American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2439 NOVEMBER 12, 1970

A Pseudoarthrosis in the Forelimb of a Sloth (*Choloepus didactylus*)

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INTRODUCTION

One of the several mechanisms of physiological adaptation possessed by vertebrate bony tissue is its potential to develop an articulation when the surfaces of two bones rub against each other (Murray, 1937; Bock and von Wahlert, 1965). Articulations developing in this manner are grouped together under the general heading of pseudoarthroses, although their structure can vary from synarthroses to diarthroses. Typically, pseudoarthroses are the results of fractures in bones that failed to unite and fuse solidly so that the broken ends of the bones continue to rub against each other. Less common are pseudoarthroses resulting from the rubbing together of undamaged surfaces of two bones that are brought into contact because of a dislocation of an articulation or because of excessive growth of a bone. Although both types of pseudoarthrosal development are of interest to the student of comparative vertebrate morphology and evolution, the second method (contact of undamaged bony surfaces) is of far greater importance.

Hence any examples of natural pseudoarthroses resulting from the dislocation of joints and subsequent rubbing of the bones is of significance.

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The pseudoarthrosis on the elbow joint of a two-toed sloth to be described, developed as the result of a dislocation and the subsequent rubbing together of the head of the radius and shaft of the humerus.

MATERIAL

The pseudoarthrosis was found in the skeleton of a two-toed sloth, *Choloepus didactylus* from the collections of the American Museum of Natural History, (A.M.N.H. C.A. No. 2374). The specimen is part of the collection of the former Department of Comparative Anatomy and is currently part of the teaching collection used by vertebrate paleontology graduate students, but is included in the catalogue of specimens in the Department of Mammalogy.

No data is stated on the label of the specimen other than its presumed locality "Guiana 1936." It was probably a noncaptive individual, and fully adult as indicated by its teeth and fusion of epiphyseal plates. Aside from the dislocation of its left elbow joint, the rest of the skeleton appears normal, so that we assume the animal was in good health at the time it was collected.

DESCRIPTION

The joint between the humerus and radius of the left arm was dislocated at some time during the animal's life, presumably as a result of a blow to the forearm. The ulna was broken by this blow and failed to heal. Only a short fragment of the proximal end of the left ulna (fig. 6A) was present in the specimen. The distal portion of the left ulna may have been lost during or after preparation of the skeleton, or it may have degenerated following the failure of the ulna to heal; we suspect the latter. In any case, no evidence is available indicating that the distal portion of the left ulna was in contact with the remaining proximal part after the fracture of the bone. The left radius was dislodged from its normal articulation on the capitulum of the humerus and pushed slightly proximally so that its head rested on the flattened distal shaft of the humerus next to the entepicondylar foramen. Following the dislocation, a new and presumably usable articulation developed between the humerus and radius. The rearrangement of the limb elements shown in figure 1A is a reconstruction of the disarticulated bones. A slight roughness on the shaft of the left radius suggests that the broken end of the ulna abutted against the radial shaft.

This rearrangement of the limb elements involved more than just a displacement of these bones. The shapes of the old articular surfaces

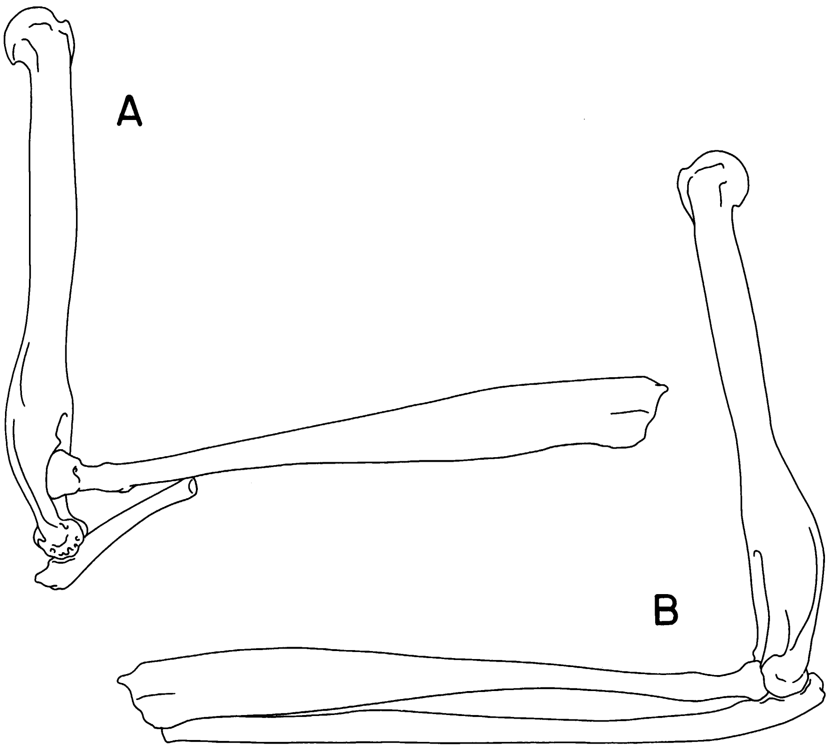

FIG. 1. Forearm of *Choloepus didactylus,* A.M.N.H. C.A. No. 2374. A. Left forearm showing pseudoarthrosis between radius and humerus. B. Right forearm showing normal articulations. Approximately ×.5 life size.

were modified radically and new ones formed. The proximal head of the normal right radius (fig. 2B) is slightly expanded with the articular surface forming a shallow concave depression, the capitular depression, which fits onto and slides over the rounded capitulum of the humerus (figs. 3B, 4). The proximal head of the left radius, which forms part of the pseudoarthrosis, is expanded into a bulbous knob with a convex, rather than a concave, articular surface (fig. 2A). The articular surface and neck of the left radius is pitted, but the existing bone appears hard and strong. The new articular surface of the radius has a dense, smooth, polished appearance, except for the pitting. We believe that these pits may have been filled with blood vessels in life. A comparison of the right and left radii (fig. 2) shows them to be of similar size and shape except for the described differences in the proximal head and neck.

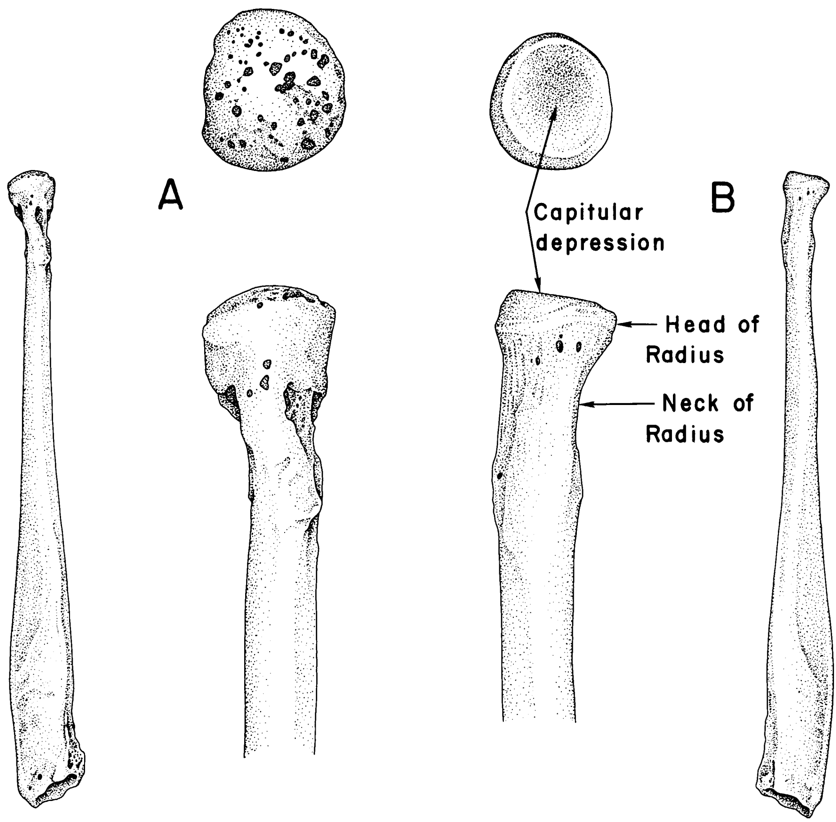

FIG. 2. *Choloepus didactylus,* A.M.N.H. C.A. No. 2374. A. Left radius showing details of new convex articular surface. B. Right radius showing normal concave articular surface.

The distal third of the humerus of the sloth is normally broader than the rest of the shaft and flattened, with a large entepicondylar foramen on its inner margin (figs. 3B, 4). The head of the left radius rested on this flat portion of the humeral shaft just proximal to the radial fossa and lateral to the entepicondylar foramen. A shallow, concave articular surface developed in this flat surface; the cavity approximates closely the convex end of the radius (figs. 3, 5). This cuplike articular surface of the humeral half of the pseudoarthrosis is sufficiently deep to cause a low bulge on the posterior surface of the bone; this bulge does not show on the illustration (fig. 5A). The articular surface of the humerus is also pitted, but like the head of the left radius, the bone appears hard, dense,

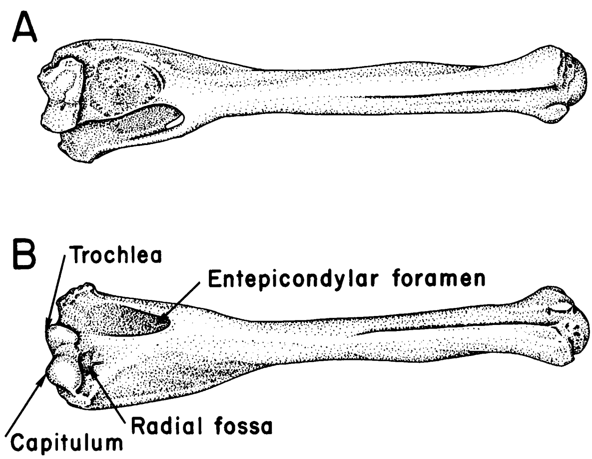

FIG. 3. *Choloepus didactylus,* A.M.N.H. C.A. No. 2374. A. Anterior surface of left humerus showing new cup-shaped articular surface. B. Anterior surface of normal right humerus.

and smoothly polished. No indications exist of arthritic development on the pseudoarthrosis. The trochlea and capitulum of the left humerus are still well formed and appear functional with the exception of a small irregular lip of bone bordering the outer edge of the capitulum (fig. 5); the shape and surface roughness of this bony lip suggest that it is an arthritic development. The radius no longer articulates with the capitulum and the articulation between the ulna and trochlea is subjected to a different pattern of stresses depending upon the action of muscles still attaching to this remnant of the ulna. The growth of new bone along the edge of the capitulum is presumably arthritic, but is less than expected at these nonoperational (or reduced operational) joint surfaces. The bone around the new articular surface on the humerus medial to the external condyle is rugose, and the entepicondylar foramen is enlarged over the size of the foramen in the right humerus.

The left ulna was evidently broken and only the proximal third remains. The preservation of the ulna is slightly different from the other bones as it is brown in color, whereas the other bones are white, and the bone of the ulna is much less dense and appears to be composed of spongy bone. Most likely, modification occurred in the bone of the ulna because it is under a new pattern of stress. The new pattern is presumably pure tension along its longitudinal axis. The associated compression stress along the longitudinal axis, as is normal for the long bones of the limbs,

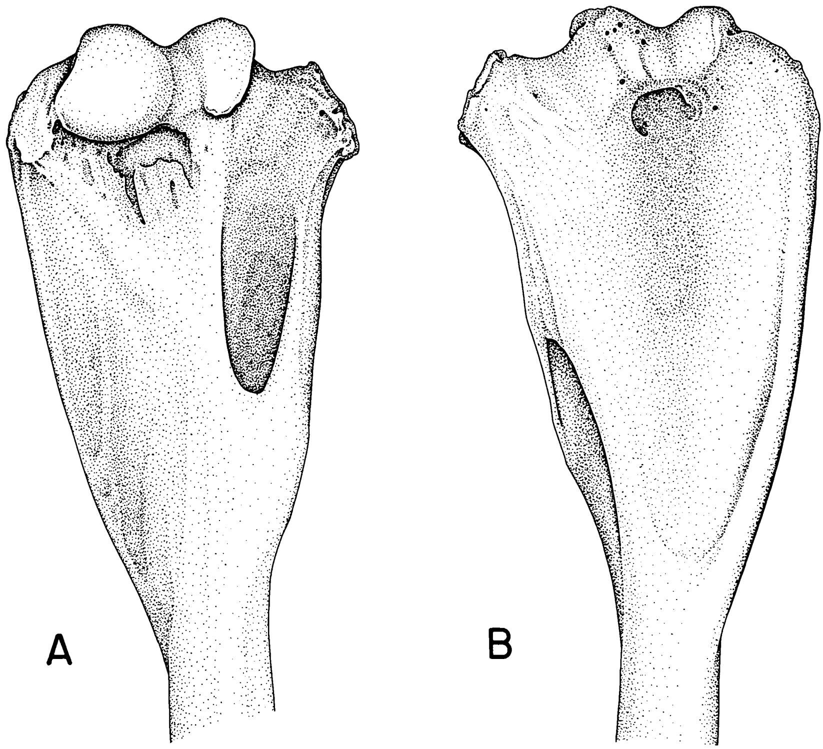

FIG. 4. *Choloepus didactylus,* A.M.N.H. C.A. No. 2374. A. Anterior surface of right humerus. B. Posterior surface of right humerus.

is lacking in the remnant of the ulna. The broken end is rounded off symmetrically. The radial notch of the left ulna is smaller than that in the right ulna, whereas the semilunar notch is larger in the left ulna. The olecranon is thicker and longer in the left ulna than in the normal right one. These changes in the ulna are most likely the result of modified muscle forces acting upon the left ulna. Presumably the muscles attaching to the proximal end of the ulna remained attached to the remnant of the left ulna which probably acted like an articular sesamoid bone, but no longer carried compressive stresses along the longitudinal axis of the forearm. These changes in the functional properties of the left ulna could account for the obvious morphological modifications in the olecranon and the semilunar notch. Separation of the radius from the ulna is responsible for the reduction in the size of the radial notch in the left ulna.

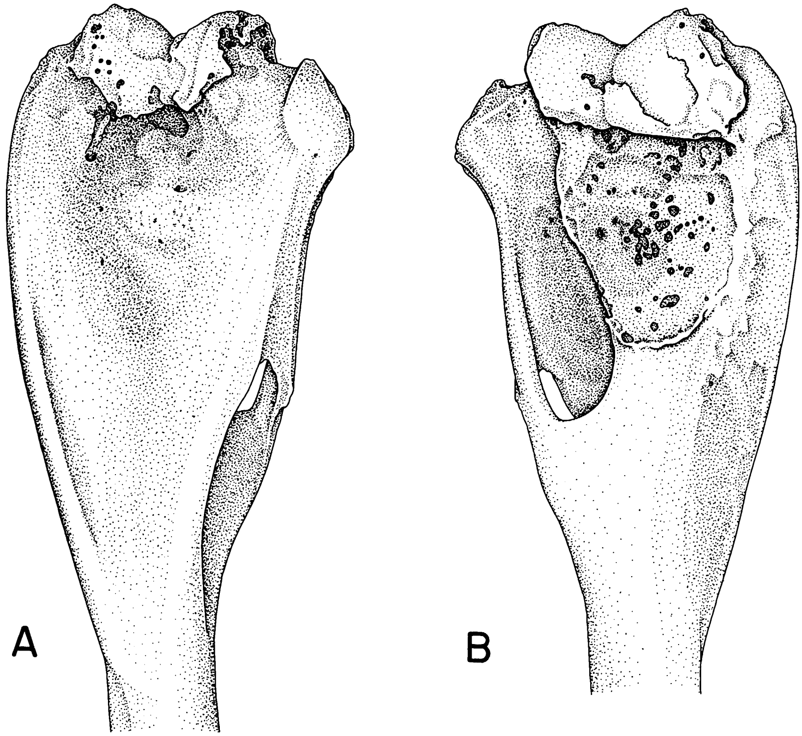

FIG. 5. *Choloepus didactylus,* A.M.N.H. C.A. No. 2374. A. Posterior surface of left humerus. B. Anterior surface of left humerus. Note rough bone along edges of capitulum and trochlea and along outer edge of humerus next to new articular surface.

DISCUSSION

The life history of this individual sloth is not known, but judging from the well-formed and reasonably normal shape of the trochlea and capitulum of the left humerus and the normal morphology of the other arm bones, the dislocation of this joint took place after the animal was fully grown and the epiphyseal plates were fully ossified. The smooth and fully congruent articular surfaces of the pseudoarthrosis indicates that this sloth lived for some time after the new joint had become fully developed and that the animal was in good health at the time it was collected.

When we place the new convex head of the left radius into the depression in the shaft of the humerus in the position shown in figure 1, the

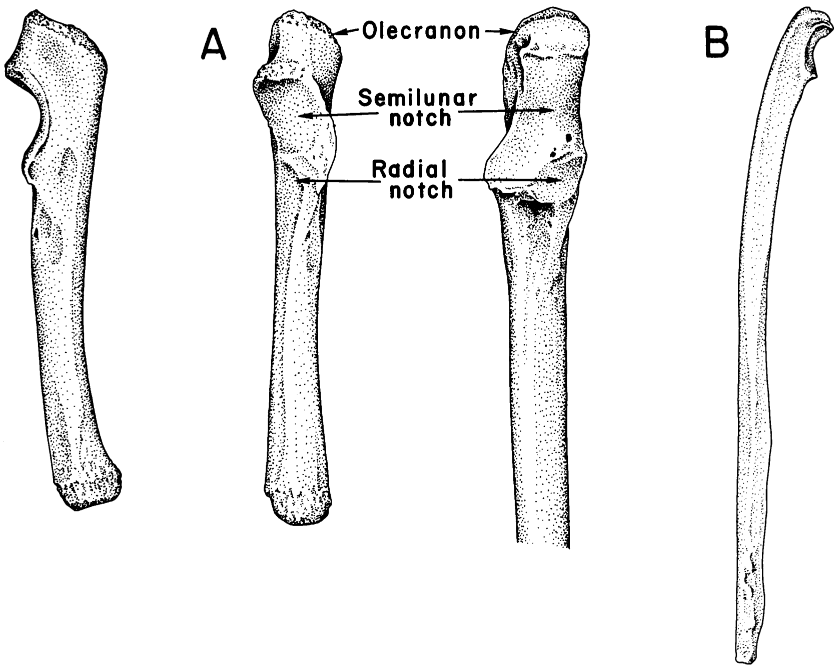

FIG. 6. *Choloepus didactylus,* A.M.N.H. C.A. No. 2374. A. Left ulna fragment showing changes in semilunar and radial notches and lengthening of olecranon. B. Right ulna showing normal length and structure of this bone.

close fit of the surfaces of the pseudoarthrosis can be seen. Although the thickness of the pads of articular cartilage is not known, we assume that they were thin. Rotating the radius while holding it against the humerus shows that the excursion of the left forearm with respect to the humerus falls somewhat short of that possessed by the normal arm, but was sufficient to provide the animal with a good amount of motion in the same planes utilized by the normal arm.

The reversal of the shape of one articular surface and the development of a new articular surface to form a new usable joint is a demonstration of the great plasticity of vertebrate bone. These pseudoarthroses, whether resulting from breaks in bones or from the rubbing together of two undamaged bony surfaces are of interest to evolutionary biologists because they indicate that individual animals are able to sustain considerable damage and still survive in good physiological condition and presumably to leave offspring. Moreover, these naturally occurring pseudoarticulations provide important evidence for the evolutionary mechanisms involved in the evolution of new articulations (Bock, 1959, 1960; Bock and Morioka, 1968). Occasionally, but rarely, these new articulations appear within the limits of an embryonic bone, such as the nasal-frontal hinge, or within the pterygoid or at the anterior end of the jugal bar in the skull of some birds, in which cases pseudoarthroses that develop at the fracture within a bone provide an analogous example. (See also, Frazzetta, 1970, for a discussion of a similar example in the upper jaw of boid snakes.)

But of far greater importance are the evolutionary origins of new articulations where the surfaces of two bones contact and rub against each other. The appearance of the mammalian dentary-squamosal articulation is a classical example; others include the mandible-basitemporal articulation in many birds (Bock, 1960) and the peculiar mandibular-ectethmoid articulation (Bock and Morioka, 1968) in two genera of honeyeaters (Meliphagidae:Aves). In all these cases, nonarticular surfaces of two bones came into contact because of increase in length of one or both bones and hence started to rub against each other because of the normal movements of the bones. These nonarticular bony surfaces modified into typical articular surfaces during the life of the individual, forming a pseudoarthrosis which may be a synarthrosis or diarthrosis as demonstrated by the variation in the structure of the mandible-basitemporal articulation in different families of birds. Moreover, the pseudoarthrosis has appeared because of the potential of physiological adaptation of vertebrate bone, and not because of the appearance of any genetical material for the particular articulation. In some of these examples, the pseudoarthrosis is not only functional but also permits new and important functions associated with generally new biological roles of great selective advantage. The pseudoarthrosis just described in the left elbow of this two-toed sloth is an excellent analogous example of a fully developed and apparently functional pseudoarthrosis that resulted from the contact of two undamaged bony surfaces, of which one of the surfaces was nonarticular; the significance of this example to evolutionary biologists is increased because of the rarity of such naturally occurring cases.

SUMMARY

A pseudoarthrosis between the left radius and humerus resulting from a dislocation of the elbow is described in *Choloepus didactylus.* The shape of the radial articular surface had changed from a concave to a convex surface and a new cup-shaped articular surface had formed on the shaft of the humerus. The pseudoarthrosis was apparently fully functional at the time the animal was collected. The development of pseudoarticula-

tions through the process of physiological adaptation following dislocations of bones in which a nonarticular bony surface is modified into an articulating surface provides an insight into the evolutionary mechanisms involved in the origin of many new articulations, such as the dentary-squamosal joint in mammals.

ACKNOWLEDGMENTS

We wish to thank Mrs. Frances Jewel for the care and skill she used in drawing the set of excellent illustrations of the bones. This study was done with support of a grant from the National Science Foundation (GB-6909x).

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