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THE PECTORAL GIRDLE AND FORELIMB OF THE BASAL THEROPOD *HERRERASAURUS ISCHIGUALASTENSIS*

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ABSTRACT—New specimens of *Herrerasaurus ischigualastensis* shed light on the structure and function of the pectoral girdle and forelimb in early theropod dinosaurs. As in tetanurian theropods, the scapulocoracoid has a broadly expanded acromion and strap-shaped scapular blade. The forelimb is less than one-half the length of the hind-limb and is specialized for prey capture and manipulation. The short proximal segments of the forelimb provide mechanical advantage and are marked by prominent tuberosities. The well-ossified carpus is divided into two functional units, one composed of the radiale and ulnare and the other composed of a centrale and distal carpals, and is designed functionally for dorsoventral extension and flexion of the manus against the forearm. The manus is longer than the humerus, radius, or ulna and is specialized for grasping and raking, as shown by the marked metacarpal extensor depressions, long penultimate phalanges, and trenchant unguals in digits I–III. Upon flexion or extension, the unguals of digits I–III converge. Manual digits IV and V are very reduced, and the phalangeal formula is 2–3–4–1–0.

Increase in the length of the deltopectoral crest and decrease in the length of manual digit IV and loss of its terminal ungual constitute the only dinosaurian synapomorphies in the pectoral girdle and forelimb. Many previously cited dinosaurian synapomorphies in the pectoral girdle and forelimb cannot be substantiated. Several synapomorphies in the scapula and manus unite *Herrerasaurus ischigualastensis* with other theropods.

INTRODUCTION

The pectoral girdle and forelimb in herrerasaurid dinosaurs was poorly represented in the original materials of *Herrerasaurus ischigualastensis* and *Staurikosaurus pricei.* In *H. ischigualastensis,* only humeral fragments were preserved (Reig, 1963), and in *Staurikosaurus pricei,* only the distal end of the scapular blade and humerus were mentioned (Colbert, 1970). The supposed humeral fragment in *S. pricei,* furthermore, was misidentified and does not pertain to the forelimb (Galton, 1977:238).

Reig (1963:fig. 5B) noted the presence of the coracoid, humerus, and radiale in material he referred to *Ischisaurus cattoi,* which is now regarded as a junior synonym of *H. ischigualastensis* (Novas, 1993). More recently, Novas (1986) and Brinkman and Sues (1987) described portions of the scapulocoracoid and humerus in *Frenguellisaurus ischigualastensis* (Figs. 1, 2) and *Staurikosaurus pricei* (MCZ 7064), respectively. These remains are also referable to *H. ischigualastensis* (Novas, 1993).

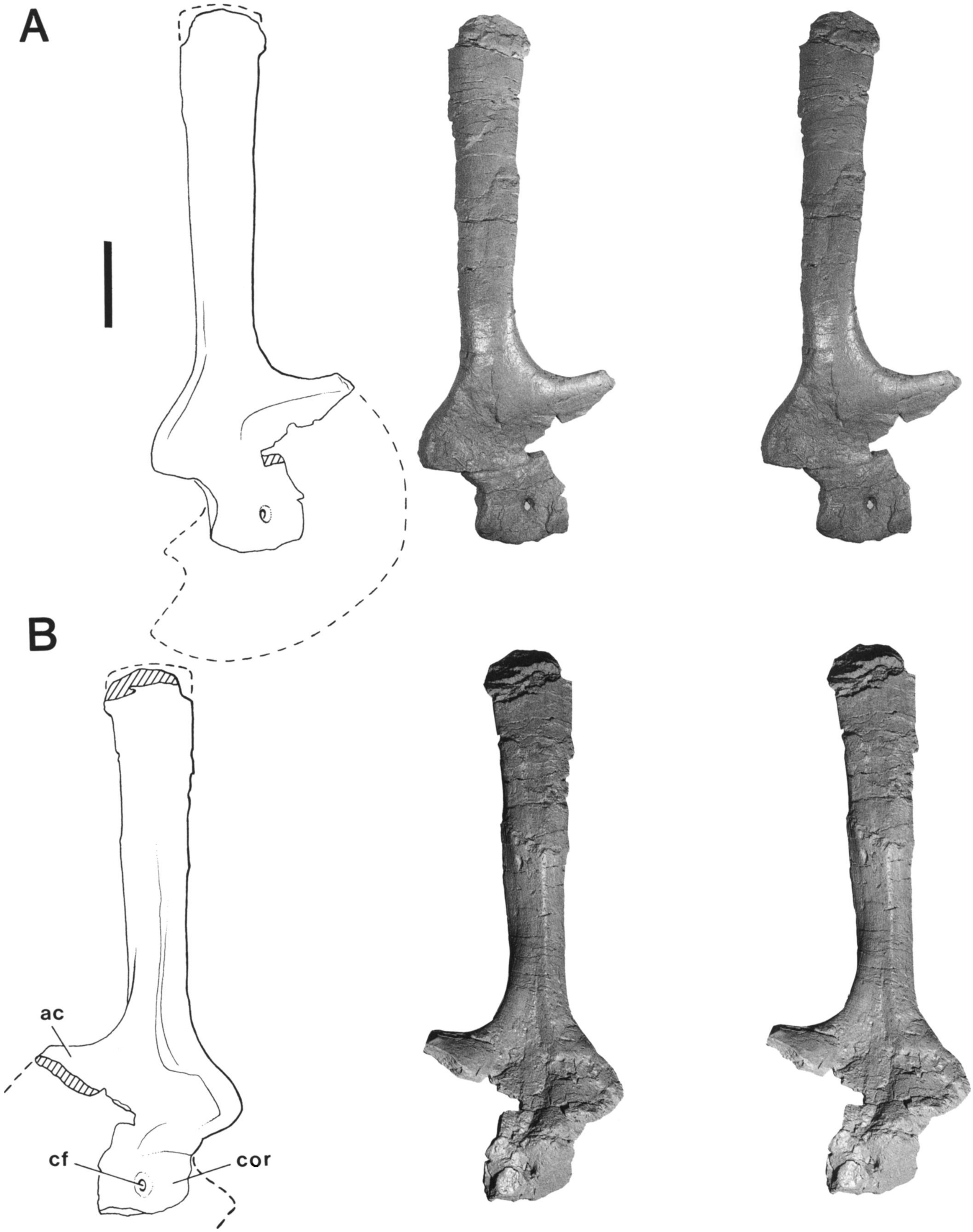
Recent work in the Ischigualasto Formation of northwestern Argentina resulted in the discovery of articulated remains of the pectoral girdle and forelimb of *H. ischigualastensis* (Sereno et al., 1988; Sereno and Novas, 1992). The following description and functional interpretation is based primarily on these materials.

Institutional abbreviations—MACN, Museo Argentino de Ciencias Naturales, Buenos Aires; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge; **MLP**, Museo de La Plata, La Plata; **PVL**, Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan; **UCMP**, Museum of Paleontology, University of California, Berkeley.

MATERIALS AND METHODS

Much of the description is based on a single articulated postcranial skeleton of *H. ischigualastensis* that preserves a portion of the scapular blade and a complete left forelimb (Figs. 3–15; PVSJ 373). Additional material pertaining to the pectoral girdle and forelimb of this species includes the following: PVSJ 380, right scapula and nearly complete, articulated right carpus and manus; PVSJ 407, articulated left pectoral girdle and forelimb lacking the phalanges; MACN 18.060, left and right humeri, proximal ends of the ulnae, and a left radiale (Reig, 1963:fig. 5; formerly *Ischisaurus cattoi*); MLP 61–VIII–2–3, right coracoid, both humeri, and fragmentary ulnae; MCZ 7064, partial right scapulocoracoid and partial right and left humeri (Brinkman and Sues, 1987:figs. 2, 3; formerly attributed to *Staurikosaurus pricei*); PVSJ 53 and PVSJ 409, partial scapulocoracoids (Figs. 1, 2; Novas, 1992a:fig. 2E; PVSJ 53, formerly *Frenguellisaurus ischigualastensis*).

The following technique was used to remove color distractions in fossil material prior to stereophotog-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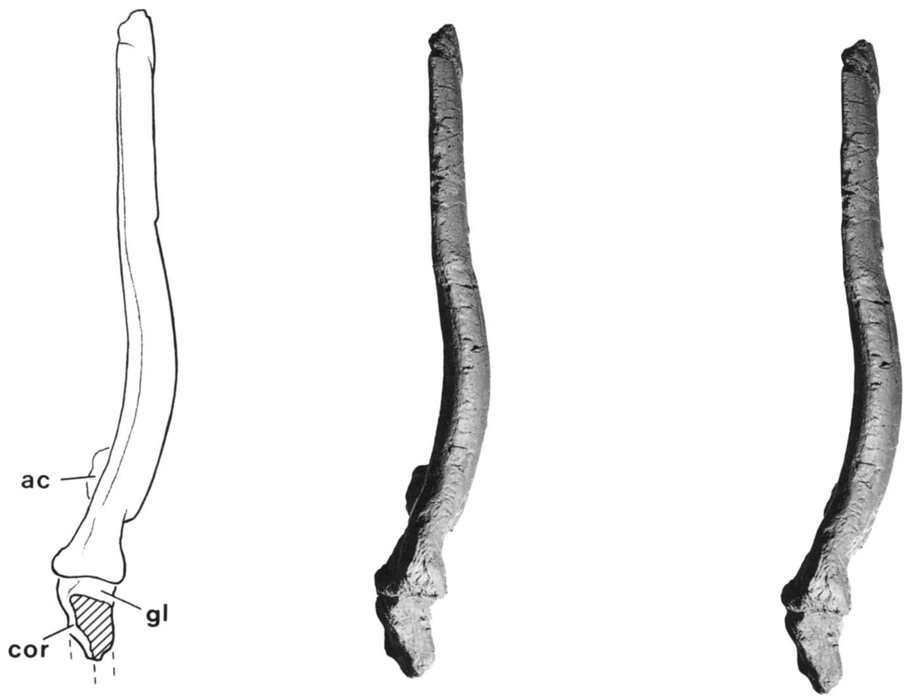

FIGURE 2. Stereopair of the right scapulocoracoid of *Herrerasaurus ischigualastensis* (PVSJ 53) in ventral view. Cross-hatching indicates broken bone surface. Abbreviations: **ac**, acromion; **cor**, coracoid; **gl**, glenoid. Scale as in Figure 1.

raphy (L. Meeker, pers. comm.): Bone surfaces were sprayed with a very thin coat of Blair dulling spray to provide a suitable base for neutral grey Windsor and Newton gouache, which was applied with a small brush. Highlights were enhanced as necessary with Aqua Net hair spray. Bone surfaces were subsequently cleaned with water and a small brush.

DESCRIPTION

Pectoral Girdle

The pectoral girdle appears to consist of paired, typically co-ossified scapulocoracoids. Clavicles and sternal plates may not have been present, although none of the postcranial skeletons is well enough preserved to demonstrate their absence.

Scapula—Except for portions of the acromion, all other parts of the scapula are known (Figs. 1, 2, Table 1; Brinkman and Sues, 1987:fig. 2). Most of the lateral surface of the platelike acromion is gently depressed (Fig. 1A). The thickened dorsal margin of the acromion turns sharply away from the scapular blade, forming an angle to the blade of less than 90°. The anterior margin of the acromion is arched and bevelled and meets the dorsal margin at a distinct corner. When the axis of the blade is inclined at 45° above the horizontal (Fig. 16), the glenoid faces posteroventrally and slightly laterally.

The strap-shaped scapular blade expands only slightly toward its distal end. Its maximum distal width is less than twice the minimum width at the proximal end, and thus the blade is more straplike than that in

TABLE 1. Measurements (mm) of the right scapula in *Herrerasaurus ischigualastensis* (PVSJ 53). Abbreviation: ( ) = estimated.

Maximum length	285
Maximum proximal width	
(lip of glenoid to acromion)	(135)
Depth of glenoid	32
Scapular blade	
Maximum length	220
Minimum proximal width	33
Maximum distal width	50
Maximum proximal thickness	21

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FIGURE 1. Stereopairs of the right scapulocoracoid of *Herrerasaurus ischigualastensis* (PVSJ 53) in lateral (**A**) and medial (**B**) views. Cross-hatching indicates broken bone surface. Abbreviations: **ac**, acromion; **cf**, coracoid foramen; **cor**, coracoid. Scale bar equals 5 cm.

TABLE 2. Maximum length (mm) and comparative ratios of forelimb and hind-limb long bones in *Herrerasaurus ischigualastensis* (PVSJ 373). Humeral length is estimated from the proportions of the humerus and forearm in PVSJ 407 and from humeral proportions in MACN 18.060. Hind-limb measurements represent an average of left and right sides. Abbreviations: F = femur; H = humerus; Mc = metacarpal; Mt = metatarsal; R = radius; T = tibia; ( ) = estimated.

Humerus	(175)
Radius	153
Metacarpal III	62
Femur	350
Tibia	320
Metatarsal III	165
H + R + Mc3/F + T + MtIII	0.47
H/R	1.14
R/McIII	0.94
F/T	1.09
T/MtIII	1.94

Staurikosaurus (MCZ 1669). The proximal end of the scapular blade is elliptical in cross-section. In medial view (Fig. 1B), the scapular blade is thickened and marked by a distinct crest, which is offset toward the posterior margin of the blade. In posterior view (Fig. 2), the blade is arched to accommodate the curvature of the ribcage.

Fusion between the scapula and coracoid is not strictly correlated with size. The scapula-coracoid suture is closed in both small (PVSJ 407) and large individuals (Fig. 1B; PVSJ 53, MCZ 7064). In another relatively large specimen (PVSJ 380), however, the suture remains open, with the scapula and coracoid disarticulated.

Coracoid—The coracoid has a semicircular shape and is broader anteroposteriorly than dorsoventrally (Fig. 1A; MLP 61–VIII–2–3; MCZ 7064; Brinkman and Sues, 1987:fig. 2). The middle and anterior portions of the acromion are platelike. The coracoid foramen passes through the coracoid ventral to the suture with the scapula. The coracoid is thickened near the glenoid cavity, where it forms the ventral two-thirds of the socket. The ventral end of the coracoid is deflected medially and projects posteriorly as a short, triangular posterior process. The posterior process and glenoid are separated by a broad notch, in which is located a marked oval depression.

Forelimb

Compared to the hind-limb, the forelimb is short in *H. ischigualastensis* (Fig. 16). Based on epipodial, propodial and metapodial measurements (Table 2), the forelimb is slightly less than one-half (47 percent) the length of the hind-limb. Within the forelimb, the manus is proportionately elongate (Tables 3, 4). The manus, for example, is considerably longer than the humerus, radius, or ulna. In the manus, digits I–III are relatively long, with metacarpal III exceeding one-third of the length of the ulna. Manual digits IV and V, in contrast, are strongly reduced (Fig. 15).

In *H. ischigualastensis,* all of the long bones of the forelimb are hollow including all of the non-ungual phalanges of the manus (Fig. 15A). All of the long bones of the hind-limb and the vertebral centra also show marked hollowing, which has been cited as a theropod synapomorphy (Gauthier, 1986; Sereno et al., 1993).

In the following account, the humerus, ulna, and radius are described with their long axes oriented vertically. The carpus and manus, on the other hand, are described in a horizontal plane, with the extensor surface of the manus facing dorsally and the flexor surface facing ventrally.

Humerus—The convex head of the humerus occupies the majority of the proximal end (Fig. 3, Table 3). In proximal view, the head is kidney-shaped, with the concave border facing anteromedially (Fig. 3C). A deep trough separates the head from an unusually prominent, finger-shaped medial tuberosity (broken away in MCZ 7064; Brinkman and Sues, 1987:fig. 3A). The prominence and shape of the medial tuberosity are diagnostic for *H. ischigualastensis*. The medial tuberosity projects dorsally, with a flattened lateral surface that is canted at approximately 45° to the axis of the proximal end of the humerus (Fig. 3C). The medial surface of the tuberosity is convex and marked by rugosities, particularly on its anteromedial side.

In anterior view, the humeral shaft is nearly straight. In lateral view, the shaft is slightly sinuous, with the proximal end inclined posteriorly and the distal end curving slightly anteriorly (MACN 18.060).

The distal end of the humerus has well developed ulnar and radial condyles and prominent medial and lateral epicondyles (Figs. 4, 5; PVSJ 373, MACN 18.060, MCZ 7064; Brinkman and Sues, 1987:fig. 3C, D). The saddle-shaped radial condyle is strongly convex anteroposteriorly and gently concave transversely (Figs. 4A, 5C). The articular surface rounds onto the anterior surface of the humerus, above which is a marked depression (Fig. 4A). The posterior margin of the radial condyle, in contrast, is bordered by a low transverse ridge (Figs. 4B, 5C). In distal view, the radial condyle is trapezoidal, with the greatest dimension on the lateral side, and merges with the ulnar condyle. The ulnar condyle is kidney-shaped in distal view (Fig.

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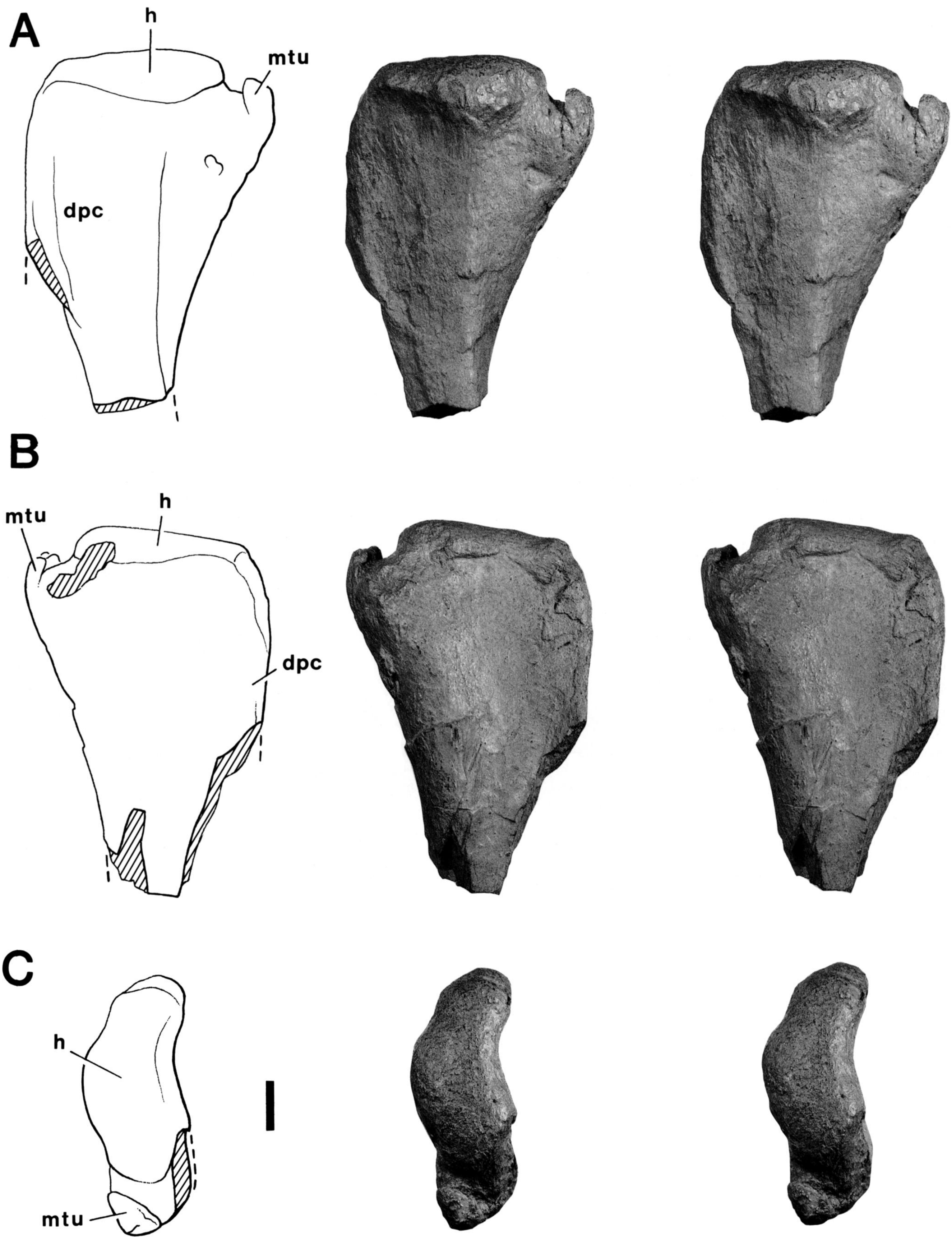
FIGURE 3. Stereopairs of the proximal end of the left humerus of *Herrerasaurus ischigualastensis* (PVSJ 373) in lateral (**A**), medial (**B**), and (**C**) proximal views. Cross-hatching indicates broken bone surface. Abbreviations: **dpc**, deltopectoral crest; **h**, head; **mtu**, medial tuberosity. Scale bar equals 1 cm.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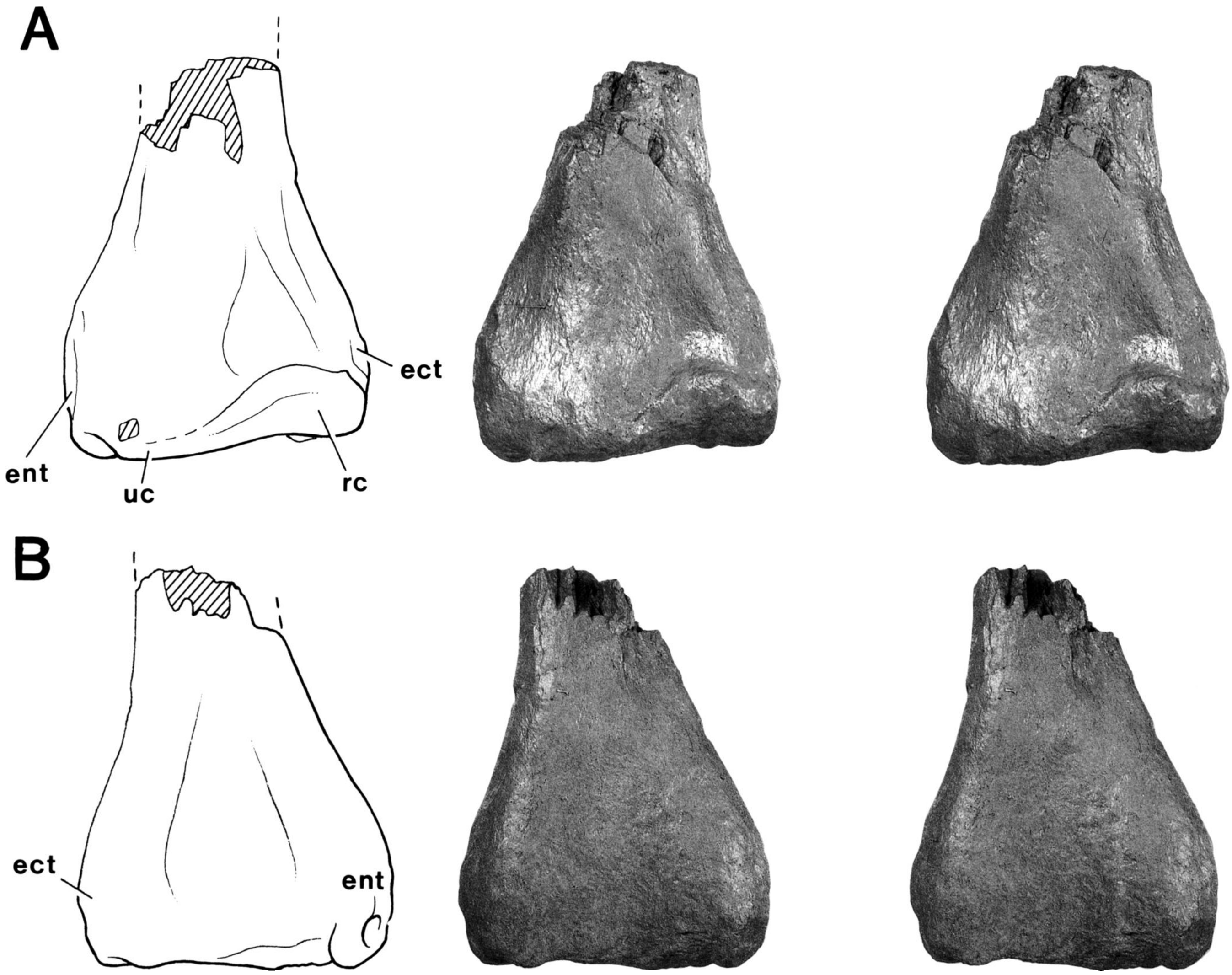

FIGURE 4. Stereopairs of the distal end of the left humerus of *Herrerasaurus ischigualastensis* (PVSJ 373) in anterior (**A**) and posterior (**B**) views. Cross-hatching indicates broken bone surface. Abbreviations: **ect**, ectepicondyle; **ent**, entepicondyle; **rc**, radial condyle; **uc**, ulnar condyle. Scale bar as in Figure 3.

5C), with the transverse axis of the condyle bowed anteriorly. The ulnar condyle faces distally and rounds onto the posterior side of the distal end of the humerus.

Epicondylar rugosities are well developed on both lateral and medial sides of the distal end of the humerus (Figs. 4, 5). The form of the entepicondyle, in particular, is diagnostic for *H. ischigualastensis* (PVSJ 373, MACN 18.060, MCZ 7064; Brinkman and Sues, 1987: fig. 3D). In distal view, the entepicondyle is separated from the ulnar condyle by a shallow groove (Fig. 5C). The anteromedial and posteromedial surfaces of the entepicondyle are marked by rugose depressions (Fig. 5B). The anteromedial depression is elliptical and oriented vertically. The posteromedial depression, which is positioned closer to the distal end, is subcircular with a raised rim. The ectepicondyle, a rugose swelling on the lateral side of the distal end (Fig. 5A), is not clearly separated from the adjacent radial condyle. In lateral view, a deep circular depression is present very near the articular surface of the radial condyle (PVSJ 373, 407, MACN 18.060; MCZ 7064).

Ulna—The proximal end of the ulna is deeper than broad and has a prominent olecranon process (Figs. 7, 8). The oval proximal articular surface has a shallow central depression and a trough along its medial margin (Fig. 8A). Anterior and posterior margins of the proximal end are pitted for ligamentous attachments. On the lateral side of the proximal end, a concave facet is present for articulation with the proximal end of the radius (Fig. 7B).

The ulnar shaft is subtriangular in cross-section and curves slightly medially in its distal one-half. Anterior, medial, and lateral ridges pass along the length of the shaft. The anterior ridge extends from the proximal

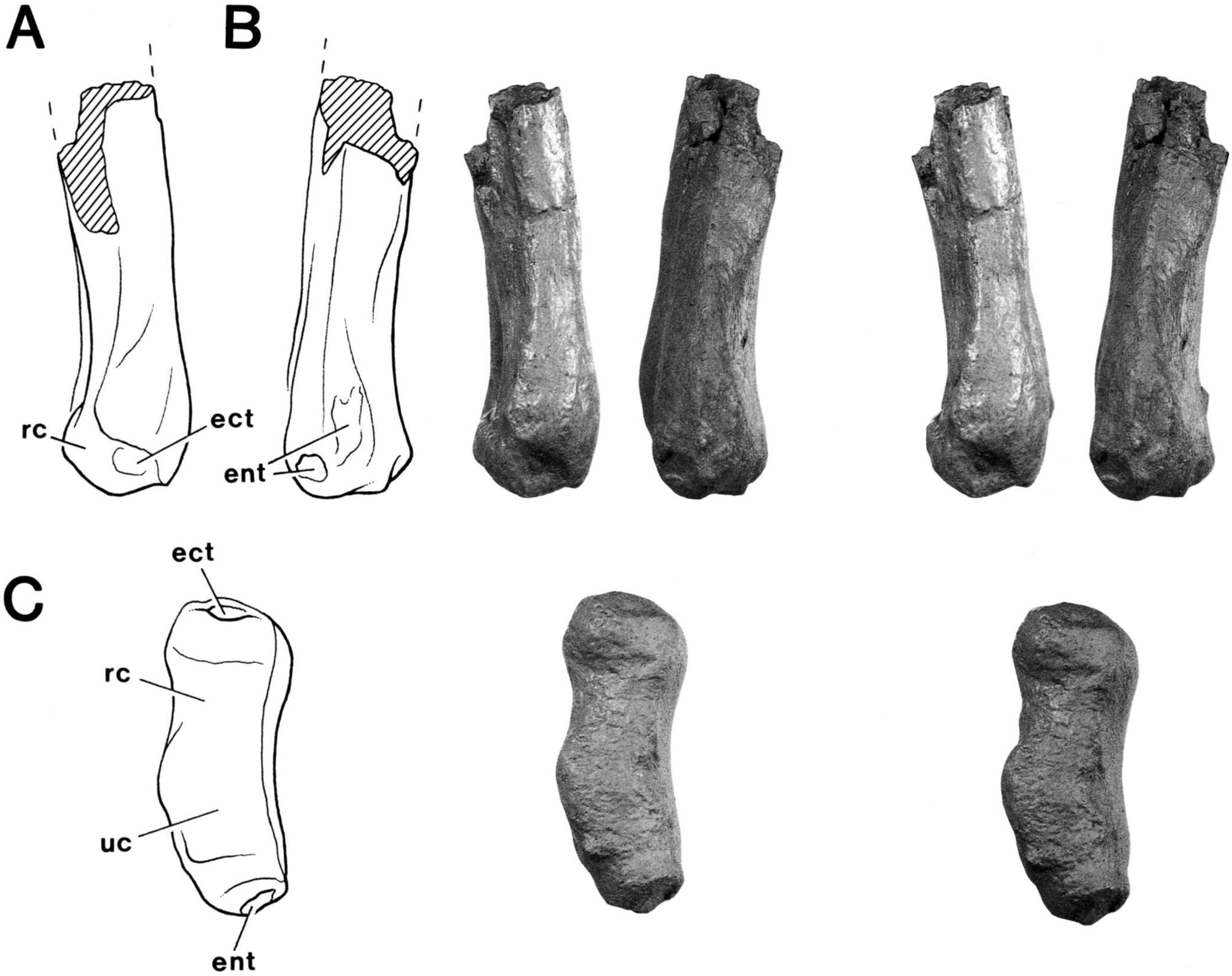

FIGURE 5. Stereopairs of the distal end of the left humerus of *Herrerasaurus ischigualastensis* (PVSJ 373) in lateral (**A**), medial (**B**), and (**C**), distal views. Cross-hatching indicates broken bone surface. Abbreviations as in Figure 4 and scale as in Figure 3.

end to the articular surface for the ulnare at the distal end and is particularly sharp where it passes near the biceps tuberosity on the radius (Fig. 8A). The proximal end of the medial ridge forms the medial margin of the olecranon process. At mid-shaft, the medial ridge ends but reappears again toward the distal end, where it is marked by a raised rugosity (Fig. 7A). The proximal end of the lateral ridge forms the posterior margin of the articular surface for the radius (Fig. 7B). Proximally, this ridge is broader and somewhat rounded. In its distal two-thirds, this ridge forms a sharp crest that faces the shaft of the radius and may represent the attachment site of an interosseous membrane between the radius and ulna. Near its distal end, the lateral ridge curves onto the posterior face of the ulna, forming the edge of an articular surface for the distal end of the radius.

The distal end of the ulna is slightly expanded in anterior view. The convex distal articular surface is fitted to the concave proximal articular surface of the ulnare (Figs. 8A, 9B). In distal view, the articular surface is semicircular, with a nearly straight posterior margin that is oriented along an anterolateral–posteromedial axis. The distal articular surface rounds onto the anterior side of the ulna, suggesting that the ulna–ulnare joint would have permitted the carpus and manus to flex against the forearm. Just proximal to the distal articular surface, a raised, subtriangular rugosity faces anterolaterally toward the distal end of the radius, suggesting that strong ligaments may have bound the distal ends of the radius and ulna (Fig. 9B).

Radius—The proximal end of the radius is slightly less robust than the distal end. The proximal articular surface is elliptical with an anteromedial–posterome-

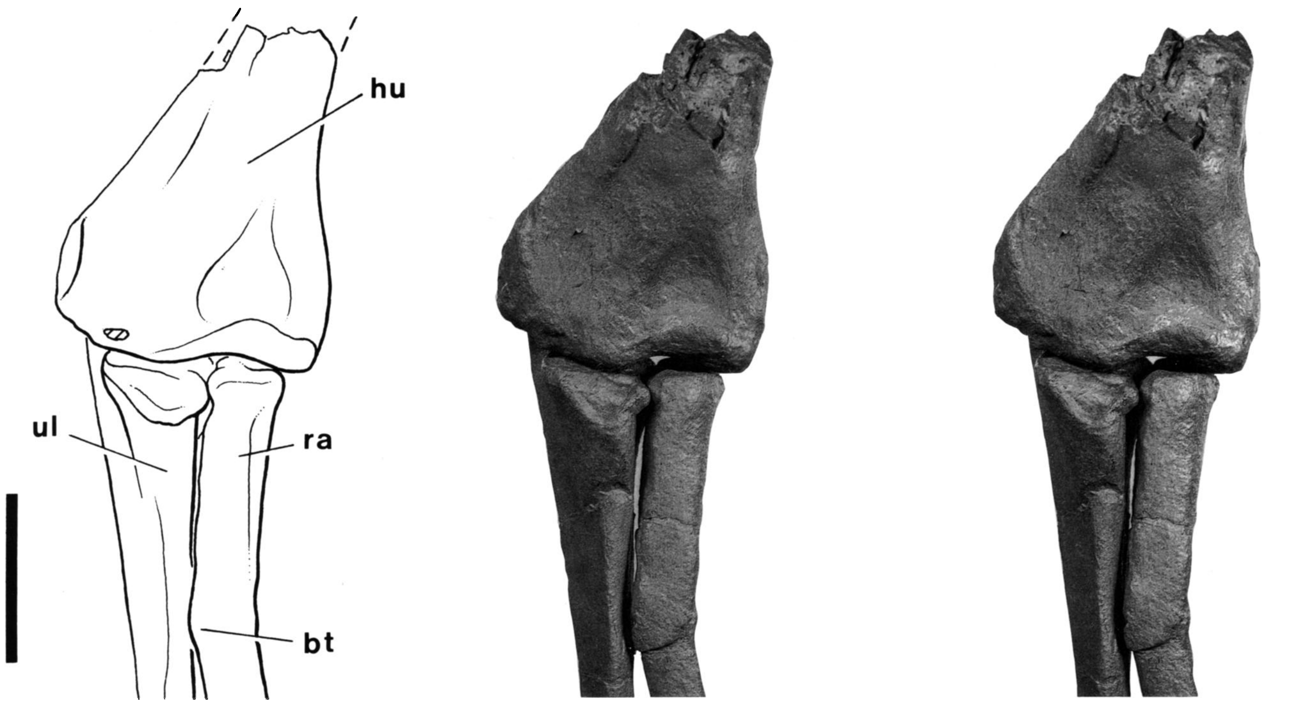

FIGURE 6. Stereopair of the left elbow joint of *Herrerasaurus ischigualastensis* (PVSJ 373) in anterior view. Abbreviations: **bt**, biceps tubercle; **hu**, humerus; **ra**, radius; **ul**, ulna. Scale bar equals 5 cm.

dial major axis. The posterior apex of the articular surface projects proximally as a heel, the posterior aspect of which is swollen and rugose (Figs. 7B, 8B).

The radial shaft has a sigmoid curve in anterior view

TABLE 3. Measurements (mm) of the humerus, radius, and ulna in *Herrerasaurus ischigualastensis* (PVSJ 373, 407). Measurements are from the left side. Abbreviation: ( ) = estimated.

	PVSJ 373	PVSJ 407
Humerus		
Maximum length	(175)	170
Maximum proximal width	55	—
Maximum distal width	50	(37)
Deltopectoral crest length	—	77
Anteroposterior shaft diameter	—	18
Ulna		
Maximum length	167	168
Anteroposterior shaft diameter	10	11
Radius		
Maximum length	153	—
Anteroposterior shaft diameter	10	11

(Fig. 8A). The proximal one-third of the shaft is closely fitted to the ulna, with low rugosities on its medial side. The anterior margin of the shaft forms a prominent crest, or biceps tuberosity, near the distal end of this section of the shaft (Figs. 7, 8A). Distal to this tuberosity, the radial shaft arches away from the ulnar shaft. Although the radius is fractured in several places, it is clear that this is the natural curvature of the shaft. A low, rounded lateral ridge becomes sharper and curves onto the medial side of the shaft near its contact with the ulna (Fig. 7B). The distal one-third of the shaft is subtriangular in cross-section, with a distinctly flattened lateral surface.

The distal end expands abruptly along its medial and posterolateral margins and is truncated at an oblique angle to the axis of the shaft. The distal articular surface is oval with an anteromedial–posterolateral major axis. The distal end thus has a more transverse orientation and is rotated only slightly relative to the proximal end. The pitted, concave distal articular surface opposes the smooth, concave surface on the radiale (Fig. 9A). The intervening space must have been filled with articular cartilage that appears to have been anchored to the pitted distal end of the radius. The rounded

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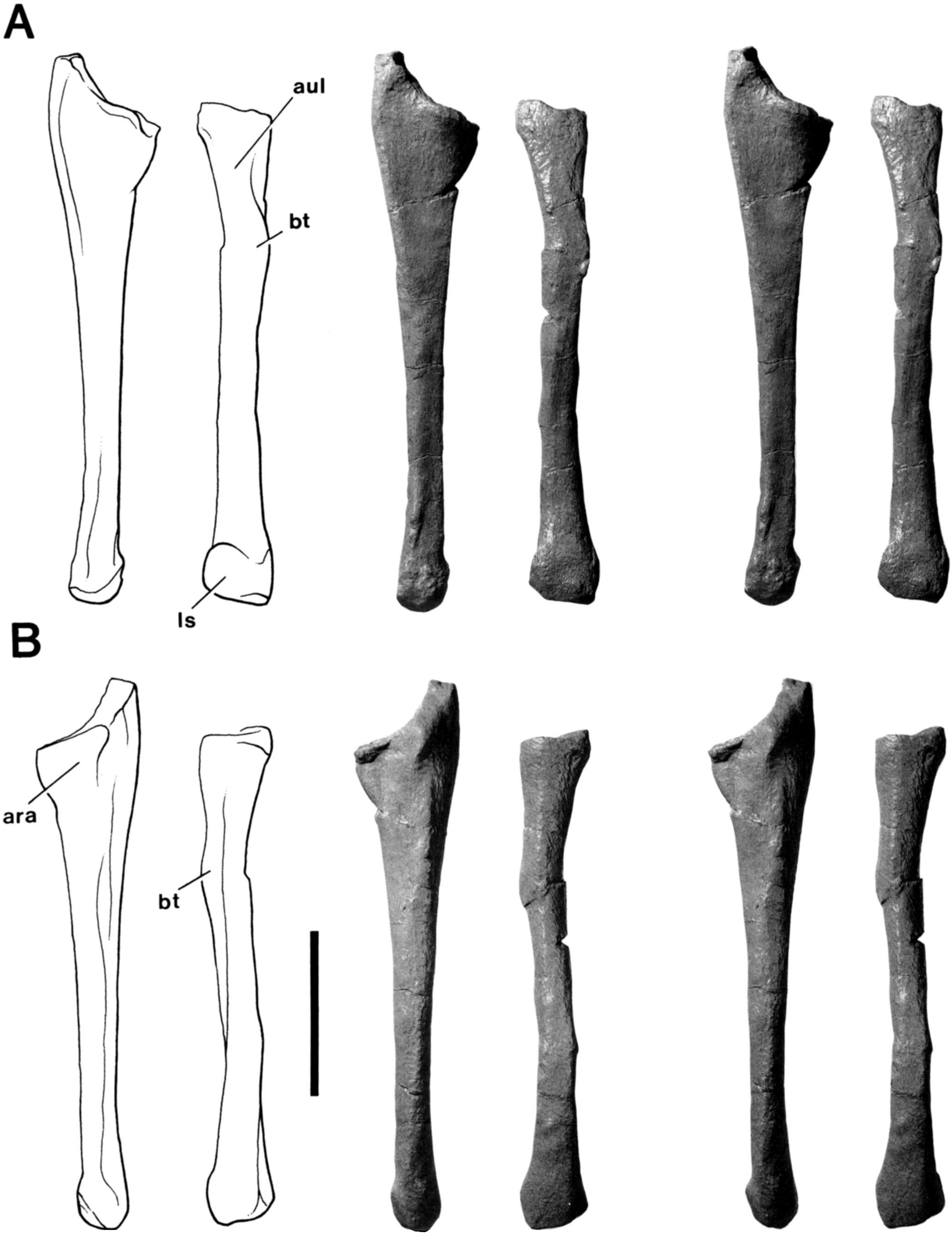
FIGURE 7. Stereopairs of the left radius and ulna of *Herrerasaurus ischigualastensis* (PVSJ 373) in medial (**A**) and lateral (**B**) views. Abbreviations: **ara**, articular surface for the radius; **aul**, articular surface for the ulna; **bt**, biceps tubercle; **ls**, ligament scars. Scale bar equals 5 cm.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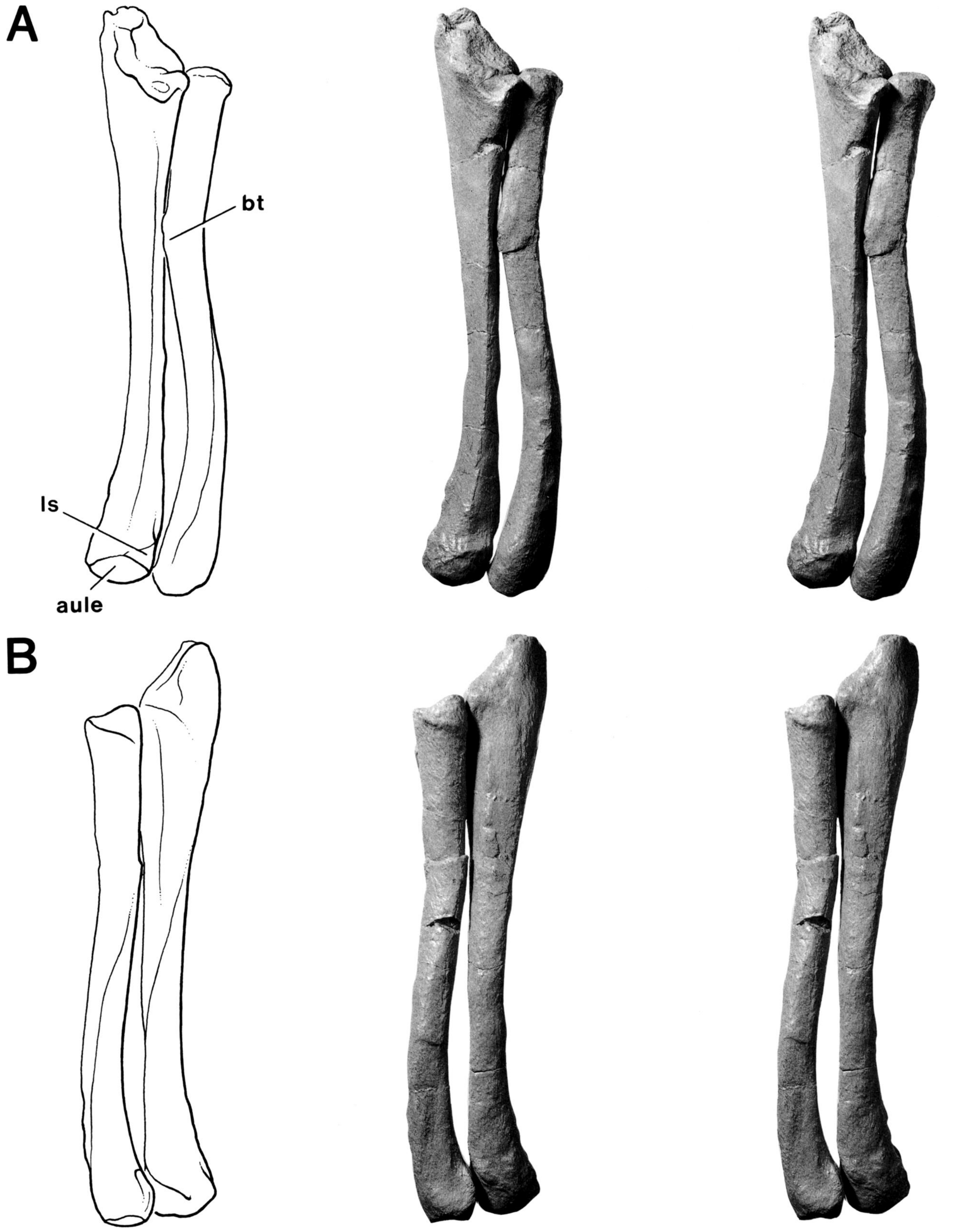

FIGURE 8. Stereopairs of the left radius and ulna of *Herrerasaurus ischigualastensis* (PVSJ 373) in anterior (**A**) and posterior (**B**) views. Abbreviations: **aule**, articular surface for the ulnare; **bt**, biceps tubercle; **ls**, ligament scars. Scale bar as in Figure 7.

anteromedial margin of the distal end is rugose and articulates in a shallow trough near the distal end of the ulna (Fig. 8).

Carpus—The carpus is known from one well-preserved, articulated left carpus (PVSJ 373), two additional left carpi (PVSJ 380, 407), and one disarticulated left radiale (MACN 18.060). Only two proximal carpals, the radiale and ulnare, are present. An intermedium, which occurs in some dinosaurs (e.g., *Camptosaurus*; Gilmore, 1909), is not present and has been lost or completely co-ossified with one of the proximal carpals. Five additional carpals are situated distal to the radiale and ulnare. One of these is situated between proximal and distal carpals and thus is identified as a centrale. The remaining four carpals articulate distally with the metacarpals and are identified by their position as distal carpals 1–4 (Fig. 9). Distal carpal 5 does not appear to have been present.

The radiale is the largest carpal and articulates proximally with the radius, laterally with the ulnare, and distally with the centrale and possibly also with the margins of distal carpals 1 and 2. The radiale has a tabular shape. The concave articular surface for the radius is oval in proximal view with angular medial and ventrolateral corners (Fig. 10B). The flat or gently concave articular surface for the ulnare is much smaller and is bevelled mediodistally. The oval distal articular surface is smaller than the proximal surface and is saddle-shaped; the dorsoventrally concave articular surface arches from the ventral side of the radiale, where it contacts the centrale, to the dorsal side, where it contacts the anterior margin of distal carpal 1 (Fig. 10A; MACN 18.060, PVSJ 373).

The ulnare is boat-shaped in lateral view (Fig. 12). The concave proximal surface is fitted to the rounded distal end of the ulna. In proximal view, it is elliptical with the long axis oriented dorsomedially. The lateral surface of the ulnare is gently arched dorsoventrally and is bevelled mediodistally, undercutting the proximal articular surface. A foramen opens into the ulnare on its lateral side (Fig. 12). The prominent dorsomedial apex of the ulnare does not articulate medially with the radiale. Contact with the radiale on its medial side is restricted, and a small foramen opens into the ulnare in this gap (Fig. 9A). The short medial articular surface of the ulnare is gently convex and fits tightly against the opposing surface of the radiale. The flat, nonarticular ventral surface of the ulnare angles ventrodistally and meets the medial surface along an angular corner. The concave distal articular surface, which is smaller than the proximal articular surface, is fitted to a broad, convex surface on distal carpal 4 (Figs. 11B, 12). The distal articular surface also contacts the centrale and distal carpals 2 and 3.

The wedge-shaped centrale inserts between the radiale and distal carpals 1 and 2. In articulation, the centrale is exposed only in ventral view (Fig. 9B). The dorsal portion of the centrale is thin and lodged in a hollow on the distal surface of the radiale.

The lozenge-shaped distal carpal 1 is the smallest distal carpal (Figs. 9A, 10A). It is approximately twice as deep dorsoventrally as broad transversely. Its gently convex proximal surface articulates against the centrale, and its distal surface overlaps the joint between metacarpals I and II. Distal carpal 1 appears to lie in natural articulation with metacarpals I and II in PVSJ 373.

Distal carpal 2 is larger and subrectangular in proximal view, with its major axis oriented dorsoventrally. It has an oval, nonarticular dorsal surface and a smaller subtriangular, nonarticular ventral surface (Figs. 9, 10A). Proximally, distal carpal 2 articulates primarily with the centrale but also contacts the dorsolateral corner of the radiale, the dorsomedial corner of the ulnare, and the dorsomedial corner of distal carpal 4. Distally, distal carpal 2 articulates primarily with metacarpal II but also overlaps the dorsomedial corner of metacarpal III and the ventromedial margin of distal carpal 3.

Distal carpal 3 is crescentic and only slightly longer dorsoventrally than distal carpal 1 (Figs. 9, 12). A small foramen opens into its ventral end. The proximal articular surface is transversely and dorsoventrally convex and articulates against the ulnare and distal carpals 3 and 4. The distal articular surface is concave dorsoventrally and gently convex transversely. It articulates primarily against the lateral margin of metacarpal III but also contacts metacarpal IV and possibly the edge of metacarpal V. The tip of distal carpal 3 is visible in dorsal view of the carpus (Fig. 9A).

Distal carpal 4 is the largest distal carpal and has an irregular shape (Figs. 9B, 10B, 11B, 12). In proximal view, distal carpal 4 is subquadrate, with a convex articular surface for the ulnare (Figs. 10B, 12). The distal surface is strongly bevelled laterodistally. It articulates primarily against distal carpals 2 and 3 but also contacts the lateral one-half of the proximal end of metacarpal IV and the rounded proximal end of metacarpal V (Fig. 11B). A subtriangular nonarticular surface on distal carpal 4 is exposed in ventral view of the carpus (Figs. 10B, 11B). The ventrolateral and ventromedial corners of this surface are developed as rounded prominences, which appear to have been positioned proximal to the bases of metacarpals IV and V, respectively.

Manus—The manus is preserved in three specimens (Figs. 13–15, Table 4), two of which are nearly complete (PVSJ 373, 380). Five digits are present. Digit III and metacarpal III are the longest manual digit and metacarpal. Digit II and metacarpal II and digit I and metacarpal I are successively shorter. The base of the metacarpus is transversely arched (Fig. 15B). Digits IV and V are very reduced and are positioned ventral to metacarpal III.

Metacarpal I is stout with a basal width and minimum shaft diameter greater than in the other metacarpals (Figs. 11, 14, 15). The proximal articular surface of metacarpal I is gently convex. The proximal one-third of the shaft has a subtriangular cross-section, with perpendicular lateral and ventral surfaces and a broad dorsomedial surface. The lateral side of the shaft

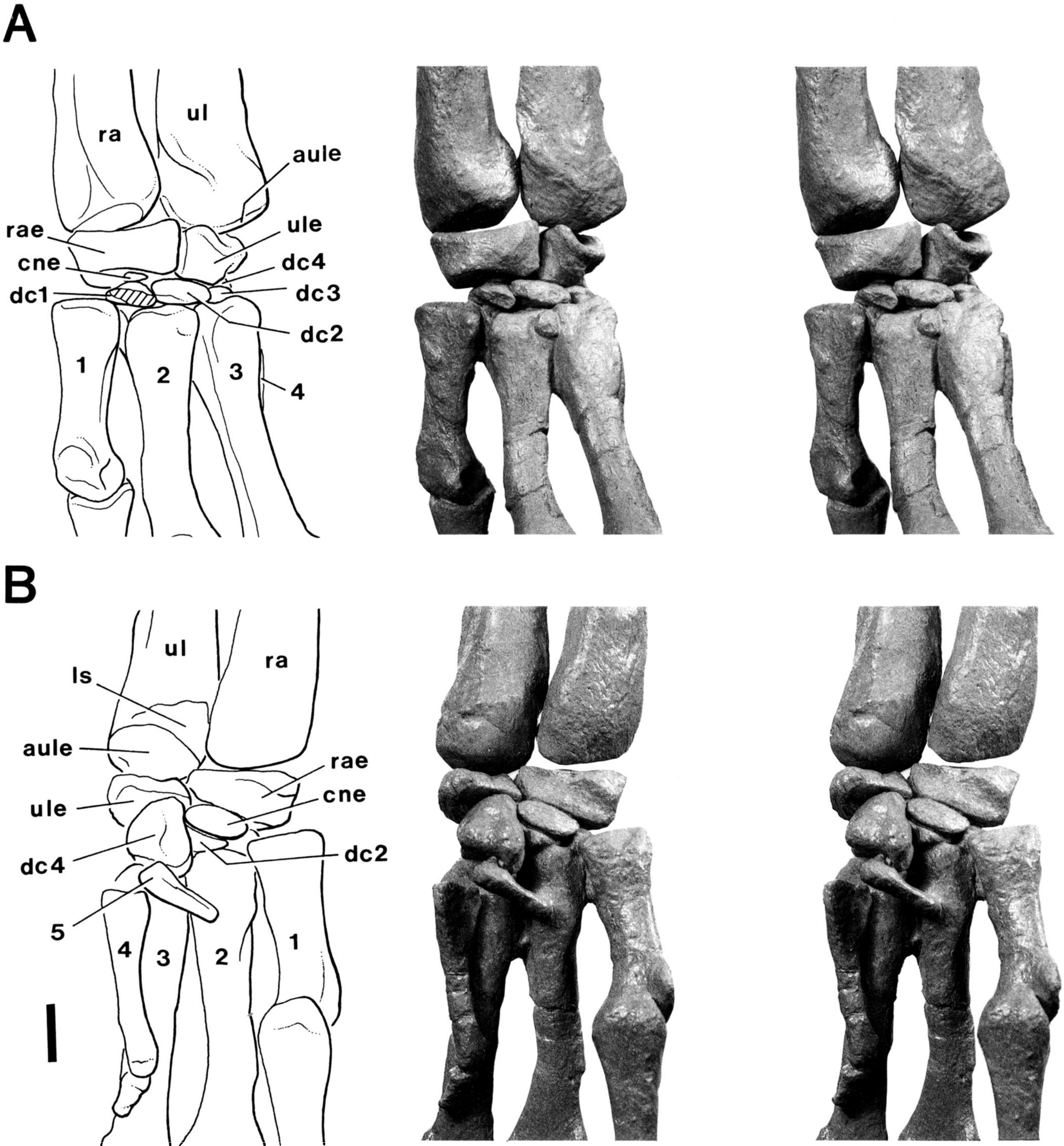

FIGURE 9. Stereopairs of the left wrist joint of *Herrerasaurus ischigualastensis* (PVSJ 373) in dorsal (**A**) and ventral (**B**) views. Cross-hatching indicates broken bone surface. Abbreviations: 1–5, metacarpals I–V; **aule**, articular surface for the ulnare; **cne**, centrale; **dc1-4**, distal carpals 1–4; **ls**, ligament scars; **ra**, radius; **rae**, radiale; **ul**, ulna; **ule**, ulnare. Scale bar equals 1 cm.

is flattened for articulation against metacarpal II (Figs. 14A, 15B). The lateral distal condyle extends farther distally than the medial distal condyle, such that in dorsal view the axis through the distal condyles is offset about 30° from the perpendicular to the shaft axis (Fig. 11A). In addition, the distal condyles are rotated relative to the proximal end. Using the vertical articular plane between metacarpals I and II to orient metacar-

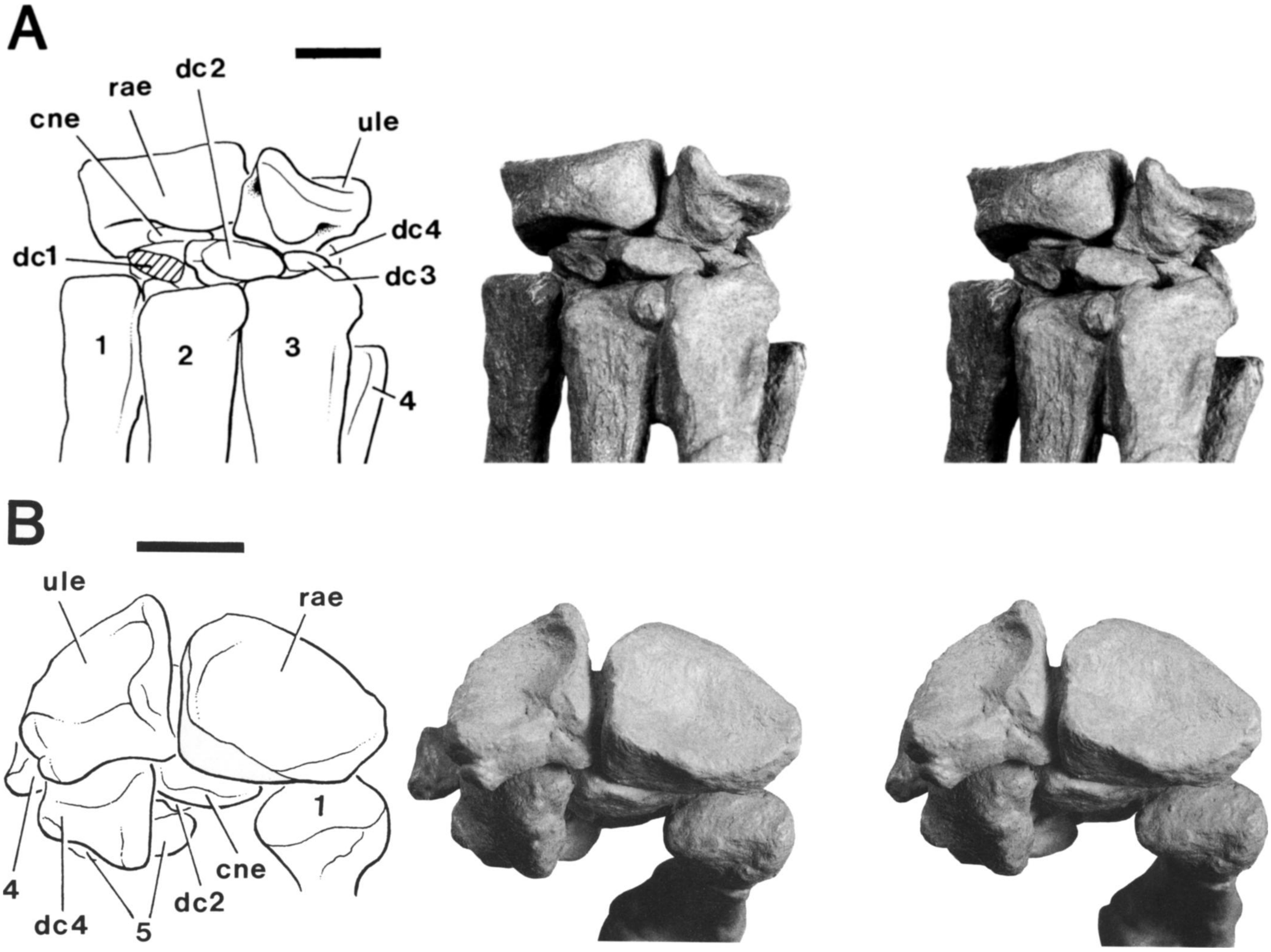

FIGURE 10. Stereopairs of the left carpus of *Herrerasaurus ischigualastensis* (PVSJ 373) in dorsal (**A**) and proximal (**B**) views. Cross-hatching indicates broken bone surface. Abbreviations as in Figure 9. Scale bars equal 1 cm.

pal I, the transverse axis through its distal condyles is rotated approximately 30 degrees counterclockwise from the horizontal (Fig. 14A). The lateral distal condyle is also deeper dorsoventrally and broader transversely than the medial distal condyle. A shallow, crescentic extensor depression is present with a low rim that arches across the dorsal surface of the distal end between the distal condyles (Figs. 11A, 15A).

Metacarpal II is more than 90 percent of the length of metacarpal III (Figs. 11A, 14, 15, Table 4). The proximal articular surface is flat and bevelled toward the dorsal edge. The proximal one-third of the shaft has a subrectangular cross-section, with the long axis oriented dorsoventrally (Fig. 14B). Medial and lateral sides of the proximal shaft are flattened for articulation against metacarpals I and III, respectively (Figs. 11A, 14B). In lateral view, the axis of the shaft is bowed ventrally (Fig. 14B). The distal condyles are rotated counterclockwise as in metacarpal I but to a lesser degree (Fig. 14A, B). The lateral distal condyle is broader transversely and extends slightly farther distally, as in metacarpal I (Figs. 11B, 14B). The dorsal extensor depression is deeper than in metacarpal I and is slightly asymmetrical, with a more complete rim on the medial side (Fig. 11A).

Metacarpal III has a concave proximal articular surface. The proximal one-third of the shaft is subtriangular in cross-section, with flat articular surfaces on the medial and ventrolateral sides for metacarpals II and IV, respectively (Figs. 11A, 12, 14C). The lateral shaft margin is sharp with a prominent rounded lip. In lateral view, the shaft is bowed ventrally as in metacarpal II. The lateral distal condyle is broader transversely than the medial distal condyle, and the distal condyles are rotated counterclockwise (Fig. 14C), as in metacarpals I and II. In contrast to metacarpals I and II, however, the medial distal condyle is deeper dorsoventrally and extends slightly farther distally. The dorsal extensor depression is as deep as that in metacarpal II (Fig. 11A).

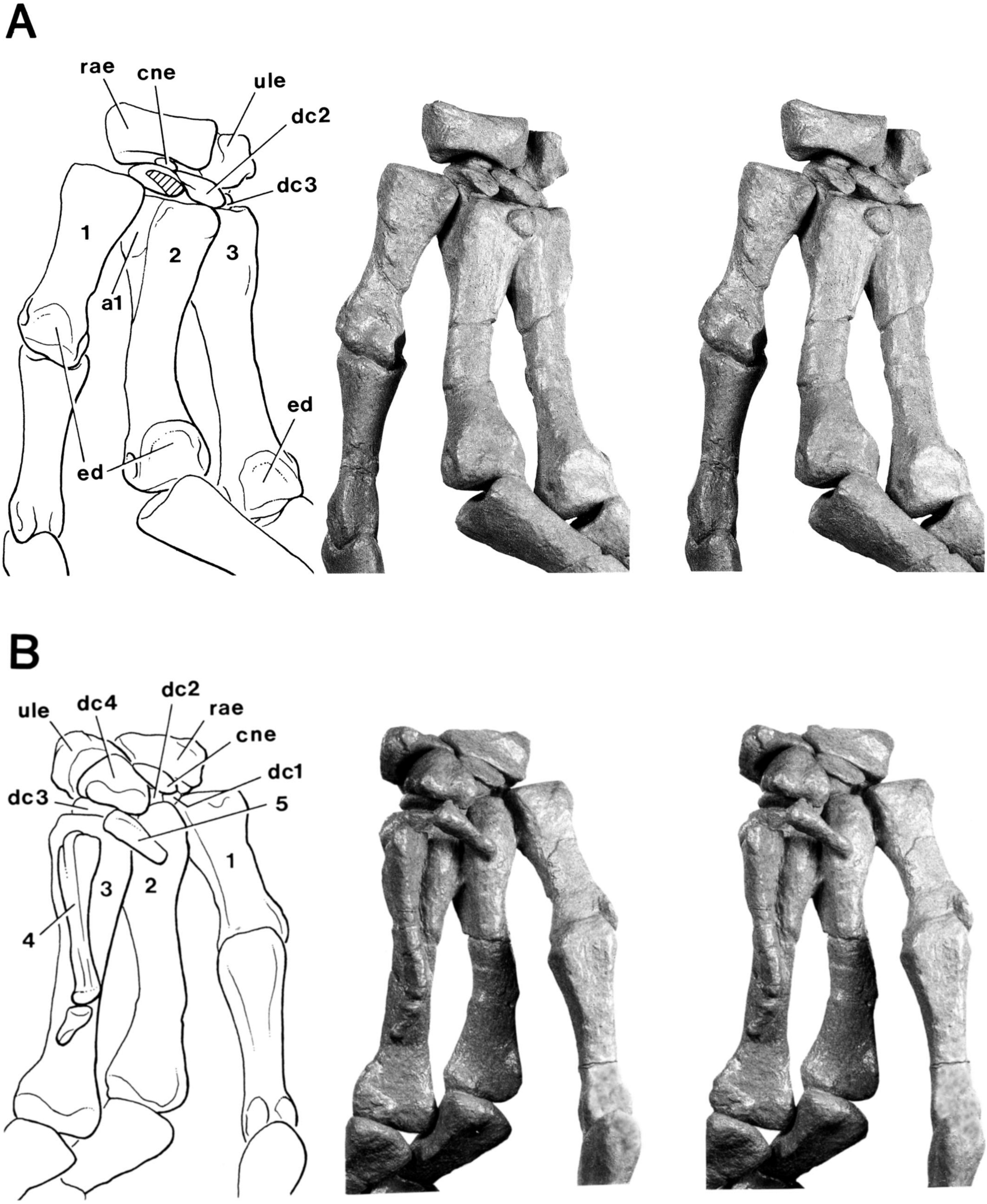

FIGURE 11. Stereopairs of the left carpus and metacarpals of *Herrerasaurus ischigualastensis* (PVSJ 373) in dorsal (**A**) and ventral (**B**) views. Cross-hatching indicates broken bone surface. Abbreviations: **a1**, articular surface for metacarpal I; **ed**, extensor depression. Other abbreviations and scale bar as in Figure 9.

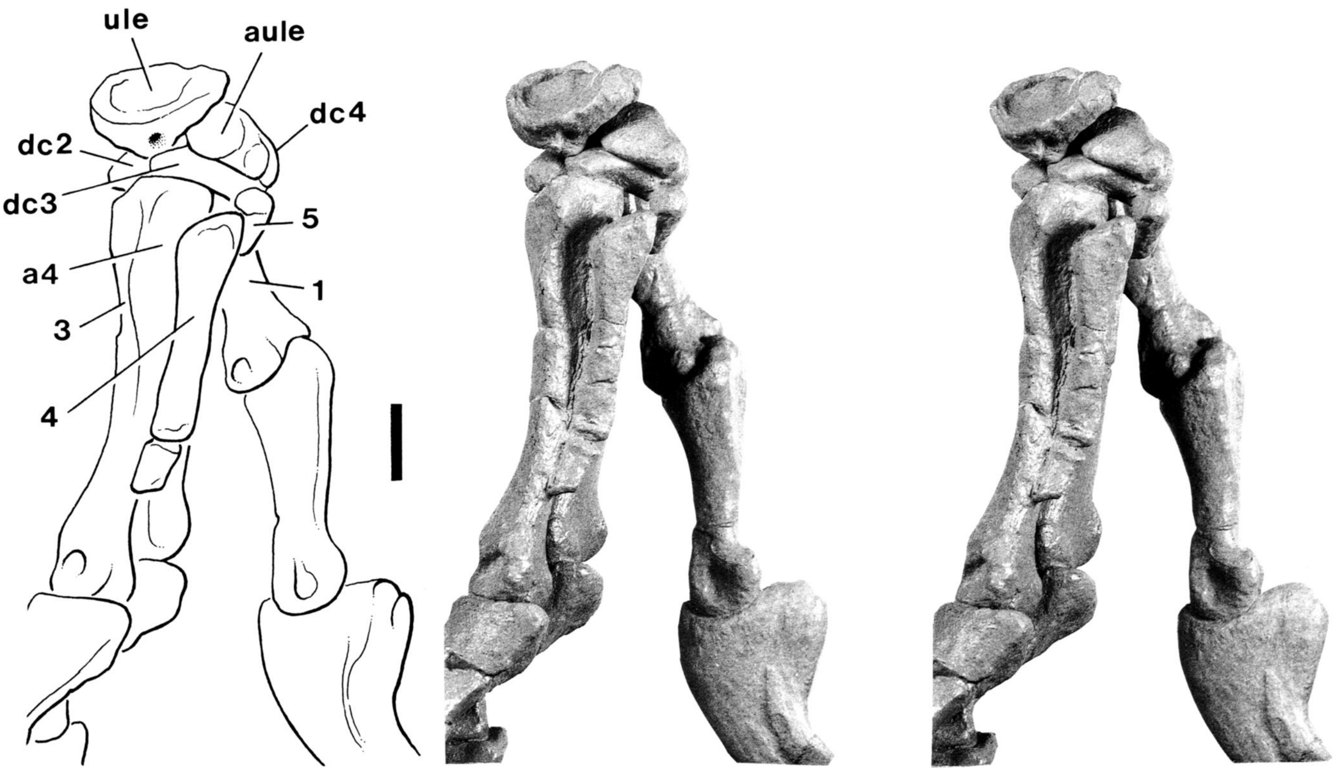

FIGURE 12. Stereopairs of the left carpals and metacarpals of *Herrerasaurus ischigualastensis* (PVSJ 373) in lateral view. Abbreviations as in Figure 9. Scale bar equals 1 cm.

Metacarpal IV is very slender and is just over one-half of the length and width of metacarpal III (Figs. 12, 14D). Metacarpal IV has the form of a miniature ulna. The flat, triangular proximal articular surface is inclined at approximately 45° from the prominent ventrolateral corner. Proximally, metacarpal III articulates with distal carpals 3 and 4. The proximal one-third of the shaft is subtriangular in cross-section, with a flattened dorsomedial surface that articulates against the ventrolateral side of metacarpal III. At mid-length, the shaft has a subcircular cross-section, and the distal one-third is dorsoventrally flattened. The rounded distal articular surface has rudimentary condyles but lacks collateral ligament pits.

Metacarpal V is rod-shaped and approximately one-half the length of metacarpal IV (Figs. 9B, 11B). The proximal end is somewhat bulbous, and both proximal and distal ends are rounded. The distal two-thirds of the shaft has an oval cross-section and is dorsoventrally flattened. Metacarpal V articulates proximally with the ventral surface of distal carpal 4 and possibly the lateral margin of distal carpal 3. It is positioned on the ventral aspect of the metacarpus and would not have been exposed in anterior view of the manus (Fig. 15A). Metacarpal V appears to have been oriented parallel to the other metacarpals (PVSJ 407).

The phalangeal formula is 2–3–4–1–0. The phalanges of the inner three digits are long and slender with well developed ginglymoid condyles, deep collateral ligament pits, and marked dorsal extensor pits (Figs. 13–15). The penultimate phalanges in digits I–III are elongate, exceeding the length of the preceding metacarpal or phalanx (Table 4). The relative length of the penultimate phalanx in digit III is variable; it exceeds the length of the preceding phalanx in PVSJ 380 but is subequal in PVSJ 373 (Table 4). The large unguals of digits I–III are strongly transversely compressed and recurved.

Phalanx 1 of digit I is approximately 115 percent of the length of metacarpal I. The proximal articular surface is subtriangular with a robust subrectangular ventral intercondylar process (Fig. 14A). As in all non-ungual phalanges, a shallow longitudinal depression is present on the ventral side of the shaft (deeper in PVSJ 380). The distal condyles are rotated approximately 15° in a clockwise direction relative to the base of the phalanx, which is opposite to the direction of rotation in the shaft of metacarpal I (Fig. 14A). The symmetrical distal ginglymoid is narrow and deeply cleft. During flexion of the phalanges of digit I, the rotation of the distal condyles results in medial deflection of the ungual.

The ungual of digit I is slightly shorter, deeper, and transversely thicker than the unguals of digits II and III (Fig. 14). In the larger manus PVSJ 380, the unguals are more recurved and the flexor tubercles are more

TABLE 4. Measurements (mm) of the manus in *Herrerasaurus ischigualastensis* (PVSJ 373, 380). Measurements are from the left side except as indicated otherwise. Ungual length is measured perpendicular to a chord across the proximal articular end. Abbreviations: r = right side; ( ) = estimated.

	Maximum length	
	PVSJ 373	PVSJ 380
Digit I		
Metacarpal I	37	44
Phalanx 1	42	56
Ungual	(36)	42
Digit II		
Metacarpal II	58	66
Phalanx 1	36	47
2	37	51
Ungual	(38)	47
Digit III		
Metacarpal III	62	74
Phalanx 1	34r	44
2	(28)	35
3	32	40
Ungual	(38)	—
Digit IV		
Metacarpal IV	33	—
Phalanx 1	10	—
Digit V		
Metacarpal V	15	—

prominent. The unguals are symmetrical about the sagittal plane and each has a well developed flexor tubercle and groove for the ungual sheath.

Phalanx 1 of digit II is shorter than phalanx 1 of digit I with more robust shaft dimensions (Fig. 14A, B). As in phalanx 1 of digit I, the proximal articular surface is subtriangular. The short ventral intercondylar process is subrectangular. The distal condyles are rotated clockwise approximately 10 to 15°, as in the proximal phalanx of digit I (Fig. 14A, B). The lateral distal condyle extends slightly farther distally than the medial distal condyle, and the medial collateral ligament pit is shallower than its opposite.

Phalanx 2 of digit II is subequal to, or slightly longer than, phalanx 1 (Fig. 14B). The triangular proximal articular surface of this phalanx, which is much narrower than in the proximal phalanges of digits I and II, is asymmetrical to accommodate the asymmetrical distal condyles of phalanx 1. The ventral intercondylar process is more pointed than in the preceding phalanx, and the apex is offset to the medial side (Fig. 15C). The distal condyles are symmetrical and are not rotated relative to the base of the phalanx, although the medial condyle is somewhat narrower and offset slightly dorsally relative to the lateral condyle.

The ungual of digit II is very similar to that of digit I. Indeed, it would be difficult to distinguish between the manual unguals were they disarticulated. As noted above, the proximal end is slightly shorter dorsoventrally and the ungual is somewhat longer than that in digit I, as measured along the perpendicular to a vertical line passing through the proximal articular surface (Table 4).

Phalanx 1 of digit III is slightly shorter than metacarpal I (Fig. 14C). The proximal articular surface is subtriangular, symmetrical, and proportionately broader than the bases of the other proximal phalanges. The distal condyles are asymmetrical, with the lateral distal condyle broader and extending farther distally than the medial distal condyle. As in the proximal phalanges of digits I and II, the distal condyles are rotated in a clockwise direction relative to the base of the phalanx (Fig. 14C).

Phalanges 2 and 3 of digit III are proportionately narrower than phalanx 1 (Fig. 14C). The medial distal condyle of phalanx 2 is somewhat broader and deeper than the lateral distal condyle. Phalanx 3 is longer than phalanx 2 and is slightly shorter than phalanx 1 (Table 4). The distal condyles of phalanx 3 are narrower than those in phalanges 1 and 2.

The ungual of digit III is slightly longer and more shallow than the unguals of digits I and II.

The single phalanx of digit IV is very short and reduced (Figs. 11B, 12, 14D). A low crest is present on the ventral aspect of the shaft. The distal end has a rounded articular surface without condyles. There are no additional phalanges in either digits IV or V (PVSJ 373, 380).

DISCUSSION

Phylogenetic Comparisons

In recent years, cladistic assessments of basal dinosaur phylogeny have placed *H. ischigualastensis* as an outgroup to Saurischia and Ornithischia (Gauthier, 1984, 1986; Gauthier and Padian, 1985; Brinkman and Sues, 1987; Benton, 1990; Sereno and Novas, 1990; Novas, 1992a). The discovery of more complete remains of *H. ischigualastensis* and of another primitive dinosaur, *Eoraptor lunensis,* has forced a re-assessment of this view. *H. ischigualastensis* and its contemporary *E. lunensis* both appear to represent basal theropods (Sereno and Novas, 1992; Novas, 1992b; Sereno et al., 1993). Several synapomorphies in the pectoral girdle and forelimb unite *H. ischigualastensis* and other theropods, such as the proportionately elongate manus (more than 50 percent of the length of the humerus plus radius; Fig. 16), extensor depressions on the distal ends of metacarpals I–III (Fig. 11A), and the extreme reduction of manual digits IV and V (Fig. 15, Table 5; Sereno et al., 1993:fig. 3). A full analysis of the theropod affinity of *H. ischigualastensis* will be presented elsewhere.

This paper concerns only the pectoral girdle and forelimb of *H. ischigualastensis.* The following discussion outlines eight autapomorphies in the pectoral girdle and forelimb of *H. ischigualastensis* (autapomorphies 1–8; see Appendix for character-state distributions). The pectoral girdle and forelimb in *H. is-*

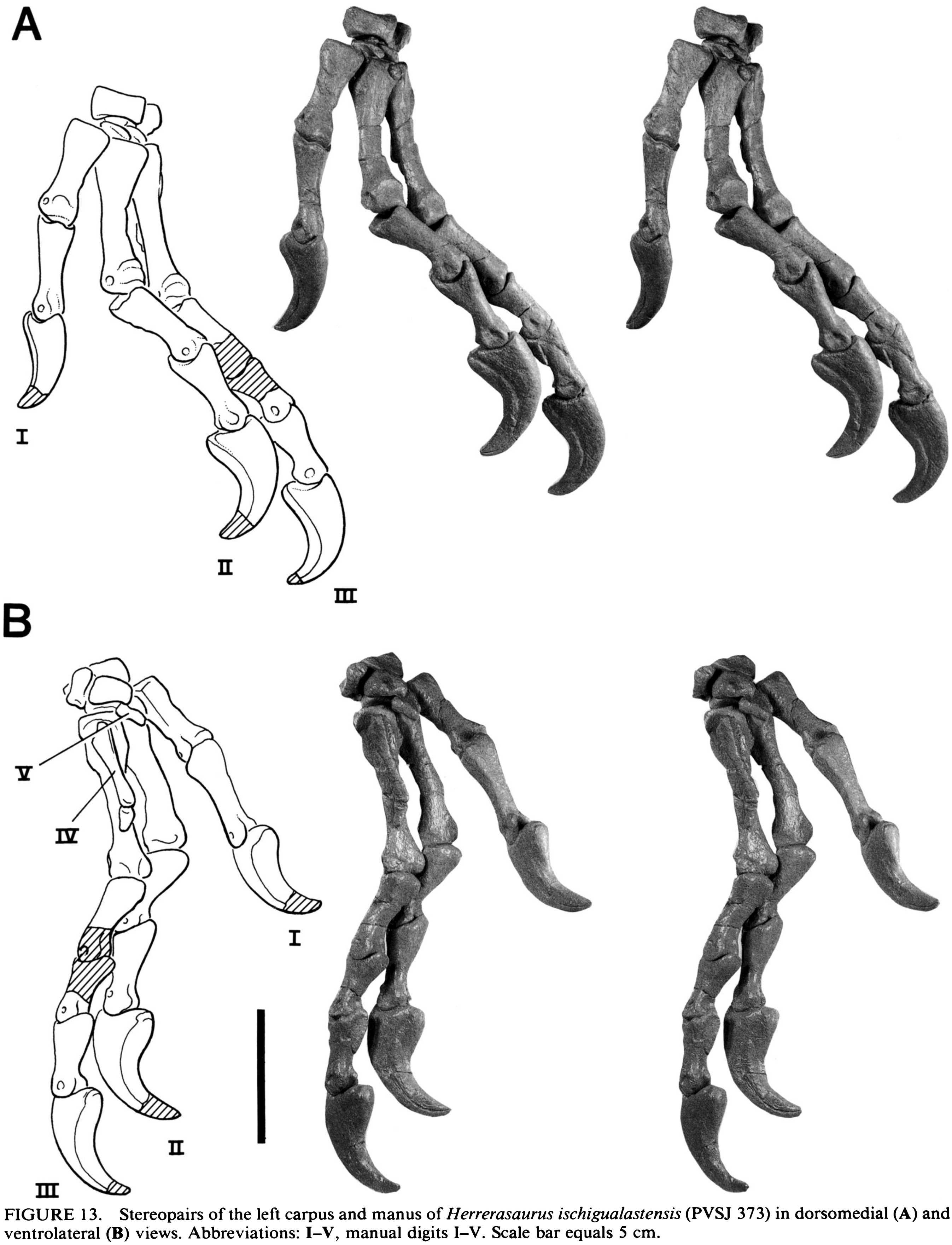

FIGURE 13. Stereopairs of the left carpus and manus of *Herrerasaurus ischigualastensis* (PVSJ 373) in dorsomedial (**A**) and ventrolateral (**B**) views. Abbreviations: **I–V**, manual digits I–V. Scale bar equals 5 cm.

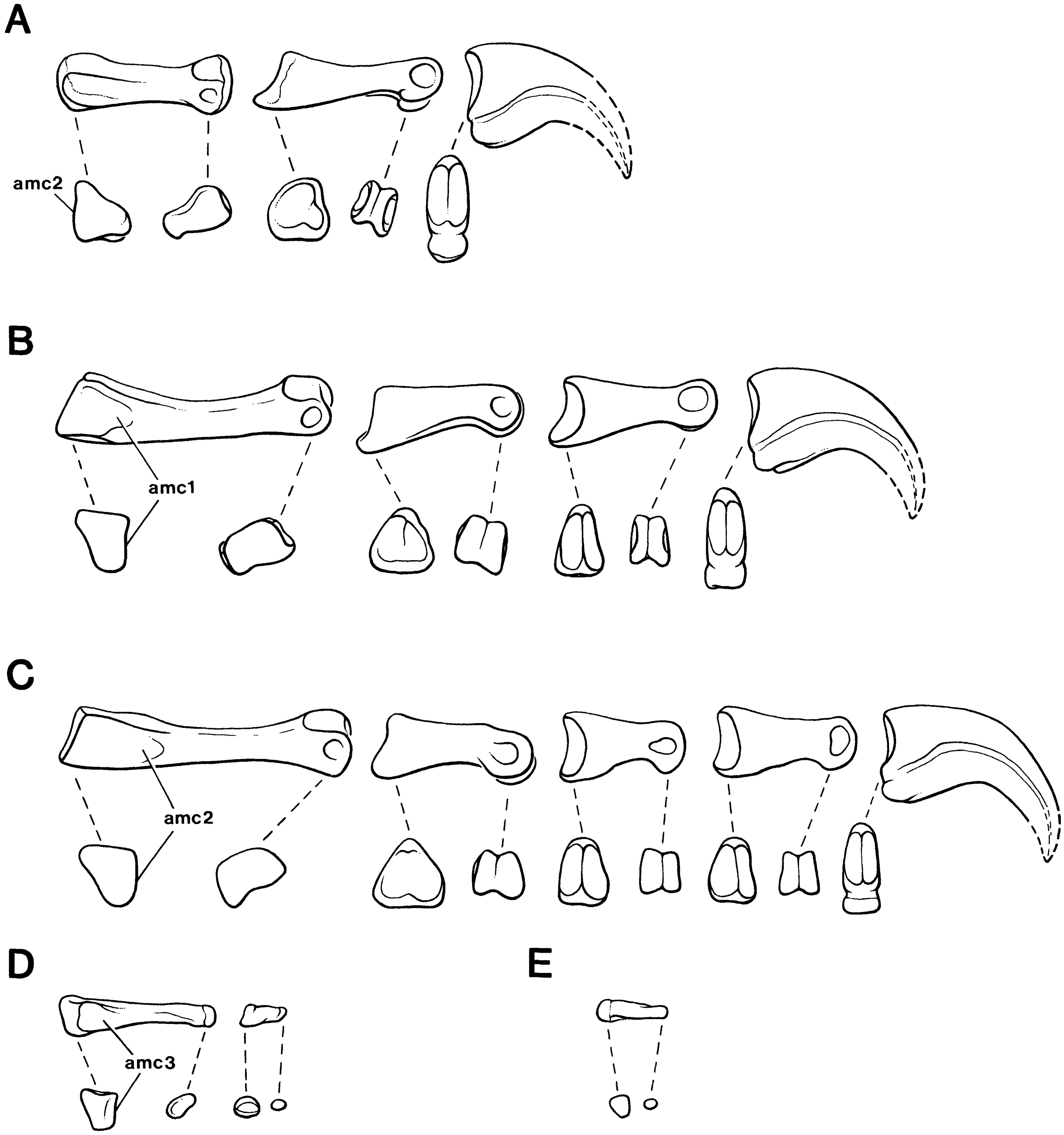

FIGURE 14. Metacarpals and phalanges of the left manus of *Herrerasaurus ischigualastensis* (PVSJ 373) in lateral view with proximal and distal views of each element. **A–E**, digits I–V, respectively. The bones are drawn in lateral view with the base of each element positioned in a horizontal plane, as seen in the proximal views. Distal views thus show the presence and magnitude of rotation in the shaft of each element. Portions of phalanges 1 and 2 in digit III are reversed from the right manus. Abbreviations: **amc1–3**, articular surface for metacarpals I–III.

chigualastensis also have important ramifications for character distributions at the base of Dinosauria. Two dinosaurian synapomorphies are described (synapomorphies 9, 10; see Appendix for character-state distributions), and previously cited dinosaurian synapomorphies in the pectoral girdle and forelimb are evaluated.

Autapomorphies in the Pectoral Girdle and Forelimb of *Herrerasaurus ischigualastensis*—(1) *Abrupt increase in width of scapula at acromion* (Figs. 1, 16). In *H. ischigualastensis,* the acromion expands abruptly from the anterior margin of the scapular blade at an angle that approaches 90°. The proximal portion of the left scapula in *Staurikosaurus* (MCZ 1669), in contrast,

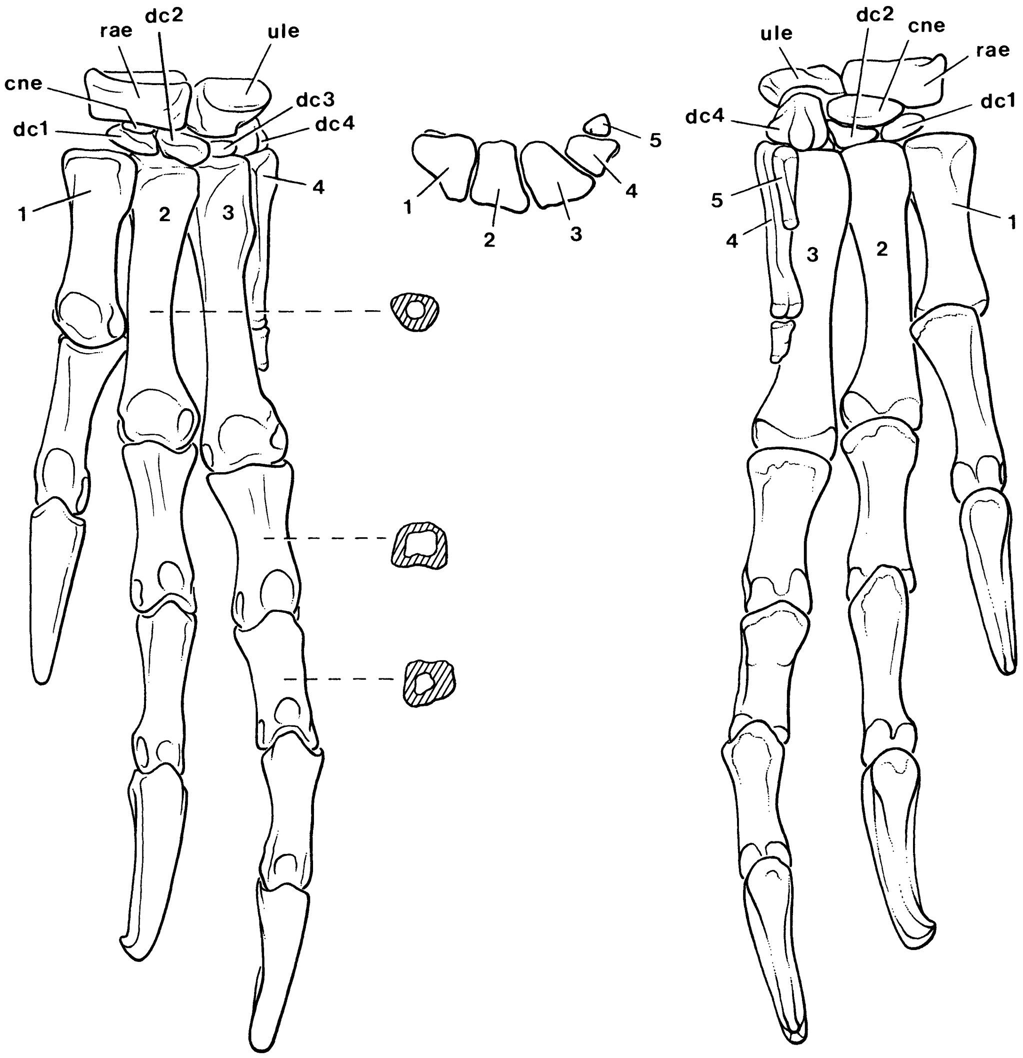

FIGURE 15. Reconstruction of the left carpus and manus of *Herrerasaurus ischigualastensis* (based on PVSJ 373). Left, dorsal view of left carpus and metacarpus; right, ventral view of carpus and metacarpus; center, proximal view of metacarpals I–V. Abbreviations as in Figure 9.

TABLE 5. Maximum length (mm), comparative ratios of metacarpals III–V, and manual phalangeal formula in *Herrerasaurus ischigualastensis* (PVSJ 373), other dinosaurs (*Lesothosaurus diagnosticus,* Sereno, 1991a; *Heterodontosaurus tucki,* Santa Luca, 1980; *Camptosaurus dispar,* Gilmore, 1909; *Massospondylus carinatus,* Cooper, 1981; *Coelophysis bauri,* Colbert, 1989), and pterosaurs (*Eudimorphodon ranzii,* Wild, 1978). Metacarpal measurements for *Massospondylus* are estimated from Cooper (1981:fig. 35), and the measurement for metacarpal III in *Eudimorphodon* is estimated from Wild (1978:fig. 17). Abbreviations: Mc = metacarpal; X = digit absent; ( ) = estimated.

	McIII	McIV	McV	McIV/McIII	McV/McIII	Phalangeal formula
Herrerasaurus	62	33	15	0.53	0.24	2-3-4-1-0
Coelophysis	36	32	—	0.89	—	2-3-4-1-X
Massospondylus	(49)	(44)	(27)	0.90	0.55	2-3-4-3-2
Lesothosaurus	13	9	5	0.69	0.39	2-?-?-?-1
Heterodontosaurus	21	15	8	0.75	0.38	2-3-4-2-1
Camptosaurus	76	60	40	0.79	0.53	2-3-4-2-1
Eudimorphodon	(25)	29	—	1.16	—	2-3-4-4-X

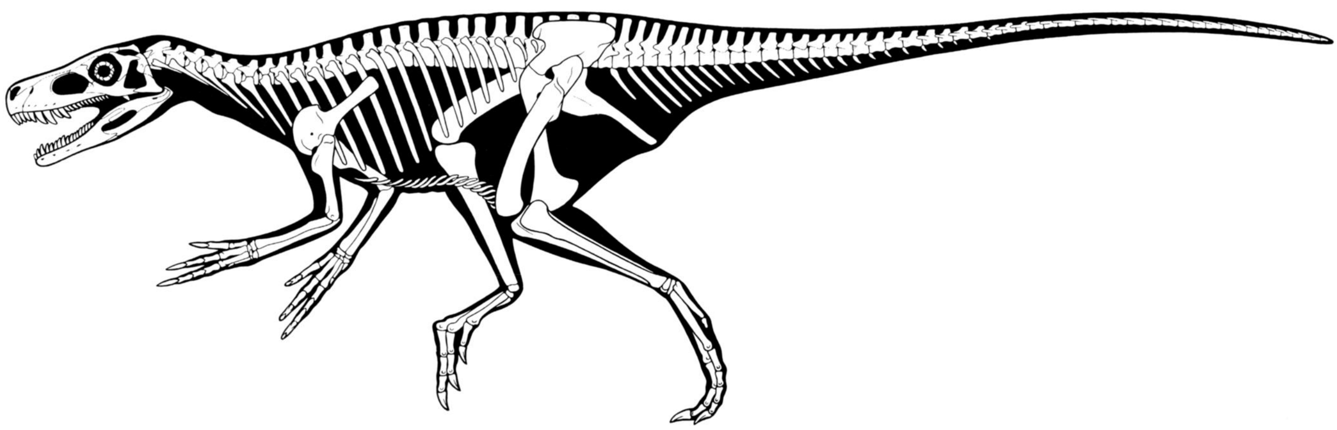

FIGURE 16. Skeletal reconstruction of *Herrerasaurus ischigualastensis* based on MCZ 7064, PVL 2566, PVSJ 53, 373, 407 (modified from Sereno and Novas, 1992).

does not appear to expand nearly as abruptly as in *H. ischigualastensis,* although it is only partially preserved. Nor does the acromion expand as abruptly in basal ornithischians (e.g., *Lesothosaurus, Heterodontosaurus*), basal sauropodomorphs (e.g., *Plateosaurus*), *Eoraptor* (Sereno et al., 1993), or ceratosaurian theropods (e.g., *Coelophysis, Dilophosaurus*). Abrupt expansion of the acromion also occurs in stegosaurs, sauropods, segnosaurs, and tyrannosaurids (Weishampel et al., 1990). Given their distant relationship to *H. ischigualastensis,* the condition of the acromion in this species must have arisen independently.

(2) *Humeral medial tuberosity prominent, separated by groove from head* (Fig. 3). In *H. ischigualastensis,* the medial tuberosity on the proximal end of the humerus projects proximally as a prominent process. In most dinosaurs, the medial tuberosity is low and poorly separated from the head of the humerus. In the ceratosaurians *Dilophosaurus* (UCMP 37302) and *Syntarsus* (Raath, 1977:fig. 13), the medial tuberosity is bulbous and separated from the humeral head by a trough. Nevertheless, other ceratosaurians (e.g., *Ceratosaurus,* UUVP 549) and other dinosaurs do not exhibit a hypertrophied medial tuberosity as occurs in *H. ischigualastensis.*

(3) *Circular pit on humeral ectepicondyle* (Fig. 5A). The distal end of the humerus has several unusual features in *H. ischigualastensis.* A circular pit is present on the margin of the ectepicondyle. A similar pit or depression has not been described in other dinosaurs.

(4) *Prominent humeral entepicondyle with anterior and posterior depressions* (Fig. 5B). The entepicondyle has anterior and posterior depressions that are located above another circular pit. The entepicondyle in the advanced ceratosaurian *Syntarsus* has these features (Raath, 1977:fig. 13), although they are absent in other theropods (e.g., *Dilophosaurus, Liliensternus, Coelophysis, Allosaurus*). The unusual form of the entepicondyle in *H. ischigualastensis* thus appears to have evolved in parallel in *Syntarsus.*

(5) *Saddle-shaped ulnar condyle of humerus* (Figs. 4A, 5C). The ulnar condyle is saddle-shaped, which appears to be unique among dinosaurs. In other dinosaurs, the ulnar condyle is convex. Because the forelimb is not known in *Staurikosaurus,* the autapomorphies in the humerus may eventually characterize other herrerasaurids.

(6) *Concavoconvex ulna–ulnare articulation with size disparity* (Figs. 9, 10B). In *H. ischigualastensis,* the ulna–ulnare articulation is strongly concavoconvex, with size disparity between opposing surfaces. The smaller concave articular surface of the ulnare must have slid across the larger convex surface at the distal end of the ulna (Fig. 17). This carpal configuration is not known elsewhere among dinosaurs. The carpus is not preserved in the immediate dinosaurian outgroups "*Lagosuchus*" and *Lagerpeton.* In pterosaurs, the ulna articulating in a concavity formed by the fused proximal carpals (Wellnhofer, 1978). The opposing surfaces, however, are equal in size, and there is no development of a sliding articulation like that in *H. ischigualastensis.*

(7) *Centrale distal to radiale* (Fig. 9). In *H. ischigualastensis,* a centrale is located distal to the radiale and is exposed only in posterior view, a carpal configuration that is unique among archosaurs. In dinosaurs, a centrale (i.e., an element situated between the proximal and distal carpals) has been described only in the ornithischian *Heterodontosaurus* and the ornithomimid *Struthiomimus.* In *Heterodontosaurus,* in contrast to the condition in *H. ischigualastensis,* the centrale is located distal to the ulnare (or co-ossified intermedium–ulnare; Santa Luca, 1980:fig. 15). In *Struthiomimus,* the centrale is located distal to the intermedium and lateral edge of the radiale (Nicholls and Russell, 1985:fig. 6). In *H. ischigualastensis,* in contrast, the centrale articulates in a ventrally facing concavity on the radiale. A centrale is absent in the well-ossified carpi of other basal dinosaurs (e.g., *Massospondylus,* Cooper, 1981; *Coelophysis,* Colbert, 1989; *Allosaurus,* Madsen, 1976; *Camptosaurus,* Gilmore, 1909).

(8) *Distal carpal 4 enlarged* (Figs. 9B, 12, 15C). Fi-

nally, in *H. ischigualastensis,* distal carpal 4 is large and specialized. It is the most massive distal carpal and projects posterior to the remainder of the carpus, supporting digits IV and V. In other saurischians, the number of distal carpals is reduced; distal carpal 5 is absent and distal carpal 4 is either reduced or absent (e.g., *Massospondylus,* Cooper, 1981; *Coelophysis,* Colbert, 1989; *Allosaurus,* Madsen, 1976; *Struthiomimus,* Nicholls and Russell, 1985). In some ornithischians, distal carpals 4 and 5 are present (e.g., *Heterodontosaurus,* Santa Luca, 1980; *Camptosaurus,* Gilmore, 1909) but they are not large. The size, shape, and position of distal carpal 4 in *H. ischigualastensis* are unique among dinosaurs. As is the case with several of these autapomorphies, the condition is not known in *Staurikosaurus* or in the dinosaurian outgroups "*Lagosuchus*" and *Lagerpeton.*

Dinosaurian Synapomorphies in the Pectoral Girdle and Forelimb—Bakker and Galton (1974) outlined a proposal for dinosaurian monophyly, and they and several subsequent authors have described or listed many dinosaurian synapomorphies. More than a dozen of these involve modifications in the pectoral girdle and forelimb (Table 6). Few of these characters could be investigated previously in herrerasaurids, because only the distal end of the scapula was described (Reig, 1963; Colbert, 1970; Reig also figured the humerus of *Ischisaurus cattoi,* now regarded as a junior synonym of *H. ischigualastensis*; Novas, 1993). The new material of *H. ischigualastensis* provides an opportunity to re-examine dinosaurian synapomorphies in the pectoral girdle and forelimb. Two synapomorphies are present in the dinosaurian forelimb (characters 9–10; see Appendix for character-state distributions).

(9) *Deltopectoral crest length 35 percent or more of humeral length.* In *H. ischigualastensis,* the length of the deltopectoral crest is more than 40 percent of the length of the humerus, as the chord from the proximal end of the humerus to the apex of the crest (Reig, 1963: fig. 5B). In the basal ornithischian *Lesothosaurus* (Thulborn, 1972) and in many other ornithischians (e.g., *Hypsilophodon,* Galton, 1974), the deltopectoral crest is approximately 35 percent of humeral length. In other ornithischians, prosauropods, and basal theropods, the length of the deltopectoral crest exceeds 40 percent that of the humerus. In contrast, the length of the deltopectoral crest in "*Lagosuchus*" (Bonaparte, 1975) is only 30 percent that of humeral length. In pterosaurs, the hatchet-shaped deltopectoral crest never exceeds 30 percent of humeral length and is usually considerably less (Wellnhofer, 1978). In crurotarsal archosaurs, the apex of the deltopectoral crest is proximally positioned with a length to the apex usually less than 25 percent of humeral length (e.g., *Parasuchus, Postosuchus*; Chatterjee, 1978, 1985). Bakker and Galton (1974; Table 6:character 7) first recognized the increased length of the deltopectoral crest among dinosaurs.

(10) *Manual digit IV only slightly longer than or shorter than metacarpal III with three or fewer phalanges* (Fig. 15; Table 6:character 13, in part). In *H. ischigualastensis* and other dinosaurs, the length of digit IV is reduced and the terminal ungual is absent. In *H. ischigualastensis* and nearly all other dinosaurs, manual digit IV is either shorter than, or only slightly longer than, metacarpal III. Dinosaurs only have three phalanges in digit IV, and the last phalanx is not an ungual. The manus in *Iguanodon* and hadrosaurs constitutes the single exception among dinosaurs, in which digit IV extends well beyond metacarpal III and often bears a flattened ungual. This condition constitutes a reversal that is related to the unusual digitigrade posture of the manus in these advanced ornithopods. Among dinosaurian outgroups, manual digit IV is considerably longer than metacarpal III. In pterosaurs, four phalanges are present in manual digit IV (Wellnhofer, 1978), and there appears to be four (or possibly five) phalanges in this digit in crurotarsal archosaurs (Chatterjee, 1978, 1985), although articulated external digits among basal archosaurs are rare.

The additional dinosaurian synapomorphies cited in the pectoral girdle and forelimb are problematic. The absence of an interclavicle, an elongate scapular blade, a relatively short forelimb, and a hatchet-shaped deltopectoral crest (Table 6:characters 1, 3–6) characterize more inclusive groups within Archosauria and have been discussed at length elsewhere (Sereno, 1991b). A posteroventrally facing glenoid (Table 6:character 2), likewise, is not a dinosaurian synapomorphy because the glenoid faces posteriorly and ventrally, rather than laterally, in the dinosaurian outgroup "*Lagosuchus*" (Bonaparte, 1975) and in many crurotarsal archosaurs. The laterally facing glenoid in pterosaurs is a modification for flight and does not represent the plesiomorphic condition for Ornithodira.

TABLE 6. Pectoral girdle and forelimb characters cited by previous authors as dinosaurian synapomorphies. Author abbreviations are listed parenthetically in chronological order. Abbreviations: B1 = Benton, 1984; B2 = Benton, 1990; BG = Bakker and Galton, 1974; G = Gauthier, 1986; GP = Gauthier and Padian, 1985; N = Novas, 1992a; P1 = Paul, 1984a; P2 = Paul, 1984b.

Pectoral girdle

1. Clavicle–interclavicle brace absent (P2).
2. Posteroventrally facing glenoid (BG, P1, B2).
3. Scapula at least 3 times longer than basal width (G).
4. Elongate coracoid (P2).

Forelimb

5. Forelimb about one-half as long as hind-limb (B1).
6. Hatchet-shaped deltopectoral crest (P1).
7. Elongate deltopectoral crest (BG, B1, B2).
8. Digit I medially divergent (BG, P1).
9. Metacarpal I short and stout (BG).
10. Phalanx 1 of digit I long and strong (BG).
11. Ungual of digit I trenchant (BG).
12. Digits II and III long, subparallel, and subequal (BG).
13. Digits IV and V short or reduced (BG, GP, G, N, B2).
14. Unguals enlarged (P1).

The medial divergence of manual digit I and the relative size of its ungual have been cited alternatively as a saurischian synapomorphy (Gauthier, 1986:17), a dinosaurian synapomorphy (Table 6:characters 8, 11), or a synapomorphy of a more inclusive group including all ornithodirans (Gauthier, 1986:43). Indeed, medial offset of the distal condyles of metacarpal I may also characterize primitive archosauriforms (Sereno and Arcucci, 1990:32–33). It has not been established that the distal condyles of metacarpal I are offset in a peculiar fashion in all dinosaurs. An enlarged ungual on digit I is problematic as a dinosaurian synapomorphy, given the small ungual in basal ornithischians (Sereno, 1991a) and the presence of a large ungual in pterosaurs (Wild, 1978). The manus, furthermore, is not preserved in the immediate dinosaurian outgroups "*Lagosuchus*" and *Lagerpeton.*

Many of the remaining proposed dinosaurian synapomorphies do not appear to accurately describe anatomical variation in basal dinosaurs or dinosaurian outgroups. The coracoid, for example, has been cited both as more elongate in dinosaurs (Table 6:character 4) or as smaller with a subcircular profile (Gauthier, 1986:43, Ornithodira). The relative size or shape of the coracoid does not appear to be diagnostic for Dinosauria. Likewise, strong recurvature of the manual unguals (Table 6:characters 11, 14) probably constitutes a theropod (Gauthier, 1986:21), rather than a dinosaurian, synapomorphy. The manual unguals are strongly recurved in *H. ischigualastensis,* in other theropods, and in digit I of prosauropods, but are not so recurved in most ornithischians. Among dinosaurian outgroups, pterosaurs (Wellnhofer, 1978) and possibly ornithosuchids (Walker, 1964:fig. 10f) have strongly recurved manual unguals. The condition is unknown in the dinosaurian outgroups "*Lagosuchus*" and *Lagerpeton,* which most likely were predatory bipeds that may well have had recurved manual unguals for prey capture.

Shortening of metacarpal I has been suggested as a dinosaurian synapomorphy (Table 6:character 9). Metacarpal I is short in *H. ischigualastensis* and in other theropods (less than 65 percent of the length of metacarpals II or III in *H. ischigualastensis* and *Coelophysis bauri*; Colbert, 1989) but is longer in basal ornithischians and sauropodomorphs (less than 75 percent of the length of metacarpals II or III in *Lesothosaurus diagnosticus* and about 85 percent in *Massospondylus carinatus*; Sereno, 1991a; Cooper, 1981). Among dinosaurian outgroups, the manus is not preserved in "*Lagosuchus*" and *Lagerpeton.* In pterosaurs, metacarpal I is subequal to metacarpals II and III, but in more distant outgroups metacarpal I is significantly shorter than either metacarpals II or III (e.g., *Parasuchus,* Chatterjee, 1978; *Euparkeria,* Ewer, 1965). Thus, it is possible that metacarpal I was significantly shorter than metacarpals II and III among dinosaurian precursors.

The unusual length of phalanx 1 of digit I in the manus has been cited as a dinosaurian synapomorphy (Table 6:character 10) or alternatively as a saurischian synapomorphy (Gauthier, 1986:17). In *H. ischigualastensis* and other theropods, phalanx 1 indeed is long relative to metacarpal 1; phalanx 1 is at least 90 percent, and often more than 100 percent, of the length of metacarpal I in *H. ischigualastensis* (114 percent) and other theropods (e.g., *Coelophysis,* 107 percent) and is longer than other proximal phalanges in the manus. The unusual length of phalanx 1 in theropods, however, appears to be correlated with elongation of the penultimate phalanges in digits II and III as an adaptation for grasping (Gauthier, 1986:20; cited as a theropod synapomorphy). Thus the penultimate phalanges in digits II and III are also longer than preceding phalanges in *Herrerasaurus* and other theropods and independently in the ornithischian *Heterodontosaurus,* all of which have a long grasping manus. Among other dinosaurs, phalanx 1 is long relative to metacarpal I only in forms in which digit I is hypertrophied compared to other manual digits (prosauropods, *Psittacosaurus*) or undergoing reduction and co-ossification (*Camptosaurus*). In these cases, the penultimate phalanges of digits II and III are not longer than preceding phalanges. Among dinosaurian outgroups, it is clear that the penultimate phalanges of manual digits I–III are elongated in all pterosaurs (Wild, 1978; Wellnhofer, 1978; Gauthier, 1986) but not among crurotarsal archosaurs. Thus, elongation of the penultimate phalanges (including phalanx 1 of digit I) appears to be correlated with a grasping manus in pterosaurs, *Heterodontosaurus,* and theropods and is absent plesiomorphically in ornithischians (e.g., *Lesothosaurus*; Sereno, 1991a) and sauropods (e.g., *Shunosaurus*; Zhang, 1988). Elongation of phalanx 1 of digit I does not constitute an unequivocal dinosaurian or saurischian synapomorphy.

Reduction in manual digits IV and V compared to digits II and III is often cited as a dinosaurian synapomorphy (Table 6:characters 12, 13). A good case can be made supporting the reduction in length and loss of the terminal ungual in digit IV as a dinosaurian synapomorphy (see synapomorphy 10 above), acknowledging the fact that the manus is not preserved in the immediate dinosaurian outgroups "*Lagosuchus*" and *Lagerpeton.* Reduction of digit V, however, cannot be substantiated as a dinosaurian synapomorphy for the following reasons. Among major dinosaurian subgroups, digit V is consistently reduced or absent only in theropods (Gauthier, 1986:20). In most ornithischians, in contrast, the shaft diameter of metacarpal V is not drastically reduced compared to metacarpals II and III, and the shaft length often approaches 50 percent that of metacarpal III (e.g., *Lesothosaurus, Hypsilophodon, Camptosaurus*; Sereno, 1991a; Galton, 1974; Gilmore, 1909). In sauropodomorphs, the shaft diameter of metacarpal V is subequal to that in metacarpal III, and the shaft length exceeds 50 percent of the latter (e.g., *Massospondylus, Shunosaurus*; Cooper, 1981; Zhang, 1988).

Considering phalangeal number in manual digit V, several ornithischians and sauropodomorphs retain two phalanges (e.g., *Heterodontosaurus, Camptosaurus, Massospondylus, Shunosaurus*; Santa Luca, 1980; Gilmore, 1909; Cooper, 1981; Zhang, 1988). Although these phalanges are reduced and do not include a terminal ungual, it has not been established that the phalanges are any better developed in dinosaurian outgroups. The manus is not preserved in "*Lagosuchus*" or *Lagerpeton,* and in pterosaurs digit V is absent (Wellnhofer, 1978). In some crurotarsal archosaurs, phalangeal number is reduced (e.g., *Riojasuchus,* Sereno, 1991b). In extant crocodilians, manual digit V usually retains three phalanges including a reduced ungual (Romer, 1956:fig. 183), although digit V is slender and only one-half the length of digit III (Romer, 1956: 408). In summary, there is no convincing evidence to support as dinosaurian synapomorphies reduction in the strength and/or length of either digit V or metacarpal V or reduction in the number of phalanges in digit V.

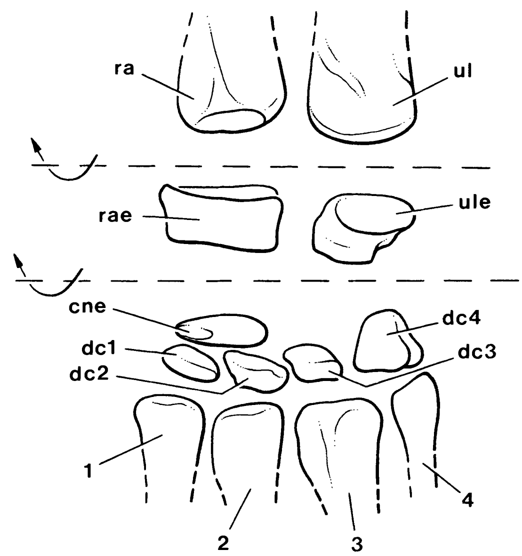

FIGURE 17. "Exploded" view of left wrist joint in *Herrerasaurus ischigualastensis,* showing the two principal axes of flexion and extension. The proximal rotational axis (located proximal to the wrist, with the forelimb in natural articulation) permitted approximately 30–35° of flexion of the carpus and manus against the forearm. The distal rotational axis (located distal to the wrist, with the forelimb in natural articulation) permitted approximately 10–15° of flexion of the centrale, distal carpals, and manus against the forearm and proximal carpals. Abbreviations as in Figure 9.

Forelimb Function

Elbow Joint—Manipulation of the distal end of the humerus and the radius and ulna (Fig. 6) suggests that the forearm could flex and extend against the humerus through an arc of approximately 60° but could not rotate about its long axis. Maximum extension appears to occur when the radius and ulna are inclined at approximately 30° to the long axis of the humerus, as seen in lateral or medial views (further extension results in disarticulation of the radial condyle of the humerus and the proximal end of the radius). Maximum flexion appears to occur when the radius and ulna are positioned at approximately 90° to the long axis of the humerus (additional flexion results in disarticulation of the ulnar condyle of the humerus and the proximal end of the ulna).

The structure of the elbow joint does not permit rotation about the axis of the forearm (i.e., pronation–supination of the manus). Rotation is prevented by the form of the articulations between the humerus and radius and between the radius and ulna. The saddle-shaped radial condyle on the humerus (Fig. 5C) limits movement of the concave proximal end of the radius to flexion and extension rather than rotation. The flat articular surface between the proximal ends of the radius and ulna (Fig. 7) does not permit rotation without disarticulation. In natural position, the manus would be positioned close to a vertical plane (Fig. 16), with the palmar surface facing medially and slightly ventrally (depending on the degree of adduction of the elbow joint).

Wrist Function—The well-ossified carpus in *H. ischigualastensis* appears to be divided into two functional units, one composed of the proximal carpals and the other composed of the centrale and distal carpals (Fig. 17). The radiale and ulnare have smooth proximal articular surfaces that permit dorsoventral flexion and extension of the carpus and manus against the forearm (Fig. 17, proximal axis). Evidence for this rotary articulation is most apparent in the ulnare, the concave proximal surface of which slid against a larger convex articular surface on the distal end of the ulna. The articular surface on the ulna for the ulnare is positioned on the posterior aspect of its distal end (Fig. 9B). Maximum extension of the carpus and manus at this joint, therefore, would occur with the manus and forearm positioned in a single plane (Fig. 9). The radiale has a transversely elongate, concave proximal articular surface (Fig. 10B) that appears to have functioned in unison with the ulnare (Fig. 17). In contrast to the ulnare, however, the radiale must have slid against a cartilage pad at the distal end of the ulna, because the opposing surface at the distal end of the radius is flat and pitted (Fig. 9A).

A second rotational articulation is present between the proximal carpals and the centrale and distal carpals (Fig. 17, distal axis). The smooth, convex proximal articular surfaces of the centrale and distal carpals slid against smooth, concave distal surfaces on the radiale and ulnare (Figs. 10–12). These articular surfaces are approximately equal in area, which suggests that maximum movement along this second joint was less than that between the forearm and proximal carpals. With maximum flexion of both carpal units, the manus would rotate posteriorly to an angle of approximately 45° to the axis of the forearm. The second rotational articulation may also have permitted limited inversion and eversion of the manus, because the conjoined proximal articular surfaces of the centrale and distal carpals is transversely convex (Fig. 10A).

The function of the wrist joint described above in *H. ischigualastensis* is unusual among dinosaurs, which usually show a close functional union between the forearm and proximal carpals. It also differs markedly from the form and function of the carpus in maniraptoran theropods, which have eliminated flexion and extension of the manus at the wrist joint in favor of inversion and eversion (Ostrom, 1969).

Manual Grasping and Raking—The length of the forelimb and proportions within the forelimb suggest that the manus was specialized for powerful grasping and raking. The forelimb is less than one-half of the length of the hind-limb (Table 2, Fig. 16) and thus is clearly specialized for prey capture and manipulation rather than locomotor support. Within the forelimb, the proximal segments are short, increasing the mechanical advantage of proximal forelimb muscles. Thus the ulna and radius nearly equal the humerus in length, the manus exceeds both the humerus, ulna, and radius in length, and phalangeal length in digits I–III is substantially greater than their respective metacarpal lengths. The presence of powerful forelimb musculature is suggested by the stout proportions of the humerus, ulna, and radius and marked muscular and ligament attachments, such as the prominent, strongly deflected deltopectoral crest, elaborate epicondylar rugosities, and well-developed biceps tubercle on the radius.

Grasping movement is enhanced by the flexible carpus, the elongate penultimate phalanges in digits I–III, and the convergence of these digits toward the center of the palm during flexion. Because the interphalangeal joints are nearly symmetrical, deflection of the digits during flexion is due to asymmetry in the distal condyles of the metacarpals. The medial distal condyle in metacarpals I and II is shorter, deflecting the phalanges of digits I and II laterally during flexion, whereas the lateral distal condyle of metacarpal III is slightly shorter, deflecting the phalanges of this digit medially during flexion.

Digits I–III also converge during extension, which presumably would enhance raking function. Marked extensor depressions on the distal ends of metacarpals I–III suggest that the phalanges of digits I–III could be extended to an angle nearly perpendicular to their respective metacarpals. In this hyper-extended position, the unguals of digits I–III would converge toward one another, as occurs in other theropods (e.g., *Syntarsus,* Galton, 1971; *Dilophosaurus,* Welles, 1984). The unguals of digits II and III converge to form a functionally unified raking claw. Trenchant unguals also enhance grasping and raking functions.

CONCLUSIONS

New specimens provide a detailed understanding of the morphology and function of the pectoral girdle and forelimb in the basal theropod *H. ischigualastensis.* Two aspects of the forelimb appear to constitute dinosaurian synapomorphies, an increase in the length of the deltopectoral crest to 35 percent of humeral length and reduction in the length and distal phalanges of manual digit IV. In other regards, the pectoral girdle and forelimb clearly resemble that in other theropods, as shown by the strap-shaped scapular blade, elongate manus, strong reduction of digits IV and V, metacarpal extensor depressions, hollow phalanges, elongate penultimate phalanges, and trenchant unguals.

The forearm is stiff and is incapable of significant pronation or supination of the manus. The carpus is divided into two functional units and appears to be capable of flexing the manus against the forearm at an angle of approximately 45°. In contrast to the condition in maniraptoran theropods, inversion and eversion of the manus appears to have been restricted. The manus is specialized for grasping and raking as in other theropods, with the trenchant unguals of digits I–III converging upon flexion or extension.

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APPENDIX

CHARACTERS AND TAXON–CHARACTER MATRIX

The coding and distribution of 10 characters is shown below for *Herrerasaurus ischigualastensis, Staurikosaurus pricei,* other basal dinosaurs (*Coelophysis bauri, Plateosaurus engelhardti, Lesothosaurus diagnosticus*), "*Lagosuchus*" *lilloensis,* pterosaurs, and crurotarsal archosaurs. This information is tabulated to show the distributions of character-states discussed in the text; it is not a matrix for the analysis of basal dinosaur phylogeny. *Lagerpeton chanarensis* is not included because none of the pectoral girdle or forelimb is preserved. Characters 1–8 are interpreted as autapomorphies of *H. ischigualastensis* and are included in a revised diagnosis of this species (Sereno, in preparation). Characters 9 and 10 are interpreted as dinosaurian synapomorphies that unite *H. ischigualastensis* and other dinosaurs. "*Lagosuchus*" *lilloensis* and pterosaurs serve as successive outgroups (Sereno, 1991b; Novas, 1992a). Character information for basal dinosaurs is based on Colbert (1970, 1989), Galton (1977), Huene (1926), Madsen (1976), Reig (1963), Sereno (1991a), and Thulborn (1972).

Herrerasaurus ischigualastensis

1. Anterior contour of scapula from blade to acromion: gradual expansion to acromion (0); abrupt increase in width (1).
2. Humeral medial tuberosity: low, rounded (0); prominent, separated by groove from head (1).
3. Circular pit on distal margin of humeral ectepicondyle: absent (0); present (1).
4. Prominent humeral entepicondyle with anterior and posterior depressions: absent (0); present (1).
5. Ulnar condyle of humerus: rounded (0); saddle-shaped (1).
6. Ulna–ulnare articular surface: subplanar (0); concavoconvex with size disparity (1).
7. Centrale distal to radiale: absent (0); present (1).
8. Distal carpal 4 size: less than (0), or more than (1), one-half of the ulnare.

Dinosauria

9. Deltopectoral crest length (humeral head to crest apex): less than 30 percent (0), or 35 percent or more (1), of humeral length.
10. Manual digit IV length and number of phalanges: much longer than metacarpal III, with 4 phalanges (0); slightly longer or shorter than metacarpal III, with 3 or fewer phalanges (1).

	Characters	
Taxa	5	10
Herrerasaurus ischigualastensis	11111	11111
Staurikosaurus pricei	0????	?????
Coelophysis bauri	00000	00011
Plateosaurus engelhardti	00000	00011
Lesothosaurus diagnosticus	10000	00?1?
"*Lagosuchus*" *lilloensis*	00000	00?0?
PTEROSAURIA	00000	00000

Character-state abbreviations: 0 = plesiomorphic state; 1 = apomorphic state; ? = not preserved/unknown.