, diverse fish fauna from the Scaat Craig site (*12*). The labeling of parts (*1*) reflects a series of hypotheses about similarity and homology within and between taxa, and the more different isolated bone are from comparable forms, the harder these hypotheses are to substantiate. In the case of fragmentary material, these hypotheses are tested by discovery of more complete individuals. Figure 1E is a geologically contemporaneous fossil bone from Frasnian-age deposits in the Canadian Arctic that could be interpreted as a humerus. It is not identical to GSM 104536, but in certain respects it is more conventionally humerus-like (note the L-shaped form and the better-developed proximal shaft). Indeed, many of the features that Ahlberg uses to unite GSM 104356 with tetrapods can be inferred from this bone. However, this is not a humerus. It is part of the gill skeleton of a large porolepiform sarcopterygian fish, and we know that porolepiforms are represented in the Scaat Craig fauna (*12*). This kind of comparison underscores the difficulties with interpreting isolated bones: This hypobranchial was preserved as part of an articulated cranium. The diversity of these gill bones is poorly understood. Given this paucity of knowledge and our concerns with the morphological interpretation of GSM 103456 itself, we suggest that it is set aside from discussions of tetrapod limb evolution pending the discovery of more complete material.

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