Yale PEABODY MUSEUM
OF NATURAL HISTORY

BULLETIN OF THE PEABODY MUSEUM OF NATURAL HISTORY

In publication since 1925, and originally a monograph series, the *Bulletin of the Peabody Museum of Natural History* publishes peer-reviewed contributions on original research in the natural sciences represented by the collections of the Yale Peabody Museum of Natural History's curatorial divisions, covering diverse topics that include evolution, phylogeny, taxonomy, systematics, biology, botany, zoology, invertebrate and vertebrate paleontology, and paleoecology, paleobotany, and archaeology.

Full monographs of *Bulletin* numbers 1 through 46 are available for download at peabody.yale.edu.
Beginning with Volume 47, fully indexed published *Bulletin* articles
are available online through BioOne Complete.

Yale University provides access to these materials for educational and research purposes only. Copyright or other proprietary rights to content contained in this document may be held by individuals or entities other than, or in addition to, Yale University. You are solely responsible for determining the ownership of the copyright, and for obtaining permission for your intended use. Yale University makes no warranty that your distribution, reproduction, or other use of these materials will not infringe the rights of third parties.

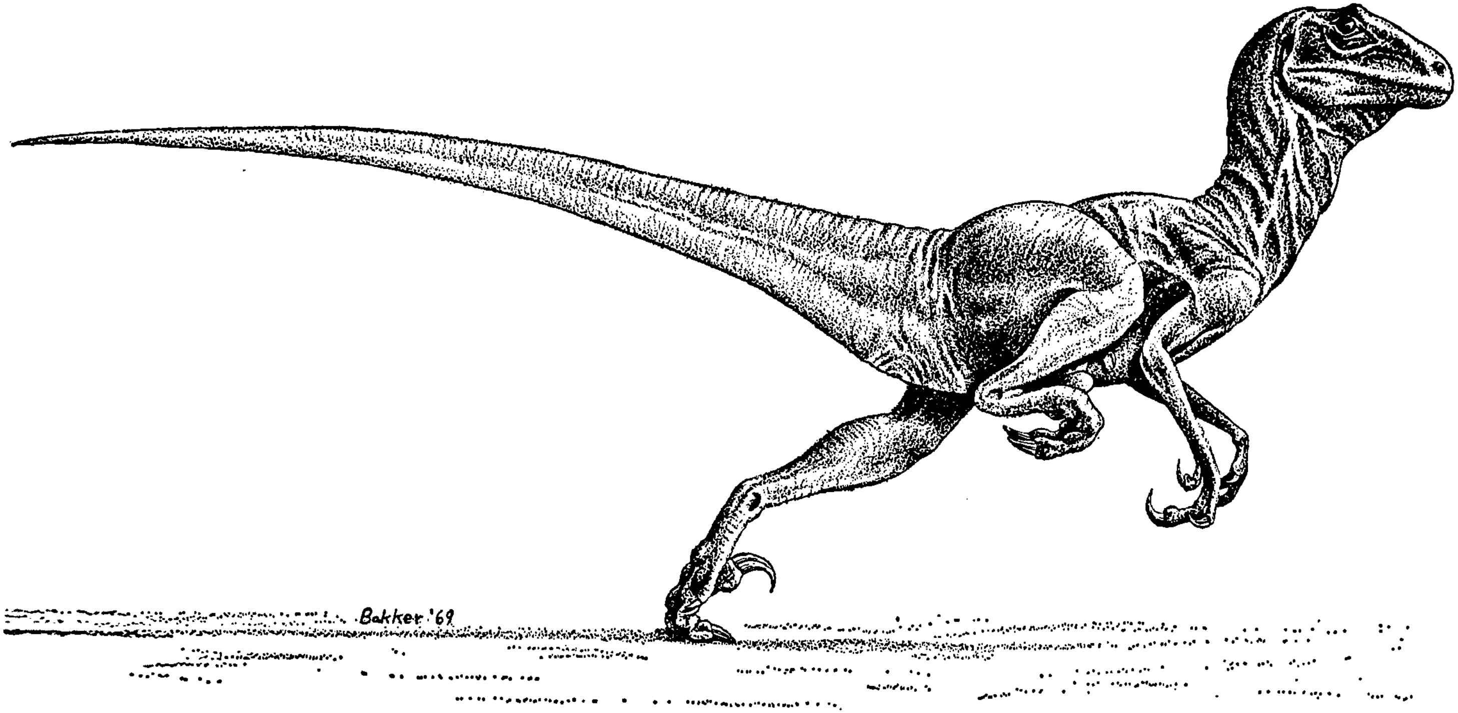
This work is licensed under the Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License. To view a copy of this license, visit http://creativecommons.org/licenses/by-nc-sa/4.0/ or send a letter to Creative Commons, PO Box 1866, Mountain View, CA 94042, USA.

PEABODY MUSEUM OF NATURAL HISTORY, YALE UNIVERSITY
170 WHITNEY AVENUE, P.O. BOX 208118, NEW HAVEN CT 06520-8118 USA
PEABODY.YALE.EDU

Osteology of *Deinonychus antirrhopus*, an Unusual Theropod from the Lower Cretaceous of Montana

JOHN H. OSTROM
Peabody Museum of Natural History
and Department of Geology and
Geophysics, Yale University

BULLETIN 30 • July 1969
PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY
NEW HAVEN, CONNECTICUT


Bakker '69

Bulletins published by the Peabody Museum of Natural History, Yale University, are numbered consecutively as independent monographs and appear at irregular intervals. Shorter papers are published at frequent intervals in the Peabody Museum *Postilla* series.

The Peabody Museum Bulletin incorporates the *Bulletin of the Bingham Oceanographic Collection,* which ceased independent publication after Vol. 19, Article 2 (1967).

Communications concerning purchase or exchange of publications should be addressed to the Publications Office, Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520, U.S.A.

Printed in the United States of America

CONTENTS

LIST OF FIGURES v
LIST OF TABLES vii
ABSTRACTS (ENGLISH, GERMAN, RUSSIAN) 1
1. INTRODUCTION 5
  ACKNOWLEDGMENTS 6
2. STRATIGRAPHIC AND LOCALITY DATA 7
3. SYSTEMATICS 11
4. GENERAL DESCRIPTION 14
  THE CRANIAL SKELETON 14
    SKULL 14
      Maxilla 17
      Premaxilla 18
      Nasal 19
      Lachrymal 20
      Postorbital 21
      Squamosal 22
      Jugal 23
      Quadratojugal 24
      Pterygoid 25
      Ectopterygoid 26
      Palatine 27
      Vomer 28
    MANDIBLE 29
      Dentary 29
      Splenial 30
      Angular 31
      Surangular 32
      Prearticular 33
      Articular 34
    DENTITION 36
  AXIAL SKELETON 41
    VERTEBRAL COLUMN 41
      Cervical vertebrae 41
        Atlas 42
        Axis 44
        Posterior cervicals 46
      Dorsal vertebrae 51
        Anterior dorsals 51
        Posterior dorsals 53
      Sacral vertebrae 57
      Caudal vertebrae 60
      Chevrons 65
      Origin and function of caudal rods 68

Dorsal Ribs 80
  Cervical ribs 80
  Thoracic (dorsal) ribs 82
Sternal Ribs and Gastralia 84
  Sternal ribs 86
  Gastralia 87
Appendicular Skeleton: Pectoral Girdle and Forelimb 89
 PECTORAL GIRDLE 89
  Scapula 89
  Coracoid 90
 FORE LIMB 90
  Humerus 90
  Ulna 94
  Radius 96
  Carpus 97
   Radiale 98
   Ulnare 99
  Manus 101
   Metacarpus 103
   Phalanges 105
 FUNCTIONAL SIGNIFICANCE OF THE MANUS 108
Appendicular Skeleton: Pelvis and Hind Limb 111
 PELVIS 111
  Ilium 111
  Ischium 112
  Pubis 113
 HIND LIMB AND FOOT 116
  Tibia 116
  Fibula 119
  Tarsus 119
   Astragalus 120
   Calcaneum 122
   Tarsal III 122
   Tarsal IV 123
  Pes 124
   Metatarsus 124
   Phalanges 131
 FUNCTIONAL SIGNIFICANCE OF THE PES 139
5. HABITS OF *DEINONYCHUS* 141
6. AFFINITIES OF *DEINONYCHUS* 145
 COMPARISON OF *Deinonychus* AND CERTAIN OTHER THEROPODS 149
 ORIGIN OF DROMAEOSAURIDAE 161
ADDENDUM 163
LITERATURE CITED 164

FIGURES

1. Maps locating the three *Deinonychus* sites 7
2. The Yale *Deinonychus* quarry 8
3. Stratigraphic sections at the two principal *Deinonychus* sites 9
4. Reconstruction of the skull and lower jaw 15
5. Reconstruction of the palate 15
6. Maxilla, premaxilla and nasal 17
7. Lachrymal 20
8. Postorbital 21
9. Squamosal 22
10. Jugal 23
11. Quadratojugal 24
12. Pterygoid 25
13. Ectopterygoid 26
14. Palatine 27
15. Vomers 28
16. Reconstruction of lower jaw, internal view 29
17. Dentary 30
18. Splenial 31
19. Angular 32
20. Surangular 33
21. Prearticular 34
22. Articular 35
23. Maxillary and premaxillary teeth 38
24. Premaxillary teeth 39
25. Comparison of anterior and posterior tooth serrations 40
26. Atlas 42
27. Atlas 43
28. Axis 45
29. Fourth (?) cervical vertebra 47
30. Seventh (?) cervical vertebra 48
31. Reconstruction of the cervical series 49
32. First dorsal vertebra 52
33. Fourth (?) dorsal vertebra 54
34. Eleventh (?) dorsal vertebra 55
35. Caudal series 61
36. Detail of caudal vertebrae 62
37. Reconstruction of a mid-caudal vertebra and chevron 63
38. Proximal caudal vertebra 64
39. Mid-caudal vertebra 66
40. Proximal chevrons 66
41. Reconstruction of chevron types 67
42. Transverse section of a mid-caudal vertebra 70
43. Enlarged transverse section of chevron rods 71

44. Transverse section of a mid-caudal vertebra 72
45. Enlarged transverse section of prezygapophyseal rods 73
46. Transverse section of a mid-caudal vertebra 74
47. Enlarged transverse section of prezygapophyseal rods 75
48. Transverse section of a mid-caudal vertebra 76
49. Enlarged transverse section of chevron rods 77
50. Cervical ribs 81
51. Dorsal ribs 83
52. Abdominal ribs and gastralia 85
53. Reconstructed cross section of the rib cage 88
54. Scapula 90
55. Humerus 91
56. Humerus 93
57. Comparison of selected theropod humeri 94
58. Ulna 95
59. Radius 97
60. Carpalia 99
61. Reconstruction of epipodial-carpus joint mobility 100
62. Reconstructed manus, dorsal view 104
63. Digits of the manus, medial view 106
64. Ilium 112
65. Ischium and pubis (?) 114
66. Tibia and fibula 117
67. Tibia and fibula 118
68. Astragalus and calcaneum 121
69. Distal tarsals 123
70. Relationship of distal tarsals and metatarsals 124
71. Left pes 125
72. Metatarsal I 126
73. Reconstructed pes, dorsal view 130
74. Reconstructed pes, medial view 132
75. Digits of pes, medial view 134
76. Limits of extension and flexion of pes digit II 135
77. Comparison of ungual form in *Deinonychus, Allosaurus, Ornithomimus and Ornitholestes* 136
78. Ungual form and mechanics in *Deinonychus, Allosaurus* and *Ornitholestes* 138
79. Skeletal reconstruction of *Deinonychus* 142
80. Comparison of pedal digit II of various theropods 152
81. Comparison of the pes in various theropods 155
82. Comparison of the manus in various theropods 159
83. Suggested phylogeny of the Dromaeosauridae 162

TABLES

1. Skull and mandible dimensions in *Deinonychus* 16
2. Dental serration counts in some theropods 40
3. Morphology of *Deinonychus* cervical vertebrae 49
4. Measurements of *Deinonychus* vertebrae 58
5. Morphology of caudal vertebrae in some tetrapods 78
6. Measurements of the scapulae of *Deinonychus* 89
7. Measurements of the fore limb of *Deinonychus* 96
8. Measurements of the manus of *Deinonychus* 101
9. Measurements of the pelvis of *Deinonychus* 113
10. Measurements of the hind limb of *Deinonychus* 119
11. Measurements of the pes of *Deinonychus* 127
12. Selected anatomic ratios of some theropods and ratites 146
13. Identification of the type *Dromaeosaurus* and *Deinonychus* foot bones 150

ZUSAMMENFASSUNG

Es liegt eine eingehende Beschreibung des Skelettbaus und Anpassungsmerkmalen des *Deinonychus antirrhopus* Ostrom (1969) vor, ein sehr ungewöhnlicher, fleischfressender Dinosaurier (Ordnung Saurischia, Unterordnung Theropoda) aus der Cloverly Formation (Untere Kreide) von Montana (USA). Die Spezies ist gekennzeichnet durch eine Anzahl von Merkmalen, die auf ein besonders aktives und bewegliches Tier hinweisen, schnellfüssig und sehr räuberisch in seinen Anlagen. Der normale tridactyl theropod pes ist abgeändert in einen didactyl Fuss (die Zehen III und IV). Die Zehe hat eine besondere Struktur, offensiv oder räuberisch, die von einer sichelförmigen, scharfen Klaue gehalten wird. Von besonderer Bedeutung ist die Tatsache, dass die offensive Struktur sich am Fusse eines obligatorischen Zweifüsslers befindet. Das Vorderbein ist lang, sowie der Fuss mit seiner langen und schlanken Zehe, die von einer grossen sehr räuberischen, zurückgebeugten und scharfen Kralle gehalten wird. Die Handwurzel ist einmalig unter niederen Wirbeltieren in der Form der proximal verbindenden Fazetten von der Speiche und der Elle, die ein ausgedehntes Anzieh-Abzieh und Drehungsstrecken der Manus erlaubt. Der Wirbelbau zeigt eine fast horizontale Haltung des Rückenwirbels mit einer ausgeprägten aufwärts gerichteten Kurve der Halswirbel, ännlich wie das von grossen Recente Ratiten. Die Schwanzwirbel, (ausgenommen die meist proximalen Teile) sind einzigartig in der Entwicklung von stark verlängerten prezyapophysalen Fortsätzen und vorderen Chevron-Fortsatzen, die acht bis zehn Wirbel lang hinausragen. Die Schwanzwirbel sind nicht verwachsen und Gelenkschleimendflächendes Wirbelzentrums sind in allen Zygapophysen vorhanden. Man glaubt, dass die Schwanzgurte mit der Sehne des Streckenmuskels und Beugemuskels verknöchert ist und die Aufgabe hat der Schwanzbeuger oder Versteiffer zu kontrollieren. Der Schwanz wird als ein dynamisches Gleichgewicht bezeichnet der sich als ein steifer Korper verhält anstatt einer Anzahl von getrennten aber verkrüppelten Bestandteilen, die mit den Trägheitsmomenten von allen Teilen in eine gleichzeitig einwirkende Kraft (oder Gegenkraft) zusammengesetzt wird.

Deinonychus ist sehr nah verwandt mit dem *Dromaeosaurus albertensis* und es wird hier auf den Dromaeosauridae (= Dromaeosaurinae von Matthew und Brown, 1922) verwiesen. Ausserdem wird auf die Familie der *Velociraptor mongoliensis, Saurornithoides mongoliensis* and *Stenonychosaurus inequalis* verwiesen.

РЕЗЮМЕ

Дано детальное описание скелетной анатомии и приспособленностей *Deinonychus antirrhopus* Ostrom (1969), очень необыкновенного хищного динозавра (отряд Saurischia, подотряд Theropoda) из формации Кловерлы (нижний мел) Монтаны. Верста характеризуется многими особенностями, указующими на крайне активное и подвижное животное, быстроногое и очень хищного образа жизни. Стандартная трехпалая тероподная стопа модифицирована в двупалую (III и IV палец). II палец специализировался в структуру для нападения, носящую большой серповидный, острый коготь. Особенно значителен тот факт, что эта структура для нападения находится на стопе обязательно двуногого животного. Передние конечности долги, кисть тоже; ее долгие и тонкие пальцы носят большие когти, загибающиеся назад и острые, облика очень типичного для хищных. Запястие единственное для нижних позвоночных по облику проксимальных сочленовных поверхностей лучевой и локтевой косточки кисти; этот облик позволял значительное приведение-отведение и супинацию-пронацию кисти. Позвоночная структура указывает на почти горизонтальную позицию спинных позвонков, с отчетливой кривизной вверх шейной серии, в целом очень похожа на ту современных бегающих. Хвостовые позвонки (с исключением самых проксимальных) единственные по развитию крайне удлиненных презигапофизов, а также передних шевроновых отростков простирающихся длинной восьми до десяти позвонков. Хвостовые позвонки не слились между собой, нормальные синовиальные сочленовные поверхности находятся на всех зигапофизах. Мы считаем, что шевроновые отростки были окостененными сухожилиями хвостовых разгибающих и сгибающих мышц — M. extensor caudae lateralis (= M. sacrococcygeus dorsalis lateralis млекопитающих) — и действовали как контролированные хвостные "изгибатели" или укрепители. Наша интерпретация — что этот хвост был динамическим стабилизатором, действующим как одно жесткое тело. Ближайший родственник *Deinonychus* — *Dromaeosaurus albertensis;* мы относим *Deinonychus* к семейству Dromaeosauridae (= Dromaeosaurinae Matthew and Brown, 1922). Мы тоже относим к этому семейству *Velociraptor mongoliensis, Saurornithoides mongoliensis* и *Stenonychosaurus inequalis.*

1. INTRODUCTION

During the summer of 1964, an expedition from Yale University's Peabody Museum under the author's direction explored exposures of the Cloverly Formation (Early Cretaceous) in Wyoming and Montana in search of fossil vertebrate remains. Among the important discoveries made was that of the spectacular little carnivorous dinosaur described here—an animal so unusual in its adaptations that it undoubtedly will be a subject of great interest and debate for many years among students of organic evolution. Although of modest size, this creature was one of the most unusual of all dinosaurs and provides entirely new insight on the classification of predaceous dinosaurs and on the surprisingly sophisticated capabilities possessed by some theropods.

At the very moment of discovery, it was evident from the few fragments exposed on the surface that we had stumbled across something very unusual and quite unlike any previously reported dinosaur. Excavation began immediately and was continued over the remainder of that field season and much of the following two summers. To date, more than 1000 incredibly well-preserved bones, representing at least three individuals, have been recovered from the site. In many instances, preservation is superior to that of the Oligocene White River series or of the Miocene John Day beds. This unusual preservation permitted a more detailed analysis than is generally possible for Mesozoic remains and was a major factor underlying the functional interpretations presented here.

At the time we made our discovery we were unaware of the existence of remains of this animal in any museum. Almost two years later, I found the fragmentary remains of two specimens in the collections of the American Museum that had been collected more than 30 years earlier by Barnum Brown from two sites on the Crow Indian Reservation in Montana. These specimens had been partly prepared, but never studied and no report had been issued. It is only by chance that they are included in the present study because some time during the 30-odd years since their collection they were moved from their logical place in the American Museum collections. Through the courtesy of Dr. Edwin H. Colbert, these materials have been placed in my hands for study and description.

Specimens referred to in this report are maintained in the paleontologic collections of the following institutions, the names of which are abbreviated as follows:

AMNH — American Museum of Natural History
NMC — National Museum of Canada
PU — Princeton University
ROM — Royal Ontario Museum
USNM — United States National Museum
YPM — Peabody Museum of Natural History, Yale University: Vertebrate Paleontology Collection
YPMOC — Peabody Museum of Natural History Osteology Collection

ACKNOWLEDGMENTS

During the preparation of this report I profited greatly through discussions with many colleagues. I gratefully acknowledge contributions by Edwin H. Colbert, A. W. Crompton, D. A. Russell, J. A. Hopson, Peter Galton, F. A. Jenkins, J. S. McIntosh and R. T. Bakker. I am also indebted to Dr. Colbert for making available Barnum Brown's field records and for permission to include several American Museum specimens in this study. Also, I thank Dr. Russell for providing materials from the collections of the National Museum of Canada. Ward Whittington prepared nearly all of the illustrations, Robert Bakker prepared the skeletal reconstruction and the life restoration of the frontispiece. Rebekah Smith drafted the locality maps and stratigraphic columns. The photographs are by A. H. Coleman and Thomas Brown, with the exception of the 1966 photograph of the Yale quarry site that was kindly provided by Ronald Brown, now of the American Museum of Natural History. I am grateful to all for their contributions. My thanks must also go to Louise Holtzinger who typed the entire manuscript, and to Jeanne E. Remington, whose editorial skills greatly improved this paper.

I am deeply indebted to Nell and Tom Edwards who graciously gave us permission to explore and collect within the limits of their ranch near Bridger, Montana. Without their cooperation and assistance this study would have been impossible.

Finally, and most important of all, I wish to pay special tribute to the technical skills of John Thomson, Ronald Brown and Peter Parks who prepared all of the Yale *Deinonychus* material. Without their delicate touch and great patience, much of the evidence about this most unusual of dinosaurs would still be undecipherable. Figures 35 and 36 are eloquent testimony of their skills.

The discovery of *Deinonychus* and the present report were made possible by grants from the National Science Foundation (GB-1015 and GB-3638). It has been published with the aid of a National Science Foundation Publication Grant (GN-528).

2. STRATIGRAPHIC AND LOCALITY DATA

All the known specimens of *Deinonychus* were collected at three localities in southern Montana (Fig. 1). The first collections were made by Barnum Brown in

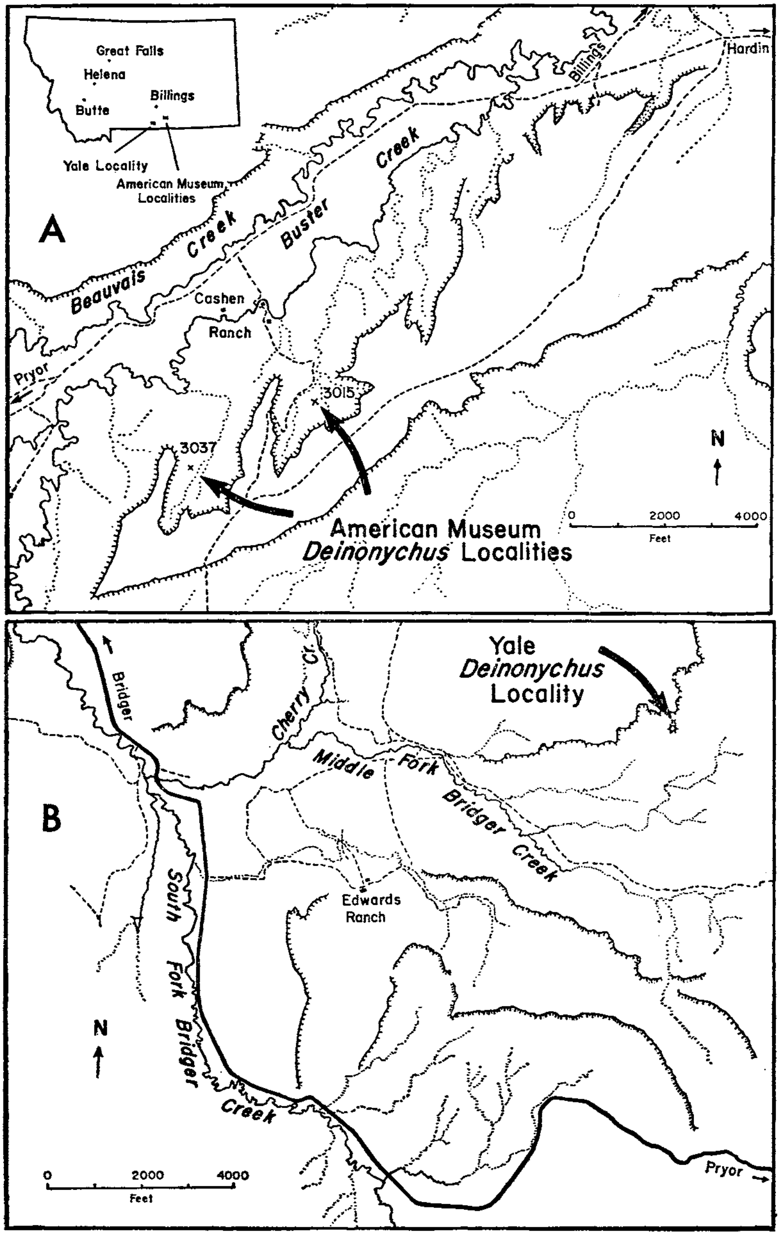


FIG. 1. Locality maps of the American Museum (A) and the Yale (B) *Deinonychus* sites in southern Montana.

1931 and 1932 on the Cashen Ranch in the Crow Indian Reservation some 30 miles (48 km) southeast of Billings, Montana. The first specimen (AMNH 3015), apparently discovered by Brown himself, consists of the major part of a poorly preserved skeleton lacking the skull. Specimen 3037 (AMNH), consisting of several dozen fragments (chiefly from the manus and pes), was found the following year at a second site slightly more than half a mile (0.8 km) from the original find. The first specimen was recovered from a small excavation (AMNH Locality 31–7) situated in the NW ¼ of Section 33, T.4 S., R.29 E., Big Horn County, Montana, approximately half a mile (0.8 km) southeast of the Cashen ranch house on Beauvais Creek (Fig. 1A). Specimen 3037 (AMNH) was collected at AMNH Locality 32–8 in the N.E. ¼ of Section 32, T.4 S., R.29 E., Big Horn County, Montana. The Yale *Deinonychus* collections were made at a single site shown in Figure 2 (YPM Locality 64–75) approximately 7 miles (11 km) southeast of Bridger, Montana, some 35 miles (56 km) west and south of the American Museum localities noted above. The Yale quarry is situated in the N.E. ¼ of Section 17, T.7 S., R.24 E., Carbon County, Montana, approximately 1.5 miles (2.4 km) northeast of the Edwards Ranch (Fig. 1B).

FIG. 2. The Yale *Deinonychus* quarry, southeast of Bridger, Montana. Photograph by Ronald Brown, August, 1966.

A majority of the fossil remains recovered from the Yale site occurred as associated but disarticulated bones. Notable exceptions are the three remarkable caudal series (YPM 5201, 5202 and 5203), a left pes (YPM 5205) and a nearly complete left manus (YPM 5206). The disarticulated occurrence of most of the other skeletal elements found in this quarry made it impossible to establish definite individual associations in many instances. Accordingly, wherever there was doubt regarding the association of several elements or groups of elements, these were catalogued as separate specimens. Consequently, the Yale *Deinonychus* materials have been catalogued as more than 50 separate entries, although they may in fact represent as few as three individuals. In spite of this, I believe that YPM 5203 (a caudal series), 5205 (left and right pes), 5206 (left and right manus) and 5210 (several vertebrae and an incomplete skull and jaws) belong to a single individual because of distinctive preservation common to these alone and the fact that they are all slightly larger than other comparable elements obtained at the Yale site. However, owing to their separated occurrence in the quarry, I have no proof. Furthermore, I have no doubts that the remains listed from the Yale quarry belong to a single species and I have thus based the species diagnosis on the hypodigm and not on the type specimen alone.

No precise stratigraphic data were recorded by Barnum Brown for the two specimens collected by him, but thanks to an aerial photograph (Brown, 1941: 293) and a tracing paper overlay found in the American Museum files, showing the location of these and other sites, this information has been recovered. AMNH 3015 was collected very close to the middle of a chalcedony-concretion-bearing claystone (Unit V in Ostrom, MS), the Little Sheep Mudstone Member of Moberly's (1960) Cloverly Formation, 21 to 24 feet (6.4–7.3 m) below the base of a massive, grey-brown, cross-bedded sandstone (Unit VI, Ostrom, MS) and approximately 103 feet (31 m) below the thin-bedded, yellow or rust-colored sand-

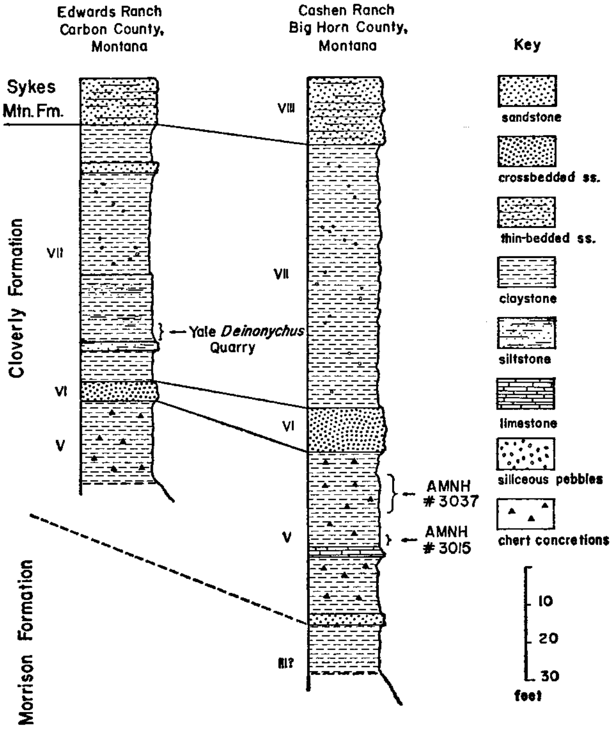


FIG. 3. Stratigraphic sections at the Yale (Edwards Ranch) and American Museum (Cashen Ranch) *Deinonychus* localities showing the levels of the three sites. Roman numerals have been assigned to parts of the non-marine section (Morrison-Cloverly Formations of some authors) by the present author (MS). Unit V corresponds in part to the Little Sheep Mudstone Member and Unit VII equals part of the Himes Member of the Cloverly Formation as defined by Moberly, 1960.

stone (Unit VIII, Ostrom, MS) that caps most of the scarps in the Beauvais Creek area and represents the terminal phase of Early Cretaceous continental deposition in the region (Fig. 3).

The exact stratigraphic position of AMNH No. 3037 is not known, but exposures in the vicinity indicated by Barnum Brown's photograph limit the level to a 10 foot (3.05 m) zone approximately 6 to 16 feet (1.8–4.9 m) below a massive sandstone (Unit VI) and approximately 70 to 80 feet (21–24 m) below the capping sandstone (Unit VIII). The level of this site also appears to fall within Moberly's Little Sheep Mudstone Member of the Cloverly Formation.

The Yale specimens were all collected from a 10 to 18 inch (25–46 cm) zone in the lower third of a brightly variegated claystone (Unit VII), 11.5 feet (3.5 m) above a fine-grained, cross-bedded sandstone (Unit VI?) and 52 feet (16 m) below Unit VIII (Fig. 3). This corresponds to the upper part of the Himes Member of Moberly's (1960) Cloverly Formation.

3. SYSTEMATICS

CLASS REPTILIA

ORDER SAURISCHIA
SUBORDER THEROPODA Marsh, 1881

FAMILY DROMAEOSAURIDAE Matthew and Brown, 1922

DEFINITION: Small to moderate-sized theropods, lightly built and bipedal in posture. Fore limb not reduced. Manus long and slender with three functional digits. Digit III moderately divergent and carpus highly specialized with asymmetrical ginglymus on radiale. Hind limb long, pes of moderate length and functionally didactyl. Digit II modified as an offensive or predatory weapon with a large, trenchant claw. Digits III and IV subequal and normal, digits I and V reduced. Eight to 9 cervical vertebrae, 13 to 14 dorsals, and 3 to 4 sacrals. Caudal series of *Deinonychus* highly modified by extremely long chevron and prezygapophyseal processes which rendered the tail virtually inflexible throughout most of its length. Comparable caudal modifications are presumed, but not known, in other taxa referred to the family.

DISTRIBUTION: Late Aptian or Early Albian to Late Campanian or Early Maestrichtian, western interior of North America and central Mongolia.

DEINONYCHUS Ostrom, 1969

Ostrom, John H. 1969. *Postilla* 128:1–17.

TYPE SPECIES: *Deinonychus antirrhopus.*

DISTRIBUTION: Late Aptian or Early Albian, south central Montana.

DIAGNOSIS: Same as for the species, given below.

DEINONYCHUS ANTIRRHOPUS Ostrom, 1969

Ostrom, John H. 1969. *Postilla* 128:1–17.

TYPE: YPM 5205, a complete left pes and an incomplete right pes.

HYPODIGM: YPM 5201, 5202 and 5203, three series of articulated caudal vertebrae.

YPM 5204, part of the atlas, the axis, fourth and fifth cervicals and the fourth, sixth, seventh and ninth dorsals.

YPM 5206, nearly complete left and right manus.

YPM 5210, an incomplete skull and jaws (vomers, left and right quadratojugals, both squamosals, a left articular, left and right pterygoids, a right ectopterygoid, right surangular, left jugal, right angular, left dentary, numerous teeth, the atlas, axis and seventh cervical, the first and tenth dorsals and an anterior (3rd or 4th) caudal.

YPM 5232, consists of the right maxilla, right and left nasals, right and left dentary, right and left (incomplete) premaxillae, right and left jugals, right squamosal, both postorbitals, right lachrymal, right and left articulars, left palatine, left angular and right quadratojugal.

YPM 5207–5209, 5211–5231, 5233–5265, various isolated and fragmentary elements.

AMNH 3015, an incomplete skeleton, lacking the skull.

AMNH 3037, fragmentary foot bones.

HORIZON: Cloverly Formation, lower part of Unit VII (= upper part of Himes Member of Moberly, 1960) and upper part of Unit V (= Little Sheep Mudstone Member of Moberly, 1960), ranging from 50 to 100 feet (15–30 m) below the Sykes Mountain Formation. (Units V and VII are defined in my report on the stratigraphy and paleontology of the Cloverly Formation—Ostrom, MS).

LOCALITIES: YPM 64–75—NE 1/4 Sec. 17, T.7 S., R.24 E., Carbon County, Montana. AMNH 31–7—NW 1/4 Sec. 33, T.4 S., R. 29 E., Big Horn County, Montana. AMNH 32–8—NE 1/4 Sec. 32, T.4 S., R. 29 E., Big Horn County, Montana.

DIAGNOSIS: A small, bipedal theropod with a moderately large head, moderately long and well-developed hind limbs, fore limbs elongated, manus long and slender in construction. Pes of medium length with four digits, the fifth represented by a vestigial metatarsal. Digital formula 2–3–4–5–0. Digits III and IV subequal in length, II specialized and bearing a very large, trenchant and strongly recurved ungual, I reduced and directed backward. Pes functionally didactyl (III and IV). Distal end of metatarsal II deeply grooved; metatarsal III not greatly compressed proximally. Articular facets of II developed to permit unusual extension but very limited flexion between first and second phalanges. Manus with three very long digits (formula 2–3–4), digits IV and V lost. Metacarpal I short and irregular in shape. Metacarpal III long, slender and divergent from II. Carpus consists of radiale and ulnare only. Radiale with well-defined asymmetrical ginglymus proximally for articulation with radius. Humerus and radius-ulna not reduced. Skull with large, sub-circular to oval orbits and three antorbital fenestrae. Supraorbital rugosities on postorbital and lachrymal. Preorbital bar slender and in weak contact with a thin, plate-like jugal. Quadratojugal very small, T-shaped, and apparently not in contact with squamosal. Nasals long, narrow and unfused. Inferior premaxillary process forms lower margin of external naris. Pterygoid very long and slender, ectopterygoid complex and pocketed ventrally. Palatine expanded, with subsidiary palatine fenestra medially. Fifteen maxillary teeth, four asymmetrical, sub-incisiform premaxillary teeth, sixteen sub-isodont dentary teeth. All teeth with anterior and posterior serrations; denticles of posterior serrations nearly twice as large as denticles of anterior serrations on all teeth. Twenty-two or 23 presacral vertebrae, 3 or 4 sacrals and approximately 40 caudals. Cervical vertebrae of moderate length, massive, platycoelous and sharply angled. Dorsals short and platycoelous to amphiplatyan with well developed hyposphene-hypantrum, and bearing short, stout neural spines. All presacrals with small but deep pleurocoels. Caudal vertebrae long and platycoelous. All caudals except the first 8 or 9 bear extremely long (up to 10 segments), rod-like, prezygapophyseal processes. Chevrons also elongated into long, paired, double bony rods extending forward beneath the preceding 8 or 9 segments. Ischium with triangular obturator process. Pubis (if correctly identified) short and greatly expanded into a subcircular, scoop-shaped element, with a distinct obturator foramen.

4. GENERAL DESCRIPTION

In the following description of the osteology of *Deinonychus,* numerous comparisons are made with corresponding elements of various other theropods, in the usual manner. Although somewhat unusual, it is appropriate at this point to draw the reader's particular attention to the apparently confusing and inconsistent implications of these comparisons. To summarize in advance, *Deinonychus* appears to have been characterized by both "carnosaurian" and "coelurosaurian" traits, a number of which have been considered as diagnostic by some authors. A tally of these features and a discussion of their possible significance is presented in the final section of this report, but in the meantime, I wish to emphasize that the osteological comparisons that occur throughout the following descriptive text should be read as comparative only, without any phylogenetic inferences whatsoever.

THE CRANIAL SKELETON

Skull

Disarticulated elements of two skulls were recovered from two widely separated points in the Yale quarry. Included were most of the dermal elements, but the skull roof and braincase were not found and these remain unknown. Many of the bones recovered are thin and extremely fragile, yet most are intact with even delicate processes preserved. The fact that only disarticulated but little-damaged elements were found suggests that the skull was very loosely bound together and probably highly kinetic.

Skull YPM 5210 consists of both squamosals and quadratojugals, parts of both pterygoids, the right ectopterygoid and palatine, right postorbital, left jugal, a partial vomer and numerous teeth. Associated with these were several parts of the mandibles; a left dentary and articular, and the right surangular, angular, prearticular and splenial. Skull YPM 5232 includes the right maxilla, nasal and premaxilla, the left nasal and premaxilla, both jugals, the right postorbital, squamosal, lachrymal and quadratojugal, and the left palatine and postorbital, plus numerous teeth. Collected near the site of these skull elements, but not clearly associated with either individual, were a left ectopterygoid and a right pterygoid (YPM 5233) and a fragmentary left pterygoid (YPM 5239). The lower jaws are represented by a left dentary, both articulars and a left angular. Other mandibular elements recovered nearby were a left splenial (YPM 5237) and a right surangular (YPM 5234).

The skull, as reconstructed from these elements and shown in Figures 4 and 5,

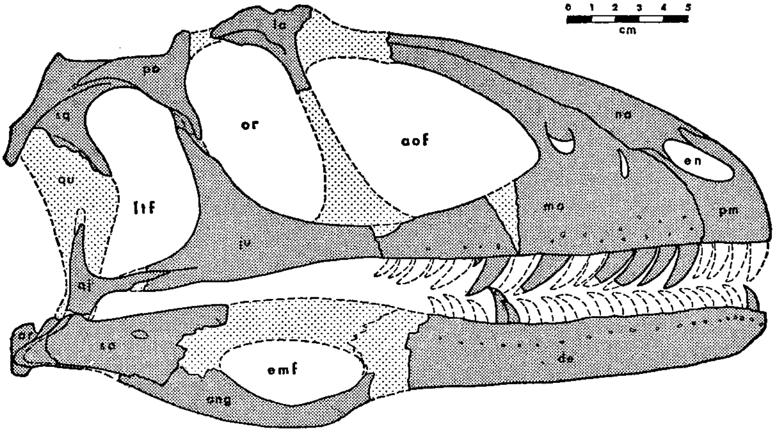


FIG. 4. Restoration of the skull and mandible of *Deinonychus antirrhopus*. Dark stippling indicates known elements, light stippling indicates unknown parts. Based on elements from at least two skulls, so proportions are only approximate. Notice the two small anterior antorbital fenestrae and the relatively large external mandibular fossa. Abbreviations: ang—angular; aof—antorbital fenestra; ar—articular; de—dentary; emf—external mandibular fossa; en—external naris; ju—jugal; la—lachrymal; ltf—lateral temporal fenestra; ma—maxilla; na—nasal; or—orbit; pm—premaxilla; po—postorbital; qj—quadratojugal; qu—quadrate; sa—surangular; sq—squamosal.

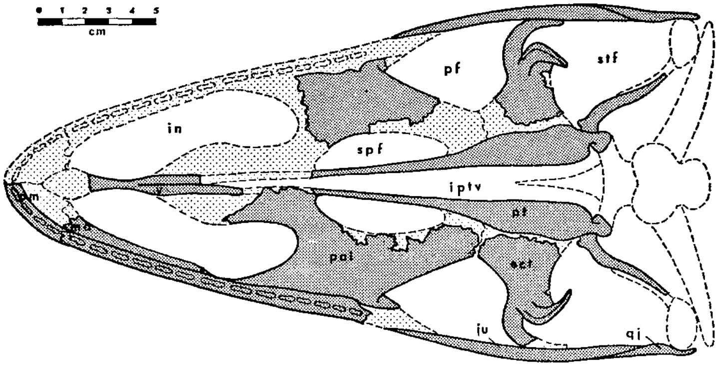


FIG. 5. Restoration of the palate of *Deinonychus antirrhopus*, based upon disarticulated elements from at least two skulls. Dark stippling indicates known elements, light stippling unknown regions. Proportions are only approximate. Abbreviations: ect—ectopterygoid; in—internal naris; iptv—interpterygoidal vacuity; ju—jugal; ma—maxilla; pal—palatine; pf—palatine fenestra; pm—premaxilla; pt—pterygoid; qj—quadratojugal; spf—subsidiary palatine fenestra; stf—subtemporal fossa; v—vomer.

is moderately long, approximately 300 to 320 mm, with moderate to large-sized orbits (probably oval) and lateral temporal fenestrae. Three antorbital fenestrae are present, of which the two anteriormost are of small size. The posterior antorbital fenestra is larger than the orbit and triangular in shape. The skull appears to have been low, measuring approximately 110 to 115 mm in height at the postorbital bar, or approximately one third of the cranial length.

TABLE 1. Estimated skull and jaw dimensions of *Deinonychus antirrhopus* (based on YPM 5210 and 5232)

Greatest length of skull	320 mm
Greatest width of skull	150 mm
Greatest height of skull	115 mm
Maxillary tooth row length	130 mm
Upper tooth row length	160 mm
Orbit height	75 mm
Orbit length	?50 mm
Lateral temporal fenestra height	80 mm
Lateral temporal fenestra length	?35 mm
Principal antorbital fenestra height	60 mm
Principal antorbital fenestra length	?80 mm
Lower jaw length	310 mm
Dentary tooth row length	140 mm
Maximum lower jaw depth	?50 mm

A convenient index of head size is the ratio of skull length to length of the presacral vertebral column. Neither of these dimensions is known exactly in *Deinonychus*, so a precise ratio is not possible. However, using what I consider to be reliable estimates of 30 to 32 cm for the skull (based on the two Yale skulls) and 80 to 85 cm for the presacral series (based on the American Museum skeleton and a presacral count of 23), this ratio must have been .35 to .40. This is a surprisingly high value; in fact it is exceeded only by that of *Tyrannosaurus* among adequately known theropods. A comparison of skull/presacral ratios in various theropods is as follows:

Ornithomimus[1] *altus* (AMNH 5339)	.15
Coelophysis longicollis (AMNH 7224)	.23
Ornitholestes hermanni (AMNH 619)	.24
Allosaurus[2] *fragilis* (USNM 4734)	.28
Deinonychus antirrhopus	.35–.40
Tyrannosaurus rex (AMNH 5027)	.41

The following cranial elements are not known: basioccipital, exoccipital, supraoccipital, basisphenoid, laterosphenoid, opisthotic, parasphenoid, presphenoid, orbitosphenoid, parietal, frontal, prefrontal, prootic, quadrate.

---

[1] I consider *Ornithomimus* and *Struthiomimus* as synonyms.

[2] I prefer Marsh's (1877) name *Allosaurus* on the grounds that Leidy's (1870) type of *Antrodemus valens* (USNM 218, a posterior half of a caudal centrum) is indeterminate; it could belong to *Ceratosaurus* or *Allosaurus*. There is no way to establish which of these two large Morrison theropods is represented by Leidy's vertebra. Marsh's excellent topotype of *Allosaurus* (USNM 4734) provides an adequate basis for the taxon, supplementing the poor type specimen (YPM 1930).

MAXILLA

The right maxilla of YPM 5232 is nearly complete and only slightly crushed (Fig. 6). In lateral view, it is triangular in shape, with the narrow apex directed forward and the rear margin deeply emarginated by the anterior boundary of the large antorbital fenestra. The upper margin forms a nearly straight, forward-sloping contact with the nasal. The anterior margin curves downward to form a moderately broad, digitate suture with the premaxilla. The inferior margin is straight and not curved or undulating as in *Allosaurus, Gorgosaurus* and *Tyrannosaurus.* Posteriorly, both upper and lower processes taper gradually to restricted contacts with the lachrymal and jugal respectively.

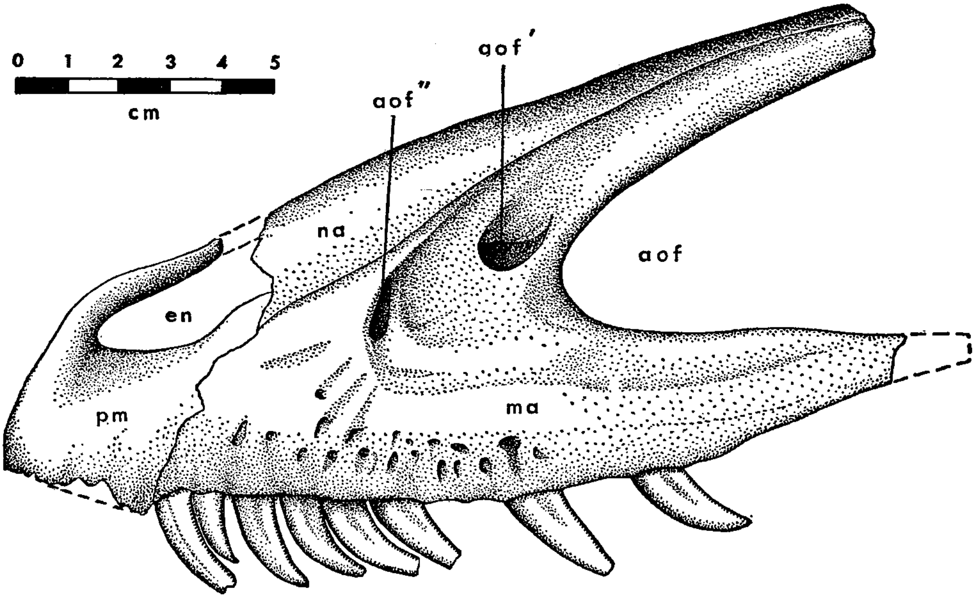


FIG. 6. Snout of *Deinonychus antirrhopus,* skull YPM 5232, right side viewed in reverse. Notice the subsidiary antorbital fenestrae. Abbreviations: aof—antorbital fenestra; aof' and aof''—subsidiary antorbital fenestrae; en—external naris; ma—maxilla; na—nasal; pm—premaxilla.

The alveolar groove contains 7 functional teeth, 3 incompletely erupted replacement teeth and 5 additional vacant alveoli, for a total of 15 maxillary teeth. This compares with 16 to 18 in *Allosaurus,* and 13 and 12 respectively in *Gorgosaurus* and *Tyrannosaurus. Coelophysis* bears 16 to 22 maxillary teeth and *Ornitholestes*[3] has 9 or 10.

The largest tooth is situated at about mid-length of the tooth row. The last 4 to 6 alveoli appear to have contained somewhat smaller teeth than those preserved along the remainder of the tooth row. The lateral surface above the alveolar margin is marked by numerous foramina arranged in two more or less distinct rows

---

[3] Examination of the type specimens has led me to conclude that *Ornitholestes* and *Coelurus* may not be synonymous. Until thorough comparisons can be made, I prefer to consider these as distinct and to use *Ornitholestes* in reference to the American Museum specimens and *Coelurus* for the Yale specimens.

that roughly parallel the alveolar border. Smaller foramina are situated irregularly between or above these rows. Presumably these foramina were vascular routes. No interdental plates are preserved.

The posterior maxillary margin defines the anterior limits of a large antorbital fenestra, apparently triangular in shape, judging from the preserved fragments of other bordering elements. Immediately anterior to this fenestra is a small, semicircular, accessory antorbital opening that is best described as a second antorbital fenestra. Anterior and slightly below this secondary fenestra is a narrow, nearly vertical, curved slit. This may correspond to the postnarial foramen described by Gilmore (1920) in *Ceratosaurus*, but on size alone it perhaps should be considered a third antorbital fenestra. The maxilla does not contribute to the narial opening, being separated from it by inferior processes of the nasal and premaxilla.

The medial surface of the maxilla (YPM 5232) is partly obscured by the left premaxilla, nasal and the vomers. The most prominent feature visible is a medially directed shelf or ledge, some 15 to 20 mm above the internal alveolar margin, that appears to extend the entire length of the maxilla. Anteriorly it is a thin plate of bone with a rather sharp medial edge, but posteriorly it forms a rounded ridge. This appears to have been nearly horizontal and probably represents the lateral portions of a secondary palate the remainder of which was cartilaginous or membranous. Ascending from this ledge, subparallel to the external maxillary surface, is a thin bony lamina that defines a narrow lateral space situated medial and ventral to the second antorbital fenestra. A thin pillar of bone extends from this lamina dorsolaterally to join the bony bar separating the two largest antorbital fenestra. Thus there appears to have been a well-defined lateral chamber of unknown function associated with the two anterior antorbital fenestrae, and perhaps extending forward to the external nares.

PREMAXILLA

Both premaxillae are preserved in YPM 5232, but the left element is severely crushed. The right premaxilla (Fig. 6) is complete except for the extremities of the maxillary and nasal processes. The main body of this bone is subrectangular with nearly vertical anterior and posterior margins. The upper margin is deeply embayed by the narial opening which is limited anteriorly and dorsally by a thin, slightly sinuous, parallel-sided, superior process. A longer, tapered, inferior maxillary process defines the lower margin of the narial opening and joins the upper anterior edge of the maxilla in a squamose articulation. The nearly vertical posterior margin provides a firm, digitate sutural union with the anterior margin of the maxilla. The median articular surface is almost completely smooth and flat, with only faint rugosities near the tip of the upper (nasal) process and just above the alveolar border. This would seem to indicate that the mid-line suture between the two premaxillae was not particularly firm.

The alveolar margin is slightly irregular due to breakage of the thin bone laminae around the alveoli, but it probably was straight or only slightly curved upward anteriorly toward the mid-line. There are four alveoli, one of which contains a strongly asymmetrical replacement tooth.

The external premaxillary surface is marked by a number of foramina arranged in several rows from 5 to 12 mm above the alveolar border, just as in the maxilla. These presumably were for passage of vascular elements, perhaps related to dental lamina. The area immediately beneath the narial opening is depressed, forming a concavity perhaps twice as large as the narial opening, suggesting that at least part of the nasal capsule was situated external to the bony snout elements—the premaxilla and nasal.

The internal premaxillary surface is marked by several irregular depressions and minute foramina in the region just above the alveolar margin. There also is a distinct medially projecting ridge that extends up and back along the base of the lower or maxillary process. This appears to be a continuation of the similar feature noted on the internal maxilla surface.

NASAL

Both nasals are preserved almost intact in YPM 5232 (Fig. 6). The nasal is a long narrow bone, perhaps equal to half the total skull length. The posterior extremity is not preserved in the materials at hand so the actual maximum length is not known. The most surprising feature of the nasal is its extreme narrowness, a condition that approaches that of *Tyrannosaurus;* the maximum preserved width is 17 mm compared with an incomplete length of 143 mm. Anteriorly, the nasal is L-shaped in cross-section, with the medial, horizontal lamina considerably thicker (3.2 mm) than the nearly vertical, lateral lamina (1.7 mm). The width of the dorsally facing medial lamina ranges from about 7 mm anteriorly to approximately 17 mm at the incomplete posterior end. The sharp, 90° angulation between the dorsal and lateral surfaces anteriorly fades into a rounded surface posteriorly and ultimately merges with the ventral border and the contact with the maxilla. Thus, posteriorly, the nasal forms only a narrow, dorsally directed surface, whereas anteriorly it forms both dorsal and lateral surfaces. The two nasals meet in a straight, edge-to-edge contact 1.5 to 2.5 mm thick. Their very narrow, flat dorsal surfaces indicate that the midline region of the snout upper surface was unusually narrow (no more than 35 mm above the principal antorbital fenestrae) and sharply delimited from the lateral snout surfaces. From this it is clear that the maxillae and premaxillae sloped laterally at a lower angle than was characteristic of most other theropods.

The nasal contacted the maxilla in a nearly straight, edge-to-edge junction anteriorly, but posteriorly it appears to have been a rather broad, tongue-and-groove-like union. Immediately above the maxillary articulation at the level of the middle antorbital fenestra there is a distinct but narrow groove with three moderate-sized, oval foramina. The dorsal surface features a number of smaller foramina, most of which are irregularly placed, but among these are six rather prominent, dorsally directed foramina that are arranged in a straight line and spaced exactly 10 mm apart. I do not recall any record of such a condition in other theropods and I have no explanation for this pattern.

Anteriorly the nasal is deeply emarginated by the posterior margin of the oval, external narial opening. A rather robust superior process extends forward and downward to underly the upper process of the premaxilla. The former is deeply grooved for reception of the upper premaxillary process. The lower process of the nasal is less robust than the upper, but it too is grooved on its underside for reception of the inferior premaxillary process. Thus, the junctions between nasal and premaxilla appear to have been quite firm.

LACHRYMAL

A nearly complete right lachrymal (Fig. 7) was recovered a few inches from the maxilla described above (YPM 5232), but unfortunately no contact between the two is preserved. This bone is T-shaped, with the cross-bar considerably more robust than the vertical shaft. In fact, the vertical shaft is remarkable because of its slender nature, in marked contrast to the robust preorbital bar of *Allosaurus, Ceratosaurus, Gorgosaurus* and *Tyrannosaurus,* and apparently also of most "coelurosaurs." Unfortunately the lower extremity is not preserved, but the several jugals recovered indicate that the junction of the jugal and lachrymal was very weak and quite unlike that of most other theropods. *Velociraptor* (AMNH 6515), however, appears to have a similarly reduced preorbital bar. The upper part of the lachrymal shaft is pierced by a narrow lachrymal duct passing from the orbital cavity to the antorbital fenestra.

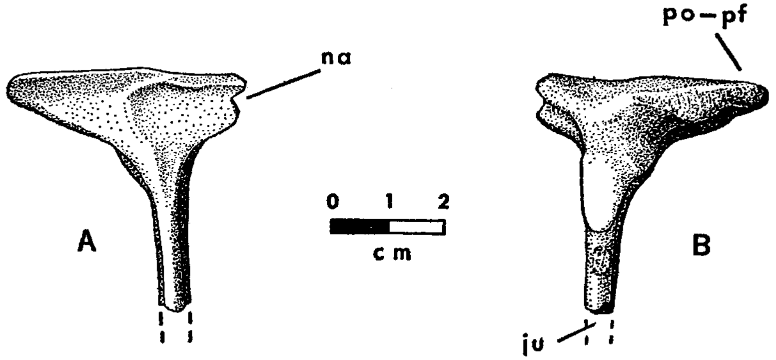


FIG. 7. Right lachrymal (reversed) of *Deinonychus antirrhopus,* YPM 5232, in medial (A) and lateral (B) views. Abbreviations: ju—jugal process; na—contact of the nasal; po-pf—postorbital-postfrontal process.

The upper portion of the lachrymal is triangular in dorsal aspect, with a prominent rugose boss projecting laterally at the dorsoanterior margin of the orbit. This rugose sculpturing extends down the shaft and across the upper part of the lateral surface, but is most strongly developed on the orbital rim. The dorsal surface is narrow (17 mm) and nearly flat and is oriented perpendicular to the ventral shaft.

The anterior half of the upper edge of the internal surface bears a distinct groove that probably represents the articulation with the nasal, but there is no recognizable scar for contact with either the prefrontal or frontal. As with the nasal the remarkable feature of the lachrymal is its restricted transverse dimension, which indicates that the skull was either extremely narrow at this point, or the frontals and posterior extremities of the nasals were unusually broad. In the absence of a skull table and contacts between the nasal, maxilla and lachrymal, it is not possible to reconstruct the exact form of the snout, but the nasals and lachrymals indicate that the preorbital portion of the skull was probably distinctly triangular in section, narrow above and broad below.

POSTORBITAL

This element is represented by two nearly complete bones, a left from skull YPM 5232 and a right from skull YPM 5210, (Fig. 8), plus a fragmentary right postorbital (YPM 5232). This small sample shows some variation, chiefly in the degree of robustness, probably a reflection of age differences. The postorbital is triradiate, with a thin posterior process extending to the squamosal and forming the dorsal limit of the lateral temporal fenestra, a somewhat stouter ventral process which meets the ascending process of the jugal and a massive and externally rugose, dorsal process that bends medially as a thick, vertical lamina to meet the frontal. The latter contact is in the form of an extensive digitate suture, whereas the posterior process fits into a tapered groove on the external surface of the squamosal and the ventral process is joined by a shallow overlapping contact of the jugal dorsal process. Like the lachrymal, the dorsal portion of the postorbital is marked by moderate rugosities or sculpturing. The remaining external surface is quite smooth and flat, but the internal surface bears a prominent and sharply defined vertical ridge which descends from the broad frontal suture down the inner surface of the jugal process toward the contact with that bone. In part, this feature contributed to the posterior wall of the orbit, separating that cavity from the temporal fossa behind. It also probably marks the lateral limits of the area of origin of part of the M. adductor mandibulae externus (Luther, 1914; Lakjer, 1926).

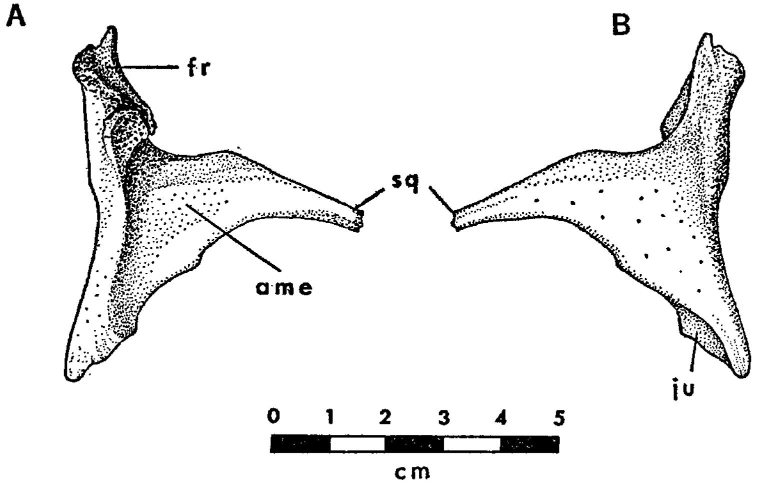


FIG. 8. Right postorbital of *Deinonychus antirrhopus*, YPM 5210, in medial (A) and lateral (B) views. Abbreviations: ame—area of origin of the external mandibular adductors; fr—frontal suture; ju—jugal process; sq—squamosal process.

SQUAMOSAL

Three squamosals are known: two from skull YPM 5210 and a fragmentary right squamosal from YPM 5232 (Fig. 9). This is a complexly shaped bone which cannot be described in a few words. It bears no less than five tapered processes by which it meets the postorbital, quadrate, parietal and the paroccipital process. The main portion is a strongly curved sheet of bone, convex dorsolaterally and strongly concave medially. The concave surface delimits the upper posterolateral margins of the temporal muscle chamber. Externally, a posterior, ventrolaterally directed process extends outward, away from a pronounced ventral concavity—the articular cotylus for the dorsal head of the quadrate. Anterior to this is a large, tapered, blade-like process that extends ventrally with a shallow groove facing posteriorly for contact with the upper part of the quadrate shaft. This process forms the upper posterior limit of the lateral fenestra and in part defines the lateral limits of the mandibular muscle chamber. A two-pronged anterior process, marked by a deep lateral groove, provides a tongue-and-groove union of the squamosal and postorbital and forms a stout upper temporal arch. Dorsal and

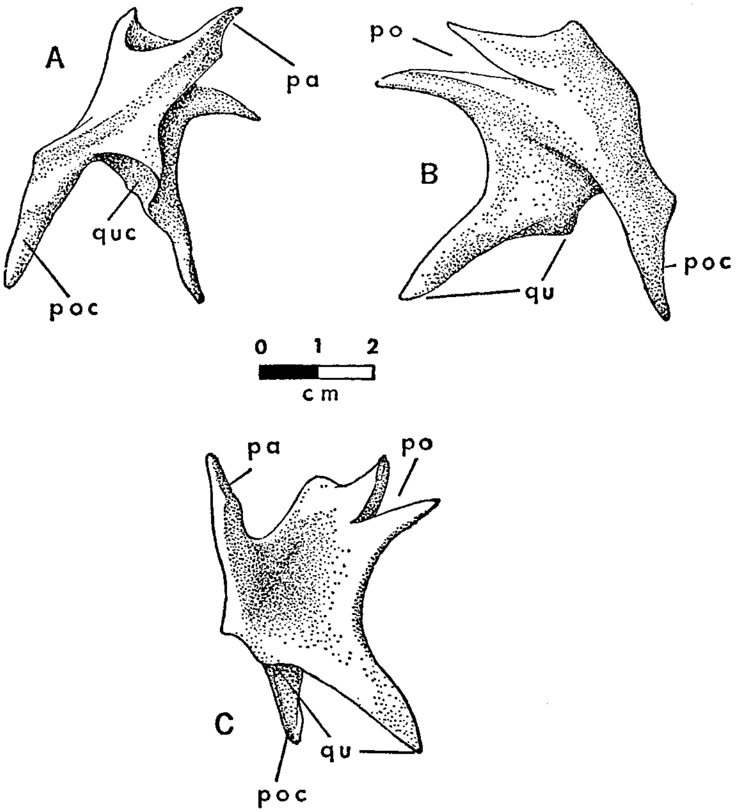


FIG. 9. Right squamosal (reversed) of *Deinonychus antirrhopus*, YPM 5210, in posterior (A), lateral (B) and anterior (C) views. Abbreviations: pa—articular surface for the parietal; po—articulation with postorbital; poc—articulation with paroccipital process; qu—articular contact with quadrate; quc—cotylus for quadrate.

medial to the quadrate cotylus the fifth process extends medially and forward to contact the parietal.

Without the adjacent bones, it is impossible to record the exact size and shape of the temporal fenestrae. However, the shape of the squamosal indicates a superior temporal fenestra of at least moderate size. The lateral fenestra was quite deep dorsoventrally and may have been slightly restricted from behind at about mid-height, as it is in nearly all "carnosaur" skulls. Without knowledge of the quadrate, however, the precise shape is in doubt.

JUGAL

Both jugals are known from skull YPM 5232 and the left jugal, complete and uncrushed, was recovered from skull YPM 5210 (Fg. 10). The jugal is a thin plate

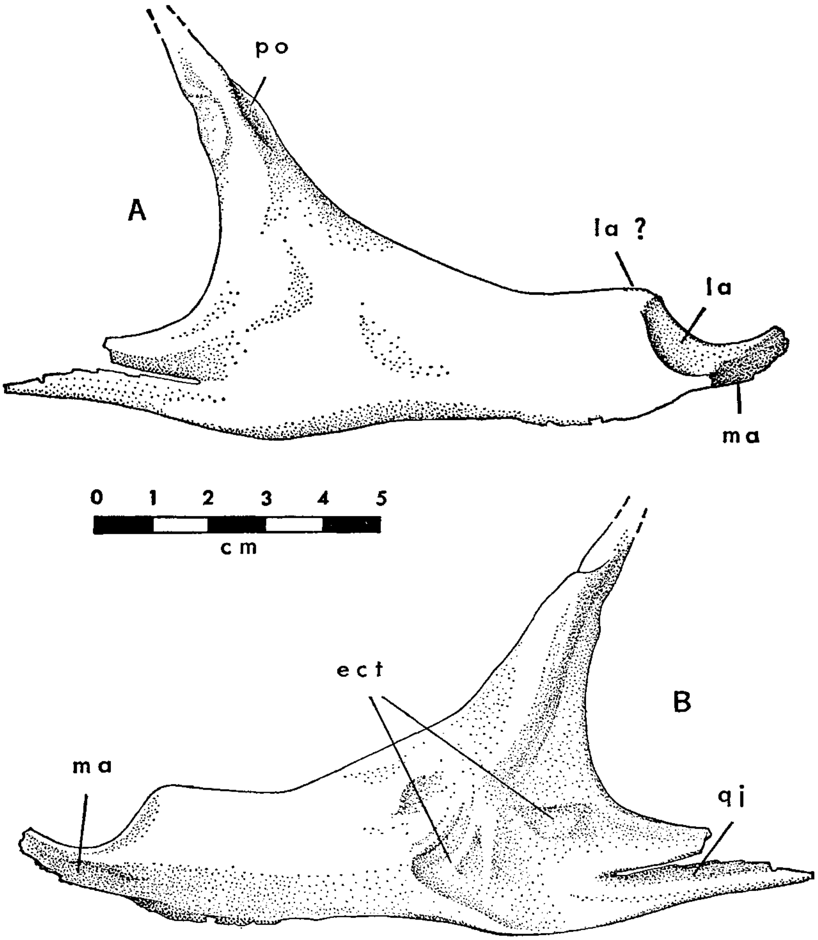


FIG. 10. Right jugal of *Deinonychus antirrhopus,* YPM 5210, in lateral (A) and medial (B) views. Abbreviations: ect—articular scars of ectopterygoid; la and la?—lachrymal contact with jugal; ma—articular area of maxilla; po—articulation area of post-orbital; qj—articulation area of quadratojugal.

of bone almost triradiate in shape. Anteriorly a thin but deep process meets the posterior ramus of the maxilla in a weak overlapping contact. Posteriorly, a thin, tapered, two-pronged process contacted the quadratojugal in what appears to have been a weak tongue-and-groove articulation. Dorsally, a somewhat more robust, grooved process met the postorbital. The latter separated the orbit and lateral temporal fenestra. The posterior process marks the ventral limit of the lateral fenestra. The sweeping curve of the upper margin of the jugal indicates an orbit of large, if not unusual, size.

The external surface is smooth and gently undulated, and, with the exception of articular surfaces for the adjacent elements mentioned above, is unmarked. The internal surface is similar except for a large and irregular depression at the base of the ascending (postorbital) process. This depression, which is the most prominent scar on this element, marks the articulation area of the ectopterygoid.

The most remarkable feature of the jugal is the lack of any recognizable contact with the lachrymal. There are clear scars for internal and external overlapping of the anterior and posterior process by the maxilla and quadratojugal respectively, but there is only the faintest suggestion of contact with a preorbital bar just behind the junction with the maxilla.

QUADRATOJUGAL

This element is represented by two complete bones of skull YPM 5210 and an incomplete right quadratojugal from skull YPM 5232. The quadratojugal is a T-shaped bone, with the cross-bar oriented almost vertically (Fig. 11). The latter is the most robust portion, forming a thick, broad blade that apparently overlapped the lower part of the quadrate shaft superficially. Extending forward from this is a delicate process that expands ventrally near its anterior limit to fit into the groove or slit of the two-pronged posterior jugal process. This clasping junction of the jugal and quadratojugal does not appear to be a particularly solid union, nor does the overlapping contact with the quadrate, but it seems unlikely that there was any significant degree of quadrate mobility.

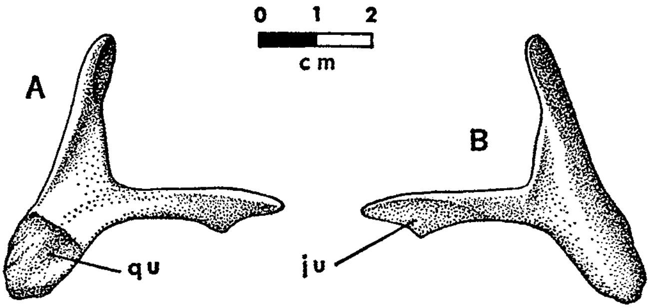


FIG. 11. Right quadratojugal (reversed) of *Deinonychus antirrhopus*, YPM 5210, in medial (A) and lateral (B) views. Abbreviations: ju—articular surface for jugal; qu—articular surface for quadrate.

PTERYGOID

Considering the delicate nature of the palatal bones it is remarkable that any part of the palate of *Deinonychus* can be reconstructed at all. Between the two skulls, the pterygoids, ectopterygoids, palatines and vomers are known and only the anterior part of the palate remains in some doubt. The pterygoid is represented by a nearly complete left and a fragmentary right pterygoid from skull YPM 5210. Two additional incomplete pterygoids were recovered from the Yale quarry. These probably belong to the other skull (YPM 5232), but because they were widely separated and situated at some distance from other skull elements they have been catalogued separately (YPM 5233 and 5239).

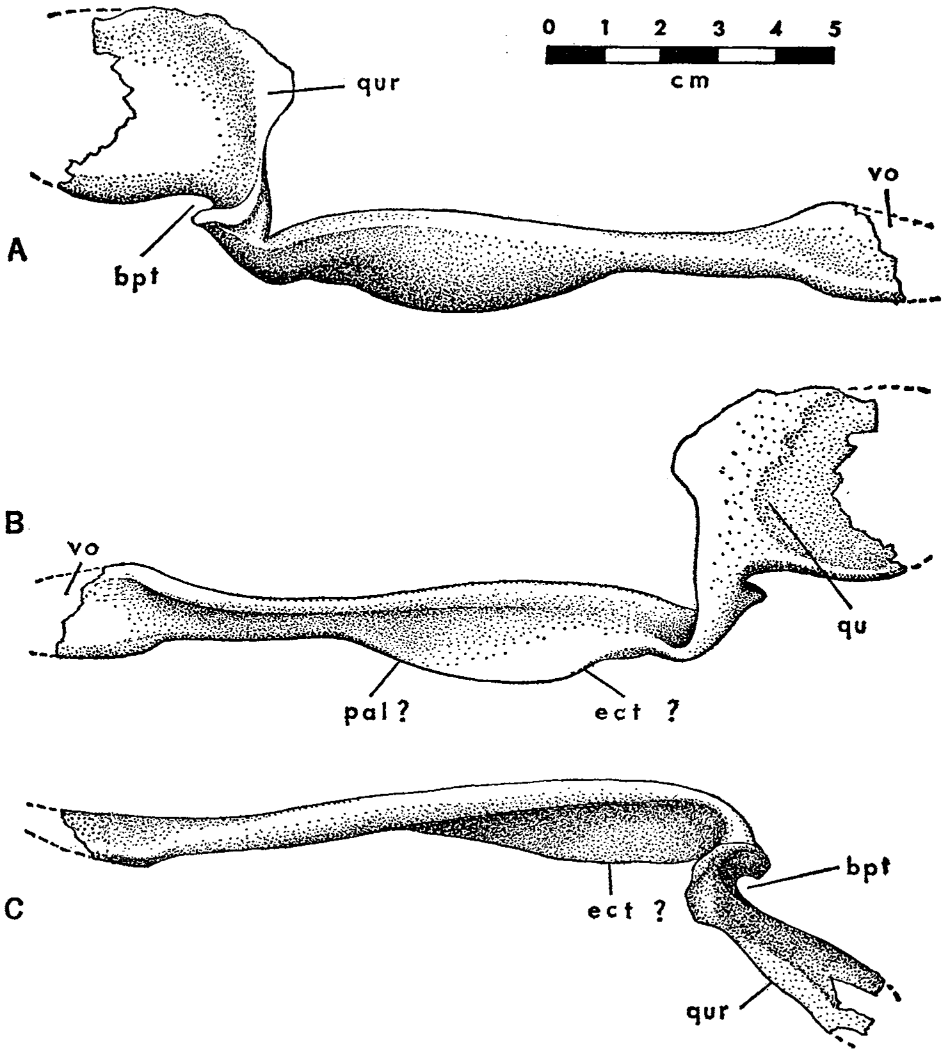


FIG. 12. Left pterygoid of *Deinonychus antirrhopus*, YPM 5210, in medial (A), lateral (B) and dorsal (C) views. Abbreviations: bpt—basipterygoid notch; ect?—probable region of contact with the ectopterygoid; pal?—probable region of contact with the palatine; qu—squamose contact with quadrate; qur—quadrate ramus; vo—vomer process.

The pterygoid is very thin and long, probably exceeding half of the basal skull length (Fig. 12). A well-developed articular surface for the basipterygoid process of the basisphenoid exists in the form of a dorsoposteriorly facing concavity. Extending caudally and outward from this is a very thin but high vertical flange, the quadrate ramus. This flange thins markedly posteriorly and none of the specimens include any part of the "paper thin" posterior margin. Two of them (YPM 5210 and 5233), however, preserve distinct impressions of the anterior limits of the squamose contact with the pterygoid wing of the quadrate on the lateral surface, indicating that this ramus of the quadrate extended forward almost to the level of the basipterygoid articulation. Such extensive overlap of the quadrate and pterygoid suggests that there was little if any streptostyly.

The palatine ramus extends forward as a nearly straight, oval rod, apparently separated from its counterpart by a narrow interpterygoid fissure. Immediately anterior to the basipterygoid process a thin sheet of bone curves down and out from the main shaft. This diminishes anteriorly to a point approximately 70 mm anterior to the basipterygoid articulation where the pterygoid consists of a simple shaft about 7 by 4 mm. Further forward the palatine process expands to a vertical sheet of bone of unknown height (more than 15 mm high by 2.5 mm in maximum thickness). The anterior extremity is not known. None of the articulations with other palatal elements are preserved, although two of the pterygoids are nearly complete, and the vomers were in contact with one of these. Presumably, the ectopterygoid met the pterygoid in a squamose, overlapping articulation with the down-curving sheet of bone immediately anterior to the basipterygoid articulation. The palatine may have made contact in this region also.

The quadrate ramus is comparable to that known in *Allosaurus* and *Tyrannosaurus*, but the narrow form of the anterior or palatine process is quite different from that of *Allosaurus* or *Tyrannosaurus*.

ECTOPTERYGOID

This element is represented by a single bone from each of the two skulls. Triradiate in shape (Fig. 13), it bears a stout, lateral process which curves posteriorly

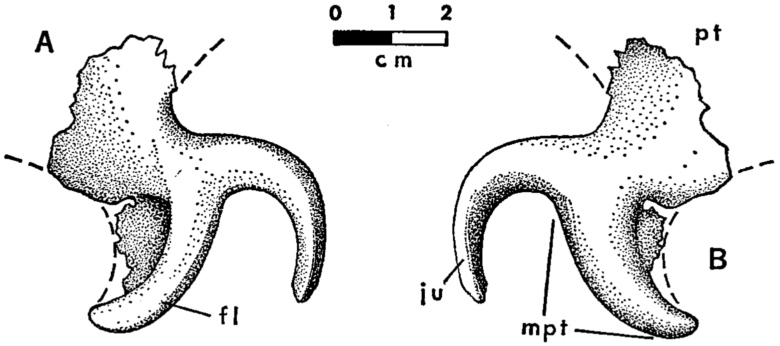


FIG. 13. Right ectopterygoid (reversed) of *Deinonychus antirrhopus*, YPM 5210, in ventral (A) and dorsal (B) views. Abbreviations: fl—"pterygoid" flange; ju—articulation with the jugal; mpt—possible origin area of the M. pterygoideus; pt—pterygoid ramus.

to contact the inner surface of the jugal in a broad overlapping union. A more robust, hook-shaped process extends back and down, forming the usual ventral, ectopterygoid (pterygoid) flange. On the underside of this ventral flange, facing medially and slightly forward is a deep and pronounced pocket or concavity of unknown function. This feature might be described as a "carnosaurian" character, for it is present in *Allosaurus* and *Tyrannosaurus* and apparently also in *Gorgosaurus,* but is absent in *Coelophysis* and perhaps in *Ornitholestes.* Extending medially from the bases of these two hook-shaped processes is a broad, thin lamina—the pterygoid process—which presumably joined the ventral extension of the palatine process of the pterygoid. A small oval pit, marking the dorsal surface of this process at its junction with the jugal process, may be related to the origin of the M. pterygoideus dorsalis. The ectopterygoid seems to have been a robust brace between the marginal elements of the skull and the medial elements of the palate, separating the palatine fenestra anteriorly from the subtemporal fossa behind.

PALATINE

The palatines are known from a nearly complete right palatine (Fig. 14) from skull YPM 5210 and an incomplete left element from the second skull (YPM

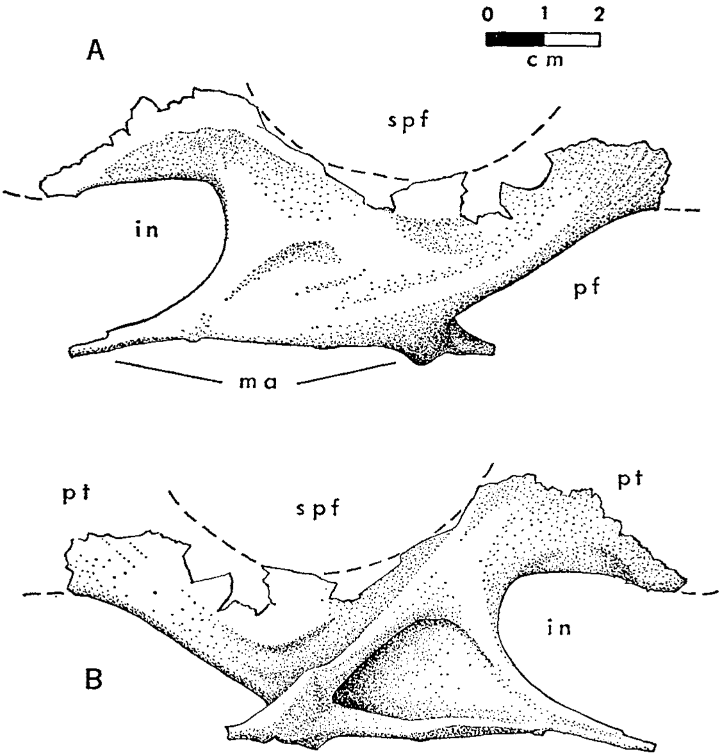


FIG. 14. Right palatine of *Deinonychus antirrhopus,* YPM 5210, in ventral (A) and dorsal (B) views. Abbreviations: in—internal naris; ma—maxillary border; pf—palatine fenestra; pt—pterygoid processes; spf—subsidiary palatine fenestra.

5232). The palatine is a large, flat, quadriradiate bone of surprising thinness that apparently formed most of the palate. Anteriorly it is deeply emarginated by the posterior margin of the large internal naris. The posterior border defines the anterior limits of the large palatine fenestra. The medial parts of both preserved palatines are damaged and incomplete, but both possess what appear to be incomplete natural margins defining an additional (subsidiary) palatine fenestra between the palatine and the anterior process of the pterygoid (Figs. 5 and 14). Among theropods, I know of no similar subsidiary palatine fenestra, except in *Ornithosuchus.* Walker (1964) illustrated a narrow, fissure-like fenestra between the palatine and pterygoid, but this opening is defined laterally, medially and posteriorly by the pterygoid; the palatine contributes only to its narrow anterior margin. In *Deinonychus,* this subsidiary palatine fenestra appears to have been limited by the pterygoid medially and the palatine laterally. The functional significance of this opening is not known.

Although a thin sheet of bone, the palatine is reinforced on its dorsal surface by three thick ridges or struts which radiate from the posterolateral corner junction with the maxilla. A lateral strut extends forward along the lateral edge, reinforcing the union with the maxilla. A second strut extends anteromedially reinforcing the lamina of bone between the choana and the "subsidiary" palatine fenestra. A third strut passes posteromedially between the latter and the large palatine fenestra and reinforces the anterior margin of that opening.

The palatine joined the maxilla in a long, grooved, buttressed union. Contacts with other palatal elements are not preserved, but they appear to have been of an overlapping, squamose kind, rather than digitate or edge-to-edge contacts.

VOMER

The vomers are incompletely known in both of the above skulls. In skull YPM 5210, incomplete fused vomers (Fig. 15) were associated with the left pterygoid, but no articular contacts are preserved. The vomers are preserved in near normal position in YPM 5232. The vomers appear to have been vertical plates of bone, some 15 mm or more in height, situated in or close to the mid-line and extending

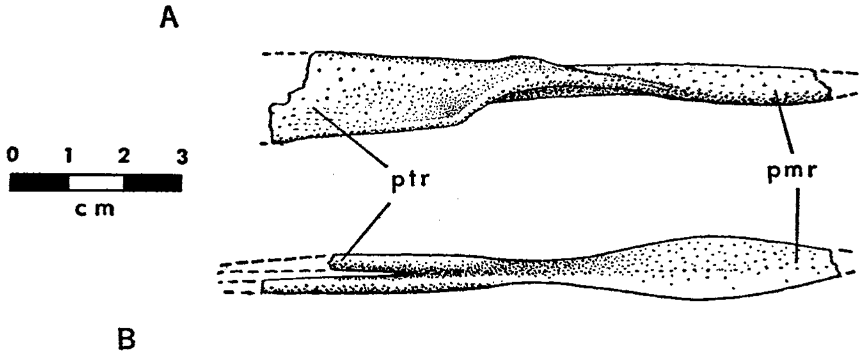


FIG. 15. Vomers of *Deinonychus antirrhopus,* YPM 5210, in right lateral (A) and ventral (B) views. Abbreviations: pmr—premaxillary ramus; ptr—pterygoid rami.

between the anterior extremities of the pterygoids and the premaxillae (Fig. 5). In all probability they separated the internal nares, but this cannot be demonstrated with the material presently available. The paired condition of the vomers is evident posteriorly, but anteriorly the two vertical lamina unite with only narrow dorsal and ventral grooves marking the mid-line and the paired construction. The anterior extremities are not preserved, but anteriorly the vomers seem to expand laterally into a mid-line element of moderate width and shallow depth, slightly concave ventrally. Whether this expansion had the diamond shape characteristic of *Ornithosuchus* and *Tyrannosaurus* is not known.

MANDIBLE

The lower jaws are known from disarticulated elements of two individuals (YPM 5210 and 5232). Mandibular elements represented are the dentary, splenial, surangular, angular, prearticular and articular. No coronoid is known, but it may well have been present. The mandibles are surprisingly shallow for their length and in this respect are distinctly "coelurosaurian," resembling *Coelophysis* and *Velociraptor* in particular (Figs. 4 and 16).

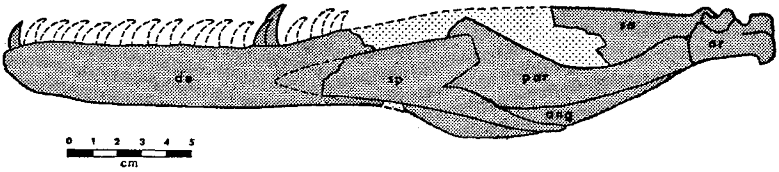


FIG. 16. Restoration of right mandible of *Deinonychus antirrhopus*, in internal view. Based on disarticulated elements so proportions and arrangements are only approximate. Dark stipple indicates known elements, light stipple unknown portions. Abbreviations: ang—angular; ar—articular; de—dentary; par—prearticular; sa—surangular; sp—splenial.

DENTARY

The dentary is long and shallow, with the inferior margin subparallel to the alveolar margin. The left dentary of YPM 5210 appears to have a complete row of 16 alveoli (although the posterior extremity is missing). The slightly smaller left dentary of YPM 5232 (in which the posterior dentary extremities are also missing) also bears 16 alveoli, with a functional tooth present in number 15 and a replacement tooth preserved in the last alveolus (Fig. 17). A dorsal expansion of the Meckelian canal extends almost to the upper dentary margin immediately behind this last alveolus, thus establishing a maximum number of 16 teeth. There are no interdental plates present on the dentary.

The symphysial suture is represented in both dentaries by nearly flat, elliptical, mid-line surfaces marked by faint, nearly horizontal, longitudinal striations. These suggest a highly mobile symphysis. The medial surface is widely open behind, exposing the deep but narrow Meckelian canal, which tapers sharply anteriorly although it persists as a shallow, but well-defined, open groove over most of the anterior half. Anteriorly, this groove terminates in a small foramina beneath

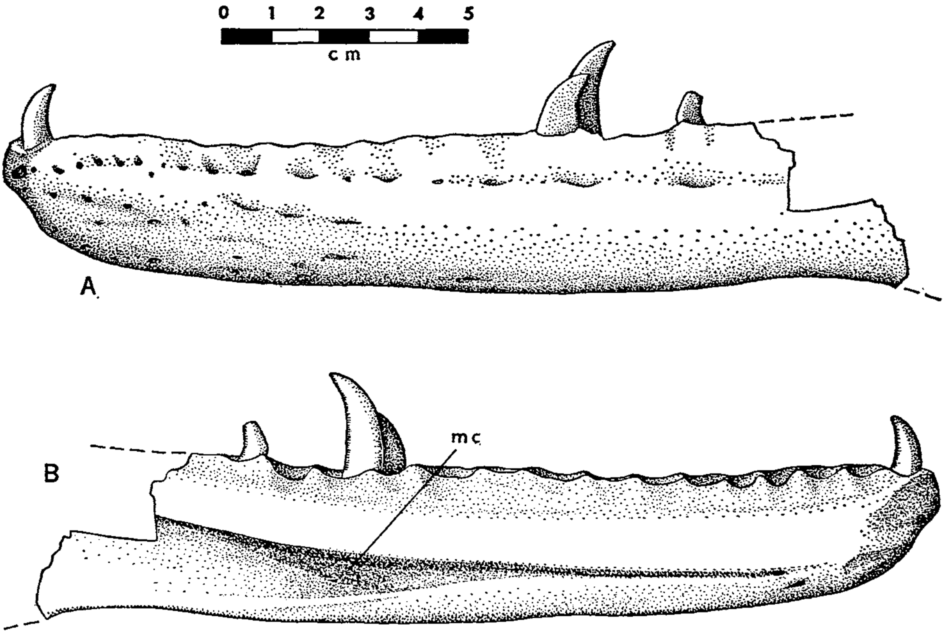


FIG. 17. Left dentary of *Deinonychus antirrhopus*, YPM 5232, in lateral (A) and medial (B) views; mc—Meckelian canal.

the third or fourth alveolus. Immediately anterior to this is a slightly larger elongate foramina which may communicate with an anterior extension of the Meckelian canal.

The lateral dentary surface is unsculptured, although slightly irregular in texture. Like the maxilla, it is marked by numerous foramina which are arranged in more or less distinct rows. The most obvious is an upper row of well-defined, circular foramina closely spaced anteriorly, but becoming progressively more widely spaced posteriorly. Below this upper row, are less distinct rows of more irregularly spaced foramina, including a final row just above the ventral margin of the dentary. The anteriorly situated foramina generally extend inward and backward, whereas the posterior foramina pass inward and forward. The function of these foramina is not known, but vascular and nerve passage to superficial tissues seems probable.

SPLENIAL

Three splenials are among the mandibular elements recovered from the Yale site, a left (YPM 5210) and two rights for which quarry data were lost. It is presumed that they belong to the two skulls known from that quarry, but in the absence of quarry data they have been catalogued separately (YPM 5237 and 5238). None of these bones are complete, but No. 5237 (Fig. 18) is nearly so. The splenial is a thin and long, wedge-shaped bone with a rather stout, rounded ventral margin. Anteriorly, a thin, probably triangular, lateral lamina overlapped the inner

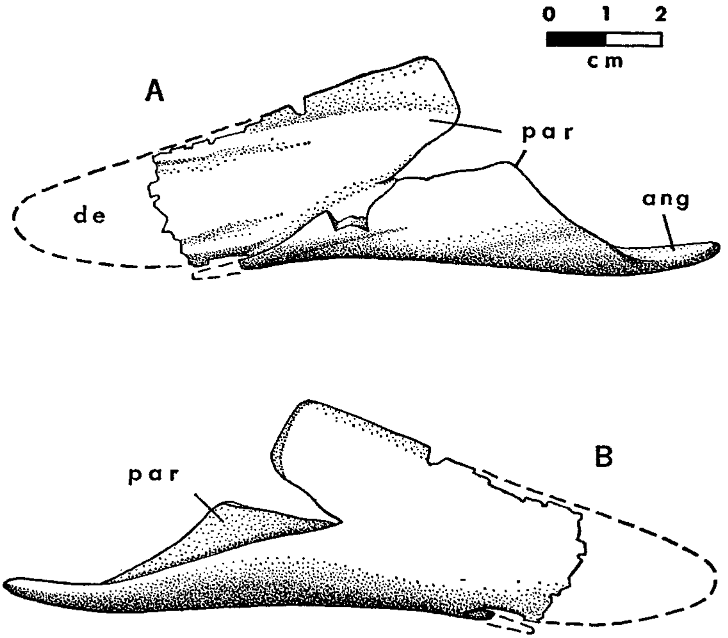


FIG. 18. Left splenial of *Deinonychus antirrhopus*, YPM 5237, in lateral (A) and medial (B) views. The rostral extremity of the prearticular apparently lay external to the upper (internal) flange. Abbreviations: ang—angular; de—dentary contact; par—areas of contact with the prearticular.

surface of the dentary. This lamina increases in height posteriorly to about midlength, where it ends in a dorsoposteriorly directed flange which is separated by a long V-shaped notch (infra-Meckelian fossa) from the ventroposterior or angular process. The latter is a stout, slightly curved, tapering process that extends back beneath the anterior extremity of the angular. The upper surface is a shallow groove which narrows and deepens anteriorly, passing between the lateral and medial lamina. The medial lamina of the splenial is less than half the height of the lateral lamina, its upper margin slopes forward to form a thin anterior process separated from the lateral lamina by a narrow, elongate notch. No sutural scars are recognizable and contacts with the dentary, angular and prearticular probably were rather loose.

ANGULAR

Two angulars are known, one from each of the skulls from the Yale site. Neither is complete and little can be said about precise relationships to adjacent jaw elements. Anteriorly, the angular consists of a stout, slightly curved process, triangular in section, which presumably met the dentary anteriorly and the splenial and prearticular dorsomedially. Caudally, it expands into a strongly curved and very thin sheet of bone which overlapped the ventrolateral portion of the surangular. The dorsal margin is well preserved in both specimens and clearly shows the inferior limits of a very large external mandibular fossa (Fig. 19). Although the

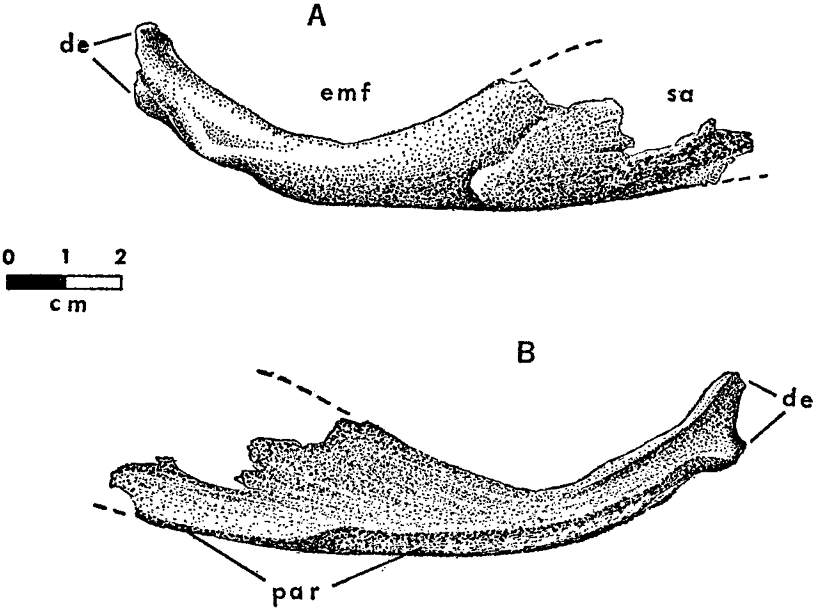


FIG. 19. Right angular (reversed) of *Deinonychus antirrhopus*, YPM 5210, in lateral (A) and medial (B) views. Abbreviations: de—articular contact for dentary; emf—external mandibular fossa; par—suture with prearticular; sa—surangular process.

anterior part of the surangular is missing and thus the actual size and shape of this fossa cannot be determined, it is quite evident that it was relatively much larger than in most other theropods. Only *Ornithosuchus*, which Walker (1964) considered a primitive carnosaur, may have possessed a larger external mandibular fossa.

SURANGULAR

A single incomplete surangular is known from the Yale site, but because it was found isolated from all the other cranial elements, it could not be positively associated with either of the known skulls. Hence it has been catalogued separately (YPM 5234; Fig. 20). This is a flat bone which formed a large part of the external surface of the posterior third of the lower jaw. It overlaps the inferior lateral surface of the articular posteriorly and anteriorly must have joined the dentary in a squamose articulation. It probably formed the entire upper external margin of the mandible behind the tooth row. The stout upper border is reinforced by a medially projecting ridge that probably extended the entire surangular length and formed the upper margin of the dorsomedially facing adductor fossa (Meckelian fossa of some writers). A prominent triangular process rises from the dorsal margin opposite the position of the glenoid. This corresponds to and lies against a dorsolateral projection of the articular. In front of this is a broad but shallow depression that extends medially and appears to be an anterolateral extension of the articular facet of the glenoid. The caudal extremity is not preserved, but its outline is preserved on the lateroinferior surface of the articular as a triangular flange that overlaps the articular. The anterior portion of the surangular also is

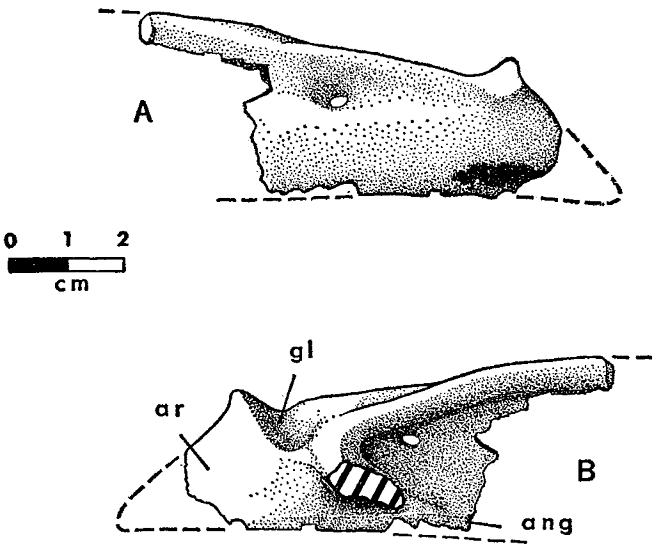


FIG. 20. Right surangular (reversed) of *Deinonychus antirrhopus*, YPM 5234, in lateral (A) and medial (B) views. Abbreviations: ang—articular contact with angular; ar—surface of articulation with articular; gl—external margin of glenoid. (Broken surface indicated by heavy inclined lines.)

not preserved, but there can be little doubt that it formed the upper limits of the external mandibular fossa. The external surface is unsculptured, but is marked by a large shallow depression at the center of which is a small oval surangular foramen approximately 2.5 cm anterior to the position of the glenoid. This foramen is minute compared with that of *Tyrannosaurus* or *Gorgosaurus,* but neither *Allosaurus* or *Ceratosaurus* have this foramen. The inner surangular surface is marked by a stout, wedge-shaped process that buttressed the prearticular just anterior to its union with the articular. This buttress also formed the posterior wall of the adductor fossa. Although, incomplete, the present element appears most similar to that of *Velociraptor,* which also appears to have a small surangular foramen at almost the same position.

PREARTICULAR

A nearly complete right (Fig. 21) and a partial left prearticular are known from skull YPM 5210. This is a curved bone, with a nearly vertical, thin blade extending anteriorly and a rounded, grooved shaft reaching posteriorly. The anterior blade presumably underlapped the medial (dorsal) lamina of the splenial and extended to the posterior extremity of the dentary medial wall. Posteriorly, it butted against the anterior part of the articular. The lateral surfaces of the posterior shaft are rugose and striated, evidence of strong sutural union with the surangular and angular. The posterior shaft is further marked by a pronounced longitudinal groove, which divided the surangular contact into a short upper and a longer lower articulation. The lower surfaces extend about 15 mm in front of the upper, where they taper into a sharp crested ventral ridge. At this point, the narrow ventral surface is marked by two distinct grooves, a broad, shallow lateral

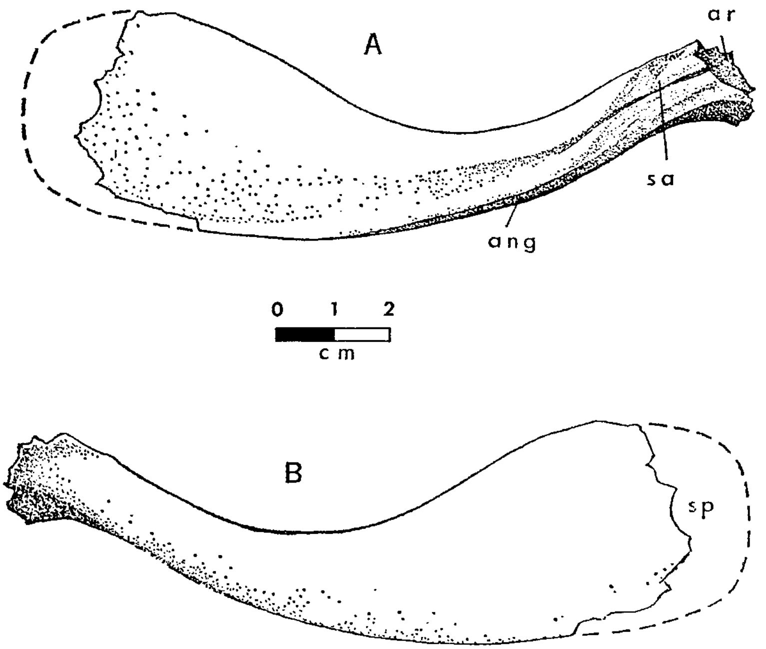


FIG. 21. Right prearticular (reversed) of *Deinonychus antirrhopus*, YPM 5210, in lateral (A) and medial (B) views. Abbreviations: ang—suture for angular; ar—articulation with articular; sa—articulation with surangular; sp—area of contact with splenial.

groove and a very narrow medial one. The lateral groove gradually fades out anteriorly, but the medial groove expands and persists nearly to the anterior extremity of the inferior margin. These features correspond to the posterior part of the ventro-medial margin of the angular (described above) and are interpreted as the sutural surfaces that joined these two bones. The dorsal margin of the prearticular forms a broad sweeping curve, which defines the lower margin of the adductor fossa.

In general form, the prearticular appears to most closely resemble that of *Velociraptor*. It is relatively longer and higher (anteriorly) and much more delicate than that of *Allosaurus*.

ARTICULAR

The articular is a massive, triangular element (Fig. 22) with a short but broad retroarticular process bearing a robust, ventro-medially directed, hook-like extremity and a longitudinally oriented, rectangular, blade-like flange projecting dorsally. The former might be the insertion site of the M. depressor mandibulae, but I suspect it is also related to the pterygoideous musculature. The ascending flange, which is situated directly behind (7 mm) the glenoid and is oriented perpendicular to the long axis of the glenoid, is the other most probable point of attachment for the depressor muscles.

Colbert and Russell (1969) described a very similar, but much more prominent, dorsally directed process in almost the same position on the retroarticular process

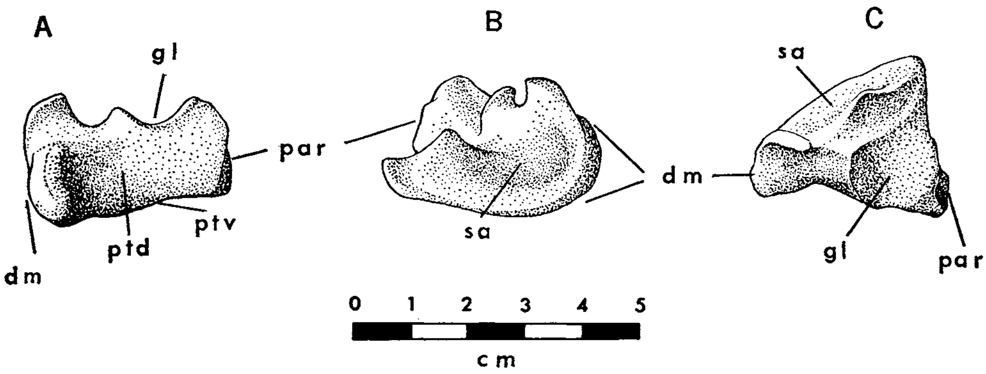


FIG. 22. Right articular (reversed) of *Deinonychus antirrhopus*, YPM 5232, in medial (A), lateral (B) and dorsal (C) views. Abbreviations: dm—area of insertion of M. depressor mandibulae; gl—glenoid; par—area of contact with prearticular; ptd—probable insertion site of M. pterygoideus dorsalis; ptv—probable insertion area of M. pterygoideus ventralis; sa—area overlain by the surangular.

of *Dromaeosaurus*. Following Bock's (1960) analysis of similar processes in certain birds, Colbert and Russell suggested that this process may have developed initially as a specialized area of insertion of the pterygoideus and depressor mandibulae muscles. They added that the extreme development of this feature in *Dromaeosaurus* may have resulted in contact with the posterior face of the quadrate when the mandible was depressed and thus it may have served as a bony stop to prevent excessive opening of the jaws. Their explanation is feasible for the very long articular process of *Dromaeosaurus*, but it does not seem feasible for the much shorter process of *Deinonychus*. A possible analogous structure is preserved in *Allosaurus fragilis (Antrodemus valens* of Gilmore, 1920), USNM 4734, but with this possible exception I do not recall a comparable feature in other theropod specimens.

The articular is defined by five surfaces: 1) the conspicuous, transverse depression of the glenoid, 2) a shallow, concave, superior lateral surface, 3) a nearly flat, inferior lateral surface (surangular contact), 4) a rectangular medial surface, and 5) a triangular, rugose anterior surface (prearticular contact). The glenoid is a broad and deeply concave trough forming the anterior half of the dorsal surface. It is longest in a transverse direction and nearly triangular in outline, the truncated apex at the rear and the longest margin forming the anterior border. Medially, the glenoid is open, but laterally it is bordered by a distinct groove trending forward and outward, which in turn is bounded by a prominent, triangular, vertical flange with the same orientation. The anterior glenoid border is broadly convex longitudinally and gently concave transversely. The posterior wall of the glenoid rises as a forward-facing buttress. The orientation of this latter surface, rising as it does to a nearly vertical transverse surface, restricts any mandible protraction and in fact appears to have provided a massive stop obstructing mandibular protraction. It furthermore suggests that the lower part of the quadrate (which is not known) sloped down and backward, as in *Ornithosuchus* and other adequately known "coelurosaurs," rather than oriented vertically or sloping forward.

The concave, nearly semicircular, superior lateral surface and the flat, inferior lateral surface are separated by a sharp longitudinal crest that extends from the anterolateral corner of the glenoid back to the curved retroarticular extremity, from which point it sweeps upward along the rear edge of the ascending retroarticular flange. The inferior lateral surface is overlain in its entirety by the posterior part of the surangular. In addition to the above crest, it is defined rather sharply by a ventral longitudinal ridge that separates this surface from the medial surface. The medial surface is smooth and slightly concave caudally where it passes to the inturned retroarticular extremity. There is no clear indication of muscle attachment on this surface, but portions of the pterygoideus may have inserted here. The triangular anterior surface lies directly in front and beneath the glenoid. It is rugose and irregular in surface texture, indicating a solid junction with the prearticular and other adjacent elements of the mandible.

Dentition

The available cranial material shows 19 teeth in the upper tooth row (4 premaxillary and 15 maxillary teeth) and 16 in the lower tooth row. Teeth in both the maxilla and dentary are sub-isodont, except at the back of the series. The right dentary of YPM 5232 contains four fully erupted teeth in the last five positions (the penultimate alveolus contains a broken replacement tooth), showing a progressive reduction in tooth size in this segment of the tooth row. A similar backward reduction in tooth size at the rear of the tooth row is indicated for the maxilla by the alveolar dimensions. No functional teeth are preserved in the only well preserved premaxilla (YPM 5232), but the alveoli are subequal in size. Isodonty of the premaxillary teeth is substantiated by four isolated premaxillary teeth associated with the disarticulated elements of skull YPM 5210, all of which are about the same height.

Maxillary and dentary teeth are all quite similar in form, being laterally compressed, sharply tapered, and recurved, and with serrated anterior and posterior edges (Fig. 23: A1, A2, A3 and A4). Tooth roots are quite long, perhaps twice as long as the enameled crown, parallel-sided and contain long, open pulp cavities. Maximum transverse and longitudinal dimensions of a given tooth occur at the upper fifth of the root, just below the limits of enamel. Below this level the root is constricted by lateral and medial grooves that extend to the root end and result in a figure-8 cross section for the root. The root appears to have been a straight shaft in both lateral and longitudinal aspects. The enameled crown curves sharply backward from the root axis and leans slightly inward. Those teeth that seem to be preserved in natural position are all directed backward, so the apex of each tooth lies well behind the rear margin of that alveolus. This appears to have been true for all maxillary and dentary teeth and it seems to have been more pronounced in *Deinonychus* than in other theropods. Compare, for example, Figure 4 and 6 with *Coelophysis, Ornitholestes, Allosaurus* or *Gorgosaurus,* where tooth apices rarely occur behind the base of the tooth.

The crowns of both maxillary and dentary teeth are slightly asymmetrical. A plane passing through the anterior and posterior serrations divides the tooth into unequal halves, a thin, slightly convex outer half and a somewhat thicker, more convex inner half (Fig. 23: A2). The lateral surfaces consistently are more convex anteriorly than posteriorly, whereas the inner crown surfaces seem to have about the same degree of curvature or convexity from front to back. Thus, a tooth appears more blade-like in external aspect and more bulbous or tusk-like in internal view. This asymmetry seems to decrease slightly toward the back of the tooth row. Gilmore (1920: p. 30) noted a similar condition in *Allosaurus.*

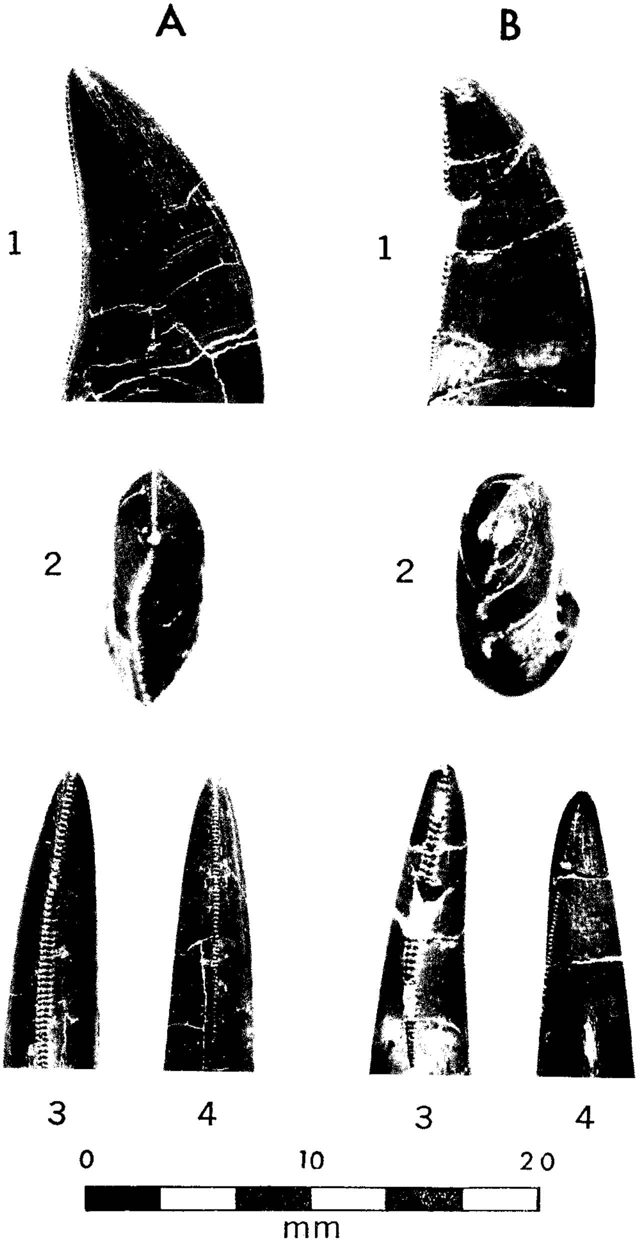
Tooth serrations extend over the entire height of the posterior margin, but vary along the leading edge from about 90 percent of tooth height to about half that. The distribution of this variant along the tooth rows is not clear, but in the specimens presently available there seems to be little variation in the length of the anterior serrated edge within the dentary series. The only available maxilla, however, indicates that the serrated leading edge is relatively shorter on posterior teeth than on anterior teeth.

A much more distinctive feature of the dentition is the size contrast between the anterior and posterior serrations (Fig. 25). The posterior serrations are approximately twice as large as the anterior serrations. There is some variation in the number of serrations per linear unit from apex to crown base, but near mid-length of the posterior edge there are 16 to 18 denticles per 5 mm, with 17 being the most frequent count. The anterior edge is much more finely serrated with 30 to 31 denticles per 5 mm. These counts compare with those in other theropods as shown in Table 2.

It is evident that in most theropod taxa anterior and posterior denticles are subequal in size, whereas in *Deinonychus* and *Velociraptor* (and perhaps *Saurornithoides*) those in front are much smaller than those of the posterior tooth edge. *Saurornithoides,* which for reasons discussed later is believed to be rather closely related to *Deinonychus,* may possess the same character, but preservation of the teeth is so poor that the condition cannot be determined. *Saurornithoides* is peculiar in that the denticles of the posterior serrations are as large as those of some much larger theropods (10 to 12 per 5 mm) but the teeth are one fifth to one tenth as large.

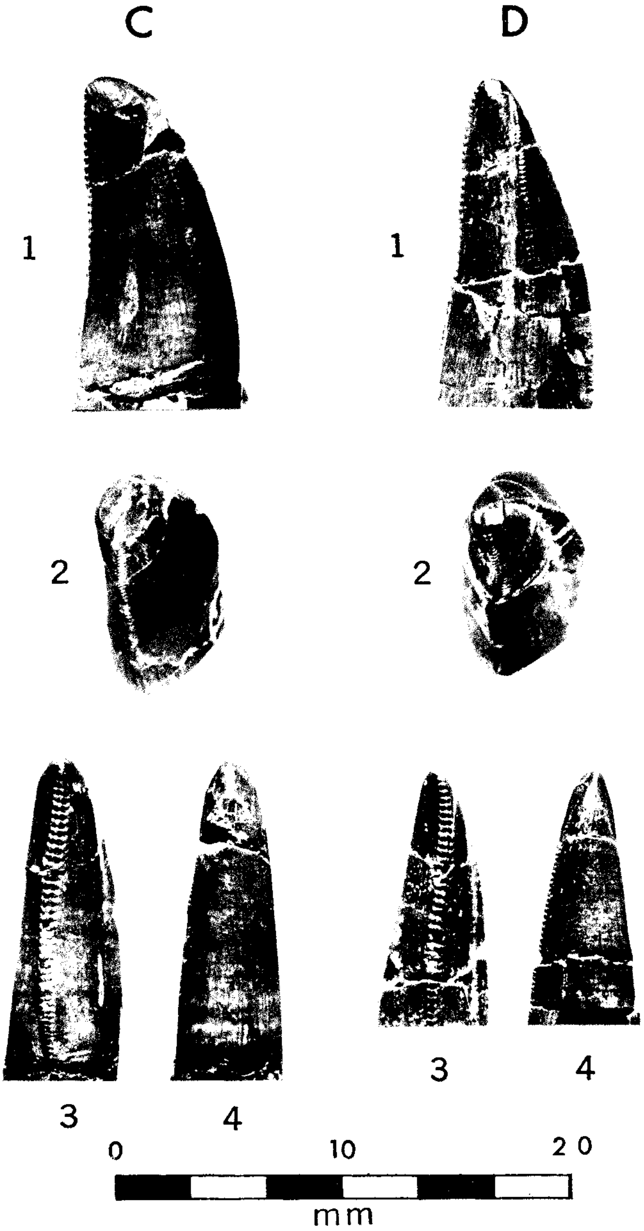
The functional significance of the disparity of anterior versus posterior serration sizes is not clear, but its rarity among theropods suggests it may be of phyletic as well as taxonomic significance.

The premaxillary teeth are quite different from the others in that they are distinctly more asymmetrical (Fig. 23B and 24C and D). They are not incisiform, as in *Gorgosaurus* (Lambe, 1917: p. 17), but resemble those of *Allosaurus.* Progressing from the last (Fig. 23B) to the first (Fig. 24C and D) premaxillary tooth, the anterior serration occupies a progressively more medial position on the tooth and the external surface becomes increasingly more convex and the inner surface less so. The latter is not flat or concave in any of the preserved premaxillary teeth, although there is a slight concave channel immediately medial to the anterior serrations. The discrepancy in size of anterior and posterior serrations persists on all premaxillary teeth and the two edges are subequal in length, both extending from apex to base of the enamel. There appears to be little variation in size among the four premaxillary teeth, in contrast to the distinct gradation recorded by Gilmore (1920: p. 30) in *Allosaurus*. There are no distinct wear facets on these or any of the other teeth, but several do show a greater degree of wear of the apex than is characteristic of most of the maxillary or dentary teeth.



FIGS. 23–24. Tooth types in *Deinonychus antirrhopus,* YPM 5210. A) maxillary or dentary tooth; B) posterior premaxillary tooth; C) intermediate premaxillary tooth; D) anterior (symphysial) premaxillary tooth. Views are medial (1), crown (2), posterior (3) and anterior (4). Notice the

Walker (1964) recorded some interesting observations on the orientation of tooth serrations in *Ornithosuchus,* noting that teeth in the premaxilla and anterior part of the maxilla possessed anterior and posterior serrations that were perpendicular to the respective tooth margins. In posterior maxillary teeth, however, the serrations are inclined obliquely toward the apex. Dentary teeth appear to have serrations more or less perpendicular to the tooth margin



medial shift of the anterior serrations in anterior premaxillary teeth. Also notice the discrepancy in size of anterior vs. posterior serrations (cf. Fig. 25).

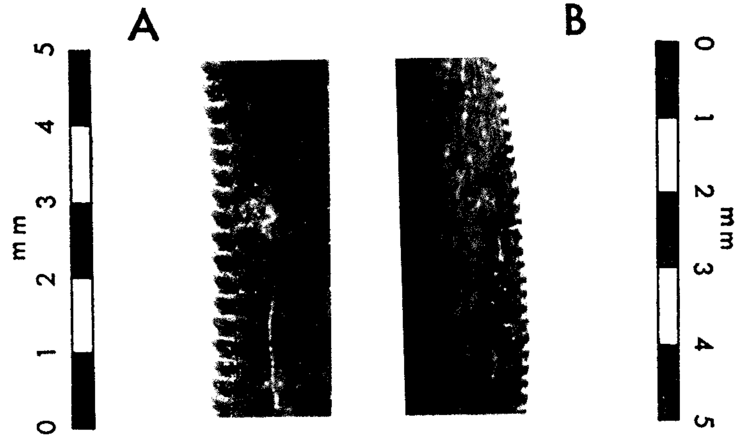


FIG. 25. Medial views, enlarged 10 times, of posterior serrations (A) and anterior serrations (B) in a single maxillary tooth (Fig. 23A) of *Deinonychus antirrhopus,* (YPM 5210), showing size differences between posterior and anterior denticles.

in the proximal half of the tooth, but in the apical half they are oblique to the margin. I have not checked this condition extensively in other theropods, but I have observed similar obliquity in teeth of *Allosaurus, Tyrannosaurus* and *Coelophysis.* How consistent or variable this condition is I do not know. The *Deinonychus* material suggests obliquity of tooth serrations may be an individual variable, or an ontogenetic variable. Every tooth in YPM 5232 (a total of 33, 14 of which are isolated teeth) shows some degree of inclination of the posterior serrations with respect to the rear tooth margin. The degree of inclination is difficult to measure precisely but appears to approximate 20° from the perpendicular. The orientation of the much smaller anterior serrations could not be determined with any precision. In YPM 5210, a total of 39 isolated teeth were closely associated with the skull elements. Of these, 25 show no obliquity at all, the serrations being perpendicular to the tooth margin. The other 14 show slight but distinct deviation from the perpendicular. YPM 5210 is slightly larger than YPM 5232, so there is a distinct possibility that obliquity may have declined with age.

TABLE 2. Dental serration counts in some theropods

	Posterior serrations per 5 mm	Anterior serrations per 5 mm
Allosaurus	10–12	10–12
Ceratosaurus	10	10
Gorgosaurus	9–12	12–13
Tyrannosaurus	6.5–8	8–9
Coelophysis	34	36
Ornitholestes	45	0
Dromaeosaurus	16	15.5
Velociraptor	25–26	38–40
Saurornithoides	10–12	?
Deinonychus	16–18	30–31

AXIAL SKELETON

VERTEBRAL COLUMN

The vertebral count is unknown for *Deinonychus,* but a close approximation can be made from the combined evidence preserved in the Yale and American Museum collections. The most complete vertebral series available is that of AMNH 3015, which includes a total of 21 presacral and 23 caudal vertebrae. Eight segments are represented from the cervical region, including an incomplete atlas intercentrum and a fragment of the axis. The cervical series apparently is not complete, but the poor state of preservation makes it impossible to determine how many segments are missing. Comparison with the extraordinarily well-preserved cervicals of the Yale specimens (YPM 5204 and 5210) suggests that the third cervical is missing in the American Museum specimen, but this cannot be certified and there may be more than one vertebra missing.

The remaining 13 presacrals of AMNH 3015, although incomplete and crushed, seem to form a continuous series. The most anterior element compares well with a "cervico-dorsal" vertebra of YPM 5210 and is judged to be the first or second dorsal. The last segment preserved in the series, although incomplete, is unmistakably a posterior dorsal, but it may not be the last presacral. It is assumed that the presacral count was 23, the usual number in theropods, and thus one dorsal vertebra, either the first or the last, is missing.

There are no sacral vertebrae preserved in AMNH 3015, but scars marking the sites of sacral rib attachments are preserved on the left ilium. Three large scars and one small anterior scar show that at least three and probably four sacral vertebrae were present. The distinctly smaller size of the anterior-most scar can be interpreted as the articulation of the transverse process of the last presacral, but without more complete material the matter must remain in doubt.

A nearly continuous series of 23 caudal vertebrae are preserved in AMNH 3015, but no positive evidence exists to establish whether the first element of this series represents the first postsacral vertebra or not. The ventral margin of the anterior face of this centrum angles back away from the vertical to form a broad, slightly rounded surface directed anteroventrally. If this represents an articular facet for a chevron, then there must have been at least one caudal segment in front of this vertebra. Comparison of the caudal series of AMNH 3015 with the three caudal series in the Yale collection (YPM 5201, 5202 and 5203) indicates at least 11 distal segments are missing from the former. YPM 5203 includes what appears to be the penultimate segment. Thus the caudal count was at least 36 and probably not higher than 40.

CERVICAL VERTEBRAE

The cervical vertebrae are all slightly platycoelous and bear robust, widely divergent zygapophyses and long, stout neural spines. The zygapophyseal facets are relatively very large and not planar, but display a distinct warp or fold near the medial margin. None of the centra are keeled and all are proportionately quite short (less than twice the centrum height). The third through seventh, at least, are strongly angled, with the anterior face of the centrum occurring well above the level of the posterior face. All centra are marked by elongate and deep lateral pleurocoels.

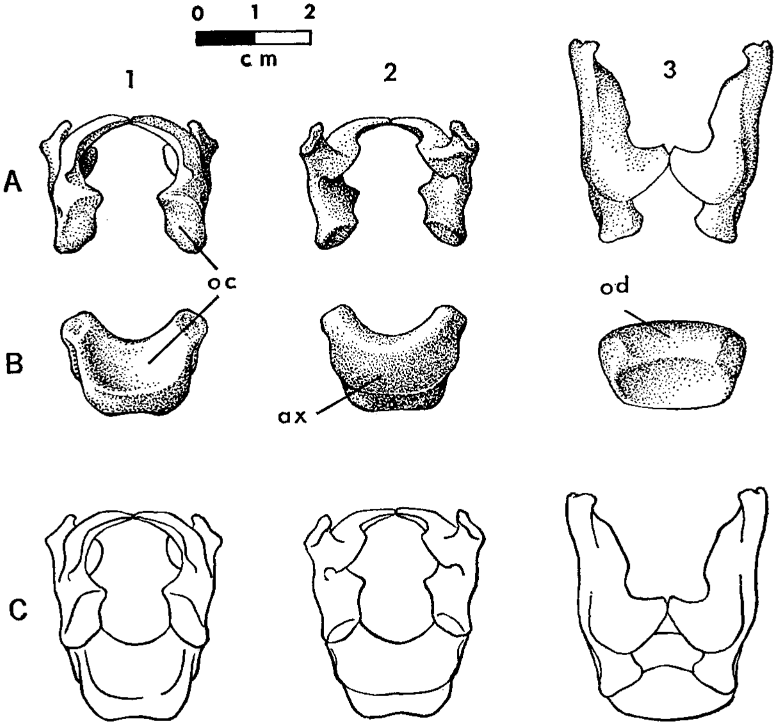


FIG. 26. Atlas of *Deinonychus antirrhopus,* YPM 5210. A) neural arch in anterior (1), posterior (2), and dorsal (3) views. B) intercentrum in anterior (1), posterior (2), and dorsal (3) views. C) outline diagrams of neural arch and intercentrum in articulation; views as in A and B. Abbreviations: ax—facet for contact with axis intercentrum; oc—facet for contact with the occipital condyle; od—concavity for odontoid process.

Atlas

The atlas (Figs. 26 and 27) is represented by an intercentrum and right half of the neural arch (YPM 5210), the left half of the neural arch from a much smaller individual (YPM 5204), and the odontoid (YPM 5204 and AMNH 3015). A fragmentary atlas intercentrum is also preserved in AMNH 3015 where it seems to be co-ossified with the axis intercentrum. The intercentrum is crescent-shaped, when viewed axially, and is largest in the transverse dimension (maximum width = 26 mm; maximum height = 20 mm). The dorsal margin is deeply notched for reception of the odontoid process. The ventral surface is only slightly convex transversely. The anterior surface is moderately

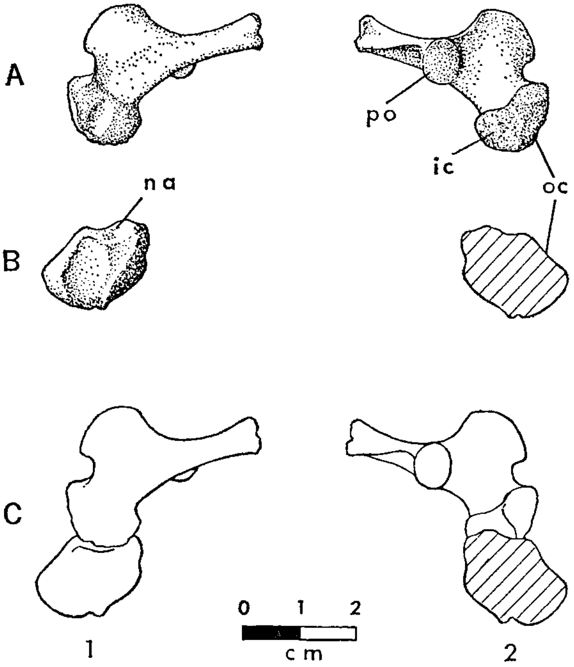


FIG. 27. *Deinonychus antirrhopus*, YPM 5210. Atlas neural arch (A) in left lateral (1) and medial (2) views, and atlas intercentrum (B) in left lateral (1) view. C) outline diagram of neural arch and intercentrum in articulation in lateral (1) and medial (2) views. (Neural arch drawn reversed from a right half.) Abbreviations: ic—articular facet for atlas intercentrum; na—facet for atlas neural arch; oc—facet for occipital condyle; po—postzygapophyseal facet.

concave for contact with the occipital condyle and faces sharply upward and forward (Gilmore [1920: p. 31] noted this same condition in *Allosaurus*). The condylar articular facet is well-defined, but the limits of the atlanto-occipital articular capsule are not clearly preserved. The posterior surface is slightly convex both transversely and vertically. The right margin of this facet is sharply defined by a lip-like margin that must represent the limits of the atlanto-axial capsule and the attachment of the capsular ligament.

The ventral surface is marked by paired, laterally placed tubercles, which are most prominent posteriorly. These are separated by a slight, median depression immediately anterior to the margin of the articular facet for the axis. Because these tubercles are situated well outside the margins of both articular capsules (atlanto-occipital and atlanto-axial), they cannot represent attachment sites of either the ventral or the anterior oblique atlanto-occipital ligaments. Also, there are no similar features preserved on the ventral surfaces of either the axis intercentrum or centrum. Accordingly these are considered the probable origin sites of M. rectus capitis anterior, the principal flexor of the atlanto-occipital joint. They might be parapophyses for articulation of atlantal ribs but this seems improbable in view of the much more dorsal position of the axial parapophyses.

Triangular, rugose, sutural surfaces for the pedicels of the neural arch are well defined on either side of the dorsal depression for the odontoid process.

These surfaces are slightly curved and are directed dorsally and slightly forward. This intercentrum differs from that of *Allosaurus* in its relatively greater height and more deeply grooved dorsal surface (for a narrower odontoid). The intercentrum of *Ceratosaurus* is low and wide like that of *Allosaurus* but the odontoid groove is deep and narrow as in *Deinonychus.* The inferior transverse outline in *Ceratosaurus,* however, is concave rather than convex.

The atlas neural arch consists of paired elements which apparently neither co-ossified nor fused with the intercentrum. Only the right half of the neural arch was found associated with the intercentrum described above (YPM 5210). This consists of a stout pedicel, a dorso-medial lamina and a posterolaterally directed articular process which bears a well-defined zygapophyseal facet. The pedicel forms two clearly separable surfaces. The ventral surface is subtriangular to oval in shape, slightly convex and appears to have been irregular or rugose in texture. This surface formed the sutural articulation with the atlas intercentrum. Separated from this by a moderate angulation is a larger, concave, oval-shaped surface that is directed forward and down. This surface is smooth and forms the upper lateral part of the articular facet for the occipital condyle.

Above the pedicel, a thin plate of bone extends toward the midline, forming a "roof" over the neural canal between the occiput and the axis. A stout postzygapophseal process extends back, out and slightly upward from the pedicel, with a prominent, oval articular facet facing ventromedially.

The atlas neural arch compares closely with that illustrated for *Ceratosaurus* (Gilmore, 1920: pl. 19) except that a prominent posteromedially directed flange is developed in *Deinonychus* behind the zygapophyseal facet. This feature extends over slightly more than half the length of the process posterior to the articular facet. Its significance is not known, but it apparently corresponds to the epipophyses that are prominently developed on succeeding cervicals.

The atlas centrum (odontoid) is fused to the axis centrum in AMNH 3015 and YPM 5204 (Fig. 28). Its upper surface is nearly flat transversely, but is slightly concave longitudinally, forming the floor of the neural canal. All other odontoid surfaces are strongly convex except for a prominent depression in the anterior extremity which probably represents the notochordal pit (although it may simply reflect contact between the occipital condyle and the odontoid). The odontoid is wider (15 mm) than it is high (9.5 mm) and is oval in longitudinal view.

Axis

The axis of *Deinonychus* is similar to that of *Allosaurus* (Gilmore, 1920: p. 33) except that it is less robust, relatively longer and bears much stouter and more divergent posterior zygapophyseal processes (Fig. 28). It is quite unlike that of *Ceratosaurus,* which has a long, transversely expanded neural spine, prominent parapophyses and a strong sagittal ventral keel.

The axis centrum is long (33.5 mm) and narrow-waisted at mid-length, has a greater diameter anteriorly (23 mm) than posteriorly (16 mm) and is

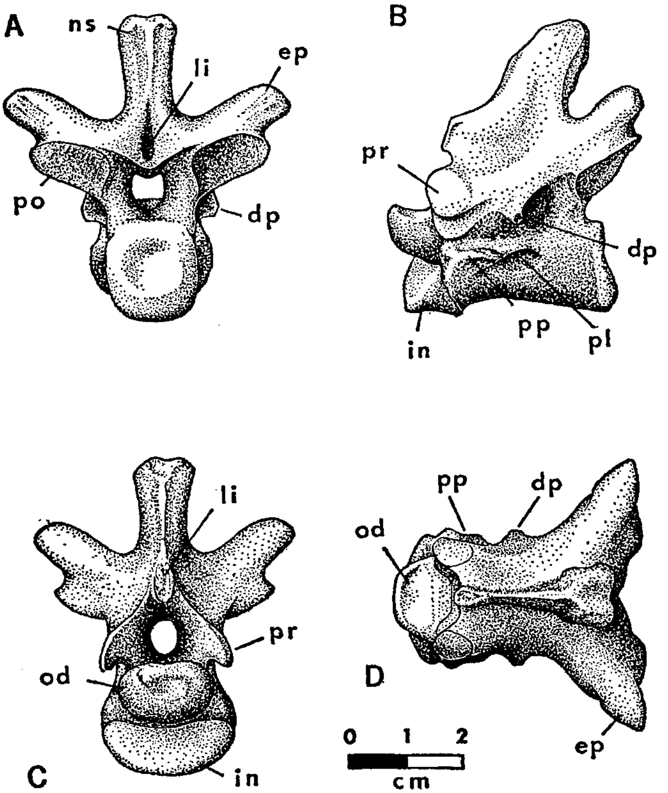


FIG. 28. Axis of *Deinonychus antirrhopus,* YPM 5204, in posterior (A), left lateral (B), anterior (C), and dorsal (D) views. The odontoid and axis intercentrum are both co-ossified with the axis centrum. Abbreviations: dp—diapophysis; ep—epipophysis; in—axis intercentrum; li—attachment scar of interspinal ligament; ns—neural spine; od—odontoid; pl—pleurocoel; po—postzygapophysis; pp—parapophysis; pr—prezygapophysis.

slightly opisthocoelous. The lateral surfaces are marked by small, but deep, oval pleurocoels. Small parapophyses are situated immediately in front of and slightly dorsal to the pleurocoels. A crescentic wedge-shaped intercentrum is fused to the anterior face of the centrum, beneath the odontoid. The intercentrum height is approximately equal to its maximum length (9 mm), its width equals 22.5 mm.

The prezygapophyses are small, flange-like structures lying lateral to the neural canal and projecting forward slightly beyond the odontoid-axis centrum suture. The articular facets are small (less than one third the area of the postzygapophyseal facets) and face upward and laterally. In sharp contrast to these are the posterior articular processes which are the dominant features of the axis. These massive processes project out and backward at approximately 45° to the mid-line and bear relatively large articular facets (greatest diameter is almost equal to the maximum posterior diameter of the centrum). Whereas the prezygapophyseal facets are nearly flat the posterior facets have a marked medial flexure which divides the articular surface into two unequal areas at approximately 90° to each other. The largest area of the facet is directed ventrally and a small medial area faces laterally. These flexed or warped zygapophyseal facets resemble the condition present in the dorsal vertebrae, but they do not form a true hyposphene-hypantrum, as in the dorsals.

The postzygapophyseal processes are surmounted by prominent projections —epipophyses—extending behind and lateral to the articular surfaces. These might have been the sites of attachment of intervertebral ligaments, but their position far lateral to the midline indicates they probably represent the insertions of cervical abductor muscles—presumably a prat o fthe transversospinalis system (either the intertransversarii dorsalis cervicis or the M. multifidus cervicis or the archosaurian equivalents). This interpretation is not entirely satisfactory, however, because the surface texture of these processes clearly indicates that whatever attached to these points extended in a caudal rather than cranial direction.

The axial neural spine extends nearly 30 mm above the neural canal (about equal to centrum length), is inclined backward about 70° from the long axis of the centrum, and is narrowly triangular in cross-section. Like the axis of *Allosaurus* and unlike that of *Ceratosaurus,* there is no longitudinal expansion of the neural spine into a broad wedge-shaped blade, except at the bases of the neural laminae (Fig. 28A). Presumably, this reflects a relatively small size for either the M. rectus capitis posterior or the M. obliquus capitis magnus, or both, but preservation does not permit any conclusion on this.

Anteriorly, the neural spine is sharp-crested, terminating in a rugose projection between and above the level of the prezygapophyses. A similar feature was noted by Gilmore (1920: p. 32-33) in *Allosaurus.* Presumably it was the point of attachment of an axial-occipital ligament. The posterior aspect of the neural spine is broad and is marked by a mid-line ridge which quite probably reflects the position of the dorsal fibers of the interspinal ligament. A deep, triangular, mid-line depression occurs at the base of the neural spine, immediately above the neural canal and between the postzygapophyses, as in *Allosaurus* but not in *Ceratosaurus.* Similar features are present on succeeding cervicals, and probably mark the position of the ventrally situated, main mass of the interspinous ligament, as in crocodilians.

Axial ribs are not known, but apparently small or rudimentary ribs were present. A slight, rugose projection (parapophysis) is situated just anterior to the lateral pleurocoel and beneath the prezygapophysis. A more prominent, but still small, diapophysis projects laterally and downward from the lateral lamina of the neural arch.

Posterior cervicals

As explained above, the complete cervical series of *Deinonychus* cannot be reconstructed at present. At least five cervical segments posterior to the axis are preserved in the American Museum specimen. These are believed to represent the fourth through eighth cervicals. Among the Yale specimens are three distinctly different, complete and near-perfect posterior cervical vertebrae from two individuals. Two of these were closely associated with an axis (YPM 5204) and are presumed to belong to the same individual (Fig. 29). The third

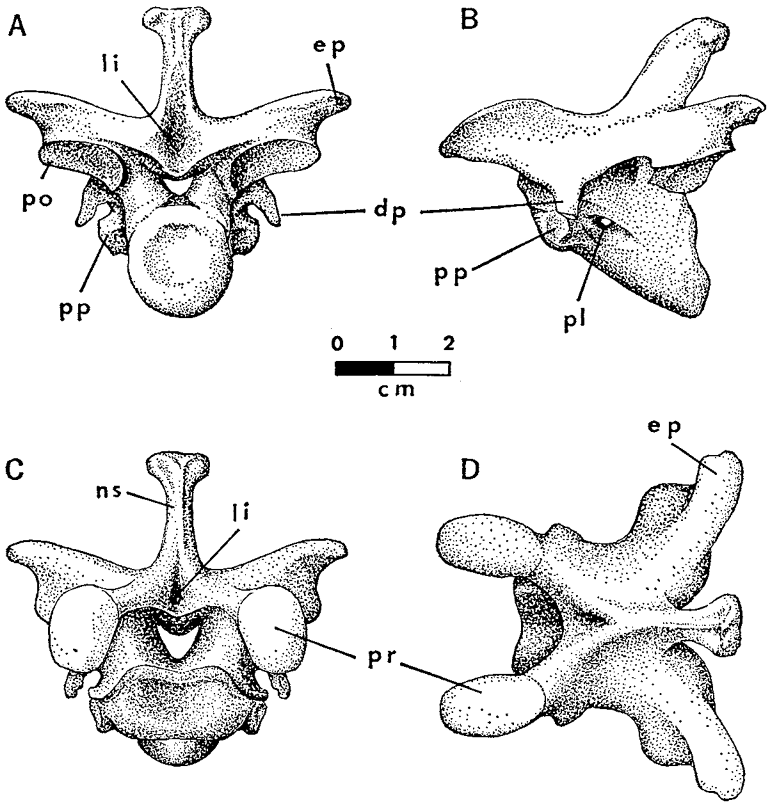


FIG. 29. Fourth (?) cervical vertebra of *Deinonychus antirrhopus*, YPM 5204, in posterior (A), left lateral (B), anterior (C) and dorsal (D) views. Notice the strong angling of the centrum and the curved zygapophyseal facets. Abbreviations: dp–diapophysis; ep–epipophysis; li–scars of interspinous ligament; ns—neural spine; pl—pleurocoel; po—postzygapophysis; pp—parapophysis; pr—prezygapophysis.

vertebra (Fig. 30), from a larger individual, was recovered from a different section of the Yale quarry approximately 15 inches (38 cm) from the atlas intercentrum (YPM 5210) referred to above. Neither of the first two can be articulated with the axis, so neither can represent the third segment. Comparison with the fragmentary cervicals of AMNH 3015 indicates they probably are the fourth and fifth cervicals. The larger vertebra (YPM 5210) is a more posterior cervical, probably the seventh or eighth.

The most conspicuous character of these vertebrae is the pronounced oblique angling of the centra (Figs. 29B, 30B and 31). Unlike a conventional vertebra in which the anterior and posterior centrum surfaces are parallel to each other and perpendicular to the long axis of the centrum, these surfaces form angles of 75° to 40° with the long axis (the floor of the neural canal) and are not parallel. Table 3 gives the geometry of known *Deinonychus* cervicals.

Similar angling of the post-axial cervicals occurs in both *Allosaurus* and *Ceratosaurus* (Gilmore, 1920: p. 30 and pl. 20) but it is not as strongly developed in either. *Gorgosaurus* and *Tyrannosaurus* also exhibit very slight angling of

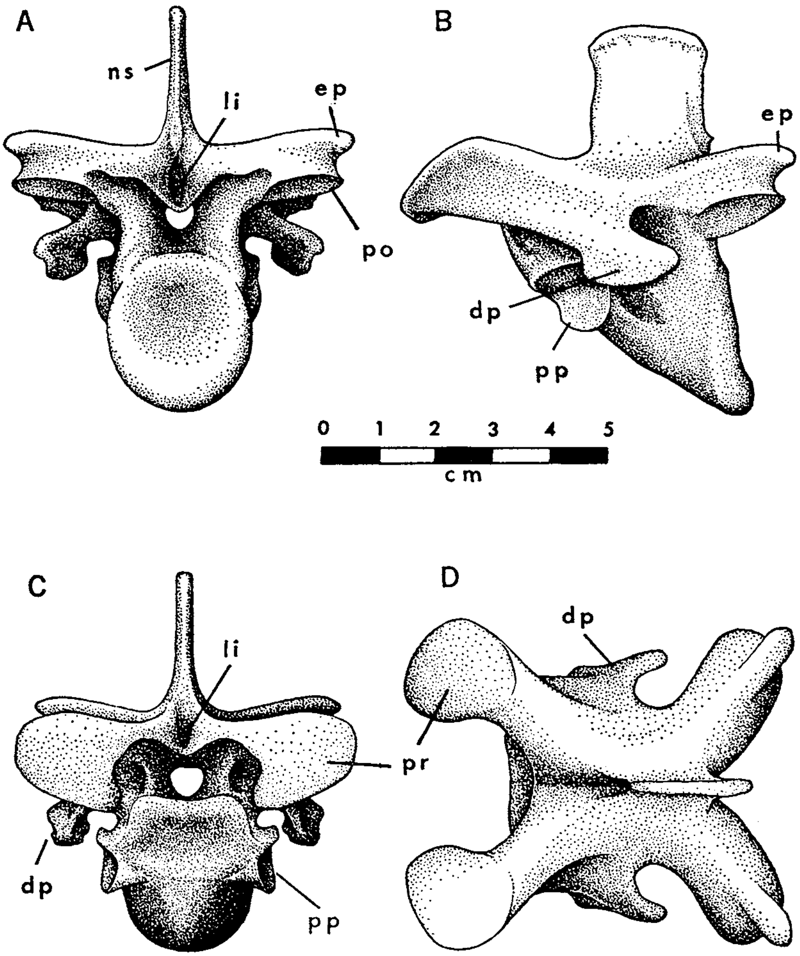


FIG. 30. Seventh (?) cervical vertebra of *Deinonychus antirrhopus*, YPM 5210, in posterior (A), left lateral (B), anterior (C) and dorsal (D) views. Abbreviations: dp—diapophysis; ep—epipophysis; li—scars of interspinous ligament; ns—neural spine; po—postzygapophysis; pp—parapophysis; pr—prezygapophysis.

the cervicals (Osborn, 1906, fig. 3). This trait may also exist in *Coelurus* (YPM 1991), but apparently is absent in *Ornitholestes* (AMNH 619) and *Ornithomimus* (AMNH 5339).

The functional significance of this angled design of *Deinonychus* cervicals is not entirely clear, but it quite obviously must have been related to natural curvature of the neck (Fig. 31). Many modern vertebrates are characterized by an arched neck, but few possess more than one or two distorted or angled cervicals. In artiodactyls, usually only the seventh (rarely the sixth and seventh) cervical is so distorted. On the other hand, some degree of angling is present in all cervicals of equids, although pronounced opisthocoely obscures this condition. Some degree of angling is present throughout the cervical series of fissipeds and is particularly well developed in felids, reaching a maximum in the lion

TABLE 3. Morphology of the cervical vertebrae of *Deinonychus antirrhopus* and *Felis leo* (attitude of centra faces relative to the floor of the neural canal)

	ANTERIOR CENTRUM FACE		POSTERIOR CENTRUM FACE	
Vertebra number	*D. antirrhopus* YPM 5204 YPM 5210	*F. leo* YPMOC 1050	*D. antirrhopus* YPM 5204 YPM 5210	*F. leo* YPMOC 1050
Atlas	—	—	—	—
Axis	—	—	75°	80°
3	?	58°	?	63°
4	51°	55°	58°	58°
5	41°	58°	58°	61°
6	?	65°	?	65°
7	45°	75°	73°	70°
8	?	—	?	—
9	?	—	?	—
First dorsal	85°	80°	85°	85°
Mid-dorsal	90°	85°	89°	85°

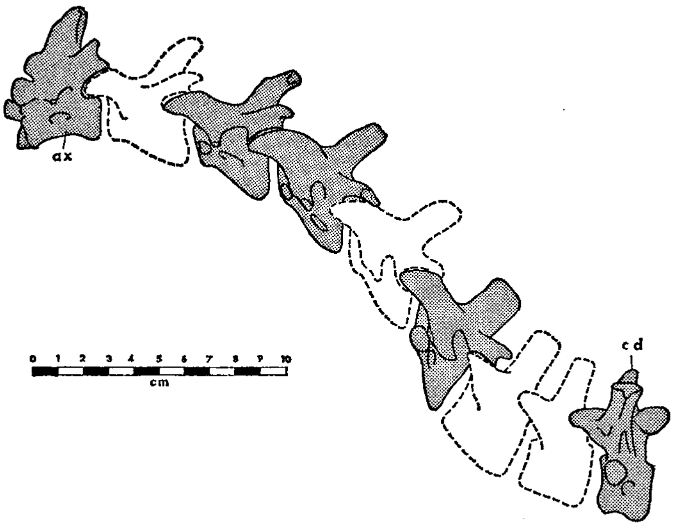


FIG. 31. Reconstruction of the cervical flexure in *Deinonychus antirrhopus*, based on the sharply angled centra of mid-cervical vertebrae. Stippled elements are represented by near perfect vertebrae in the Yale collections. Abbreviations: ax—axis; cd—"cervico-dorsal."

(*Felis leo*) and tiger (*F. tigris*). I believe comparable natural curvature was present in the cervical series of all theropods (see fig. 18 in Gilmore, 1920, for an excellent example), but it may have reached a maximum in *Deinonychus*. The geometry of lion cervicals is given, along with that of *Deinonychus*, in Table 3. The lion's neck arches up at an angle of 50° to 60° to the trend of the anterior thoracics, as a consequence of this cervical angling. The more extreme degree of centrum distortion in *Deinonychus*, suggests that this cervical series was held at an even greater angle to the dorsal series than is found in the lion. Cervical curvature could be increased, of course, by contraction of the dorsal cervical muscles.

The post-axial cervicals are all moderately platycoelous, with the posterior surface usually slightly more concave than the anterior surface. Anteriorly, the centrum is broader than deep and the anterior facet is distinctly kidney-shaped with a shallow dorsal notch defining the ventral limit of the neural canal. The posterior centrum face is circular to slightly oval in shape with the vertical dimension the largest. The centra are narrow-waisted at mid-length, slightly expanded posteriorly and have maximum widths anteriorly. The lateral surfaces are marked by deep, oval pleurocoels that appear to have penetrated completely through the centrum. None of the cervicals bear even the slightest ventral keel.

The zygapophyses are stout processes bearing large articular facets that are situated well beyond the ends of the centrum. These facets lie well lateral to but level with the neural canal, and are directed up (prezygapophyses) and forward and only slightly inward. Those of the anterior cervicals are oval and elongated longitudinally. Those of posterior cervicals are more nearly circular in shape. All cervical articular facets tend to be curved rather than planar, parallel to the longitudinal axis. In addition, all display a sharp longitudinal flex or warp near the medial edge, which divides each articular facet into a small medial surface (facing medially on the prezygapophyses) and a much larger lateral surface directed upward. These "folds" or flex lines are not parallel to the midline, but converge posteriorly and the "fold" becomes more prominent posteriorly (except for the cervico-dorsal region) reaching maximum development in the posterior dorsals. The zygapophyseal facets are progressively more widely spaced caudally. As discussed later, these zygopophyseal flexures may have restricted the degree of lateral flexion or abduction, but permitted maximum vertical flexion and extension.

The postzygapophyses of posterior cervicals, like those of the axis, are surmounted by robust tubercles or epipophyses (Gilmore, 1920: p. 36, described similar features in *Allosaurus*). The material at hand indicates that these tubercles reach their maximum development at about the fifth or sixth cervical, where they project 10 to 12 mm beyond the articular facet, and then diminish posteriorly. Most probably, they mark the insertion of cervical abductors, possibly the M. transversospinalis.

Parapophyses are prominently developed on all post-axis cervicals immediately behind the anterior face of the centrum and in front of the pleurocoel. In both *Allosaurus* and *Ceratosaurus* the pleurocoels are situated above the parapophyses rather then behind them. The parapophyses become progressively larger posteriorly, with deep, cup-like facets for the capitula.

Diapophyses are present on all post-axis cervicals. In the anterior cervicals they extend downward as small processes from the ventral region of the prezygapophyses, and are situated close to the lateral wall of the centrum. They terminate in a small oval facet just dorsal and lateral to the capitular facets of the parapophyses. On posterior cervicals, the diapophysis is more robust, and extends ventrolaterally as an elongate flange from the ventroposterior region of the prezygapophysis.

The neural spines are well developed on all cervicals, but they grade from a robust, triangular-in-section, dorsocaudally directed process with an expanded extremity in anterior segments to a tall, thin, blade-like process that rises nearly perpendicular to the neural canal in the posterior cervicals. This transition is contrary to that of *Allosaurus* (Gilmore, 1920: p. 36) where the anterior cervical spines (the axial spine excepted) are blade-like but the spines of posterior cervicals (seventh through ninth) are sub-rectangular in section and not blade-like. The latter condition also appears to be characteristic of *Gorgosaurus* and *Tyrannosaurus.* The cervical neural spines in *Ceratosaurus* are similar to those of *Allosaurus* except that those of the posterior cervicals (sixth through ninth?) are blade-like. *Coelurus* and *Ornitholestes* exhibit nearly uniform, low, but long (anteroposteriorly) neural spines and the cervicals of *Ornithomimus* apparently lack neural spines altogether.

The functional significance of this gradational change in cervical neural spines is not known either for *Deinonychus* or for other theropods. My guess at the moment is that it reflects cervical differentiation of the dorsal axial musculature—the M. spinalis and semi-spinalis. I doubt if it is related to differences in the interspinal ligaments.

All known cervicals of *Deinonychus* are characterized by deep, mid-line, triangular depressions at the base of the neural spine, both anteriorly and posteriorly. These are situated immediately above the neural canal, but are separated from it by a horizontal lamina of bone. Gilmore (1920: p. 36) noted similar features in *Allosaurus* but only on the anterior surfaces at the neural spine base. According to Gilmore this feature diminishes in size posteriorly and is absent on the ninth cervical. There is a similar diminution in *Deinonychus,* but they apparently are present on all cervicals and dorsals. As suggested above, these depressions probably mark the sites of attachment of the main mass of the cervical interspinous ligament.

DORSAL VERTEBRAE

Specimen AMNH 3015 includes 13 vertebral segments, all of which are crushed and fragmentary but recognizable as dorsals. They appear to form a continuous but incomplete series. Among the Yale specimens are six nearly perfect dorsal vertebrae (probably the first, fourth, sixth, seventh, ninth and tenth) from two individuals (YPM 5204 and 5210). Anterior centra are slightly platycoelous, posterior centra tend to be amphiplatyan. Centrum length is uniform throughout the series, but depth and breadth increases posteriorly. All centra have slit-like, lateral pleurocoels. The neural arch laps well down on the lateral surfaces of the centra and bears prominent, pedestal-like, cupped capitular articulations or parapophyses. The transverse processes are subequally developed throughout the series, with a slight backward and upward orientation. All except the first two or three dorsals bear tall and massive, rectangular neural spines, but the neural spines of the first few dorsals apparently were short and weakly developed.

Anterior dorsals

None of the present specimens permits precise separation of cervicals and dorsals, nor can it be demonstrated whether the change is gradual or abrupt.

AMNH 3015 seems to show a rather abrupt upward shift in the parapophyses and an increase in size of the transverse processes over two segments of the series. The first four centra at this point of change are strongly keeled and seem to have reduced concavity of anterior and posterior faces.

One of the unusually well-preserved "dorsal" vertebrae among the Yale materials might be considered a "cervico-dorsal" (Osborn, 1906: p. 288), because it has both cervical and dorsal features (Fig. 32). Cervical features are: 1) widely spaced articular facets; 2) articular facets are large and slightly inclined; 3) the posterior zygapophyses are surmounted by small epipophyses; 4) the neural spine is short, not blade-like or rectangular, and is transversely expanded at its summit; in general, it is quite similar to the neural spines of the fourth and fifth cervicals; 5) parapophyses are low and are at least partly borne on the centrum. Dorsal features are: 1) long, robust transverse processes that angle slightly upward and back; 2) ventral sagittal keel on the centrum;

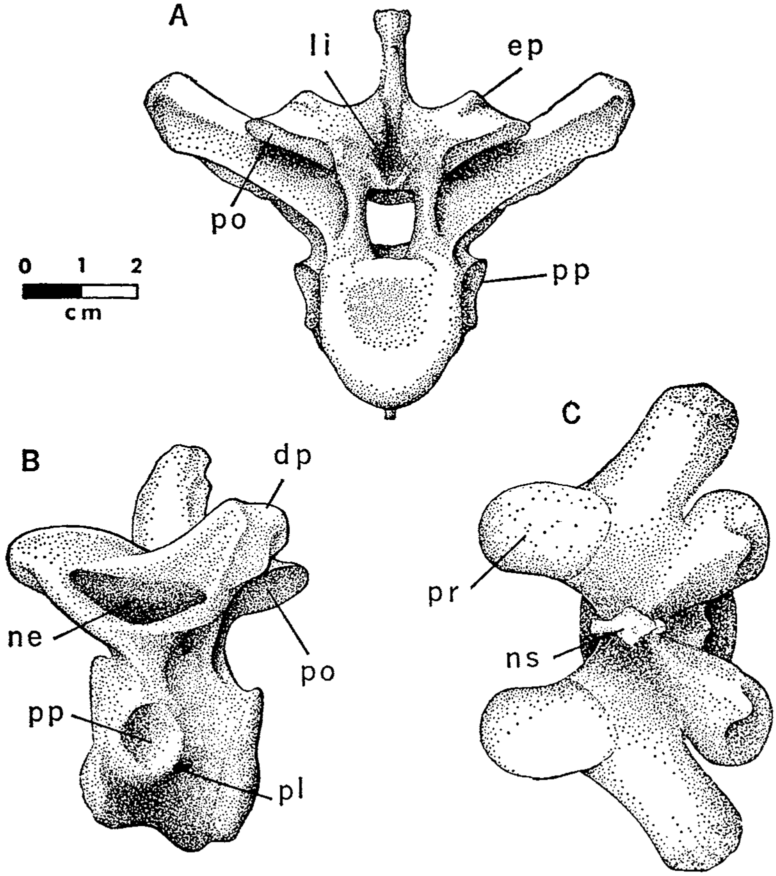


FIG. 32. First dorsal or "cervico-dorsal" vertebra of *Deinonychus antirrhopus*, YPM 5210, in posterior (A), left lateral (B) and dorsal (C) views. Notice the reduced neural spine and the planar zygapophyseal facets. Abbreviations: dp—diapophysis; ep—epipophysis; li—scar of interspinous ligament; ne—excavation of neural arch (hapidocoel = arch + hollow); ns—neural spine; pl—pleurocoel; po—postzygapophysis; pp—parapophysis; pr—prezygapophysis.

3) centrum is short and not angled, but with parallel anterior and posterior platycoelous surfaces almost perpendicular (85°) to the centrum long axis (floor of the neural canal). Comparison with the presacral series of AMNH 3015 indicates that this cervico-dorsal represents the 10th or 11th presacral vertebra. The orientation and length of the transverse processes show that the Yale vertebra bore a large rib with widely separated tuberculum and capitulum. The ninth vertebra of AMNH 3015, although incomplete, appears to have had short and downward-directed transverse processes. Hence the Yale vertebra probably represents the first dorsal—unless a segment is missing from this part of the American Museum specimen, a possibility mentioned earlier.

The centrum of the first dorsal is platycoelous—almost amphiplatyan; it is constricted at mid-length and bears a prominent ventral keel. Centrum length and height are subequal and exceed centrum width. Anterior and posterior centrum faces are oval in shape, but are impinged upon dorsally by the large, neural canal. Lateral pleurocoels occur as small, elongate depressions at mid-length. Large, cup-shaped capitular facets are well developed anterior to and above the pleurocoels.

The neural arch is a large, high and complex structure with very prominent zygapophyseal and transverse processes. The zygapophyseal facets are large and widely separated from the mid-line, as in the cervical series. Unlike the cervicals, however, these facets are inclined transversely (at about 30° to the horizontal) and both anterior and posterior facets are planar rather than folded or curved as in nearly all other presacrals. The degree of folding of the articular facets is reduced in posterior cervicals, and apparently in anterior dorsals, but is developed to a maximum degree on all other dorsals. This reduction or absence of facet flexure in the cervicodorsal region indicates that this region of the vertebral column probably had greater mobility than other sections of the presacral series. The posterior zygapophyses bear small caudally-directed tubercles, very similar to, but much smaller than the epipophyses of the cervical series. These features apparently diminished abruptly in the anterior dorsals, for none of the other dorsal vertebrae possess them.

The transverse processes are long and robust, angling up at 30° to 40° to the horizontal and backward at 30° to the transverse plane. Proximally the bases of the transverse process and of the prezygapophysis are marked by several excavations and strut-like ridges—probably an adaptation to lighten without weakening the neural arch. This condition is similar to but less extreme than that in *Coelurus* dorsals. The neural spine is short longitudinally and vertically and distinctly not blade-like. The extremity is slightly expanded. Although not as stout, it resembles the neural spines of the fourth and fifth cervicals rather than those of succeeding dorsals.

Posterior dorsals

Morphologic changes along the dorsal series are of the usual kind: progressive increase in height and width of centra (but not length), the neural spines increase in height and massiveness, reduction and loss of the ventral keel, and progressive enlargement of the capitular process. With the exception of these features, successive dorsal vertebrae are all very similar (Figs. 33 and 34).

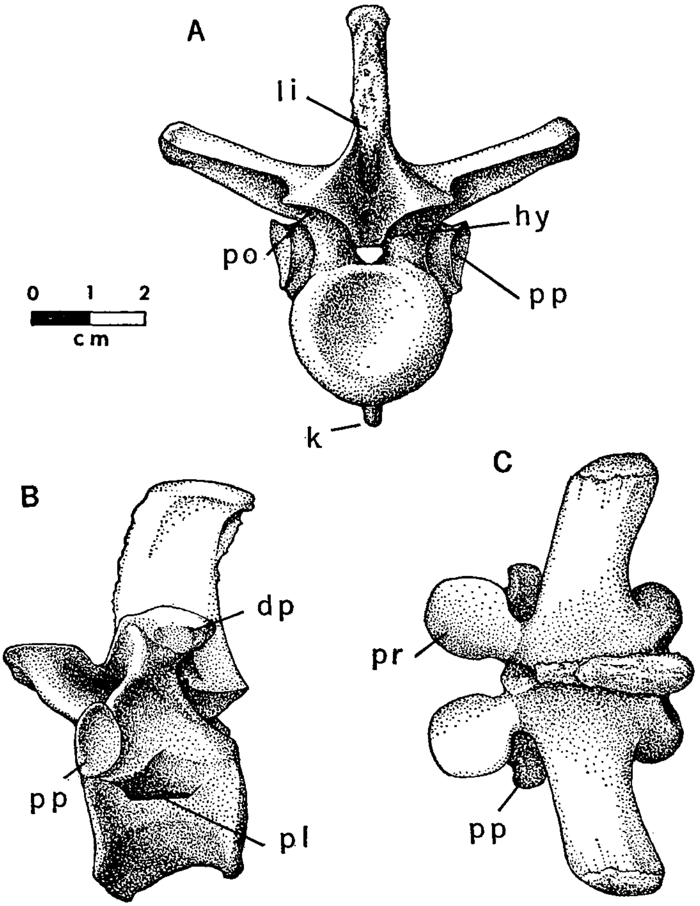


FIG. 33. Fourth (?) dorsal vertebra of *Deinonychus antirrhopus*, YPM 5204, in posterior (A), left lateral (B) and dorsal (C) views. Notice the curved form of zygapophyseal facets. Abbreviations: dp—diapophysis; hy—hyposphene; k—sagittal keel; li—scar of interspinous ligament; pl—pleurocoel; po—postzygapophysis; pp—parapophysis; pr—prezygapophysis.

The centra are amphiplatyan or slightly platycoelous and nearly circular in end view. Anteriorly, centrum length is slightly more than height or width, the latter being subequal. Posteriorly, height and width exceed the length by more than 60%. The ends of the centra flare out to maximum circumference but at mid-length the centra are constricted and lateral and ventral surfaces are strongly concave longitudinally. Anterior and posterior centrum surfaces are parallel throughout the dorsal series and perpendicular to the floor of the neural canal and none show the ventral "wedging" reported by Gilmore (1920: p. 40) in *Allosaurus* and by Osborn (1917: pl. 27) in *Tyrannosaurus*. Lateral surfaces are marked by deep, slit-like pleurocoels just beneath and parallel to the neural arch suture. Ventral keels are absent on all except the first five or six dorsals. The neural arch and spine account for nearly two thirds of the vertebral height. At the anterior limit of the arch pedicel, just above the suture, is a prominent peduncle-like process that terminates in a "cupped"

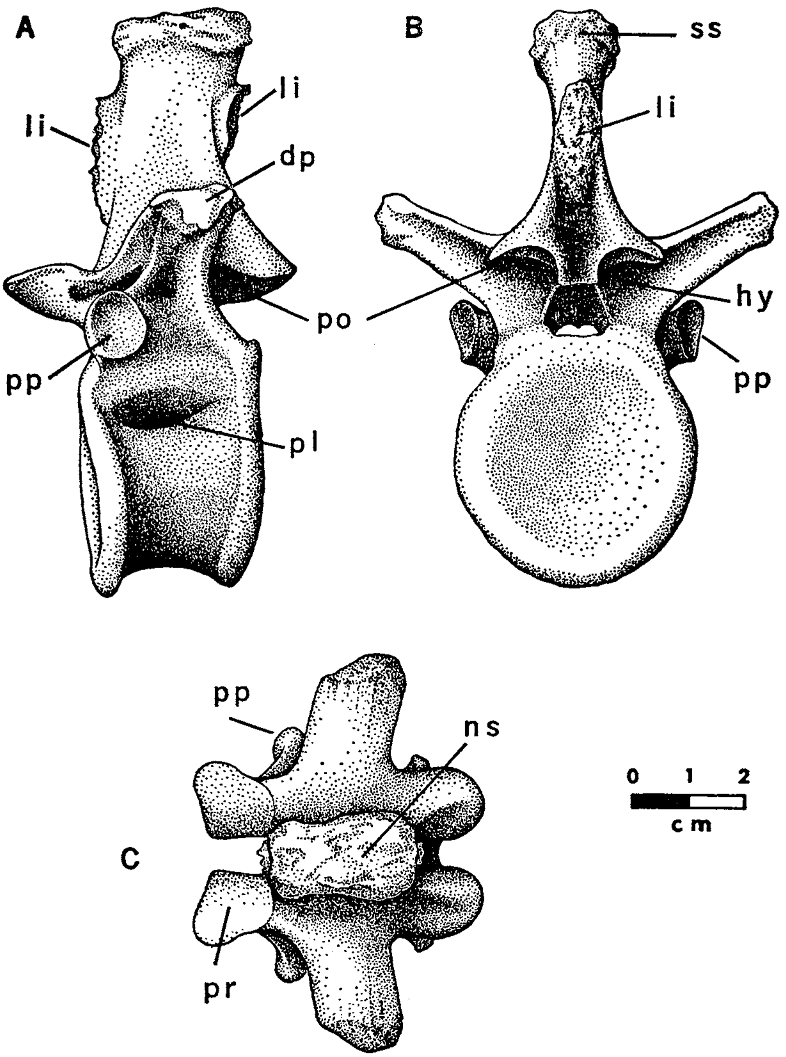


FIG. 34. Posterior (11th?) dorsal vertebra of *Deinonychus antirrhopus,* YPM 5210, in left lateral (A), posterior (B) and dorsal (C) views. The parapophysis is still well below the level of the diapophysis, so this probably is not one of the last presacrals. Notice, however, the well-developed hyposphene, the expanded summit of the neural spine and the enlarged interspinous ligament scar. Abbreviations: dp—diapophysis; hy—hyposphene; li—scars of attachment for the interspinous ligament; ns—neural spine; pl—pleurocoel; po—postzygapophysis; pp—parapophysis;; pr—prezygapophysis.

articular facet for the capitulum. These project prominently to the side below and anterior to the transverse processes.

Gilmore (1920: p. 41) notes that the transverse processes of the dorsals in *Allosaurus* gradually lengthen and assume a more horizontal and directly transverse orientation, as one progresses from front to back. These are contrary to the conditions in *Deinonychus.* The transverse processes of all dorsals extend outward, up and back, at approximately the same orientation throughout the series and the length appears to be more or less uniform in all dorsals.

The zygapophyses are considerably shorter (relatively) than in the cervicals and are placed much closer to the mid-line. The zygapophyseal facets are moderate in size and subcircular in shape. All except those of the most anterior dorsals display prominent flexures in the medial third of the facet. Prezygapophyseal facets are thus divided into a medial section that faces inward toward the mid-line (hypantrum) and an outer section amounting to 75% of the total articular facet that faces directly upward. The postzygapophyseal facets display the reverse condition, with the medial segments forming a vertical wedge (hyposphene) with laterally facing facets and the larger outer zygapophyseal surfaces facing downward and slightly outward (Figs. 33A and 34B). Whereas the traces of these flexures as developed in the cervical articular facets converge toward the mid-line caudally, in the dorsal vertebrae the flexures parallel the sagittal plane. As a result, the articular facets of successive dorsal vertebrae form a series of trough-like or grooved articular contacts. Again, the functional significance of this unusual feature is obscure, but it can be compared with the "grasping" zygapophyseal facets in artiodactyls noted by Slijper (1946) or the xenarthral facets of edentates. Whereas the "grasping facets", as usually developed in mammals (fissiped lumbars, for example), are the prezygapophyseal facets (facing up and inward), in *Deinonychus* it is the posterior facets that "grasp" (by facing down and out and "enclosing" their counterparts).

In terms of articular freedom and restriction, these opposites would seem to be adaptive equivalents—restricting the amount of intersegmental abduction, but permitting maximum sagittal flexion and extension. Accordingly, it would appear that the dorsal series (and the cervical series) had considerable flexibility in the dorsoventral plane (assuming a strong but elastic interspinous ligament), but limited freedom of lateral movement. The restricting factor, as regards abduction, is the opposite-facing segments of the two zygapophyseal facets of each segment. Because these oppose each other—or face in opposite directions—the only movement permitted by both in concert is motion parallel to both, in other words, movement in the vertical plane. Those portions of the articular facets that face in the same direction (i.e., outer portions of left and right prezygapophyseal facets facing upward) permit all degrees of freedom, the postzygapophyseal facets contacting them may move away from (perpendicular to) as well as parallel to (including transverse as well as longitudinal movement) these surfaces. With the restrictions imposed by the near vertical segments (hyposphene-hypantrum) of the zygapophysea facets, the dorsal series appears to have been dominated by sagittal flexion and extension. Lateral flexion (abduction-adduction) of the presacral column appears to have been limited to the cervicodorsal region and the most anterior cervicals, which lack hyposphene-hypantrum-like zygapophyseal facets.

With the exception of the first (and perhaps the second and third) dorsals, all dorsal neural spines are robust, rectangular blades, oriented nearly vertical (perpendicular to the neural canal), or inclined only slightly backward. All display slight to moderate expansion of the extremity, and all feature prominent mid-line depressions at the spine bases, both fore and aft, just above the neural canal. The height of the spines is not great, ranging from 1.5 to 1.75 times the length of the centrum. In all except the first two or three dorsals, the leading and posterior edges of the neural spines are marked by very prominent rugose tracts extending nearly (but never entirely) the full height of the spine. These project forward and backward toward the adjacent neural spines, and increase in prominence toward the sacrum. These features are recognizable on some of the cervical neural spines, but they are not nearly as prominent. There can be little doubt that these rugose ridges are the areas of attachment of massive and very strong interspinous ligaments. Gilmore (1920: p. 42) describes similar features in *Allosaurus,* as do Stovall and Langston (1950: p. 710) in *Acrocanthosaurus.* The latter authors thought these were for interspinous muscles, but similar features in *Crocodylus* are related to expanded interspinous ligaments along the dorsal series. Of particular interest, however, are the nearly identical, very prominent rugose tracts of the posterior dorsals of many birds—particularly ratites (*Struthio, Casuarius, Dinornis* and *Aepyornis*). Only in *Dinornis* are these tracts as prominently developed (relatively) as they are in *Deinonychus,* but they are conspicuous features in all. In modern ratites these tracts are the attachment sites of very large interspinous ligaments which fix the posterior dorsals into a strong, moderately inflexible, supporting column which projects forward *horizontally* from the sacrum and pelvis.

The apparently natural curve of the cervical vertebrae strongly suggests a horizontal posture for the main part of the dorsal series in *Deinonychus.* A cervical flexure makes no sense otherwise. But the most significant, if not conclusive, evidence for a normal horizontal attitude of the dorsal series, as illustrated in the skeletal reconstruction of Figure 79, are the prominent rugose tracts on the fore and aft edges of the dorsal neural spines and the analogy with the massive interspinous ligaments and posture of living ratites.

In this connection, it is most significant that of all the presacral vertebrae, only the atlas, axis and the "cervico-dorsals" possess completely planar zygapophyseal facets. All other presacrals bear facets with moderate to extreme (90°) flexures, which must have limited vertebral mobility primarily to the sagittal plane. The simpler nature of the cervicodorsal facets must have permitted more degrees of freedom at the base of the neck, including lateral, as well as vertical, flexion, and perhaps some twisting.

The rigidity imposed upon the dorsal series by the hyposphene-hypantrum articulations seems contrary to the optimal conditions expected in an active, bipedal predator, but precisely the same restrictions (by means of different anatomical features) occur in *Struthio* and apparently in other large ratites. Limited mobility of the thoracic series apparently is related to the primary weight-bearing function of these vertebrae that jut out horizontally from the sacrum to the base of the neck—with the rib cage, viscera, etc., slung beneath. The dorsal series is a cantilevered beam projecting forward from the pelvis. The additional rigidity required of such a cantilevered beam imposes significant restrictions in mobility, which appear to be compensated for in the cervicodorsal region.

SACRAL VERTEBRAE

As noted previously, no sacral vertebrae are preserved among the materials

TABLE 4. Measurements (in millimeters) of presacral and caudal vertebrae of *Deinonychus antirrhopus*

VERTEBRA NUMBER	MAXIMUM LENGTH OF CENTRA			MAXIMUM WIDTH (ANTERIOR) OF CENTRA			MAXIMUM HEIGHT (ANTERIOR) OF CENTRA			GREATEST HEIGHT OVERALL		
	AMNH 3015	YPM 5204	YPM 5210	AMNH 3015	YPM 5204	YPM 5210	AMNH 3015	YPM 5204	YPM 5210	AMNH 3015	YPM 5204	YPM 5210
PRESACRALS												
Atlas	—	—	—	—	—	—	—	—	—	—	—	—
Axis	—	31.5	—	—	23.0	—	—	19.5	—	—	53.4	—
3	—	—	—	—	—	—	—	—	—	—	—	—
4	—	33.0	—	24.0*	28.2	—	—	19.6	—	—	55.4	—
5	36.7	32.0	—	30.5	29.3	—	20.5	18.2	—	—	55.0	—
6	38.5	—	—	31.0	—	—	21.0	—	—	—	—	—
7	39.0*	—	41.8	—	—	34.0	25.5*	—	26.6	—	—	75.0
8	29.0*	—	—	—	—	—	30.0*	—	—	—	—	—
9	31.0*	—	—	—	—	—	30.0*	—	—	—	—	—
10	30.0*	—	29.5	—	—	28.0	—	—	28.6	—	—	71.0
11	31.0*	—	—	—	—	—	—	—	—	—	—	—
12	30.0*	—	—	—	—	—	—	—	—	—	—	—
13	30.0*	28.4	—	—	26.6	—	—	28.3	—	—	74.8	—
14	30.0*	—	—	—	—	—	—	—	—	—	—	—
15	27.0*	28.6	—	35.0*	29.6	—	—	28.5	—	—	80.0	—
16	28.5*	28.5	—	—	28.3	—	—	30.6	—	—	79.2	—
17	27.5*	—	—	—	—	—	39.0*	—	—	96.0	—	—
18	31.5*	28.6	—	—	30.0*	—	—	33.0	—	96.0	84.0	—
19	30.0*	—	30.0	36.0*	—	41.4	35.0*	—	40.0	96.7	—	100.3
20	28.0*	—	—	—	—	—	39.0*	—	—	106.0	—	—
21	27.0*	—	—	44.0*	—	—	—	—	—	—	—	—

[Atlas and presacral segments 3, 22 and 23 and caudal 1 incomplete or absent].

	AMNH 3015	YPM 5203	YPM 5210	AMNH 3015	YPM 5203	YPM 5210	AMNH 3015	YPM 5203	YPM 5210	AMNH 3015	YPM 5203	YPM 5210
CAUDALS												
1	—	—	—	—	—	—	—	—	—	—	—	—
2	33.1	—	—	32.0	—	—	25.0	—	—	—	—	—
3	37.4	—	—	31.6	—	—	24.1	—	—	>58.0	—	—
4	38.3	—	39.6	27.3	—	27.6	23.8	—	24.3	—	—	>62.0
5	39.0	—	—	27.2	—	—	—	—	—	—	—	—

TABLE 4. (continued)

	AMNH 3015	YPM 5203	YPM 5201	AMNH 3015	YPM 5203	YPM 5201†	AMNH 3015	YPM 5203	YPM 5201†	AMNH 3015	YPM 5203	YPM 5201†
6	41.4	—	—	25.8	—		23.8	—		>54.5	—	
7	43.6	45.5	—	25.5	23.5		21.0*	23.2		—	—	
8	44.5	47.6	—	24.1*	23.1		21.0*	22.8		—	>42.4	
9	47.6	50.2	—	24.0	19.3		20.7*	23.6		—	>40.3	
10	49.4*	—	—	25.0*	21.7		—	23.7		—	—	
11	50.6*	53.0	—	—	22.2		—	21.4		—	>35.1	
12	—	53.1	—	—	22.1		—	22.0		—	—	
13	—	53.2	48.3	—	—		—	—		—	—	
14	—	53.0	—	—	—		—	—		—	—	
15	47.2*	53.5*	46.6	17.2	17.2		18.5*	—		—	—	
16	48.0	52.6	46.4	16.0*	17.0		17.5*	18.5		—	—	
17	47.8	51.7	47.5	15.5	16.8		18.1	17.8		—	—	
18	46.2	50.0	46.0	15.4	15.5		17.6	—		24.7	—	
19	47.1	50.2	45.0	15.3	15.3		15.7	16.6		—	—	
20	46.6	48.3	41.6	13.4	14.6		15.5	15.8		22.4	—	
21	—	47.5	42.6	—	13.8		—	15.0*		—	—	
22	—	46.9	43.2	—	13.3		—	13.3		—	—	
23	43.5	45.2	41.6*	12.8	12.9		15.1	—		20.7	—	
24	43.2	42.8	40.0*	12.3	12.5		13.9	—		19.3	—	
25	43.0	42.0	39.4	11.6	10.5		12.6	9.8		>20.0	—	
26	41.8	41.5	35.0*	11.0	10.6		11.5	—		>17.0	—	
27	—	—	36.1	—	10.0		—	—		—	—	
28	—	37.8	35.0	—	9.0		—	—		—	—	
29	—	37.5	34.3	—	—		—	—		—	9.0	
30	—	33.6	—	—	—		—	—		—	—	
31	—	32.1	—	—	—		—	—		—	8.1	
32	—	32.3	—	—	—		—	—		—	—	
33	—	28.7	—	—	—		—	—		—	—	
34	—	24.8	—	—	—		—	—		—	—	
35	—	23.3	—	—	—		—	—		—	—	
36	—	20.1	—	—	2.6		—	3.0		—	—	

---

* approximate.

† In YPM 5201, only the length of the centra could be measured.

in present collections. Consequently, the number of sacral vertebrae is not known, although a left ilium (AMNH 3015) suggests that the number was at least three and probably four. This interpretation is based on what appear to be sutural scars on the ilium, marking the attachment sites of sacral ribs and diapophyses. Although the topography of the ilium surface is very poorly preserved there are three moderate-sized, oval-shaped areas of irregular texture situated above the pubic peduncle, the acetabulum and the ischiac peduncle. Above these are two or three smaller and less well-defined areas of similar texture. These are interpreted respectively as probable attachment sites of sacral ribs and transverse processes. Presumably the above evidence would indicate the presence of only three sacral segments, but there may have been one or more dorsals or caudals co-ossified into the sacrum which did not contact the ilium. Such a discrepancy between the number of sacral ribs and sacral vertebrae occurs in *Allosaurus* and *Ceratosaurus* (Gilmore, 1920: pls. 8 and 21). In fact, the spacing of the upper series of scars suggests a series of four segments.

CAUDAL VERTEBRAE

The caudals number no less than 36 and probably no more than 40 (based on YPM 5201, 5202, 5203 and AMNH 3015). Although this number is relatively low among theropods, the tail accounted for more than half the total length of the animal; tail length approximated 125 cm in the above individuals.

The caudal series is normal in all respects except two, but these exceptions are remarkable features that clearly establish the tail as a critical structure for maintaining balance and promoting agility. The chevrons and the prezygapophyses of all but the most anterior caudals are modified into extremely long, double, bony rods reinforcing the tail. Elongated prezygapophyses have been noted in a variety of theropods such as *Gorgosaurus, Ornithomimus, Ornitholestes, Allosaurus* and *Ceratosaurus* (Lambe, 1917: p. 28; Osborn, 1917: p. 736 and 748; Osborn, 1903: p. 462; and Gilmore, 1920: p. 47 and 99), but in none of these does prezygapophysis length exceed segment length. In *Deinonychus,* however, the prezygapophysis reaches a maximum length of at least 10 and perhaps 12 segments (Fig. 37). In the remarkable caudal series of YPM 5201 (Figs. 35 and 36) these structures are preserved as continuous bony rods, 1 to 2 mm in diameter, extending more than 430 mm over the length of 10 preceding segments. The proximal portion of the prezygapophyses are normal with distinct, almost vertically oriented, articular facets. Immediately beyond these facets, the articular processes narrow abruptly into oval-sectioned rods that bifurcate approximately 10 to 15 mm anterior to the articular facets into 2 cylindrical rods. These double rods pass forward, closely packed with similar rods from more caudad segments, in prominent bundles situated lateral to the neural arch. Each pair of prezygapophyses extends forward as a pair of double rods, clasping the short postzygapophyses of the vertebra in front and continues forward to lie parallel to and clasp the prezygapophyses of that same vertebra and those of the next 8 or 10 vertebrae beyond.

Except for the most anterior elements the chevrons are modified to very similar counterpart structures. Instead of a long blade-like spine projecting

FIG. 35. A nearly perfect caudal series of *Deinonychus antirrhopus*, YPM 5201. This series is almost a meter in length, of which approximately 60 cm are shown here.

downward and backward, most chevrons are greatly flattened dorsoventrally into narrow, flat wedges, the blunt apex of which points caudally. The anterolateral extremities are greatly elongated into double, bony rods extending at least nine segments (380 mm) forward, closely embracing the wedge-shaped body of the next chevron forward. In ventral view, the chevrons form a series of nesting V's. These interlocking haemal arches are the morphologic equivalents of the neural arches above in that successive posterior elements embrace a series of preceding segments.

FIG. 36. Detail photo of the caudal series in *Deinonychus antirrhopus*, YPM 5201, showing the prezygapophyseal rods above and the chevron rods below the centra. Approximately ×1.

Both rod types are nearly uniform in diameter over most of their length but gradually diminish from approximately 2 mm posteriorly to less than 0.3 mm at the anterior extremities. Throughout their length they are subcircular in cross section, with a well-defined concentric structure (Figs. 43, 45, 47 and 49).

The proximal 8 or 9 caudal vertebrae probably were of normal form with normal chevrons and zygapophyses. Specimen YPM 5203, consisting of a partly

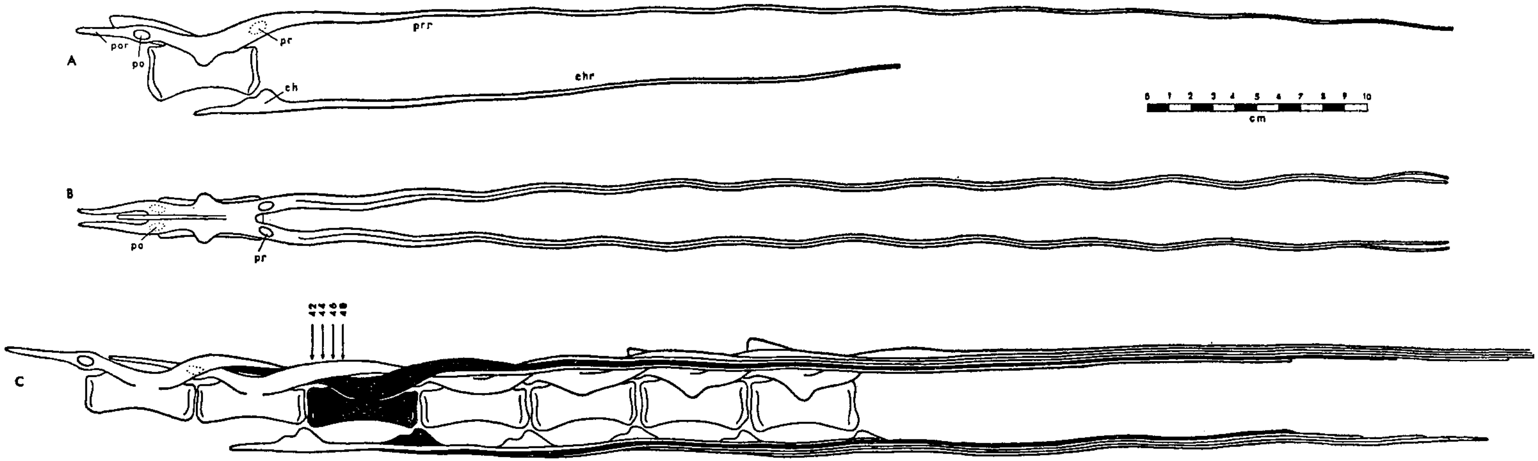


FIG. 37. Outline drawings of a single caudal vertebra and chevron of *Deinonychus antirrhopus* in lateral (A) and dorsal (B) views. C illustrates the relationship of a single vertebra and its bony rods to preceding (right) and succeeding (left) vertebrae. The arrows in C indicate the positions of the thin sections illustrated in Figs. 42, 44, 46 and 48. Abbreviations: ch—body of the chevron; chr—chevron rod; po—postzygapophyseal facet; por—postzygapophyseal rod; pr—prezygapophyseal facet; prr—prezygapophyseal rod.

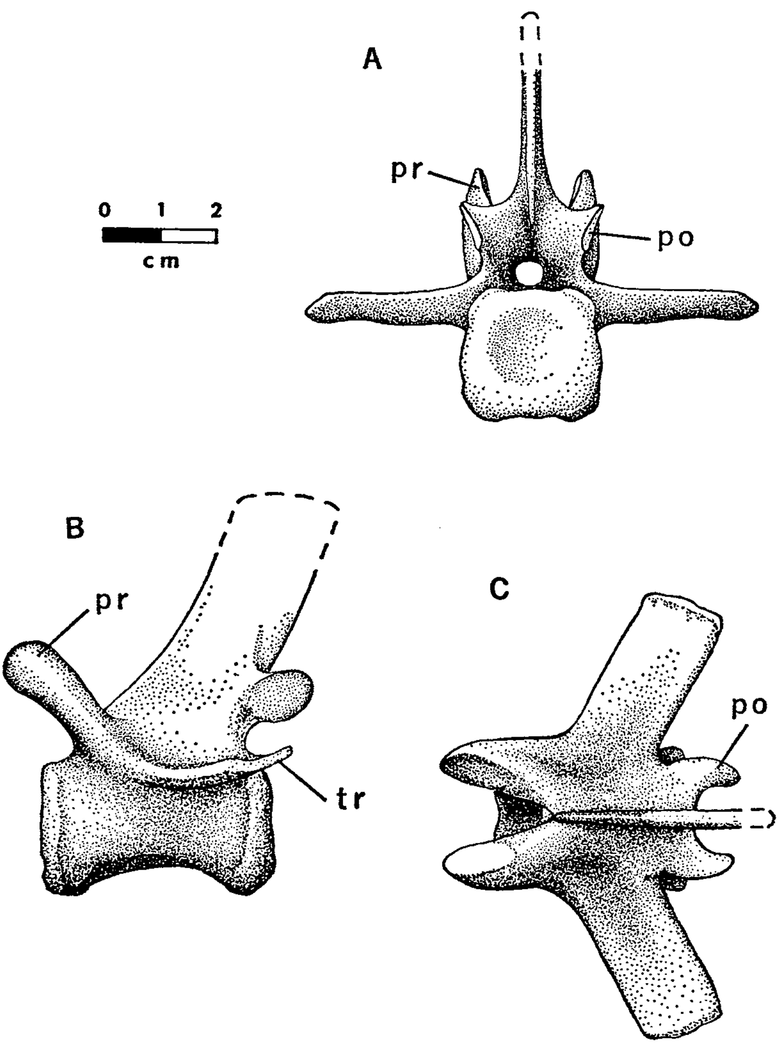


FIG. 38. Proximal (5th) caudal vertebra of *Deinonychus antirrhopus*, YPM 5210, in posterior (A), left lateral (B) and dorsal (C) views. Abbreviations: po—postzygapophysis; pr—prezygapophysis; tr—transverse process.

dissected, articulated caudal series (interpreted as the 7th through 36th segments), includes an anterior caudal vertebra (the 7th?) which is not encased in these bony rods, and although both anterior and posterior zygapophyses are incomplete, it appears to have had normal articular processes. The succeeding vertebra bears normal postzygapophyses indicating perhaps that the incomplete prezygapophyses were also normal. There are, however, 4 bony rods (2 pairs?) preserved on each side of the centrum that angle up and forward. These probably are the most anterior extensions of two chevrons several segments farther back. The chevron which articulates with this particular vertebra and the vertebra behind (the 9th?) is of normal keel-like construction. (Fig. 40).

The proximal caudals are relatively short and stout and only slightly longer than wide (Fig. 38). The centra are concave laterally, flaring out at both ends. Ventrally, all caudals are marked by a distinct, narrow and shallow longitudinal groove. In anterior vertebrae, this groove is a relatively small feature occupying only the mid-line area of the ventral surface, but in more distal centra it forms the entire ventral surface. All caudals are slightly platycoelous; none are characterized by pleurocoels.

Centrum length increases posteriorly to a maximum at the 12th to 15th segments, beyond which point it decreases progressively. Height and width diminish progressively toward the caudal extremity.

Transverse processes are stout and of moderate length (approximately equal to centrum length in anterior caudals), angling back and outward in a horizontal plane. Anteriorly, these processes are sub-circular to oval in section, becoming compressed into broad, thin, horizontal blades at about the 5th caudal, and diminishing in length posteriorly until represented by only slight ridges on the upper lateral surfaces of the 11th and 12th caudal centra. Where present, transverse processes arise from the upper lateral surfaces of the centra, although in the most anterior caudals they may develop from the neural arch. The centrum and neural arch are firmly united in all caudals, as they are in all presacrals. In fact, fusion has completely obliterated the centrum-arch sutures in all preserved caudal vertebrae. A 5th? caudal (YPM 5210) suggests that this suture may have passed beneath the transverse process.

The neural arch is low and robust in anterior caudals with stout articular processes and a thin, rectangular, blade-like neural spine that projects up and back at about 75° to the horizontal. The neural spine becomes progressively shorter and projects back at a progressively lower angle in successive vertebrae, until at the 9th caudal it consists only of a very low, but distinct ridge extending over the full length of the vertebrae and terminating in a low apex between the postzygapophyses articular facets. A very faint ridge is present on the 11th and 12th (Fig. 39), but succeeding caudals bear no sign of a neural spine.

CHEVRONS

As noted above, all except the most anterior chevrons (Fig. 40) are modified to highly specialized structures which almost duplicate on the underside of the caudal column the nesting design of neural arches and prezygapophyses above. The most anterior chevrons are not known, but it is probable that the first chevron was situated between the first and second caudal vertebrae as in *Gorgosaurus* (Lambe, 1917) and *Ceratosaurus* (Gilmore, 1920). The beveled anterior and posterior ventral margins of all the preserved caudals in AMNH 3015 support this conclusion.

The most anterior chevron preserved in natural position is associated with vertebrae that I interpret as caudals 8 and 9 (YPM 5203). This chevron (Fig. 41A) is of normal design, with a relatively short dorsoventrally projecting blade which is expanded longitudinally into a spade-shaped keel. The greatest dimension is longitudinal, near the distal extremity. Proximally the thin chevron blade flares out transversely to enclose the haemal canal. Above the haemal

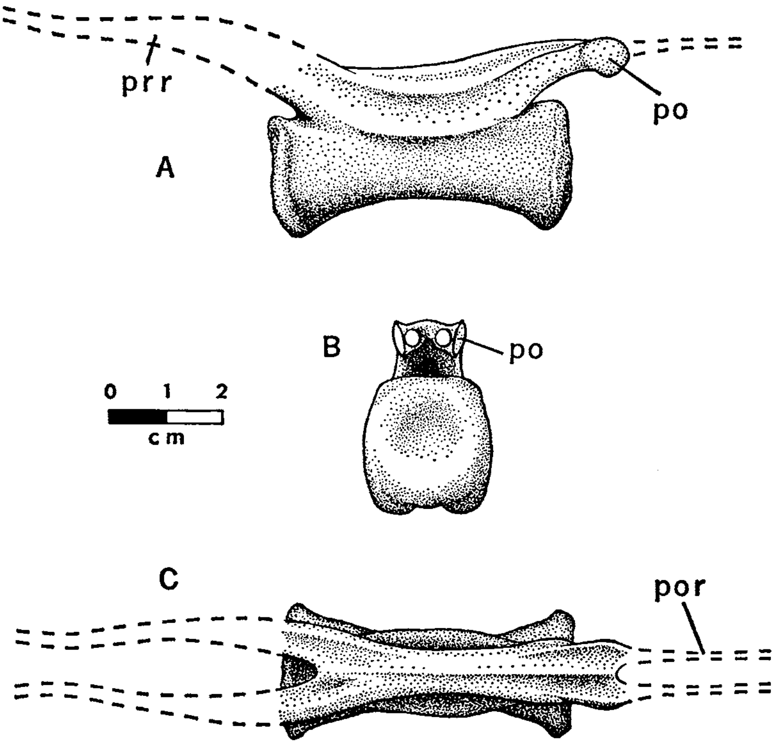


FIG. 39. A mid-caudal vertebra of *Deinonychus antirrhopus*, YPM 5203, in lateral (A), posterior (B) and dorsal (C) views. Abbreviations: po—postzygapophysis; por—postzygapophyseal rod; prr—prezygapophyseal rod.

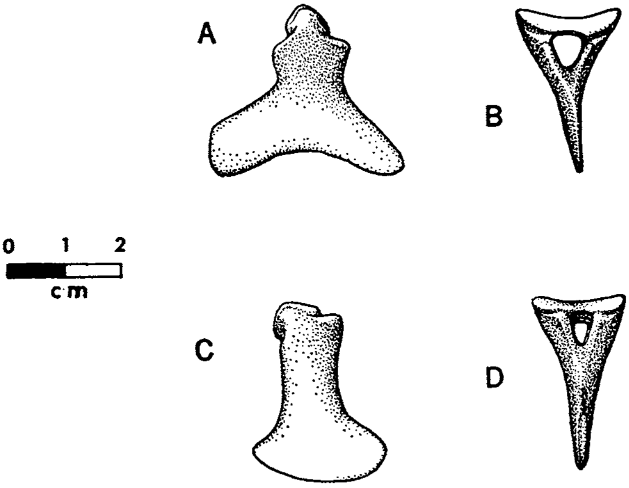


FIG. 40. Proximal chevrons of *Deinonychus antirrhopus*, YPM 5244, in left lateral (A and C) and posterior (B and D) views. Presumably that illustrated in A and B occurred anterior to the chevron of C and D, on the basis of the relative sizes of the haemal canal. This seems to be substantiated by the last normal chevron in the caudal series of YPM 5203 (see Fig. 41A).

canal, well-developed, wedge-shaped articular processes meet in the mid-line, but apparently do not co-ossify. A number of similar chevrons were found isolated in the Yale quarry and are believed to represent more proximal chevrons of *Deinonychus* (Fig. 40).

The adjacent chevron in this specimen (YPM 5203), which articulates with the 9th and 10th caudals, is totally different in form (Fig. 41B). Instead of a compressed, longitudinally expanded sagittal blade, the 9th chevron flares out transversely into a flat-bottomed, V-shaped structure the apex of which is directed caudally. The anterior ends of the V extend forward an unknown distance (at least to the anterior end of the 8th caudal) as double bony rods on each side. Clearly, this is the most proximal chevron bearing these unusual bony rods. Presumably the rods from this segment were the shortest of the entire series, although at least 9 caudals occur in front of this chevron. Chevron rods are preserved with both the 9th and 8th caudals, so those of this chevron clearly extended at least 2 segments forward, but I suspect that they did not extend much beyond the 7th caudal with the first 5 or 6 caudals entirely free of chevron rods (and probably of the prezygapophyseal rods as well). Except

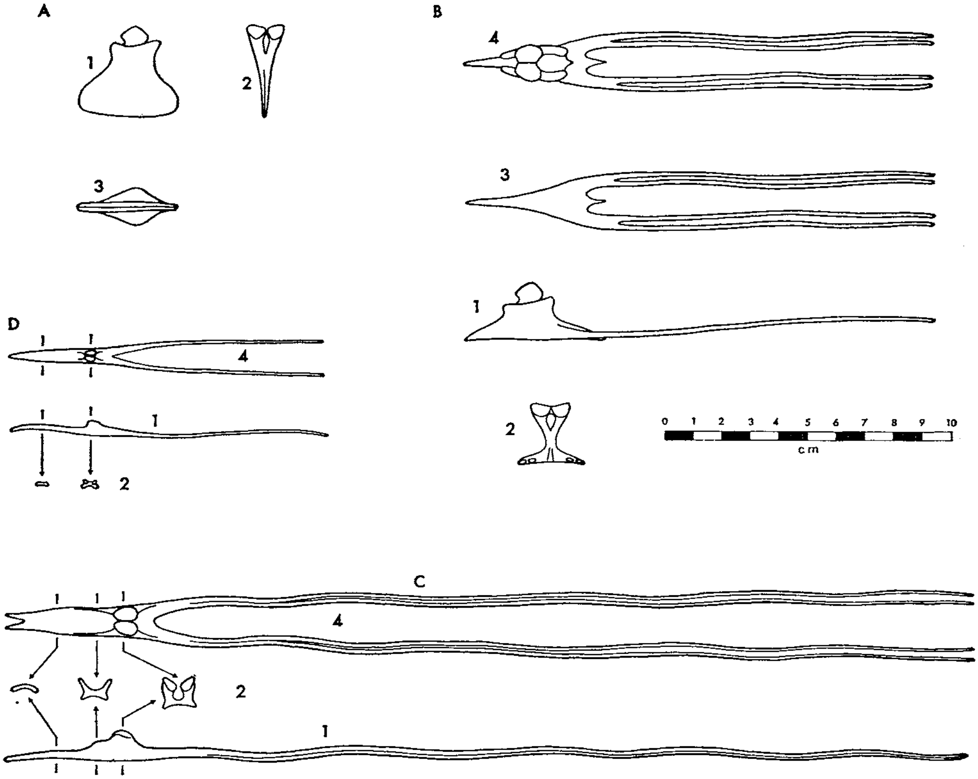


FIG. 41. Outline drawings showing the variation in chevron form in the caudal series of *Deinonychus antirrhopus* (based on YPM 5201 and 5203). A) chevron between eighth and ninth caudals (YPM 5203) in lateral (1), posterior (2) and ventral (3) views. B) chevron between ninth and tenth caudals (YPM 5203) in lateral (1), anterior (2), ventral (3) and dorsal (4) views. C) a chevron at mid-tail (YPM 5201) in lateral (1), cross-section (2) and dorsal (4) views. D) a distal chevron (YPM 5201) in lateral (1), cross-section (2) and dorsal (4) views.

for somewhat greater depth dorsoventrally, more abrupt taper of the V, and a prominent mid-line anterior projection, this element is similar to the remaining chevrons. Dorsally, it is expanded transversely to enclose the haemal canal and bears two normal, stout articular facets. More distal chevrons are progressively narrower and shallower. It is also clear that succeeding chevrons, behind the first specialized chevron, bear successively longer rods, until a maximum length of 10 or more segments is achieved. Specimen YPM 5203 has 7 rods preserved on the left side of the first specialized chevron, showing that the rods of at least the following 4 chevrons were longer.

The microscopic structure of these chevron rods is identical to that of the prezygapophyses (Figs. 43 and 49). Examination of a number of thin sections of the 14th and 15th caudals of YPM 5202 shows that there are differences in the internal structure of adjacent chevron rods. This, of course, reflects the fact that each pair of rods is sectioned at a different point in its length. For example, in Figure 49 one rod is distinctly oval in section and has a double concentric structure, whereas the adjacent rods are circular and show a simple concentric pattern. The oval rod has been sectioned close to the body of the chevron just behind the point at which the left process bifurcates.

Two basic structural types, aside from the double pattern just noted, are present within the chevron rods: 1) simple concentric structure with a solitary central cell or canal (Fig. 47), and 2) concentric shell with a compound core structure consisting of two to eight oval or subcircular canals or cells (Fig. 43C). The simple condition appears to be relatively rare, although it must be kept in mind that the thin sections available come from only one short segment of the caudal series, as shown in Figure 37. The much more numerous complex rods appear to have a central core composed of perforated but not cancelous, bone surrounded by a thick sheath of compact (periosteal?) bone. The superficial concentric pattern is remarkably similar to the dense periosteal bone of modern reptilian long bones.

ORIGIN AND FUNCTION OF CAUDAL RODS

The unusual and extreme nature of the prezygapophyseal and chevron rods in *Deinonychus* raises intriguing and important questions about development and function. It is very evident that this caudal series was highly specialized for some particular function. It is also evident that either the precise function or the overall importance of the tail in this animal's behavior and way of life was unique. The tail is a critical structure for grasping, maintaining balance, or facilitating agility in a wide variety of living vertebrates. Its function is often an essential factor in successful adaptation to particular modes of life, as in riccochetal rodents, squirrels, tarsiers, lemurs and kangaroos. But in these examples, precisely controlled mobility (and strength in the instance of the kangaroo) are essential qualities. Extreme flexibility, of course, is required for prehensile capabilities as in cebids and chameleontids. In view of the very limited degree of flexibility of most of the caudal series in *Deinonychus*, prehension may be discounted.

None of the living "tail balancers" (lemurs, squirrels, riccochetal rodents, kangaroos) possess caudal structures that even remotely resemble those of *Deinonychus*. In fact, they all display the usual mammalian pattern—the progressive diminution of both articular processes and chevrons over the length of the caudal series. Among mammals, whether the tail is an important stabilizing or balancing appendage or not, these structures are rudimentary or nonexistent beyond the fifth to eighth caudal segment, as are the transverse processes and neural spines in most instances. In living reptiles and in a majority of extinct reptiles the articular processes and chevrons persist as functional elements over most of the caudal series, but only in rhamphorhynchoid pterosaurs do we have evidence of such extreme development as in *Deinonychus*. The rhamphorhynchoid condition appears to be a parallel adaptation and I plan further study of this group.

At first glance the closely packed bundles of bony rods would appear to have completely eliminated all tail flexibility, but closer examination reveals that there is no co-ossification between adjacent rods (Figs. 42–49), no fusion of adjacent vertebrae even at the tail extremity, and no fusion of chevrons to centra. Most surprising of all, however, is the presence of distinct articular facets (synovial joints) on pre- and postzygapophyses, apparently throughout the entire length of the tail. Intersegmental mobility may have been restricted by the enclosing rods, but it was not eliminated.

Continuity of these rods with the caudal neural arches and haemal arches, together with uniform surface texture and shape with those structures, suggests that these rods are extreme elongations of normal bony processes, but it is highly unlikely that they developed from the usual centers of ossification. It seems much more reasonable that they ossified from other connective or muscular tissue during early ontogeny. Non-osseous structures present in living reptiles and mammals suggest a possible origin and a reasonable function.

Tetrapod caudal musculature consists of short intersegmental and long transsegmental muscles. The latter are typically arranged in lateral or near-mid-line dorsal and ventral positions. The lateral muscles, including the M. ilio-caudalis, M. ischio-caudalis and M. femoro-caudalis, commonly are the largest of the caudal muscles in reptiles, inserting on the transverse processes or their rudiments over much of the caudal length. These muscles are the caudal abductors or lateral flexors. Excluding the transverso-spinalis and longissimus, the other dorsal and ventral caudal muscles in reptiles (M. extensor caudae medialis, M. extensor caudae lateralis, and M. flexor caudae) are usually small muscles, except at the base of the tail. Mammals generally possess the same basic caudal muscle arrangement but the dorsal and ventral components are the largest and the lateral muscles are reduced. We can correlate the dominance of lateral caudal musculature in reptiles with the lateral, undulatory pattern of locomotion in lizards and crocodilians. We can suppose that the contrary dominance of dorsal and ventral caudal musculature in mammals is correlated with loss of the reptilian, sinuous, lateral undulations of the axial column during locomotion. Extension and flexion of the tail in or close to the sagittal plane appears to be more important than lateral flexion in mammalian tetrapods. Compare reptiles and mammals, for example, in the proportion of the caudal length that bears distinct transverse processes, the principal origin and insertion sites of caudal lateral flexors (Table 5). In those mammals that carry "dynamic

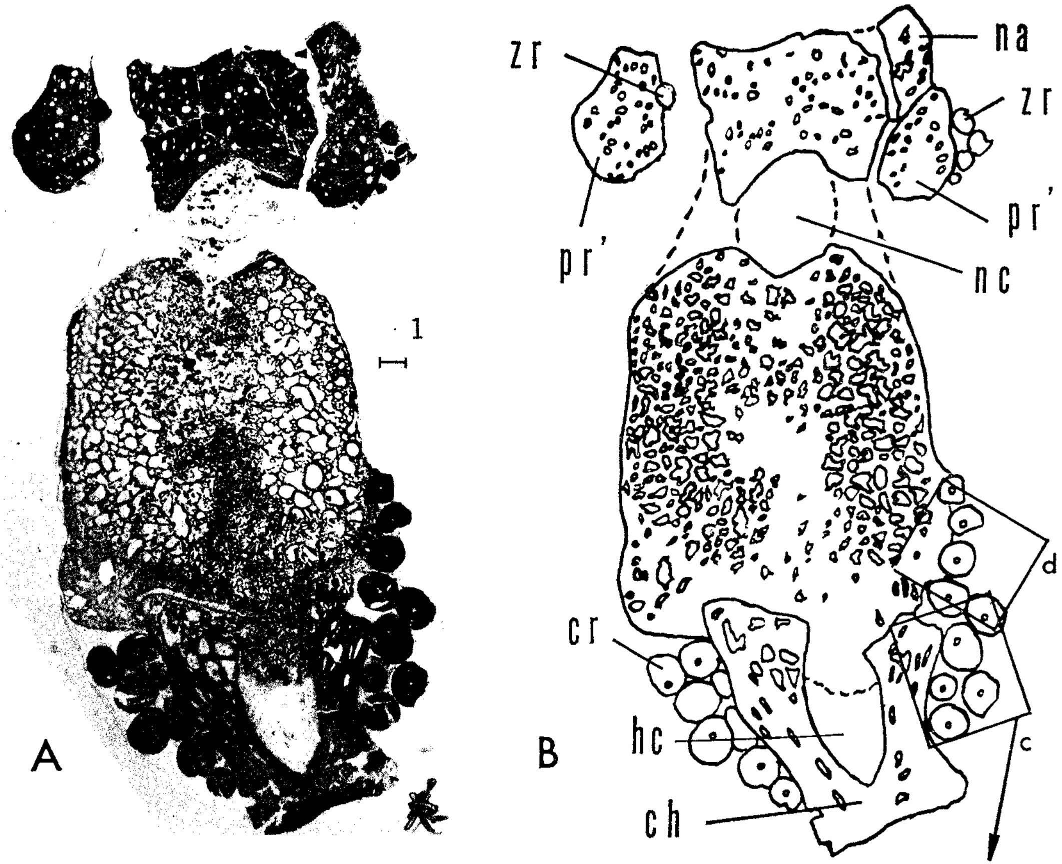


FIG. 42. (A) Transverse section (×3) through the posterior part of a caudal vertebra of *Deinonychus antirrhopus* near mid-tail (YPM 5202) showing the peculiar caudal rods. The section is oriented correctly with regard to right and left sides. The four transverse sections of Fig. 42, 44, 46 and 48 are spaced approximately 4 mm apart. The various features are identified in B. The rectangles of B indicate the areas illustrated in C and D of Fig. 43. Abbreviations: ch—chevron; cr—chevron rod; hc—haemal canal; na—neural arch; nc—neural canal; pr′—prezygapophysis of succeeding segment; zr—prezygapophyseal rod.

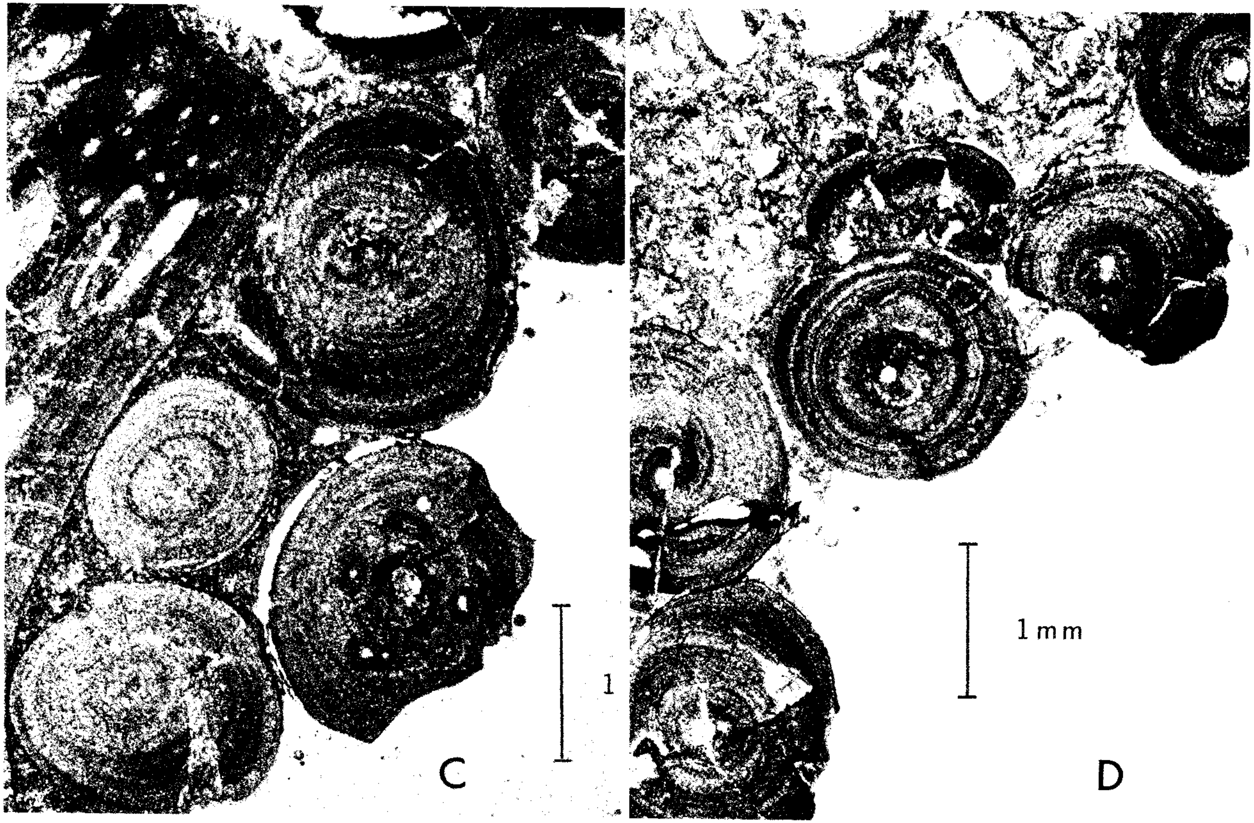


FIG. 43. Enlarged (20×) areas of previous transverse section (Fig. 42) showing concentric, "periosteal" bone of the chevron rods. Notice that some rods have simple cores, others have compound cores.

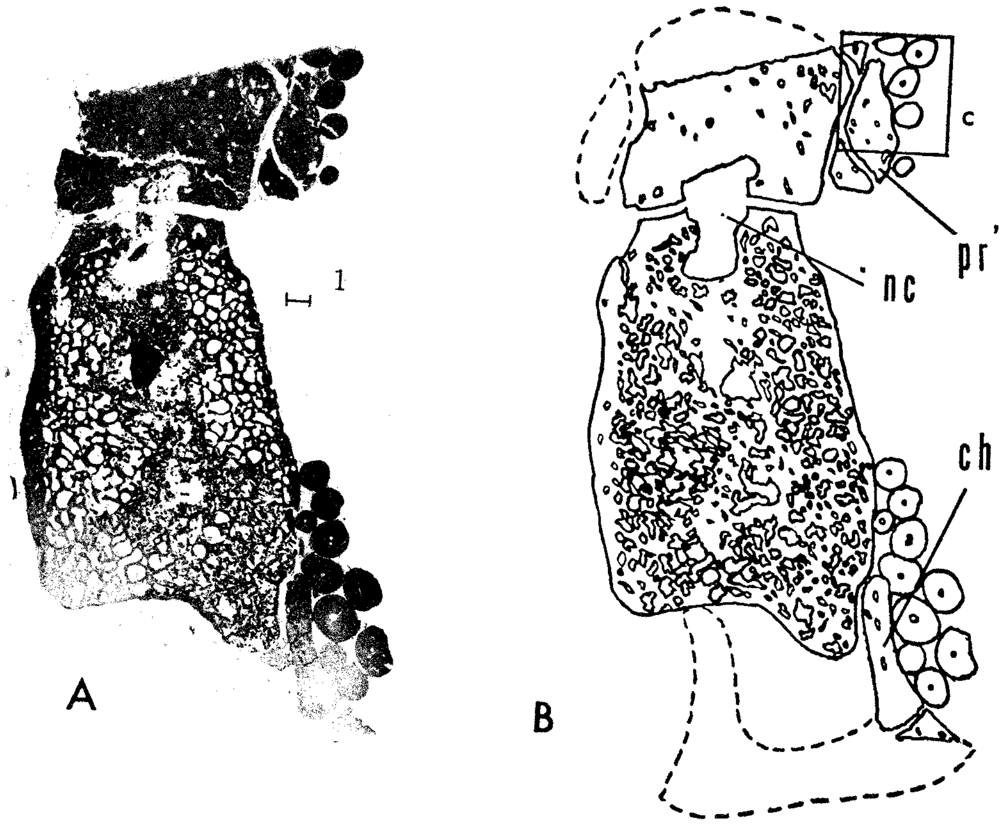


FIG. 44. Transverse section (A) approximately 4 mm anterior to that of Figure 42. The rectangle of B indicates the area enlarged in Fig. 45. Abbreviations as in Fig. 42.

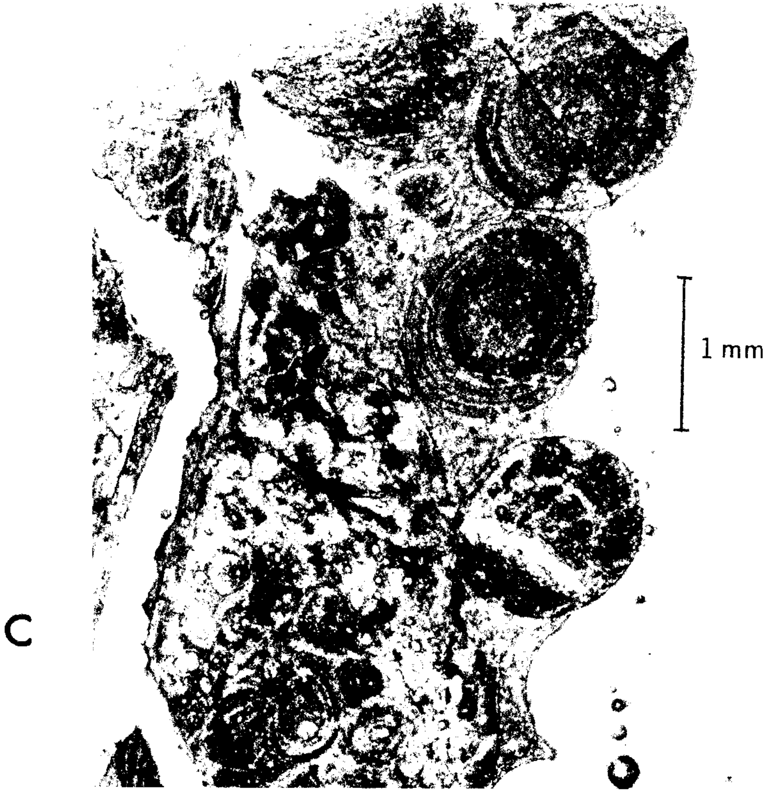


FIG. 45. Enlarged (20×) area of previous transverse section (Fig. 44) showing the concentric "periosteal" bone of several prezygapophyseal rods. Notice the typical Haversian bone of the prezygapophysis at left center. This is enclosed in a thin "rind" of layered or periosteal bone.

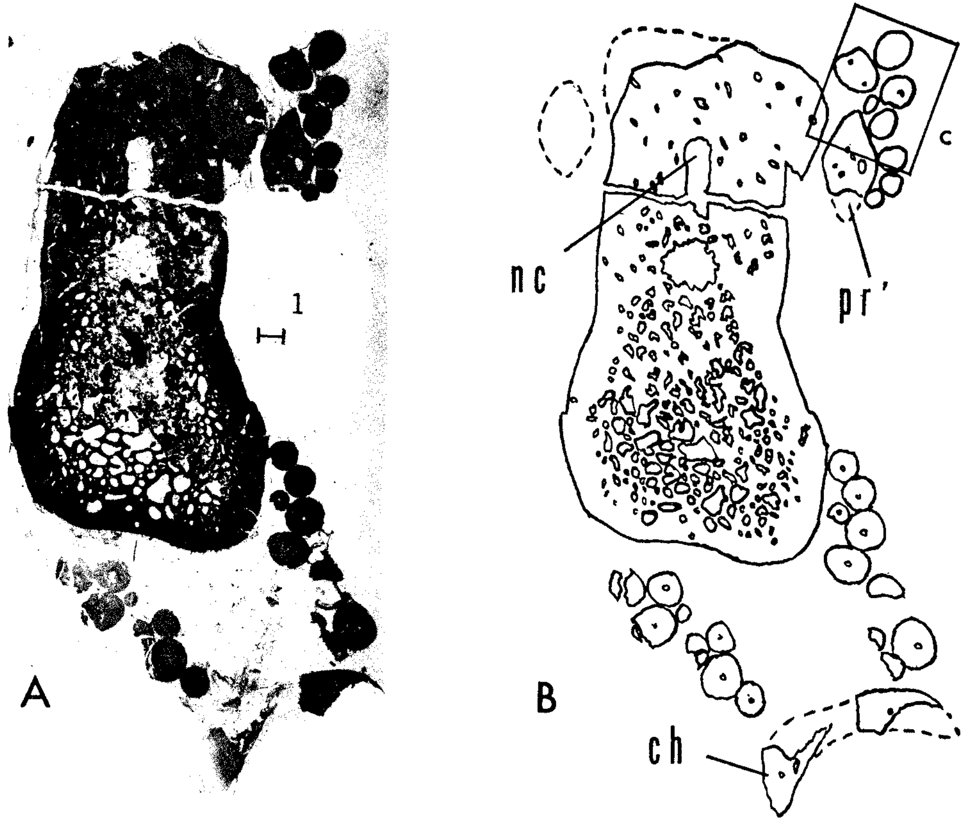


FIG. 46. Transverse section (A) approximately 4 mm anterior to that of Figure 44. Notice the smaller size of the prezygapophysis (pr′) and the very different form of the chevron (ch). Abbreviations as in Fig. 42.

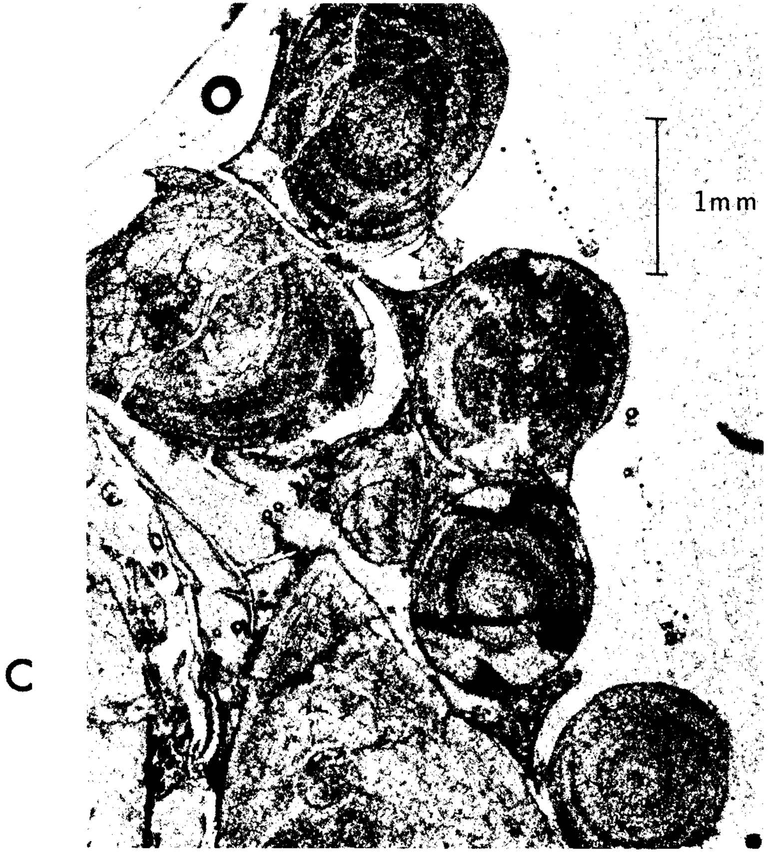


FIG. 47. Enlarged (20×) area of previous transverse section (rectangle of Fig. 46B) showing the internal structure of the prezygapophyseal rods. Notice the thin superficial zone of layered (periosteal) bone in the prezygapophysis (pr′) at bottom center. The three rods at the right are the same rods shown in Fig. 45.

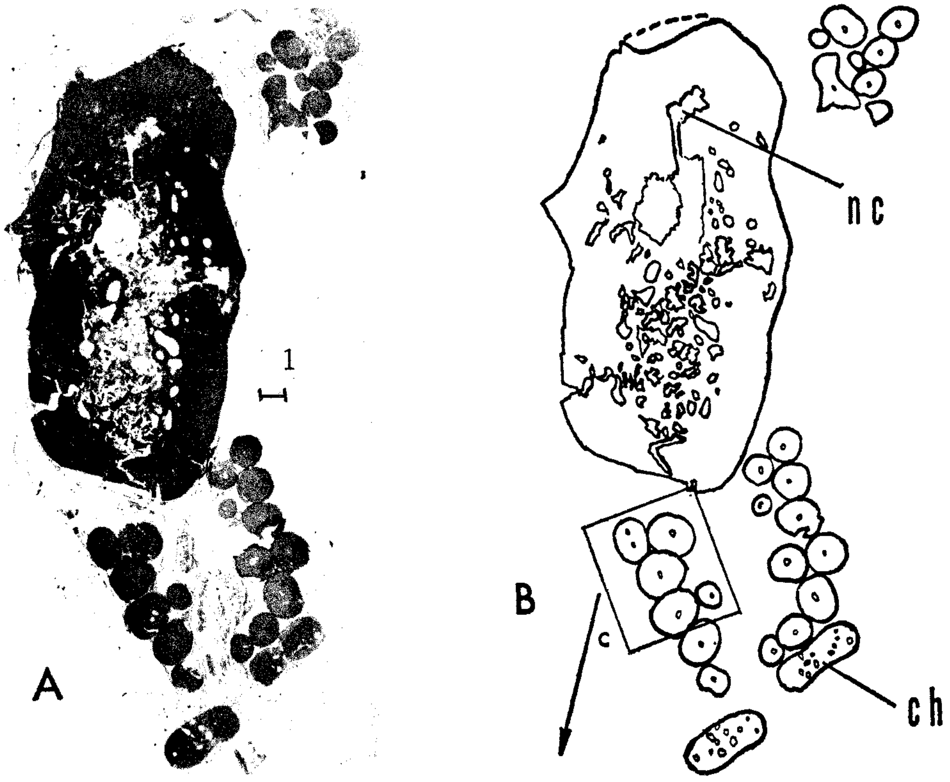


FIG. 48. Transverse section (A) approximately 4 mm anterior to that of Fig. 46. Notice the lozenge-shaped elements at the bottom of the two columns of chevron rods. These are the proximal shafts of the anterior extensions of the chevron, immediately posterior to bifurcation into double rods on each side. The contrast does not reveal the internal structure here, but both "lozenges" have two (left and right) cores of Haversian bone. Abbreviations as in Fig. 42.

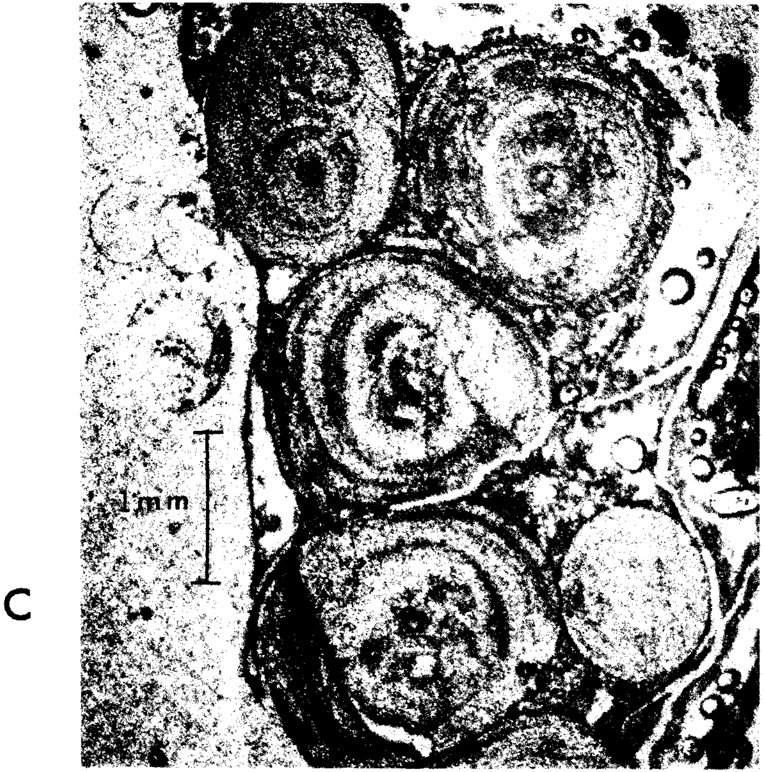


FIG. 49. Enlarged (20×) area of previous transverse section (rectangle of Fig. 48B) showing the concentric structure of chevron rods. Notice the double pattern of the upper left rod.

TABLE 5. Morphology of caudal vertebrae in some selected tetrapods

Taxon	No. of caudals with distinct transverse processes	Percent of total tail length with transverse processes
Alligator mississippiensis	18	50
Crocodylus americanus	17	48
Tupinambis teguexin	18	40
Iguana iguana	14	20
Varanus komodoensis	50	80
Varanus niloticus	51	84
Felis domesticus	7	28
Canis familiaris	7	25
Lemur catta	5	11
Tamiasciurus hudsonicus	5	12
Dipodomys ordii	4	10
Didelphis marsupialis	7	25
Macropus rufus	7 (?)	42

tails," only the proximal segments bear distinct transverse processes, involving 10 to 30 percent of tail length. Even in kangaroos (*Macropus*) distinct transverse processes occur only along the proximal 40 percent of the tail, although pronounced dorsoventral flattening of the distal centra has resulted in some transverse expansion of the vertebrae. In crocodilians and lacertilians, however, the caudal series bearing transverse processes generally ranges from 40 to 80 percent of the total caudal length.

In lizards (*Iguana, Basiliscus*) the two dorsal muscles are moderately developed. The medial muscle, M. extensor caudae medialis, lies next to the neural spines, extending from the sacrum to the distal part of the tail. Origins are on the neural spines and insertions at the bases of more caudad spines and on the neural arches. Situated lateral to this is the M. extensor caudae lateralis, which is somewhat larger and more prominent. The extensor lateralis extends posteriorly from the sacral ribs and the fascia of the M. longissimus dorsi to insert by individual tendons on the extremities of the prezygapophyses beginning with the fifth caudal vertebrae. A prominent, but not large, muscular belly is evident at the base of the tail, but beyond the seventh or eighth caudal, only bundles of thin, parallel tendons with few muscle fibers are present. The arrangement is strikingly similar to that of *Deinonychus,* as shown in Figures 35 and 36.

Ventrally, a minor long muscle lies lateral to the haemal spines, inserting by individual tendons to the bases of successive haemal arches. The origin appears to be by fleshy attachment on the ventral surfaces of the sacral and posterior dorsal centra. This is the M. flexor caudae.

In mammals, comparable extensors and flexors are strongly developed, particularly in the lemur, cat, dog, and probably also in squirrels and riccochetal rodents. The mammalian muscles are the M. sacrococcygeus dorsalis medialis, dorsalis lateralis, ventralis medialis and ventralis lateralis (Miller et al, 1964). The lateral or abductor muscles (M. intertransversarius coccygeus) are relatively small, except at the base of the tail. Again, the striking similarity of the tendon bundles and of the attachment sites of individual tendons of the M. sacrococcygeus dorsalis lateralis in the common cat, to the arrangement and "attachments" of the prezygapophyseal rods in *Deinonychus,* like the less distinct, but still similar pattern of the M. extensor caudae lateralis in *Iguana* and *Basiliscus,* is impressive evidence pertaining to the derivation of these unusual bony rods in *Deinonychus.* The chevron rods may similarly be equated with the long tendons of the M. flexor caudae of *Iguana* and *Basiliscus* or tendons of the M. sacrococcygeus ventralis lateralis in *Felis,* all of which attach to the bases of the haemal arches or the haemal processes.

If the caudal rods of *Deinonychus* were derived from the tendons of the caudal extensors and flexors, this suggests a great deal about function and development. Tendons attach to bone by means of the periosteum and the tendon sheath is usually continuous with the periosteum. Is it reasonable to suppose that osteoblasts could migrate by proliferation from the true periosteum into the tendon sheath, transforming it into "neo-periosteum"? If so, this could explain the periosteal-like, concentric structure of these caudal rods and their continuity with normal bony structures.

The possible presence of contractile tissues attached to the anterior extremities of these bony rods may account for what appears to be a paradox. On the one hand, these bundles of bony rods would have inhibited caudal flexibility; on the other hand, the retention of articular facets clearly establishes that some flexibility remained. Contraction of extensor tail muscles attached to these rods at the base of the tail would pull each pair of prezygapophyses more tightly against the preceding postzygapophyses; the result would be a more compact, interlocked series of tightly nested V's. The chevrons forming a strikingly similar series of ventral V's would similarly be nested more tightly together by contraction of the ventral flexors. The effect of simultaneous contraction of caudal extensors and flexors would be to stiffen the tail into a single unified member. Relaxation of the extensors and flexors would release the tightly nested dorsal and ventral V's, and thereby permit at least some passive, if not active, flexibility.

The normal design of the proximal caudals of *Deinonychus* indicates that considerable flexion, extension and probably abduction was possible in that region. We can suppose that medial flexors and extensors, equivalent to the M. sacrococcygeus dorsalis medialis and ventralis medialis were the primary elevators and depressors of the tail, since the dorsal and ventral sacrococcygeus lateralis muscles appear to have been modified into caudal "inflexors" or stiffeners. Moreover, because the transverse processes are limited to the first 10 caudals, we can presume that the lateral flexors or abductors were similarly restricted to this region and that all abduction, as well as flexion and extension, was effected at that region.

The remaining question is: what is the functional significance of a stiff tail? Presumably the stiffening of the tail eliminated the whiplash action that occurs with a sudden movement of a flexible or segmented series. Acting as a single rigid body instead of a series of separate, but linked, bodies, the moments of inertia of all segments are compounded into a solitary, simultaneously acting force or counterforce. Thus the angular momentum of the tail of *Deinonychus* may have been compounded whenever required, increasing the effectiveness of the tail as a dynamic stabilizer during rapid or irregular movements by the animal. (Tight rope walkers use rigid balancing poles, not lengths of flexible chain.)

The *Deinonychus* caudal adaptation probably provided controlled rigidity, but at the same time minimized the hazard of fractures that would be inherent in a series of co-ossified caudal vertebrae.

DORSAL RIBS

A large number of dorsal and abdominal ribs and rib fragments were recovered from the Yale *Deinonychus* quarry, but, owing to their disarticulated occurrence and their incomplete or distorted preservation, a complete reconstruction of the rib cage is not possible. A number of ribs were closely associated at several spots in the quarry and these probably belong to a single individual in each instance, but even these represented very incomplete remains. Most of the ribs occurred as isolated bones and cannot be referred to a definite specimen. Consequently, the following descriptions include tentative identifications that cannot be verified until additional articulated material is discovered. All of the dorsal ribs recovered are dichocephalous, as was indicated by the available vertebrae.

CERVICAL RIBS

Two distinct types of cervical ribs are known (Fig. 50) from the Yale *Deinonychus* site. Both types were closely associated with cervical vertebrae of YPM 5210. The most distinctive feature of these ribs is their short length. The fact that both kinds are equal to or shorter than the cervical centra strongly suggests that none of the cervical ribs exceeded centrum length. Short cervical ribs might be considered a "coelurosaurian" character, since they are present in *Coelophysis, Ornithomimus, Compsognathus* and possibly *Ornitholestes. Allosaurus, Gorgosaurus* and *Tyrannosaurus,* on the other hand, are characterized by elongated cervical ribs equaling or exceeding the length of three segments. The cervical series in *Deinonychus* (and of "coelurosaurs") would appear to have had greater flexibility than those of "carnosaurs."

The two pairs of elements closely associated with cervical vertebrae (YPM 5210) are interpreted as anterior or mid-cervical and posterior cervical ribs. This interpretation is based on the fact that the two heads are very close together (3 to 4.5 mm) in one pair (Fig. 50A and B) and much more widely separated (15 mm) in the second pair (Fig. 50C and D). The capitulum of each is sub-oval in shape, rugose in texture and relatively large—several times larger than the tuberculum. In these features, they correspond to the size, shape, texture and spacing of the parapophyses and diapophyses of several vertebrae which I have interpreted as anterior or middle cervicals and posterior cervicals.

In the anterior cervical ribs (Fig. 50A and B) the capitular and tubercular heads are close together, but separated by a deep longitudinal channel that is circular in section and that continues as a medial concavity on the inner surfaces of the anterior and posterior (distal) processes. The stout capitular

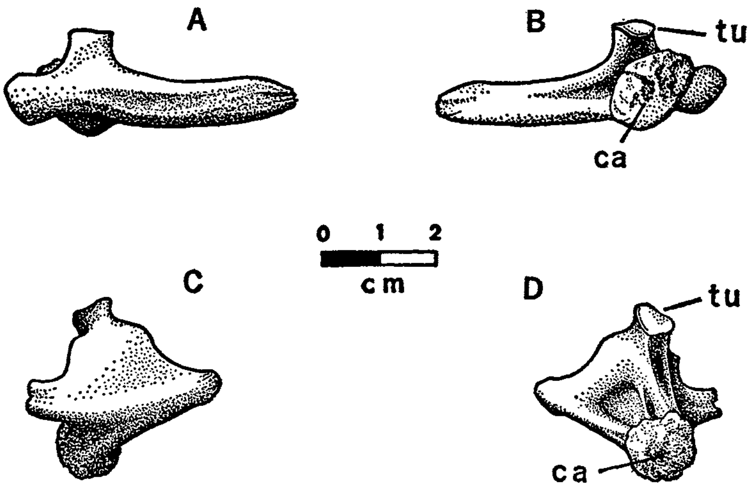


FIG. 50. Cervical ribs of *Deinonychus antirrhopus* (YPM 5210). An anterior cervical rib in lateral (A) and medial (B) views. A posterior rib in lateral (C) and medial (D) views. Abbreviations: ca—capitulum; tu—tuberculum.

and tubercular pedicels form a C-shaped structure in transverse section. Its concave inner surface has a single, small, deep pit facing posteriorly at the base of the pedicels. A short, irregular process extends forward approximately 10 mm beyond the tuberculum and the main shaft. A parallel-edged, medially concave blade extends to a posterior termination, rounded and striated, some 33 mm behind the tuberculum. The capitular process is nearly round in section and flares slightly at its extremity. The tubercular process is a compressed oval in section and is not expanded at its termination.

Closely associated with these ribs was another pair of quite different cervical ribs (Fig. 50C and D). These are distinctly triangular in shape, rather than elongated blades, with short (5 mm), irregular, anterior processes and longer (18 mm), triangular, posterior extensions. The capitulum and tuberculum are more widely separated (15 mm) and the latter is only about half the size of the former. These features correspond most closely with a cervico-dorsal vertebra, suggesting these are probably posterior cervical ribs, perhaps the eighth or ninth. Again, the capitular surface is strongly rugose, indicating that the entire cervical rib series were immovably united by digitate sutures with the cervical vertebrae. The external rib surface is moderately convex, the inner surface is strongly concave and is sculptured by a number of deep excavations at the base of the tubercular process and across the triangular posterior extension. When articulated with their respective vertebrae, these cervical ribs trended down and backward, parallel and close to the lower lateral surfaces of the centra. Posterior processes may have overlapped the short anterior process of the rib behind in the anterior half of the cervical series, but any such overlap was of limited extent—probably much less than that of modern crocodilians, and certainly far less than was characteristic of larger theropods.

The apparent correlation of long necks with short cervical ribs, and short necks with long cervical ribs tempts me to conjecture about relative degrees of flexibility and functional significance of the two kinds. But suffice it to say that although the *Deinonychus* cervical series does not seem to have been of unusual length, it clearly was quite flexible, particularly in the vertical plane.

THORACIC RIBS

As with the cervical ribs, identification of the dorsal ribs is based on vertebral evidence—the spacing, shapes and relative positions of the parapophyses and diapophyses. The number of thoracic ribs is unknown, but assuming 14 dorsal vertebrae it is probable that all bore ribs. A total of 9 left and 12 right thoracic ribs are known, plus numerous fragments. These belong to at least two individuals.

Fig. 51A shows what probably represents the first thoracic rib. It is totally different from any cervical rib and its curvature, short length and the relative positions of the two heads show it to be an anterior thoracic. The capitular and tubercular surfaces are widely separated (30 mm) and lie one above the other in a vertical plane. They are subequal in size, but the tubercular surface is more elongate and oval, whereas that of the capitulum is nearly round. Both are smooth in texture, rather than rugose, indicating greater mobility against the vertebra than appears to have been true of the cervical ribs. The capitular process is the longer and more robust of the two processes, and projects down and inward at nearly a right angle to the main rib shaft. In articulation, the capitulum extended inward to fit into the cup-like facet on the parapophysis. The tuberculum above and lateral to it articulates against the under side of the diapophysis extremity. The main shaft curves out and downward from the diapophysis. Proximally, the dorsal aspect of the shaft is raised into a thin, caudally reflected crest or ridge, which gradually diminishes distally. At mid-length the shaft is nearly oval in section; distally it terminates in a sharp tapered point with no evidence of articular contact or cartilaginous connection with a sternum or sternal ribs. Total length from tuberculum to the distal termination is 101 mm.

Posteriorly, the expected changes occur in the rib series. Successive ribs are longer, at least to the vicinity of the eighth to tenth dorsal (Fig. 51B). The capitular process becomes shorter, but no less robust, and capitular and tubercular facets are more closely spaced. In correspondence with changes in vertebral structure, the tuberculum shifts from a position above and lateral to the capitulum to a position well posterior and only slightly above the capitulum. The capitulum-tuberculum plane thus rotates from a vertical orientation at the first dorsal to one of 45° at mid-dorsal, and a nearly horizontal position at the last dorsal.

In the longest ribs available, presumably from near the middle of the series, the capitular process is still the longest and most robust of the two, is oval in section and passes medially into a thin lamina of bone extending between the two heads. The capitular surface is convex, oval and smooth. The tubercular surface is slightly smaller than the capitulum and is concave and oval. When in articulation the capitular process extends down and forward to fit into the cup-like facet of the parapophysis, the tuberculum articulating with the lateral extremity (not the underside) of the diapophysis. The rib shaft curves out and

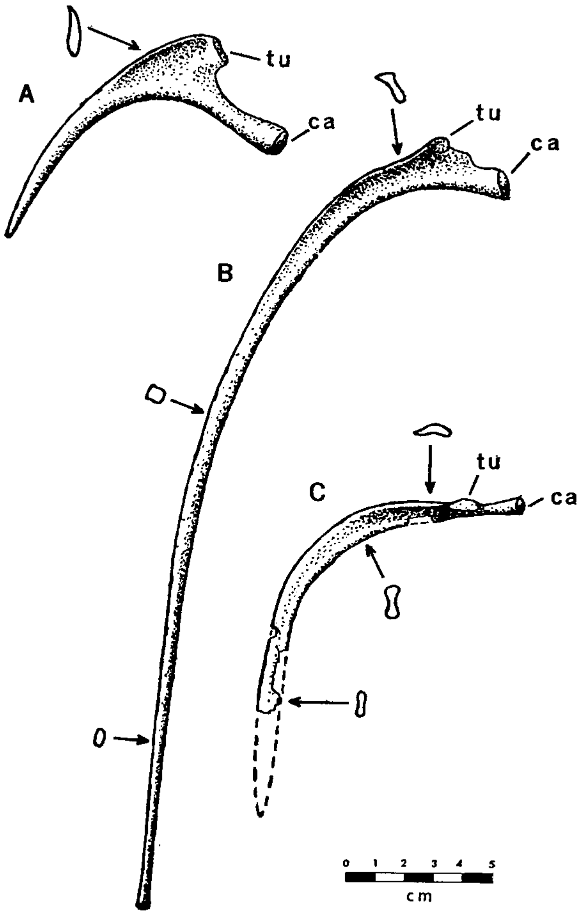


FIG. 51. Dorsal ribs of *Deinonychus antirrhopus* in posterior view. A) an anterior rib (YPM 5245); B) mid-dorsal rib (YPM 5249); C) posterior dorsal rib (YPM No. 5249). Arrows indicate location of cross sections. Abbreviations: ca—capitulum; tu—tuberculum.

down from the latter articulation. Proximally, the shaft is almost T-shaped, being expanded externally to form slight anterior and posterior "shoulders" that surmount the main shaft. This superficial expansion of the shaft diminishes distally until at mid-length only a faint groove remains on the anterior surface. The distal half of the shaft is oval in section, the greatest diameter being longitudinal, not transverse. The maximum rib length known is 300 mm, measured along the curve of the shaft from tuberculum to distal termination. Of the long ribs, six are preserved intact, with expanded distal ends that show an osseous articulation existed between the dorsal and sternal ribs.

A number of incomplete, short ribs are among the materials from the Yale site. Some of these might be from a juvenile, but on the basis of the relationship of the two heads, and in the absence of any other evidence of immature individuals at this site, I have concluded that these must represent the last thoracic ribs (Fig. 51C). One of these, from which the extremity is missing, measures 49 mm in length (from the tuberculum) and probably did not exceed 60 mm. A second rib is nearly twice as large in most dimensions and may have exceeded 100 mm in length. In a pair of slightly larger ribs (YPM 5241) the incomplete length (along the shaft curve) measures 130 mm. All of these are similar in form, but quite distinct from those previously described. First, the two heads are closer together (16 mm in the largest) and occur in a horizontal plane. The shaft projects outward, apparently nearly horizontally, and then swings sharply downward perpendicular to the capitulum-tuberculum plane. Proximally, the shaft adjacent to the heads is slightly expanded externally to form the T-shaped cross section, but this expansion abruptly diminishes distally and the shaft section has the shape of a compressed figure 8, with the transverse dimension approximately three times that of the fore-aft dimension. The distal extremity is not known. The capitular surface is convex, oval, smooth and slightly larger than the tubercular surface, which is concave and oval. In the absence of well preserved posterior dorsal vertebrae, the relationships of these processes to the vertebra are not known. Clearly, the capitulum fit into a cup-like articulation, but whether this occurred on a pronounced pedestal-like parapophysis is not known. The tuberculum appears to have contacted the lateral extremity of a relatively short diapophysis.

STERNAL RIBS AND GASTRALIA

In modern crocodilians there are two distinct series of ventral, transverse, rod-like elements that resemble the dorsal ribs. The more anterior series consists of lateral and ventral cartilaginous segments that connect the ventral extremity of each dorsal rib with the sternum or xiphisternum. Both segments are commonly calcified in crocodilians. These cartilages are properly referred to as abdominal or sternal ribs, the lateral element as the lateral or intermediate rib segment and the ventral part as the sternal rib segment.

Posterior and superficial to the sternal ribs is a series of similar, rod-like structures which are dermal in origin, are rarely, if ever, calcified and do not contact either the sternum or any of the dorsal ribs. These are gastralia (although they have been called abdominal or ventral ribs by many authors) and in crocodilians are composed of pairs of long lateral and short median elements which are joined by overlapping rather than end-to-end contacts. *Crocodylus* has 10 pairs of abdominal ribs and 7 pairs of gastralia (Romer, 1956: fig. 141).

Gastralia have been reported in several theropods (*Tyrannosaurus, Gorgosaurus, Albertosaurus, Struthiomimus* [= *Ornithomimus*] and *Allosaurus*) although in all instances these have been identified and described as abdominal ribs. Ossified sternal or true abdominal ribs, on the other hand, apparently are not known in theropods; at least they have not been reported before.

A variety of rib-like bones found at the Yale site indicates the probable presence of a ventral cuirass in *Deinonychus*. At least four distinct types of rib-like elements, all of which are readily distinguished from dorsal ribs, are represented by as many as 8 or 10 examples each. Three of these are paired, being represented in the collections by both left and right elements, and the fourth quite probably was paired also. The four kinds are of two basic types: 1)

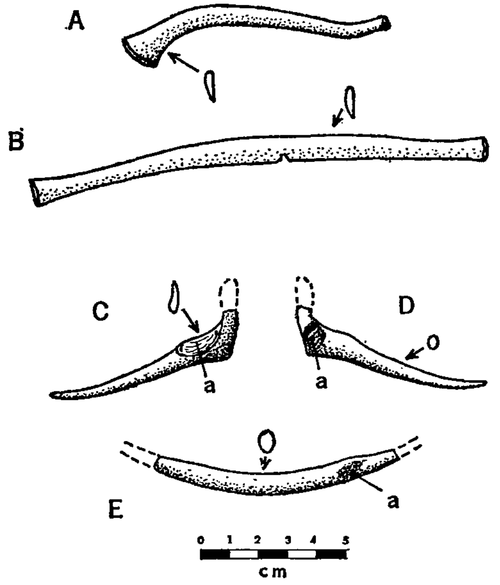


FIG. 52. Probable ventral "ribs" of *Deinonychus antirrhopus;* true abdominal or sternal ribs (A and B) (YPM 5246) and segments of gastralia (C, D and E) (YPM 5247), A is considered a lateral segment and B the sternal segment of a sternal rib. C and D illustrate a medial segment of a gastralia "rib" in ventral (C) and dorsal (D) views. E is interpreted as a probable lateral segment of a gastralia "rib" in ventral view. Articular scars are designated as "a."

flattened rods with expanded articular surfaces at each end (Fig. 52A and B), and 2) curved, tapered rods with appositional or articular scars on one or two sides, but with no evidence of terminal articulations (Fig. 52C, D and E). The former are believed to be fully ossified sternal ribs and the latter gastralia.

Osborn (1906) in his description of *Tyrannosaurus,* was the first to record the occurrence of "abdominal ribs" in theropodous dinosaurs. But the structures described (see his fig. 12) are almost certainly gastralia and not ventral extensions of the dorsal ribs. This is indicated by the overlapping, rather than end-to-end, contact of left and right elements, and by their asymmetrical form. The gastralia of *Tyrannosaurus* appear to have consisted of a series of long, tapered, lateral elements, some of which co-ossified into V-shaped, asymmetrical median bones. The lateral elements probably occurred in pairs, apparently not mirror images of each other, and were joined by overlapping contact at the mid-line.

Similar abdominal ossifications were reported by Lambe (1917) in *Gorgosaurus* and by Parks (1928) in *Albertosaurus.* Lambe and Parks also referred to these as "abdominal ribs," but again they appear to be gastralia. Lambe reconstructed the series as extending from the sternum to the pubes and consisting of paired median ventral bones overlapping at the mid-line, and short, tapered lateral bones overlapping the lateral extremities of the previous element. He also described two fragmentary bones that appear to be co-ossified left and right median elements (as in *Tyrannosaurus*), which he interpreted as the first and last abdominal ribs (Lambe, 1917: fig. 27).

Osborn (1917) also described "sternal ribs" in *Struthiomimus* (= *Ornitho-*

mimus) equating "at least thirteen rows" with the thirteen thoracic ribs (of which he could only see eleven). He interpreted these as composed of a triple series on each side (Osborn, 1917: fig. 6 and pl.XXVI) of short, slender "proximal" bones, slender "median" bones about twice as long as the proximal element, and a stout "ventral" bone about three times as long as the proximal element. The latter terminated in club-like expansions at the mid-line. It is evident in Osborn's specimen (AMNH 5339) and in his illustrations that these triplets overlapped one another, as in *Gorgosaurus.* It is also evident that, contrary to Osborn's opinion, there is neither numerical nor spatial correspondence with the 11 preserved dorsal ribs. This is verified by other ornithomimid specimens, *Struthiomimus currelli* (ROM 851) and *S. ingens* (ROM 852) (=*Ornithomimus*), as shown in Plates I and V of Park's 1933 report. In addition, these specimens show that these structures are best developed and apparently concentrated in the abdominal region immediately anterior to the pubes and diminishing forward toward the region of the sternum. On these grounds, I believe them to be gastralia and not true sternal ribs.

The triple nature of the above structures is unlike that described in *Tyrannosaurus* or *Gorgosaurus,* but it resembles the condition reconstructed by Gilmore (1920) in *Allosaurus.* Gilmore noted "double abdominal ribs" (as in *Tyrannosaurus*) but he reconstructed the ventral cuirass as composed of a series of transverse "ribs" consisting of three or four segments on each side of the mid-line or on each side of a single, V-shaped median bone (Gilmore, 1920: figs. 38 and 39). In light of the triplet design of the gastralia in *Ornithomimus,* it appears that Gilmore's reconstruction is probably correct, but I suspect that some of the elements preserved in his specimens (USNM 4734 and 8367), specifically those illustrated as C and D in Figure 38 (Gilmore, 1920), are parts of sternal ribs, rather than gastralia.

Is it possible to distinguish between gastralia and true sternal ribs if the elements are disarticulated? A very distinct difference exists in *Crocodylus* and *Alligator.* Sternal rib segments articulate with each other and the sternum or the dorsal rib by end-to-end contacts. Gastralia segments contact each other by overlapping contacts only. The *Deinonychus* material includes both of these types.

STERNAL RIBS

The two types of rib-like bones which I interpret as sternal rib segments (Fig. 52A and B) are represented by a minimum of five examples each from the Yale *Deinonychus* site. The shorter of the two (Fig. 52A) is strongly flattened, slightly curved perpendicular to the plane of flattening and is distinctly sinuous in the plane of flattening. One end is greatly expanded and moderately rugose, as though for cartilaginous contact with another element. The other end is only slightly expanded, but has a similar rough surface, apparently for cartilaginous contact with another bone. In the terminal articulations and in the curvature, both perpendicular and parallel to the plane of flattening, this bone is similar to the intermediate or lateral segment of the sternal rib in *Crocodylus,* and I have so interpreted it.

The long element (Fig. 52B) is similarly flattened, but is subequally expanded at both ends and is significantly longer than the preceding bone. Moreover, unlike the previous bone, the curvature is most pronounced perpendicular to the plane of flattening. This bone is strikingly similar to the medial or sternal segment of the sternal rib in *Crocodylus* and accordingly has been so interpreted.

In the absence of articulated material, I am unable to establish the precise relationships between the dorsal ribs, sternal rib segments and sternum, but upon comparison of the relative sizes and shapes of the rib ends I suggest that the small end of the intermediate sternal rib segment (Fig. 52A) articulated with the extremity of the dorsal rib. One end of the bone interpreted as the sternal segment (Fig. 52B) is flatter than the other and probably contacted the expanded end of the intermediate segment. Figure 53 illustrates the restored transverse section of the rib cage at about the fifth or sixth dorsal vertebra in accordance with these interpretations.

No estimate as to the number of sternal ribs is possible with the existing material. At least one or two anterior dorsal ribs appear not to have had any osseous connections with the sternum (Fig. 51A). Posterior dorsal ribs probably lacked sternal segments also.

GASTRALIA

The presence of gastralia in *Deinonychus* is indicated by numerous, asymmetrical, tapered and curved, rod-like bones apparently free of terminal articular surfaces. Most of these bear one or two articular scars (as in Fig. 52C, D and E) some distance from either end. These scars are comparable to those figured by Lambe (1917: figs. 25 and 26) and Gilmore (1920: fig. 38E) as well as the contacts of gastralia segments in *Crocodylus* and *Alligator.*

The shortest segment apparently was L-shaped when complete, is slightly compressed and bears two distinct scars on opposite sides close to the angle. The stout end is not complete in any of the material available but it appears to have been blade-like. The opposite end tapers uniformly to a point, is oval to round in section and smooth in texture, showing no sign of muscular or bony contact. Both left and right elements are present, but positive pairs have not been recognized. Some bear a prominent boss at the apex of the angle, perhaps for contact with its opposite, but this feature is absent on most specimens. The positions of the two scars suggests an overlapping of each element with those in front and behind, probably close to the mid-line. The irregular presence of a third articular scar suggests that not all members of the gastralia series met at the mid-line. Chiefly on the basis of the multiple appositional scars, I consider this to be the medial segment of a gastralia element.

A large number of curved, doubly tapered, oval to round rod-like elements, some of which bear a single, poorly defined appositional scar, (as in Fig. 52E), were scattered throughout the Yale quarry. None are complete and most are not worthy of further consideration. Those which bear the presumed articular scar may represent lateral segments of the gastralia that overlapped median segments in the manner illustrated by Lambe (1917) and Gilmore (1920), but this cannot be confirmed at present.

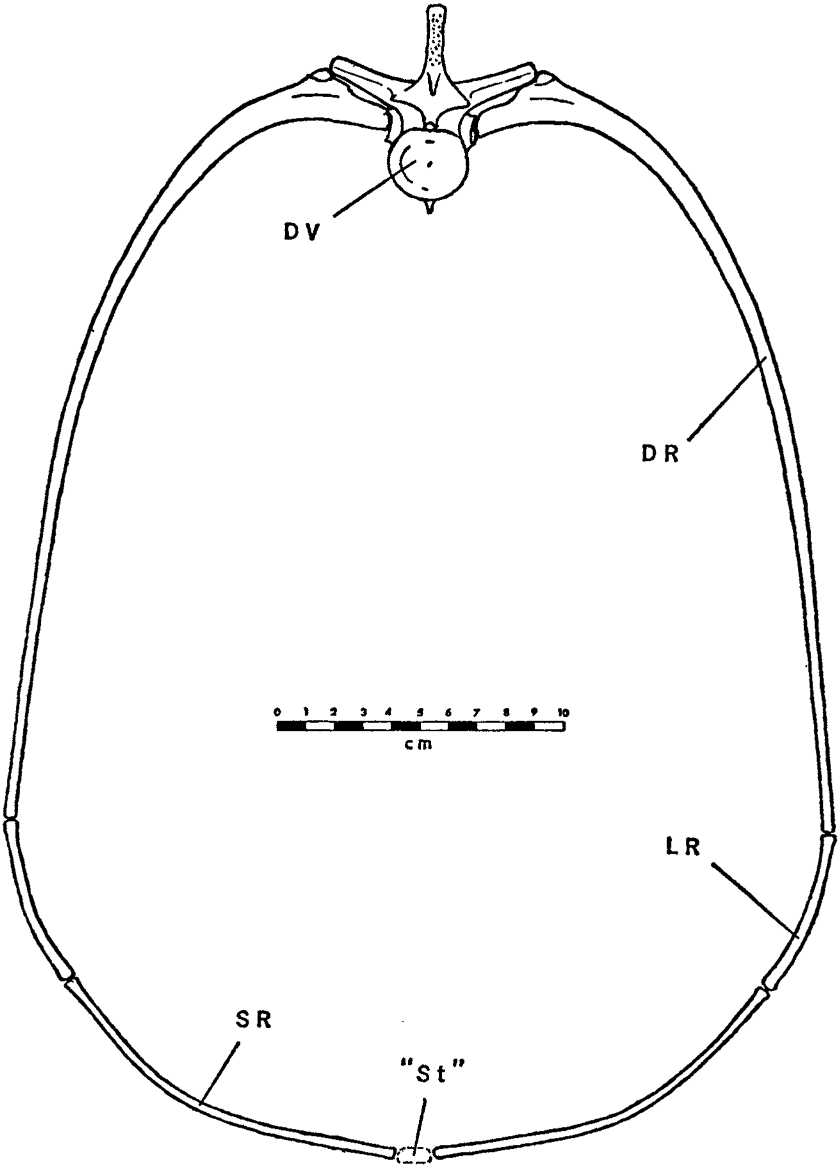


FIG. 53. A restored transverse section of the trunk of *Deinonychus* at about the sixth dorsal vertebra, showing the unusually deep thoracic region and hypothesized relationship of lateral and sternal segments (Fig. 52A and B) to the dorsal ribs. Abbreviations: DV—dorsal vertebra; DR—dorsal rib; LR—lateral segment of sternal rib; SR—sternal segment of sternal rib; "St"—sternum.

APPENDICULAR SKELETON: PECTORAL GIRDLE AND FORELIMB

Contrary to what might be described as the general condition in "carnosaurs," the forelimb and manus of *Deinonychus* are relatively large—in fact, the manus is much longer, relatively, than in any other theropod with the possible exception of *Ornithomimus*. The total length of the forelimb and manus is more than 700 mm, or much more than twice the length of the skull (approximately 320 mm). *Allosaurus* (USNM 4734) with a skull length of 605 mm has a forelimb-manus length of 948 mm. The manus is significantly longer than the humerus or the radius-ulna, and is nearly as long (300+ mm) as the skull (320 mm). In general, the manus is most similar to that of *Ornitholestes*, although much larger and more robust. It is tridactyl and without any indication of digits IV and V. The large unguals and the extreme development of flexor tubercles indicate that the manus was a powerful grasping structure, probably adapted for predation.

Pectoral Girdle

SCAPULA

Both scapulae are preserved in AMNH 3015, the left being nearly complete (Fig. 54 and Table 6). Although the extremity of the blade is missing in both, so that the maximum scapular length is not known, there is no evidence that the blade is expanded distally as in *Allosaurus* and *Tyrannosaurus*. The scapular blade is long but very slender (maximum width equals 23.5 mm) with the inferior and superior margins almost perfectly parallel. Proximally, it is robust (16 mm thick) and oval in section, but it becomes thinner (6 mm) and more blade-like distally. Both lateral and medial surfaces are convex across the width of the blade, but along its length it is strongly curved in the transverse plane conforming to the curvature of the rib cage. Proximally the scapula is expanded both transversely and longitudinally to a maximum transverse thick-

TABLE 6. Measurements (in millimeters) of the scapulae of *Deinonychus antirrhopus* (AMNH 3015)

	Left	Right
Maximum length	190*	—
Maximum blade breadth	23.5	25.0*
Least blade breadth	21.5	—
Maximum blade thickness	17.5	16.0

* = approximate.

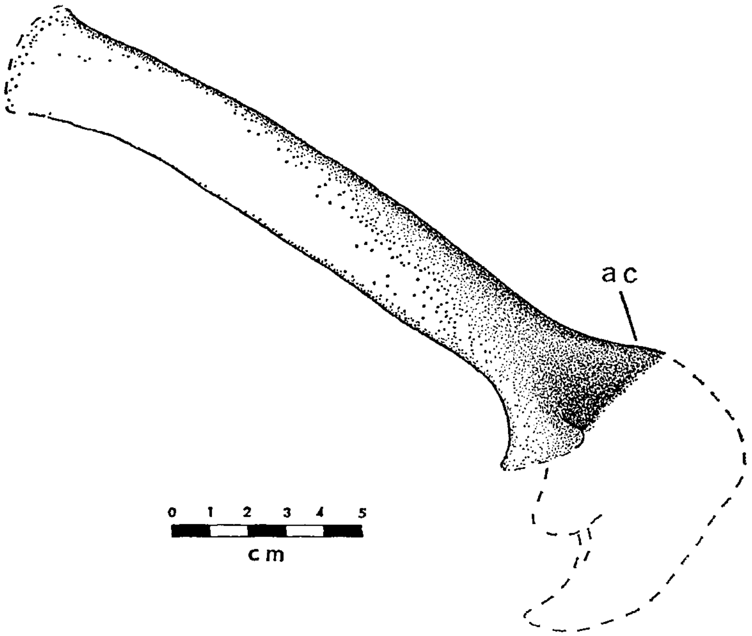


FIG. 54. Right scapula of *Deinonychus antirrhopus* (AMNH 3015) in lateral view; ac—acromial process or deltoid border.

ness of 18.5 mm and a fore-aft length of 46 mm at the upper margin of the glenoid. The acromial process or deltoid border is not greatly expanded anteriorly. Although imperfectly preserved, the glenoid appears to have been an unusually deep notch, the orientation of which can only be approximated, but which appears to have faced anteroventrally and outward. Presumably the scapulo-coracoid suture passed through its center.

In general, the scapula is most like that of *Ornithomimus* with its long, narrow, parallel-edged blade. It differs from the typical theropod scapula in the apparent absence of any significant distal expansion of the blade and the unusually small size of the acromial process (deltoid border) above and anterior to the glenoid. Both of these features may be correlated with reduction of the scapular deltoid musculature which in part is involved with humeral extension (recovery).

CORACOID

Only a small part of the left coracoid is preserved in AMNH 3015, representing the ventral margin of the glenoid. No other evidence exists pertaining to its size, shape or the nature of its junction with the scapula.

FORELIMB

HUMERUS

Both humeri are known in AMNH 3015, although neither is complete.

Portions of the shaft and the deltopectoral crest are missing from the left humerus and most of the crest is absent in the right. Nevertheless, the general form and major dimensions can be obtained (Figs. 55 and 56). The humerus, which is relatively long and slender, is much less robust than that of *Allosaurus* and compares most closely with that of *Coelurus* (YPM 2010) except that the deltopectoral crest and the internal tubercle are much more strongly developed in the present genus (Fig. 57). The shaft is slightly curved (concave anteriorly), comparable to the curvature indicated by Osborn (1917: fig. 7) for *Struthiomimus* (= *Ornithomimus*) and less than that of *Allosaurus*. The shaft is long and slender, subcircular in section over most of its length and, like all other limb bones of *Deinonychus*, is hollow. Proximally it expands abruptly into a thin but very prominent forward projecting ridge, the deltopectoral crest. As in most theropods, this crest is restricted to the proximal third of the humerus and is situated along the external side of the anterior aspect of the shaft. The apex is approximately 7 cm below the head and projects forward approximately 2.5 cm from the shaft almost perpendicular to the long axis of the humeral head.

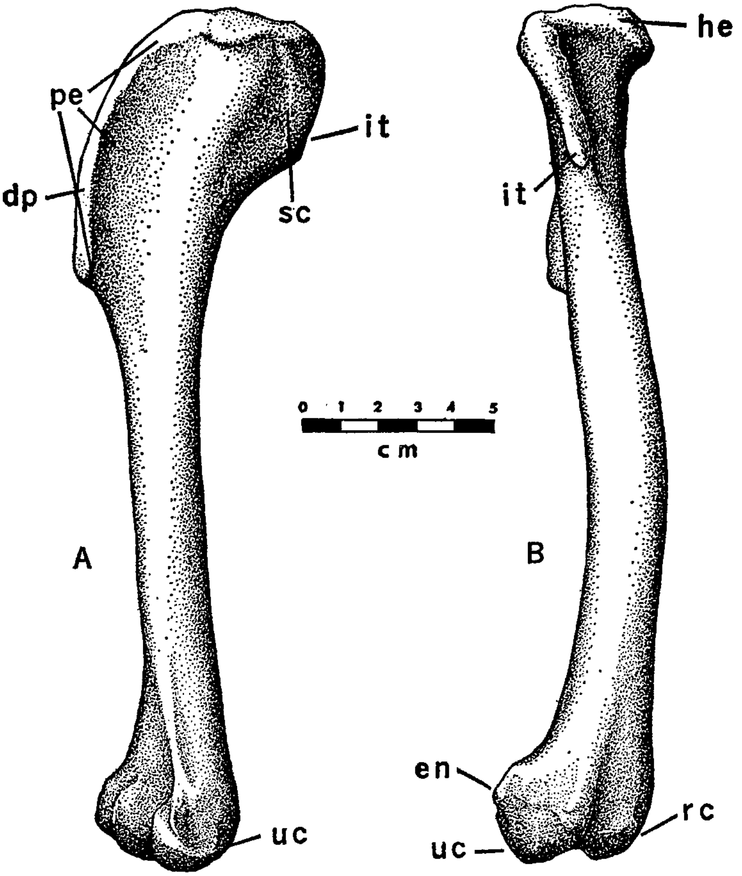


FIG. 55. Right humerus of *Deinonychus antirrhopus* (AMNH 3015) in medial (A) and posterior (B) views (reconstructed from both humeri.) Abbreviations: dp—deltopectoral crest; en—entepicondyle; he—humeral head; it—internal tuberosity; pe—probable area of insertion of the M. pectoralis; rc—radial condyle; sc—probable insertion area of the M. subcoraco-scapularis; uc—ulnar condyle.

Its distal-proximal length is relatively greater than in other theropods and the extent of its projection out from the shaft is unusual. These features may be equated with the large size of the several muscles that inserted on its inner and outer surfaces: the M. pectoralis and coracobrachialis on its inner aspect, and the clavicular portion of the deltoid and the M. brachialis and humero-radialis on the outer surface. The pectoralis and coracobrachialis are the major adductors (flexors) and long axis rotators (medial rotation or pronation) of the humerus. The M. deltoid is the principal extensor or recovery muscle of the humerus (swinging the humerus forward) and external rotator or supinator. The M. brachialis and humero-radialis are flexors of the forearm.

It is not possible with the present material to map out the respective insertion areas of the pectoralis and coracobrachialis, but the unusual projection of the deltopectoral crest must have provided greater than usual leverage for medial humeral rotation. Similarly we can correlate the somewhat greater than usual distal-proximal length of this crest with increased leverage for humerus adduction. Both capacities would be important in a raptorial forelimb and the above features correlate well with other unusual features of the forelimb.

The outer surface of the deltopectoral crest is marked by a conspicuous, broad ridge that sub-parallels the distal margin of the crest (Fig. 56). This ridge is the only feature that can be correlated with the external muscle attachments on the deltopectoral crest, and it is presumed to separate the origin area of the M. brachialis (marginal) from that of the humero-radialis (posterior), as shown in Figure 56B. The insertion of the clavicular portion of the deltoid must have occupied the remainder of the external crest surface above this ridge.

The M. brachialis and humero-radialis are the principal flexors of the forearm in lizards and crocodilians and it is presumed that they had the same function in *Deinonychus.* It cannot be demonstrated that the external ridge at the base of the deltopectoral crest marks the insertion sites of these muscles. But if it does, the prominence of the ridge and crest (compared with other theropods and with reptiles in general) would indicate that these muscles were unusually large. This in turn suggests unusually powerful forelimb flexion. Again, forearm flexion is a critical faculty in a raptorial forearm and in view of the other unusual adaptations of the forelimb of *Deinonychus,* I believe the above interpretation is reasonable.

A prominent internal tuberosity projects backward from the inner posterior surface of the humeral head as a short, rugose crest. Although much shorter and less expanded than the deltopectoral crest, this feature is considerably more developed than in any other theropod. Presumably this internal tuberosity provided attachment for the M. subcoracoscapularis on its medial surface and the M. scapulohumeralis posterior on its external surface, as in modern crocodilians. The normal function of these muscles is to adduct the humerus and rotate it laterally (supination). The crest of this ridge is rugose and expanded transversely, indicating that whatever muscles attached here were of moderate size. The extent to which this ridge projects from the humeral shaft is a measure of the significant leverage it provided for humeral rotation.

Whereas the reduced scapular blade and acromion process suggest a reduced mass for the scapular and clavicular deltoid (which typically insert on the

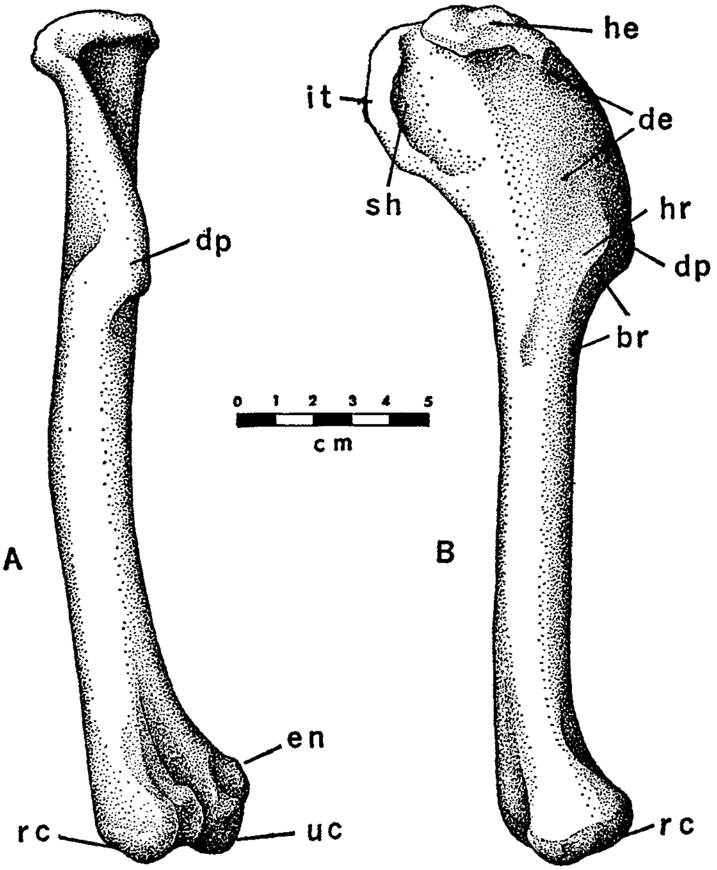


FIG. 56. Right humerus of *Deinonychus antirrhopus* in anterior (A) and external (B) views. Abbreviations: br—probable origin area of the M. brachialis; de—probable insertion area of the deltoid; dp—deltopectoral crest; en—entepicondyle; he—humeral head; hr—origin of the M. humeroradialis; it—internal tuberosity; rc—radial condyle; sh—possible insertion area of the M. scapulo-humeralis; uc—ulnar condyle. (Reconstructed from both humeri, AMNH 3015).

external surface of the deltopectoral crest), the relatively enormous size of the deltopectoral crest indicates the presence of very powerful pectoralis and coracobrachialis muscles for flexion and long axis medial rotation (pronation) of the humerus. The humeral head (and the glenoid) are too imperfectly preserved to indicate much about the articular movements possible at this joint, but the crests described above clearly establish the importance of humeral adduction, flexion *and rotation.* In addition, the conspicuous external ridge along the distal base of the deltopectoral crest indicates the probable existence of ususually powerful flexors of the forearm. In all probability these features were adaptations increasing the mobility and power of the forelimb for catching and holding prey.

Distally, the humerus shaft is expanded transversely into the usual double condyle, the outer or radial condyle being the larger of the two. The two condyles are separated by a well-developed fore-aft groove. The limits of the articular capsule are preserved in part and show that the articular surfaces extended well onto the anterior surface, but were restricted posteriorly, although full extension of the forearm appears probable. The ulnar condyle is a little more than half the size of the radial condyle and is sharply convex both transversely and longitudinally, forming a somewhat elongated ball-like surface. The long axis of the ulnar condyle roughly parallels the plane of the inner tuberosity above. The radial condyle appears to have a similar though larger form, but its axis of elongation is at some 30° to that of the ulnar condyle and is nearly parallel to the plane of the deltopectoral crest. The significance of these two parallelisms is not known. The greatest width of the distal end (across the two condyles) coincides with the greatest dimension of the head and is nearly perpendicular to the plane of the deltopectoral crest.

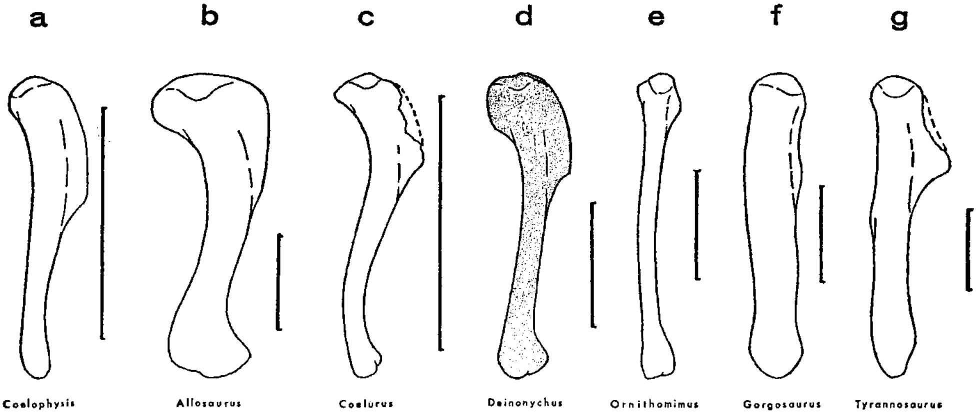


FIG. 57. Comparison of the left humeri of several theropods as seen in medial view (anterior is to the right). All are drawn to unit scale to emphasize relative robustness and dimensions of the deltopectoral crest and the internal tuberosity. All vertical lines = 10 cm. A) *Coelophysis longicollis* (AMNH 7224), (right humerus reversed); B) *Allosaurus fragilis?* (YPM 1894); C) *Coelurus agilis* (YPM 2010); D) *Deinonychus antirrhopus* (AMNH 3015); E) *Ornithomimus altus* (AMNH 5201), (right humerus reversed); F) *Gorgosaurus libratus* (NMC 2110), (right humerus reversed); G) *Tyrannosaurus rex* (AMNH 972), (right humerus reversed).

The ectepicondyle is represented by a faint ridge at the external anterior border of the radial condyle. The entepicondyle, on the other hand, exists as a small, but conspicuous knob medial and slightly above the antero-internal limit of the ulnar condyle (Figs. 55B and 56A). This feature is clearly separated from the articular capsule and is far more prominent than in any other theropod with which I am familiar. It seems reasonable to equate the greater than usual prominence of the entepicondyle with a relative increase in the power and importance of the flexors of the carpus and hand.

ULNA

The radius and ulna are well represented in the American Museum and Peabody Museum collections. Both left and right elements are nearly complete in AMNH 3015. The left radius and ulna and a partial right radius are preserved in YPM 5206, the complete left radius and ulna and right ulna are present in YPM 5220, and a nearly complete left ulna probably belonging to YPM 5206 has been catalogued separately (YPM 5230) because of its isolated position in the quarry.

The ulna (Fig. 58) is moderately robust with strongly expanded proximal and distal ends and is about 80 percent as long as the humerus. Except that it is more markedly curved, the ulna is similar in overall proportions to that of *Ornithomimus* (Osborn, 1917). The shaft is hollow and subcircular in section near midlength but becomes distinctly oval proximally and triangular distally. Except near the extremities the shaft is subequal in diameter along its length. The shaft is moderately curved, convex posterolaterally or away from the radius.

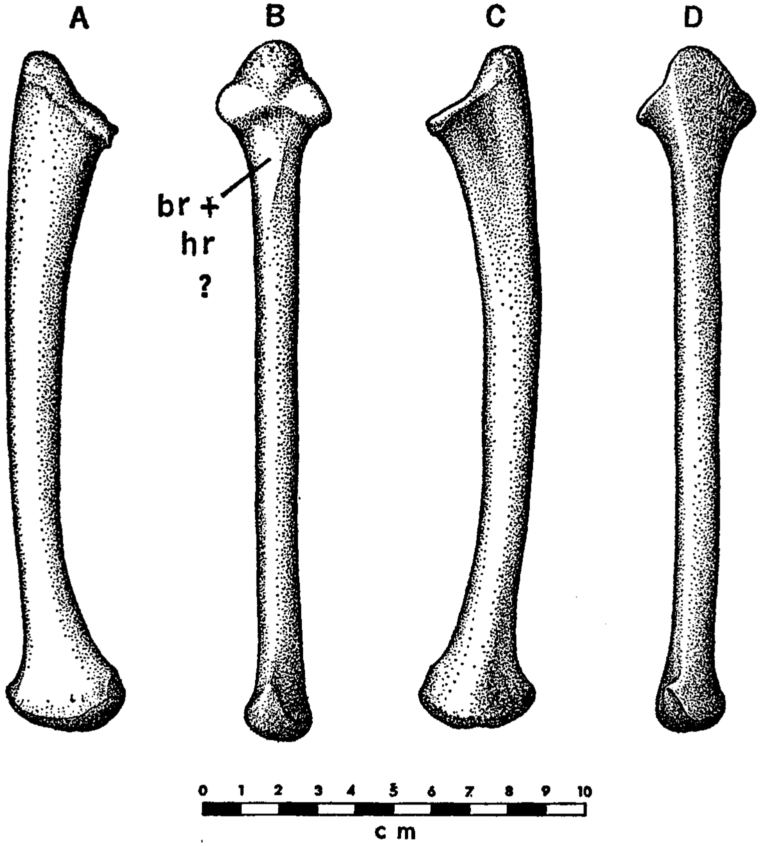


FIG. 58. Left ulna of *Deinonychus antirrhopus* (YPM 5220) in medial (A), anterior (B), lateral (C) and posterior (D) views; br + hr? possible insertion areas of the M. brachialis and M. humeroradialis.

The proximal articular surface is inclined (toward the radius) with respect to the shaft and is nearly flat, with very finely rugose texture. The latter could mean the cartilaginous articular pad was thin. The surface is triangular in shape with a slight concavity marking the radial margin. No olecranon is preserved, but due to the inclination of the articular surface, the external margin projects above the medial border of the facet. A distinct scar marks the limits of the cartilagenous pad. The gentle concavity representing the appositional surface for the radius gives way distally to a robust, short ridge which probably marks the attachment site of muscles—possibly the M. brachialis or humeroradialis or a pronator or supinator of the forearm.

The distal extremity is expanded anteroposteriorly but compressed lateromedially, forming a slightly asymmetrical, rounded distal condyle of compressed oval shape as seen in end view. Again the limits of the articular capsule are clearly demarked as a distinct angulation separates the slightly roughened texture of the extremity from the smooth surface of the shaft. A distinct rugose lip along the posterior part of the medial edge of the distal surface marks the probable site of the distal radio-ulnar ligament.

TABLE 7. Measurements (in millimeters) of the fore limb of *Deinonychus antirrhopus*

	AMNH 3015		YPM 5220		YPM 5206	YPM 5230
	Left	Right	Left	Right	Left	Right
HUMERUS:						
Length	227.0	237.0*	—	—	—	—
Distal transverse width	42.0	42.1	—	—	—	—
Proximal transverse width	36.0	41.0*	—	—	—	—
Width across delto-pectoral crest	43.5	—	—	—	—	—
Least diameter of shaft	18.0	18.2	—	—	—	—
ULNA:						
Length	—	186.0	180.0	174.2	—	—
Greatest distal transverse width	32.0	28.3	30.0	30.0	35.3	35.5
Greatest proximal transverse width	29.6	31.2	28.2	29.0	35.0	34.1
Least diameter of shaft	—	11.8	10.9	10.6	13.0	13.2
RADIUS:						
Length	172.0*	—	172.0	—	176.5	—
Greatest distal transverse width	23.8	—	21.4	—	24.9	—
Greatest proximal transverse width	—	20.6	20.2	—	23.6	—
Least diameter of shaft	8.7	10.0	9.0	—	9.3	—

* = approximate.

RADIUS

The radius is a nearly straight, cylindrical and hollow shaft only slightly shorter and more slender than the ulna (Fig. 59). Both ends are expanded, the proximal end anteroposteriorly and the distal end transversely. The long and slender form is most like the radial proportions in *Ornithomimus* and quite unlike that of any other theropod. The proximal articular surface is moderately convex, finely rugose and triangular in outline. A distinct line marks the limits of the cartilage pad. The distal condyle is strongly convex and slopes

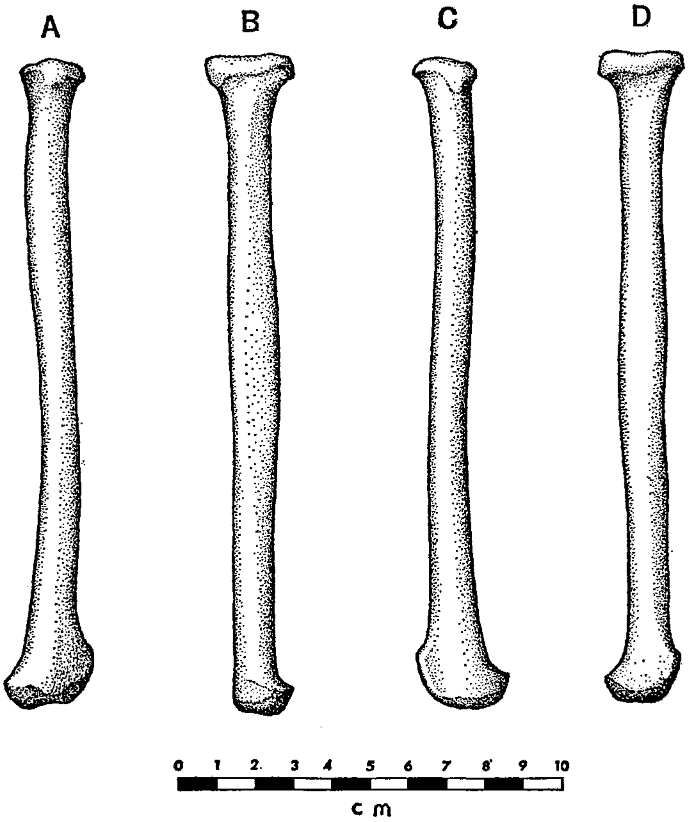


FIG. 59. Left radius of *Deinonychus antirrhopus* (YPM 5220) in medial (A), anterior (B), lateral (C) and posterior (D) views.

away from the ulna. Immediately above the distal articular surface, the shaft is expanded into a prominent lateral boss and a slight, medially placed tubercle. The function of these is not known, but they may have been attachment sites of radio-ulnar or radio-carpal ligaments.

Except for the concave radial margin of the proximal end of the ulna, scars marking appositional contacts between the radius and ulna are not well developed. This might indicate that these elements were not closely juxtaposed and some degree of pronation-supination may have been possible in the forearm. The proximal head of the radius is faintly saddle-shaped and could have permitted some long axis rotation as well as pivoting about the radial condyle of the humerus.

CARPUS

Four distinct types of mesopodials (excluding the astragalus and calcaneum) have been recovered from the three *Deinonychus* sites. Two types were associated with the manus and two with the pes at both the Yale site and American Museum site No. 31-7. It can hardly be claimed that the theropod carpus is well known, but in view of the fact that at least five carpals are known in

Allosaurus (Gilmore, 1920), *Gorgosaurus* (Lambe, 1917) and *Ornithomimus* (Osborn, 1917) and at least four and probably five are present in *Ornitholestes* and *Coelophysis,* it seems unlikely that the carpus of *Deinonychus* could have consisted of only two elements. Yet this appears to be the condition. Five specimens of each of the two known carpals are represented in the present collections. No other possible carpals are represented by even a single specimen. Other carpals may have been present but not preserved, or may have failed to ossify, but the morphology of the two known elements clearly indicates that these two bones alone composed the functional wrist joints. Two (YPM 5208) from the left carpus were collected in contact in what appears to be natural articulation. The nature of their articular facets shows that these two bones articulated directly with the three metacarpals and the epipodials with no intervening ossicles. Subsidiary ossicles may have existed, but these could not have contributed to the joints with either epipodials or metacarpals.

Both carpals (Fig. 60) are well ossified with distinct and highly finished articular facets. Each of the five examples of both kinds is so like the others that they could almost have come from the same mold. These clearly were not just irregular ossifications, but well formed elements with precise articular contacts with adjacent bones designed to permit precise movements of the wrist and hand. These movements are discussed below.

Radiale

The radiale (Fig. 60A-C) is about twice the size of the ulnare with prominent, well-defined proximal and distal articular facets. In proximal view it is subquadrangular in shape with a prominent medial projection. The anteromedial side is nearly flat with an oval area marked by small irregularly placed pits, presumably representing ligament attachments. The posterolateral surface is smaller, nearly semicircular in shape, concave and strongly pitted. The latter probably indicate a strong ligamentous union of the radiale and the ulnare. The proximal surface is saddle-shaped, strongly convex (almost circular in profile) along the long axis of the element but moderately concave across the width. Thus, it has the form of a broad, shallow groove which is strongly arched, reminiscent of the pulley-shaped distal articulations of phalanges (Fig. 60A). Unlike the latter, however, which are usually nearly symmetrical, the present surface is strongly asymmetrical, the radius of the external arc is much shorter than that of the medial arc, thus the external curve approximates 140° of arc whereas the inner curve equals only about 80°. Neither of these curves is perfectly circular, but the external arc approaches it very closely. This asymmetrical pulley-like surface clearly provided a very precise rolling movement of the carpus over the distal extremity of the radius (Fig. 61A and B). The amount of movement must have approximated the average of the two arcs or about 110°, viewed along the axis connecting the centers of the two arcs. However, due to the asymmetry, as the radiale rolls through this angle it also twists laterally (supination). The amount of supination possible at this joint has been estimated at 35° to 45° degrees (the angle between tangents drawn across the lateral and medial limits of the facet) as shown in Fig. 61B. It is particularly significant that the long axis of this articular surface is trans-

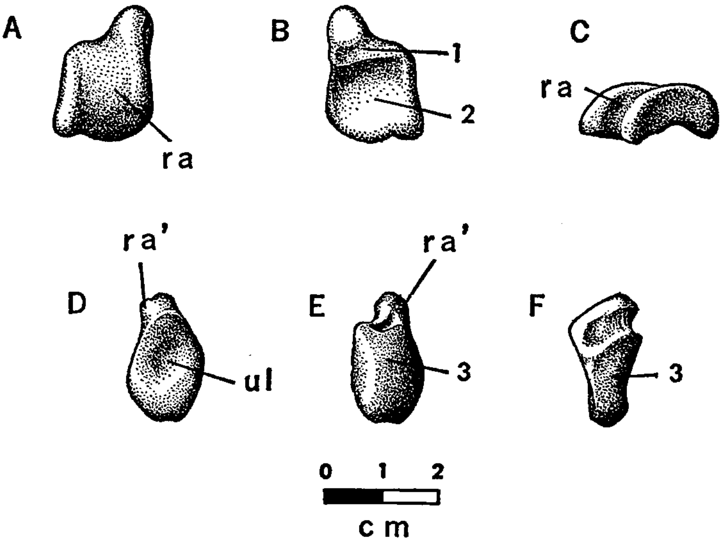


FIG. 60. Right carpalia of *Deinonychus antirrhopus*. Radiale (YPM 5211) in proximal (A), distal (B) and ventral or palmar (C) views. Ulnare (YPM 5228) in proximal (D), distal (E) and ventral or palmar (F) views. Abbreviations: ra—articular facet for radius; ra'—articular "stop" for radius; ul—articular facet for ulna; 1, 2, and 3—articular facets for metacarpals I, II and III.

verse, parallel to the plane of metacarpals I and II. Hence this joint facet produced adduction and abduction rather than flexion or extension of the digits.

From a fully pronated position of the manus, with the digits extending forward and the forearm in horizontal position in a parasagittal plane, the hand could be adducted approximately 50° and abducted nearly 45° from the parasagittal plane. During adduction, the manus supinated approximately 45°. Apparently little or no pronation occurred at this joint when the carpus was abducted beyond the parasagittal position. In other words, all pronation at the wrist occurred during the first phases of abduction from the fully adducted position.

The distal surface of the radiale is divided into two distinct facets separated by a moderate-sized, vertical ridge (Fig. 60B). Both facets are shallow concavities, the medial one being subtriangular in shape and the lateral facet quadrangular. The former is the facet for metacarpal I and the latter for metacarpal II. The two metacarpals fit these facets so perfectly and snugly there appears to have been very little mobility between the radiale and either metacarpal. Although there is no co-ossification, I believe that these three elements operated almost as a single unit.

Ulnare

The ulnare (Fig. 60D–F) is a small, oval-shaped bone, which, like the radiale, appears to have been constant in shape. It is represented by five examples from two of the three *Deinonychus* sites. On the evidence of YPM 5208 (left radiale and ulnare found in contact at the Yale quarry) this bone is reconstructed as lying ventral to the radiale and tightly appressed against the

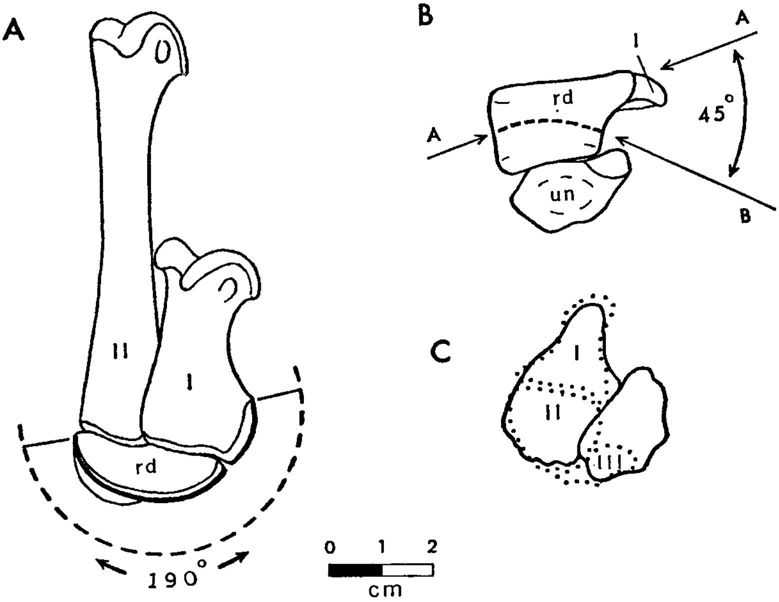


FIG. 61. Outline sketches of the carpus and metacarpus (in part) of *Deinonychus antirrhopus* illustrate the nature of the joints between the carpus and epipodials (A and B) and the carpus and metacarpals (A and C). The dashed arc of A parallels the articular arc (heavy curve) formed by the radiale and the internal proximal part of the first metacarpal. This arc covers 190° ± and produced a wide angle of adduction-abduction of the manus on the epipodials. This adduction-abduction arc was not planar, but curved (twisted) through about 45° during adduction, as is shown in B. The dashed curve of B traces the plane of adduction-abduction from a fully abducted position at left to a fully adducted position at the right. The 45° angle between arrows A and B is the amount of rotation (supination) that occurred during adduction. The dotted lines of C outline the proximal ends of the metacarpals, relative to the two carpals (solid lines). Abbreviations: rd—radiale; un—ulnare; I, II and III—metacarpals I, II and III.

pitted, concave, ventral side of that bone. Unless it did not contact the radiale at all, there seems to be no other possible position, for all other possible surfaces of the radiale are known to articulate with other elements.

The proximal ulnare surface is oval and distinctly concave. Considering the movement of the radiale against the radius, this concavity probably permitted a simple sliding movement, with some rotation, across the expanded ventral or posterior portion of the ulnar condyle. The distal surface presents another surprise. Unlike the shallow, flat facets for the first and second metacarpal, that for metacarpal III is a broad, smooth convexity which is almost cylindrical. The best specimens show this to be faintly saddle-shaped, being strongly convex vertically (short axis) and slightly concave transversely (the long dimension), as shown in Figure 60E and F. This convex facet includes almost 90° of arc in a plane which is almost perpendicular to the plane of the first and second metacarpals. A prominent boss or tubercle projects medially from this surface, presumably for attachment of a digital flexor. The dorsal aspect of this boss is quite smooth and rounded and appears to have been a ventromedial extension of the inferior part of the strongly rounded radiale facet. In fact, it can be equated with the medial extension of the broader upper curve of that surface, and appears to have been a limiting facet or stop that prevented further supination at this joint. It may even have produced a slight pronation at the final stages of adduction.

Whereas metacarpals I and II had very little articular freedom against the carpus, it is evident from the distal surface of the ulnare that metacarpal III had significant, if not considerable, mobility. Inspection of both bones has established to my satisfaction that the third metacarpal could be extended as much as 15° to 20° away from metacarpal II in a plane almost perpendicular to that of metacarpals I and II. I have no explanation for this capacity other than to relate it to the grasping powers of the hand. However, since such movement would deflect the third digit from the raptorial plane of the other digits, resulting in the third claw being directed *away* from the other claws, the functional significance of this joint must lie elsewhere.

MANUS

The manus is completely known from several magnificently preserved specimens recovered at the Yale site (YPM 5206 and 5209) plus the nearly complete hands of AMNH 3015. As noted above, the manus is remarkable for its length and the unusual size of the digits and unguals (Figs. 62 and 63). Far from being reduced, the manus of *Deinonychus* appears to have been elongated and perfected as a grasping organ. Digits I, II, and III are well developed with normal theropod formulae (2–3–4). There is no sign of either lateral digit and no indication of a vestigial fourth metacarpal in contact with metacarpal III. In general appearance the manus most resembles that of *Ornitholestes* and is quite unlike the manus of either *Allosaurus* or *Ornithomimus*, particularly in its more slender construction and more elongated elements.

TABLE 8. Measurements (in millimeters) of the manus of *Deinonychus antirrhopus*

	AMNH 3015		YPM 5208	YPM 5211	YPM 5217
	Left	Right	Left	Right	Right
RADIALE					
Length (proximo-distal)	10.1	—	10.9	12.3	10.5
Transverse width	27.0	—	29.9	30.0	24.5
Vertical height	18.7	—	18.8	18.4	17.3
				YPM 5228 Right	YPM 5242 Right
ULNARE					
Length (proximo-distal)	12.2	11.5	11.0	12.8	9.9
Transverse width	24.2	—	22.2	22.7	18.9
Vertical height	13.0	12.0	13.2	13.7	9.7
			YPM 5206 Left	YPM 5206 Right	

TABLE 8. (continued)

METACARPAL I					
Length	35.5	—	45.8	43.2	—
Distal transverse width	19.0	—	20.0	19.9	—
Proximal transverse width	16.2	—	20.8	20.9	—
					YPM 5270 Right
METACARPAL II					
Length	—	—	88.3*	93.7	93.5*
Distal transverse width	16.3	15.1	17.0	16.8	15.7
Proximal transverse width	14.5	—	13.9	13.7	12.8
				YPM 5214 Right	
METACARPAL III					
Length	73.4	—	82.0	—	—
Distal transverse width	8.1	8.6	8.9	8.8	—
Proximal transverse width	—	—	7.5	7.9	—
				YPM 5213 Right	YPM 5220 Right
PHALANGES					
I^1 Length	—	—	74.1	72.0	67.2
Distal transverse width	13.2	13.5	15.3	15.1	13.0
Proximal transverse width	—	—	19.6*	20.4	16.6
				YPM 5212 Right	YPM 5220 Left
I^2 Length along outer curve	80.0*	—	>95.0	>95.0	85.0
Height of facet	21.0*	—	23.7	23.0	21.5
Proximal transverse width	10.0	—	13.0	12.8	9.6
				YPM 5216 Right	
II^1 Length	—	62.2	54.0	55.3	—
Distal transverse width	—	14.4	15.9	15.2	—
Proximal transverse width	—	17.7	18.1*	17.7	—
				YPM 5209 Right	
II^2 Length	70.2	70.7	76.5	78.0	—
Distal transverse width	12.9	12.9	13.6	13.6	—

TABLE 8. (continued)

	Proximal transverse width	13.2	13.7	14.1	14.0	—
						YPM 5222 Right
II^3	Length along outer curve	—	—	>80.0	>90.0	>80.0
	Height of facet	15.0*	—	20.2	19.9	18.7
	Proximal transverse width	8.9	—	12.0	12.0	10.0
					YPM 5206 Right	
III^1	Length	—	21.7	29.9	30.6	—
	Distal transverse width	—	8.7	9.2	9.4	—
	Proximal transverse width	—	9.0*	9.7	10.1	—
III^2	Length	15.5*	15.2*	20.5	—	—
	Distal transverse width	9.1	9.5	9.6	—	—
	Proximal transverse width	8.8	—	10.0	—	—
				YPM 5215 Left	YPM 5209 Right	YPM 5243 Right
III^3	Length	47.3	46.1	—	52.0	48.7
	Distal transverse width	10.8	10.0	9.9	10.0	9.1
	Proximal transverse width	10.2	10.5	10.8	11.4	9.9
				YPM 5206 Left		
III^4	Length along outer curve	—	—	>54.0	>40.0	>40.0
	Height of facet	14.0*	—	15.2	14.4*	15.5
	Proximal transverse width	6.4	—	7.5	7.9	7.0

* = approximate.

Metacarpus

As in most theropods, metacarpal I is distinctly shorter, more massive and more irregular in shape than the other metacarpals. Its length is only half that of metacarpal II although both extremities and the shaft are more robust than those of II. The proximal surface is gently convex to almost flat and is triradiate in shape. Medially, this surface extends into a narrow ridge which curves proximally, hooking over the medial projection of the radiale. This ridge then sweeps distally as a broad ventromedial flange with a conspicuous curved border

—a continuation of the dorsal arc of the radiale. In fact, in dorsomedial view (Fig. 61A), it is one continuous sweeping curve from the apex of this flange along its crest and across the dorsal curve of the proximal radiale facet. The total arc of this curve is about 190°. Although it seems unlikely that the radius rotated across this combined arc to make contact with the first metacarpal, the crest of the metacarpal flange is stout and rounded and has the same texture and sharply defined borders that are present on other articular facets—suggesting that it was covered with a pad of cartilage. The fact that metacarpal I appears to have been almost immobile against the radiale, seems to add support to the possibility that the first metacarpal contributed to the carpus-epipodial joint. Its inclusion would have added several degrees of adduction and supination to manual mobility.

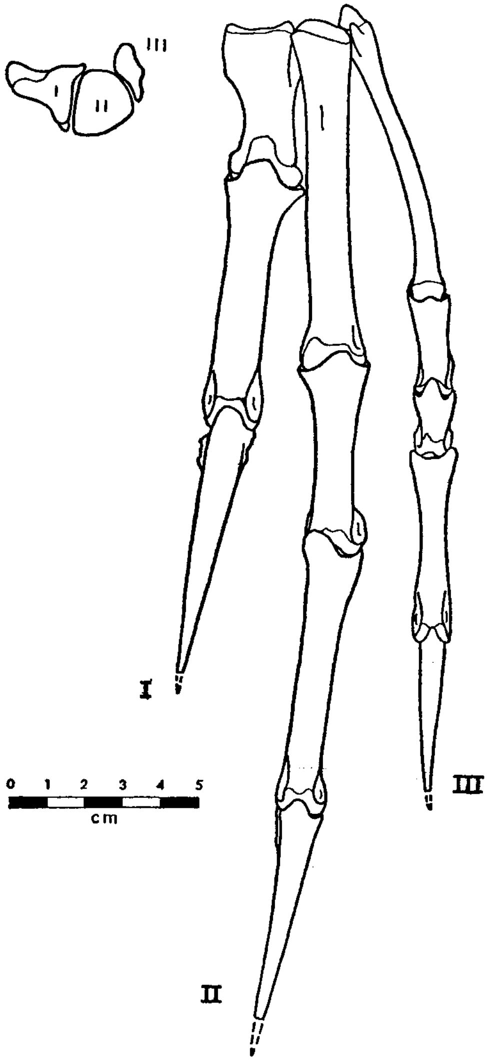


FIG. 62. The left manus of *Deinonychus antirrhopus* (YPM 5206) in dorsal aspect. The proximal ends of the metacarpals are outlined at the upper left.

The external side of metacarpal I bears a large, roughened, flat to slightly concave scar that extends almost to mid-length of the shaft. This corresponds to a counterpart feature on the medial surface of metacarpal II and establishes that these elements were tightly appressed together, and both were virtually immobile against the radiale.

The distal articular surface or head of the first metacarpal is irregularly expanded beyond the triangular shaft dimensions as an asymmetrical, quadriradiate, saddle-shaped facet. The medial and lateral margins are convex and separated by a broad and moderately deep groove. Unlike the more usual symmetrical groove and keel articulations of the phalanges, this joint must have permitted some lateral mobility as well as flexion and extension. The medial margin extends much farther back on the dorsal surface than does the lateral part.

Metacarpal II (Figs. 62 and 63) is long, quite robust and of normal theropod design. Medially it bears a distinct appositional scar from contact with metacarpal I, but no recognizable scar occurs on the lateral or ventral surface for contact with metacarpal III. The distal articulation is a normal slightly asymmetrical ginglymoid joint that permitted flexion and extension but only slight lateral or medial displacement. The asymmetry, with the lateral condyle somewhat smaller than the medial condyle, produced a slight outward rotation of the digit during flexion. The lateral and medial fossae are subcircular and extremely deep, indicating the presence of very strong collateral ligaments.

Metacarpal III (Figs. 62 and 63) presents still a third metacarpal form. It is very slender and slightly curved (concave ventrally), but is only a little shorter than the much stouter metacarpal II. The proximal facet is quadrangular and narrow, convex transversely, but distinctly concave in the vertical dimension for articulation with the broadly rounded distal surface of the ulnare. The distal end is expanded transversely and vertically into a broadly rounded condyle with only a faint groove inferiorly. Prominent fossae for collateral ligaments are present, the inner one the larger of the two.

Phalanges

The phalangeal formula is 2–3–4. All three digits terminate in large, laterally compressed, sharply recurved, trenchant claws. Those of I and II are the largest and are subequal in size. The penultimate phalanx is the longest in each digit and that of digit II is the longest element in the manus. All phalanges have well-developed and highly finished articular facets and extremely deep, subcircular pits or fossae on each side of the distal articular facet. These are the sites of attachment of collateral ligaments, the primary function of which is to prevent disarticulation of the phalanges. Their extreme development in all phalanges of *Deinonychus* indicates more than normal stresses and more than ordinary activity for the hand. The articular facets of digits I and II are of the ginglymoid type providing considerable flexion and extension but in a restricted plane. In digit I the deeply grooved distal facet of the first phalanx and the curved, ridged facet of the claw are nearly symmetrical; consequently, there was negligible rotation of the claw during flexion. In digit II, however, the distal facet of the penultimate phalanx is slightly asymmetrical. It also is inclined slightly with respect to the ridge on the proximal facet. Accordingly, the second ungual must have rotated inward (supination) when flexed against the penultimate phalanx.

The unguals are strongly curved and stout, but compressed laterally. The sides are each marked by a deep groove extending from the base of the articular facet to the extremity. The articular facet is strongly ridged and very clearly delineated from adjacent surfaces. A very large, rugose, flexor tubercle projects ventrally well below the inferior border of the articular facet, indicating the presence of powerful flexor muscles with good leverage. The unguals apparently could be flexed as much as 70° on the adjacent phalanx in both the first and second digits, as shown by the backward extension of the trochlea onto the underside of the penultimate phalanx.

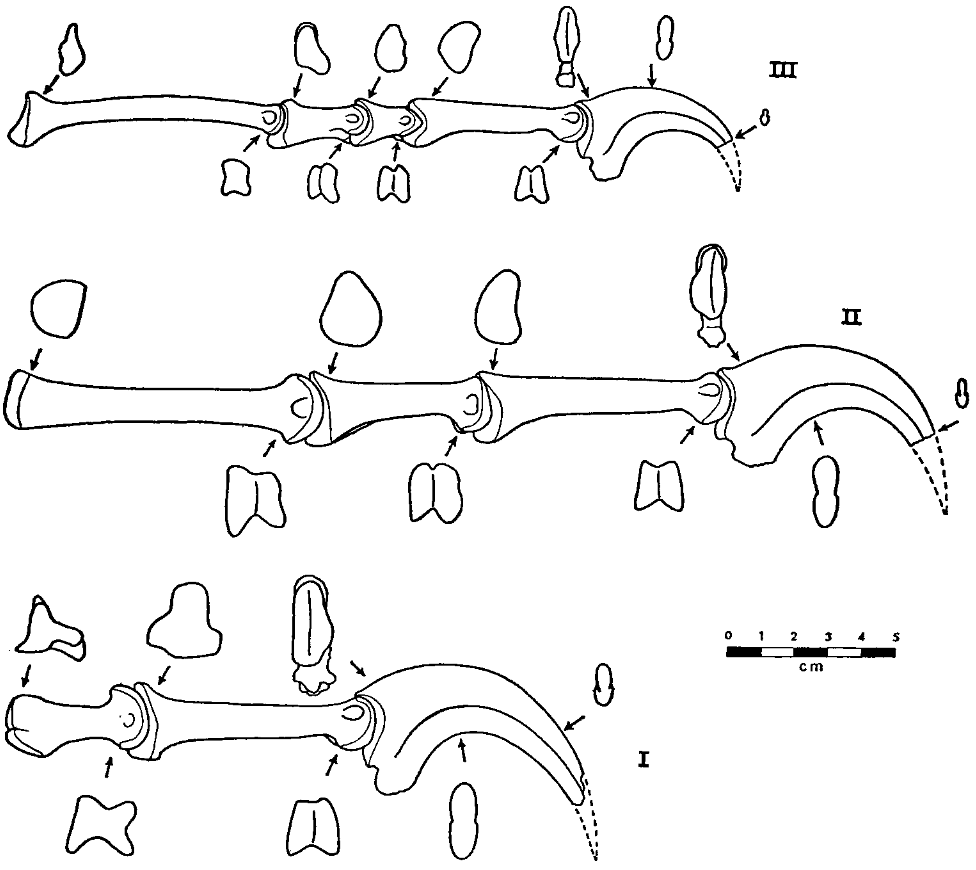


FIG. 63. The digits of the left manus of *Deinonychus antirrhopus* (YPM 5206) in medial aspect, with proximal and distal outlines.

The third digit is much more slender and delicate appearing than the other digits. It is normal in that it consists of two very short proximal phalanges and a long distal phalanx and ungual. Articular facets are well-developed and highly finished and the collateral ligament fossae are prominent, although not as deep as in the other two digits. The unusual feature in digit III is the form of the interphalangeal articulations.

The proximal facet of the first phalanx is sub-triangular and moderately concave. No ridge or keel is apparent. This permitted transverse displacement, as well as flexion and extension, against the broadly rounded distal facet of the third metacarpal. The distal articular facets of the proximal and second phalanges are not simple ginglymoid surfaces. Rather than permitting a simple hinge-like motion between the first, second and third phalanges, these two joints appear to have been restricted or limited joints. The distal facet of the first phalanx is strongly asymmetrical with a small, nearly circular (in side view) medial condyle and a much larger square lateral condyle separated by a vertical groove. The condyles extend far back on the ventral surface, but not on the dorsal surface. The proximal surface of the next phalanx consists of a large, rounded, medial ridge which fits into the vertical groove, and a triangular lateral flange which overlaps the outer surface of the lateral condyle. These are separated by a slightly curved, deep socket into which fits the ventrodistal part of the lateral condyle. The dorsal and ventral extensions of the medial ridge project proximally, overlapping the dorsal and ventral portions of the facet of the preceding phalanx to the extent that almost no flexion or extension is possible. In articulation the second phalanx appears to have been fixed in a slightly flexed position (approximately 15°).

The joint between the second and third phalanges is almost exactly the same. The chief differences are that the medial condyle of the second is triangular and the larger lateral condyle more distinctly rectangular. The former fits into a triangular depression on the inside of the inner ridge of the third phalanx and the latter is overlapped laterally by a short flange. Again, there appears to have been very little mobility at this joint, the third phalanx being fixed in a slightly flexed position.

The joint between the ungual and the third phalanx is of the normal ginglymoid type providing the usual hinge-like motion through an arc of 60° or more. It is not clear why the third digit is constructed in this manner, but an obvious result is that three relatively short phalanges are fixed into a single, more or less inflexible segment—which in effect became the *penultimate* segment. The length of this compound "phalanx" is more nearly comparable to the lengths of the other penultimate phalanges, and the joints at which flexion can take place is now reduced to two—the same number as the corresponding digit (I) on the inner side of the hand. I cannot explain this condition nor am I aware of a comparable adaptation in any other animal. I suspect, however, that it is related to the functional significance of elongation of the penultimate phalanx in the digits of the manus. I presume such elongation is related to flexion of the unguals, perhaps providing greater leverage, and to the precise way in which the claws are used. Elongated distal phalanges appear to be characteristic of all theropods (*Chirostenotes* may be an exception) but they are most evident in *Oviraptor*, *Ornithomimus* and *Deinonychus*.

Of special interest in this regard is the fact that elongated penultimate phalanges are characteristic of the pes in some birds of prey. It is not characteristic of ground or aquatic birds, however, or even of most perching birds; nor is it true of the pes or manus in most tetrapods. Among the predatory birds featuring this trait, there appears to be a correlation between claw form and phalanx length. Where the claws are highly curved and trenchant or very sharp, there often is a lengthened penultimate phalanx. Where the claws are less strongly curved, the penultimate phalanx is usually not the longest element. The most striking examples of the former is the osprey or fish hawk (*Pandion haliaetus*), well known for its skill in catching and holding fish. Other, less spectacular, examples are the red-shouldered hawk (*Buteo lineatus*), the eagle owl (*Bubo bubo*) and the barred owl (*Strix varia*).

FUNCTIONAL SIGNIFICANCE OF THE MANUS

The manus of *Deinonychus* was a highly perfected and powerful grasping structure quite unlike that of any other adequately known theropod. The most important features confirming this conclusion are the long and stout first and second digits with their large, trenchant and strongly recurved claws, the slender, abductable third digit with its unique restrictive joints, the very large flexor tubercles on all unguals, the highly perfected carpus that provided extensive and precise adduction and supination of the hand, the unusual length of all fore limb components and the great size of the deltopectoral crest and internal tuberosity. By way of contrast, the manus of *Ornithomimus*, which was described by Osborn (1917) as a prehensile or grasping hand, has subequal digits bearing rather straight, non-trenchant claws with relatively small flexor tubercles (Fig. 77e) and the wrist is unmodified and apparently relatively inflexible. The fore limb is not unusually elongated and the deltopectoral crest is surprisingly small. The manus of *Ornithomimus* was considered a grasping structure by Osborn primarily because of the nearly equal lengths of the three digits and the presumed opposability of digit I. The manus of *Ornitholestes*, which Osborn (1917) described as "subraptorial" and too feeble and reduced for "raptorial grasping," has long, unequal digits with large, recurved and trenchant claws with large flexor tubercles (Fig. 77). The carpus is not known, but the forelimb is quite long and the deltopectoral crest is relatively large.

Brown (p. 757), Osborn (p. 757) and Gregory (p. 758) (*in* Osborn, 1917) apparently agreed that the first digit could rotate on its metacarpal in *Struthiomimus* (= *Ornithomimus*), thus permitting opposition of digit I to digits II and III. It is true that this joint is not a distinct ginglymus, but I suggest that any rotation of the proximal phalanx about its long axis against the metacarpal was slight. Distinct collateral ligament fossae are present on both sides of the distal facet of the metacarpal. The existence of collateral ligaments at this joint would have severely restricted, if not prevented, rotation of the digit. Furthermore, there is no evidence on the phalanx of the attachment of a rotator muscle that had sufficient leverage to produce any meaningful rotation. The first digit was divergent in *Ornithomimus*, as it was in *Ornitholestes*, *Deinonychus* and most other theropods, thus it must have converged upon the other digits during flexion, but it appears not to have been opposable in the usual sense. The only unusual feature of the first digit is the length of the metacarpal, which is almost equal to metacarpals II and III. Consequently, the proximal joints of all three digits are situated close together, equidistant from the wrist, instead of widely spaced as in *Ornitholestes*, *Deinonychus* and other theropods. In fact, this is a unique condition among theropods that would seem to have reduced the maximum amount of digital divergence or splay and thus reduced the grasping power. The three digits appear to have functioned more as a unit than as three separate elements.

The unguals of *Ornithomimus* are not as strongly curved as in *Ornitholestes* or *Deinonychus* (Fig. 77). Osborn (1917: p.751) described them as "extremely long, slender, and slightly recurved, with strong attachments for the flexor perforans, less recurved, claw-like or raptorial than those of *Ornitholestes*." Moreover, they are broad and nearly flat on the under side and not narrow and trenchant as in a truly raptorial or grasping claw. Gregory (*in* Osborn, 1917: p. 758) noted that the wrist joint of *Struthiomimus* (= *Ornithomimus*) "was very stiff, capable of very little extension." The carpus consists of five unspecialized ossicles with no clearly defined facets. It would seem that if prehension was an important function of the manus, selection would have increased carpal mobility and this would be reflected in distinct carpal facets. The carpus of *Ornitholestes* is unknown, but those of *Allosaurus* and *Ceratosaurus* are similarly unmodified and presumably were also relatively inflexible. The apparent absence of significant carpal adduction or supination in *Ornithomimus,* both of which would seem to be essential for effective grasping with both hands, indicates that all adduction and supination of the hands must have been achieved by adduction and long axis rotation of the humerus. However, it has already been pointed out that the very reduced size of the deltopectoral crest and the internal tuberosity in *Ornithomimus* (Fig. 57) indicate that only slight and weakly powered rotational movements were possible for the humerus. The small deltopectoral crest also indicates that even forelimb adduction and retraction were feebly powered motions. Other theropods (*Ornitholestes, Coelurus, Allosaurus, Coelophysis*) have relatively large deltopectoral crests, indicating powerful adduction and retraction, and possibly pronation, but the small size of the internal tuberosity suggests only modest power for supination of the fore limb. In summary, the only obvious conclusion is that *Deinonychus* was much more highly adapted than other theropods (with the possible exception of *Ornitholestes*) for powerful grasping with the hands.

Consideration of the function of the manus in *Deinonychus* would be incomplete without some comment on the extraordinary length of both the fore limb and the manus. The unusual dimensions of these elements are perhaps best illustrated by comparison of total forelimb length with that of several other skeletal dimensions, such as skull length, hind limb length and length of the presacral vertebral column, in *Deinonychus*[4] and several other theropods. Such comparisons are given in the following ratios.

---

[4] All three of these dimensions are estimated for *Deinonychus.* The skull length is estimated at 32 cm on the basis of the two Yale skulls. The presacral length was derived from the nearly complete vertebral series of AMNH 3015 and an assumed presacral count of 23. The hind limb length, the most doubtful of these three dimensions, assumes equal lengths for the tibia and the unknown femur. This last assumption is warranted in view of femur-tibia ratios in other theropods, but even if it is in error by as much as 25% (femur length was as short as 0.75 or as long as 1.25 of tibia length—a margin of error greater than the total range of femur/tibia ratios known among all theropods), the resultant ratio of fore limb to hind would still be larger than in any other presently known theropod except *Ornitholestes.*

	Fore limb / Skull	Fore limb / Hind limb	Fore limb / Presacral column
Allosaurus fragilis	1.58	0.42	0.46
Coelophysis longicollis	1.33	0.42	0.31
Tyrannosaurus rex	0.83	0.20 ±	0.25 ±
Deinonychus antirrhopus	2.22	0.70	0.85
Ornitholestes hermanni	2.32	0.66	0.60
Ornithomimus altus	3.57	0.51	0.52

The use of three different ratios minimizes possible errors of interpretation that might result from an unusual dimension of a single comparative feature. For example: the large ratio of fore limb to skull length in *Ornithomimus* reflects the reduced size of the skull and not an excessive length of the fore limb. This is verified by the moderate ratios of fore limb to hind limb and fore limb to presacral vertebral length. On the other hand, the consistently low ratios for *Tyrannosaurus* reflect the greatly reduced length of the fore limb.

From these ratios it is evident that the fore limb of *Deinonychus* is much longer relative to other body proportions than is true of the other theropods listed, or of any other theropod that I am aware of. The differences are most obvious in the second and third ratios, but even the ratio of fore limb to skull length is surprisingly large considering the relatively large size of the skull in *Deinonychus*. If the skull of *Deinonychus* had been of more ordinary proportions (comparable to *Allosaurus*, for example) this particular ratio would have been well over 3.00. Of particular interest is the fact that among the five species listed, the *Ornitholestes* ratios are closer to those of *Deinonychus* than are any of the other ratios.

A significant feature of the fore limb of *Deinonychus* is that the manus accounts for nearly half of the total length and the three phalanges of the second digit together are longer than the radius and almost as long as the humerus. Such elongation of all fore limb components greatly increased fore limb reach and in view of the trenchant and strongly recurved form of the unguals this extended reach seems best related to predation. However, since most, if not all, theropods were predators, predatory habits alone cannot account for unusual fore limb length in *Deinonychus*. Also, the condition in "carnosaurs" commonly is just the reverse, with many species featuring greatly reduced fore limbs. I am inclined to relate fore limb length in *Deinonychus* to the unusual claw (discussed in the following section) on the second pedal digit. If this claw was used to kill prey held by the hands, the prey quite obviously could not have been held close to the body. The foot claw could only have been applied to objects held at arm's length. Moreover, it seems quite probable that on some occasions the fore limbs and hands were essential to effective use of the sickle-like foot claw, immobilizing the prey and bracing it against the retractive power stroke of the hind leg.

APPENDICULAR SKELETON: PELVIS AND HIND LIMB

PELVIS

The pelvis of *Deinonychus* is presumed to have consisted of the usual elements. Both ischia and the left ilium are preserved in AMNH 3015. A right ischium (YPM 5235) was also collected at the Yale site. The pubis, however, is a doubtful element. A very strange bone, quite unlike any bone I am familiar with, was found at the Yale site not far from the above ischium. It is my opinion that this bone is a right pubis and it is described as such below, but it must be recorded here that this identification is not proven. I have no doubts, but I must admit that colleagues who have examined this element have not always been as certain as I am.

ILIUM

The only ilium available (Fig. 64) is fragmentary and poorly preserved, so its precise shape and other details of its morphology are still unknown. It appears that the ilium was almost triangular, with a relatively short posterior blade and a very abbreviated anterior blade. Compared with that of *Allosaurus* the ilium is much shorter and the posterior blade is more rectangular and does not taper as sharply. The nearly intact dorsal margin is straight over most of its length, but curves downward caudally to terminate the posterior blade. The margin is not transversely expanded except near the caudal extremity. The anterior margin is unknown, but the thin construction of what remains of the anterior blade indicates this feature may not have reached much beyond the pubic peduncle. A thin ventral flange flares out laterally from the base of the pubic peduncle and the ventral corner of the anterior blade, somewhat like that of *Gorgosaurus* and *Tyrannosaurus,* but its extent cannot be determined. The lateral surface of the ilium appears to have been smooth and broadly concave; no muscle scars can be recognized. The inner surface bears faint striations in its upper part, probably reflecting muscle attachments (M. longissimus dorsi and M. ilio-costalis). There appears to have been a medially projecting longitudinal ridge which extended along the inner surface to the posterior extremity from above the acetabulum, but its precise shape and length is not known. The inferior part of the medial surface is irregular and marked by three (perhaps four) rugose patches that are believed to mark the attachment sites of sacral ribs.

The pubic peduncle is quite massive and sub-rectangular in section. It projects ventrally, rather than anteroventrally, and forms the anterior margin of the acetabulum. The ischial peduncle is much shorter but broader, and forms only the upper part of the posterior margin of the acetabulum. The acetabular margins are massive and strongly buttressed, providing a stout socket for the head of the femur.

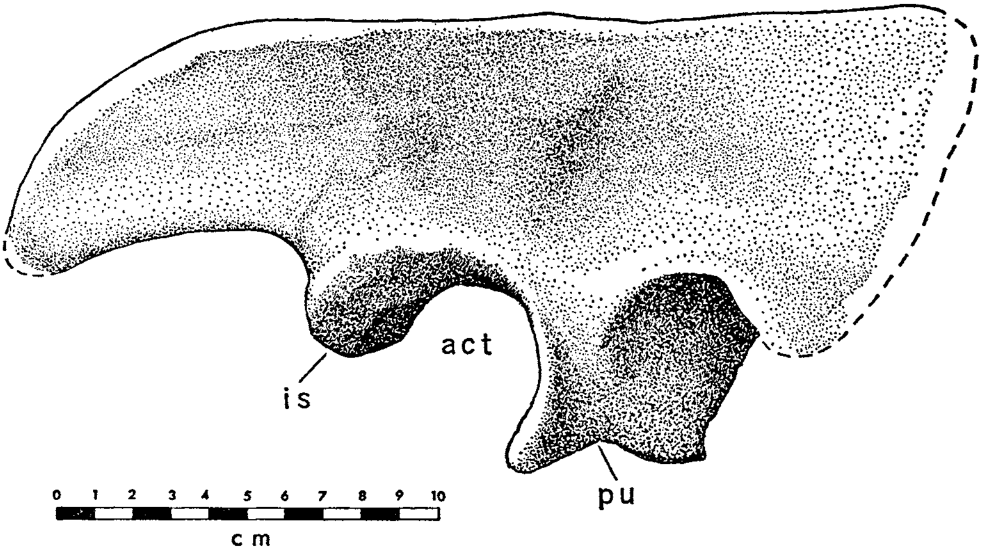


FIG. 64. Left ilium (reversed) of *Deinonychus antirrhopus* (AMNH 3015) in lateral view. Abbreviations: act—acetabulum; is—ischiac peduncle; pu—pubic peduncle.

ISCHIUM

This bone (Fig. 65A) resembles the ischium of *Gorgosaurus,* and to a lesser extent, *Tyrannosaurus,* in that it has a prominent forward-projecting triangular flange (obturator process) near mid-length of the shaft and the shaft extremity is not expanded or club-shaped. It differs from both in that the obturator process is relatively much larger in *Deinonychus* and more distally placed on the shaft. Also the shaft is straighter, although it does curve slightly caudad. Most distinctive is the size of the ischium, being much shorter relatively than in any other theropod. Generally, the ischium length is 70 to 80 percent of tibia length (= 65–75% of femur length), but in the present instance it is only about 50 percent of tibia length. The possible significance of this is discussed below.

The shaft has subparallel anterior and posterior margins, is flat internally and broadly rounded externally. The proximal end is greatly expanded longitudinally and transversely into a posterior articulation for contact with the ischiac peduncle of the ilium and an anterior expansion for union with the pubis. These articular expansions are separated by a thin, concave margin which formed the posteroventral boundary of the acetabulum. The surfaces of both the iliac and the pubic articular expansions are deeply pitted and grooved and very irregular, indicating firm digitate sutural unions with these two bones.

Distally, the anterior margin of the shaft flares out forward just proximal to mid-length into the large, triangular obturator process. This structure provided extensive area for a fleshy origin of femoral adductors (M. adductor femoris and a posterior part [3] of M. pubo-ischio-femoralis externus of Romer [1923b] or the M. ischio-femoralis and M. pubo-ischio-femoralis external of Gregory and Camp [1918]). Unlike other theropods this obturator flange lies

TABLE 9. Measurements (in millimeters) of the pelvis of *Deinonychus antirrhopus*

	AMNH 3015		YPM 5235	YPM 5236
	Left	Right	Right	Right
ILIUM				
Length	245.0*	—	—	—
Length anterior to acetabulum	100.0*	—	—	—
Length posterior to acetabulum	80.0*	—	—	—
Height above acetabulum	72.0	—	—	—
ISCHIUM				
Length (proximo-distal)	161.0*	158.0	161.0	—
Width across peduncles	66.1	66.0	63.0	—
Width across obturator process	—	—	45.8	—
Obturator process apex to iliac penduncle	127.0	128.0	116.0	—
Maximum shaft thickness	10.9	9.1	11.5	—
PUBIS				
Length (proximo-distal)	—	—	—	116.5
Length (antero-posterior)	—	—	—	99.0
Height (vertical)	—	—	—	97.0*

* = approximate.

largely in the distal half of the ischial shaft. There is no evidence of an obturator notch. The distal margin of the obturator process is slightly expanded transversely and is finely rugose, indicating that the ischia were united in mid-line along this margin.

The distal extremity of the ischium tapers abruptly and curves slightly backward. There is no evidence of a longitudinal terminal expansion of the ischium as in *Allosaurus, Ceratosaurus, Acrocanthosaurus?* and *Ornithomimus.* The ventral margin of the extremity is well scored by longitudinal grooves and ridges, possibly the origin scars of ventral caudal muscles (M. ischio-caudalis).

PUBIS

As noted above the bone described here (YPM 5236; Fig. 65B) is so unlike the pubis of any archosaur known to me that its identification as such must be provisional. In contrast to the general archosaurian pubis, this element is very short, but greatly expanded longitudinally. There is no shaft whatsoever, simply a broad plate of bone which is roughly triangular in shape.

Proximally, a very stout rugose expansion is directed upward. This is by far the most massive part of the entire bone. It corresponds roughly in size, shape and topography to the pubic peduncle of the ilium (AMNH 3015) and in texture it matches exactly the surfaces of the ischial articular contacts. A thin plate of bone extends anteriorly from this "iliac peduncle," but its upper margin is incomplete. Although this lamina is very thin, presumably it thickened dorsally and terminated in an expanded contact with the ilium. Its upper margin probably formed a short, thin-walled, inferior boundary of the acetabulum.

From the presumed ischiac articulation a very stout column extends downward to a prominent "corner," from which point it extends ventromedially. This sharp projection is appropriately situated to have been the origin site of an upper part (pars 2 of Romer, 1923b) of the M. pubo-ischio-femoralis

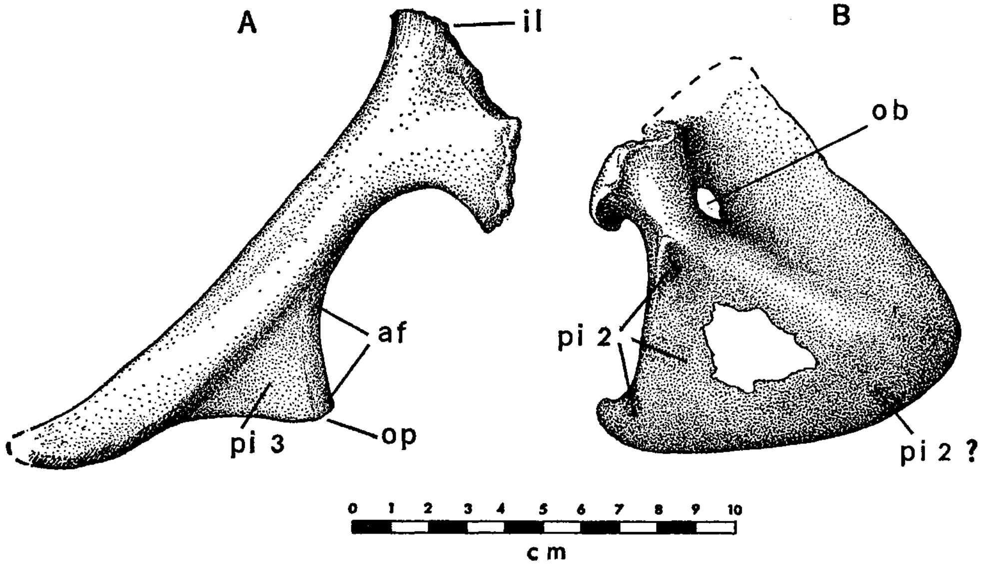


FIG. 65. (A) right ischium (YPM 5235) and (B), right pubis (?) (YPM 5236) of *Deinonychus antirrhopus,* both in lateral view. Abbreviations: af—probable area of origin of the M. adductor femoris; il—iliac articulation; ob—obturator foramen; op—obturator process; pi2—probable origin area of the M. pubo-ischio-femoralis externus, pars 2; pi3—probable origin area of part 3 of the M. pubo-ischio-femoralis externus.

externus. It seems unlikely that the M. ambiens attached at this point but this must be considered as another possibility. A broad, thin plate of bone, deeply concave medially, extends from this "corner" down and forward. The posterior margin is stout and triangular in section, but the anterior margin is very thin. The inferior margin is slightly expanded, rounded and faintly rugose in texture. Any contact along this latter margin with the opposite pubis must have been cartilaginous or ligamentous.

A moderate-sized oval foramen is situated just beneath and anterior to the "ischiac peduncle," passing up and inward. A distinct channel extends from the foramen upward across the inner surface to the posterior margin of the "ischiac articulation." This would appear to be the obturator foramen, although among theropods this feature apparently exists only in *Ceratosaurus nasicornis* (USNM 4735 and some primitive Triassic forms such as *Ornithosuchus.*

My identification of this element as a right pubis is based on the following:

a) The correspondence of its articular expansion to the pubic peduncle of the ischium.
b) A foramen which corresponds perfectly in location and orientation to an obturator foramen.
c) The size is appropriate.
d) Although primitive, the shape is not unreasonable.
e) It seemingly cannot be equated with any other bone in either theropod or ornithopod (the only two kinds of vertebrates represented in the Yale quarry).

If this identification is correct, the pubis of *Deinonychus* must be considered as primitive in shape. However, it seems unlikely that the pubis would retain such primitive character when so many other anatomical features must be considered as advanced. A more likely explanation is that the peculiar form of the pubis is not a relict condition, but a newly acquired feature, perhaps correlated with the highly specialized and extraordinary adaptation of the feet for predatory activities. It is significant that the pubis of *Saurornithoides* (which possessed a specialized pes similar to that in *Deinonychus*) appears to have been similarly expanded, but short. It is incompletely preserved, however, so its precise shape is not known.

Aside from the ventral abdominal muscles, the principal muscles attaching to the pubis, and to the obturator process of the ischium, are femoral adductors, specifically, the several parts of the M. pubo-ischio-femoralis externus (see Romer: 1923a and b). While these fibers may have contributed to the recovery stroke of the femur, their principal function was one of adduction—pulling the femur toward the sagittal plane, or to a more vertical position. Gregory (1918) considers these muscles as adductors and homologizes them with the M. obturator externus of mammals, which is an important adductor of the leg in man (Gregory, 1918: p. 533). It is unfortunate that the femur of *Deinonychus* is not known, but we can presume that these adductors inserted at points on the proximal third of the femur as in crocodilians and as reconstructed by Romer (1923b) for *Tyrannosaurus.* The expanded pubic plate of *Deinonychus* is thus probably related to expansion of the adductor muscles originating on the pubis. The unusually short pubic length may correlate with this. A consequence of shortening the pubis is to elevate the origin sites of the femoral adductors to bring these more nearly level with the insertions on the femur. Thus the adductors, although shortened, would be more nearly horizontal in orientation and more nearly perpendicular to the femur shaft. If there was no concurrent shift in adductor insertion sites, this shift of the origin level closer to the acetabulum must have increased the leverage of the hind limb adductor musculature, but the shortened fiber length would have reduced the amount of femur excursion possible (although perhaps not significantly, since these inserted close to the fulcrum). This may also be the explanation of the relatively short ischium, on which were attached the M. adductor femoris and part of the M. pubo-ischio femoralis externus.

What might account for enlargement and increased leverage of femoral adductors in *Deinonychus?* Maintenance of the femur in a nearly vertical plane close to the sagittal plane must have been important in all theropods, so why the distinctive condition here?

An important difference between *Deinonychus* and other theropods is in the foot. In other theropods the pes was clearly adapted primarily for locomotion, and any offensive or defensive adaptations were secondary. In *Deinonychus,* as is described in the following pages, the foot includes a highly specialized offensive or predatory instrument. It should be quite obvious that this device could not be used unless the animal stood on *one* leg. It is also obvious that the use of this structure necessitated significant agility and perhaps even violent activity while standing on that one limb. Under these conditions, powerful and effective limb adductors and abductors are essential to retain stable posture.

If femoral adductors were important for bipedal stability in *Deinonychus,* we should also expect to find evidence of enlarged femoral abductors. The abductor is just as critical to stable posture when support is even momentarily maintained by only one limb, because the supporting limb is fixed on the ground and cannot be moved. The body above the limb is moved toward or away from the plane of the femur by the femoral adductors and abductors. Balance is maintained by the constant interaction of these opposing muscles, keeping the center of gravity above or nearly above the supporting limb. While there are indications of some changes in the femoral adductors in the shorter ischia and pubes and the expansion of the latter, there are no clear evidences of modification of the hind limb abductors, the M. ilio femoralis and ilio tibialis. But it should be noted that all theropods have greatly expanded ilia, presumably for enlargement of the ilio-femoralis and tibialis.

Hind Limb and Foot

The femur, unfortunately, is not known, but the remainder of the hind limb and foot is known from numerous, exceptionally well-preserved elements from the Yale site and in AMNH 3015. Without the femur nothing definite can be said about hind limb proportions or femoral dimensions. However, it is probably safe to say that the femur was at least as long and probably a little longer than the tibia, as it is in all theropods except *Ornithomimus* and *Compsognathus.* The fact that the metatarsals in *Deinonychus* are not especially long (less than 50% of the tibia length compared with nearly 70% in *Ornithomimus* and *Compsognathus*) suggests that the epipodials probably were not elongated relative to the femur. Hence the hind limb appears not to have been elongated for extraordinarily fast running as in *Ornithomimus* and cursorial birds like the ostrich. Accordingly, we can presume that the femur was relatively long.

TIBIA

The tibia (Figs. 66 and 67) is known only from the right limb of AMNH 3015. The bone is nearly complete and was preserved articulated with a fragmentary fibula and the astragalus and calcaneum. It is presumed that the tibia is shorter than the femur, as in most other theropods. It is expanded at both ends, anteroposteriorly at the proximal end and transversely at the distal end. The proximal end is roughly triangular, with the narrow angle projecting forward. This anterior projection is the proximal termination of a short but stout crest (cnemial crest) that diminishes abruptly over approximately one fifth the tibia length. Posteriorly, the proximal articular surface is separated by a posterior notch into two subequal medial and lateral expansions for articulation with the two distal condyles of the femur.

The shaft is stout, but not as massive as in *Allosaurus,* straight, and oval to sub-triangular in section. Like the other limb elements, it is hollow at least at mid-shaft. Except that the proximal end is more robust, in general proportions it compares most closely with the tibia of *Ornithomimus* and is much less robust than in "carnosaurs."

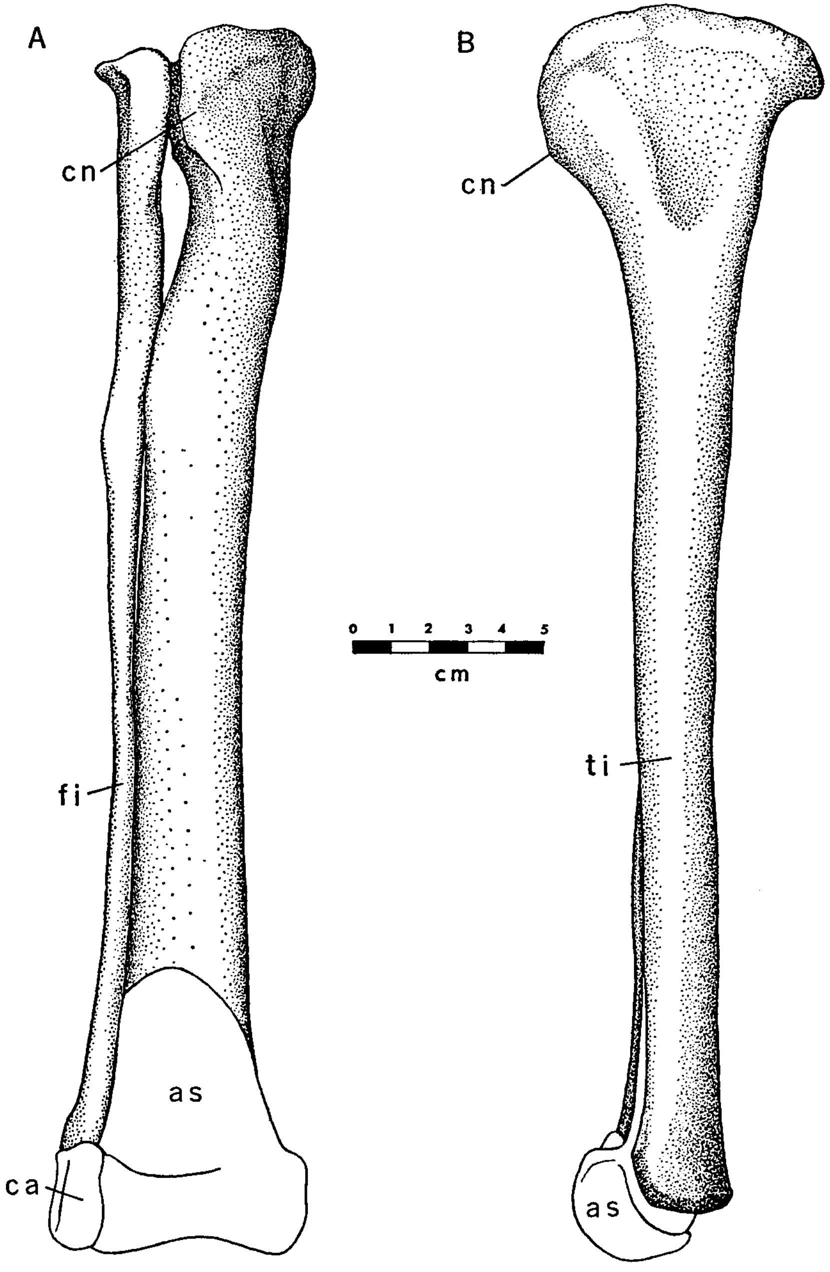


FIG. 66. Right tibia and fibula (AMNH 3015) of *Deinonychus antirrhopus* in anterior (A) and medial (B) views. Abbreviations: as—astragalus; ca—calcaneum; cn—cnemial crest; fi—fibula; ti—tibia.

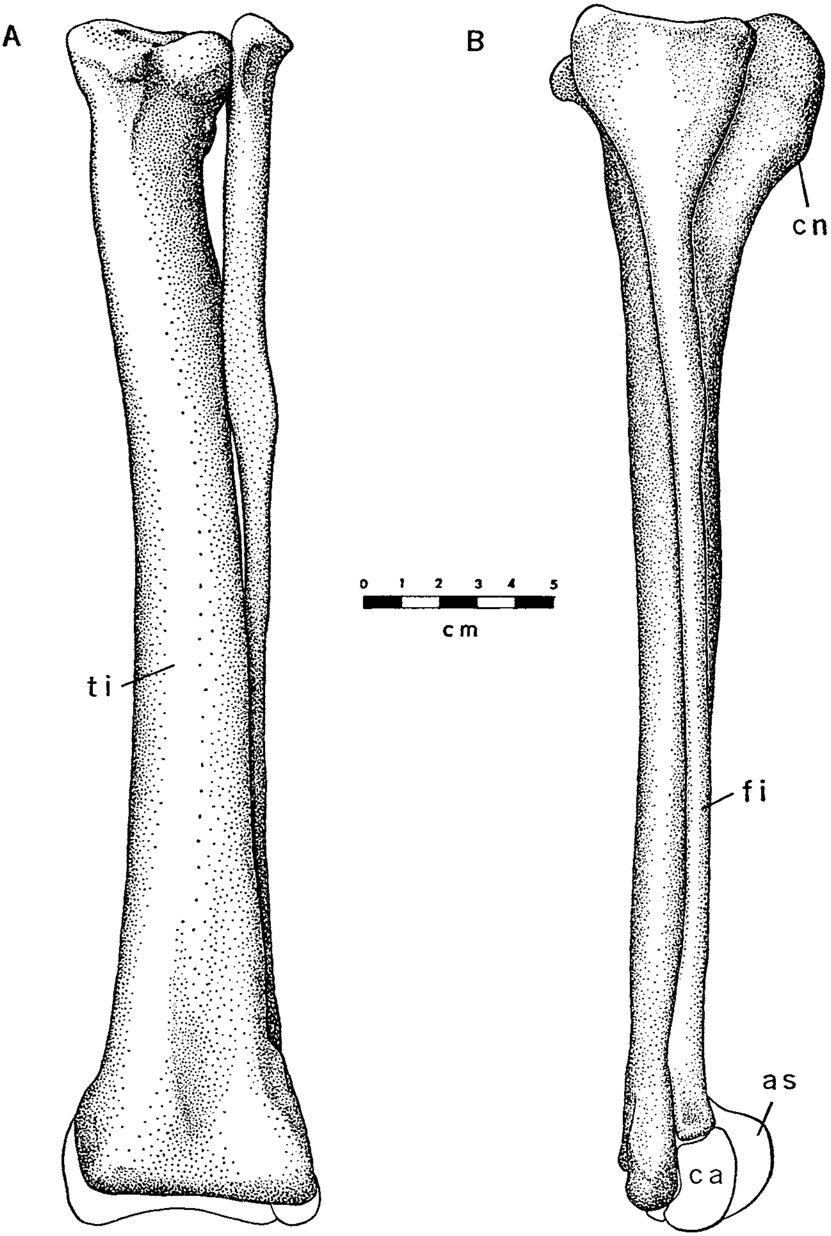


FIG. 67. Right tibia and fibula (AMNH 3015) of *Deinonychus antirrhopus* in posterior (A) and lateral (B) views. Abbreviations: as—astragalus; ca—calcaneum; cn—cnemial crest; fi—fibula; ti—tibia.

TABLE 10. Measurements (in millimeters) of the hind limb of *Deinonychus antirrhopus*

	AMNH 3015 Right	YPM 5226 Left
TIBIA		
Length	312.0	—
Length with astragalus	324.0	—
Distal width	63.3	—
Proximal width	44.8	—
Least shaft diameter	18.0	—
Maximum proximal dimension	74.0	—
FIBULA		
Length	297.0*	—
Length with calcaneum	320.0*	—
Distal width	11.0	—
Proximal width	16.0	—
Least shaft diameter	6.2	—
Maximum proximal dimension	48.4	—
ASTRAGALUS		
Length (proximo-distal)	71.0	76.0*
Maximum transverse width	59.0*	59.0
Maximum antero-posterior diameter	30.5	30.2
Least antero-posterior diameter	19.0	21.5
CALCANEUM		
Length (proximo-distal)	26.5	30.0
Transverse width	9.8	13.1
Maximum antero-posterior diameter	19.0	20.3

* = approximate.

The distal end is broad transversely (67 mm), but very narrow (17 mm) longitudinally. It cannot be viewed directly because it is largely concealed beneath the astragalus and calcaneum, but judging by the form of the tibial articular surface on an isolated astragalus and calcaneum (YPM 5226), the distal extremity of the tibia appears to have been flat (except in its posterior part) and of narrow triangular shape, tapering externally.

FIBULA

This bone is extremely slender and much less robust than the tibia (Figs. 66 and 67). The shaft apparently was straight, nearly circular in section and was appressed against the upper fourth and lower fourth of the tibia shaft. Distally, it also had extensive contact with the external edge of the astragalus ascending process, and a short narrow abutting contact with the external part of the proximal surface of the calcaneum.

Proximally, the fibula is greatly expanded fore and aft into a long, narrow, rectangular head, which adjoins the external expansion of the tibia head. Together these two surfaces articulated against the lateral condyle of the femur. The combined proximal surfaces of the tibia-fibula provided a long, broad, flat platform which rocked over the presumably strongly convex condyles of the femur.

TARSUS

The tarsus is composed of four bony elements, as in most theropods. Proximally a very large astragalus, corresponding to the large end of the tibia, and a small, disc-like calcaneum are closely applied to the tibia and fibula. Only two distal tarsals, probably tarsals III and IV, are known, but these are represented by three separate pairs (YPM 5207 and AMNH 3015) and several isolated examples (YPM 5205, 5217, 5223 and 5229). No other elements have been found at any of the *Deinonychus* sites that could possibly represent an additional tarsal and the structure of the tarsus indicates that any additional elements that may have been present did not contribute importantly to the joint between the crus and the foot. The tarsus is not well known in most theropods, so it is not clear what the normal theropod condition may have been. Three distal tarsals are preserved in the type specimen of *Gorgosaurus libratus* (NMC 2120), two distal tarsals are present in *Allosaurus fragilis* (Gilmore, 1920: p. 71),[5] but only one distal tarsal is preserved in the type of *Ceratosaurus nasicornis* (USNM 4735), (although tarsal IV was probably present, as Gilmore noted [1920: p. 110].) *Ornithomimus* (AMNH 5339) has two distal tarsals, as shown by Osborn (1917: fig. 11), although Romer (1956: fig. 191) shows three. As in other theropods, the tarsus of *Deinonychus* forms a rather simple, mesotarsal joint, a rolling, hinge-like joint between the proximal and distal tarsals.

Astragalus

The astragalus, functionally part of the crus, is situated as a cap-like addition to the distal end of the tibia. The American Museum specimen indicates that a firm union existed between these two bones, but the isolated astragalus and calcaneum in the Yale collection (YPM 5226; Fig. 68) demonstrates that they were not necessarily fused to the tibia, nor were astragalus and calcaneum fused. In general, the astragalus is remarkably similar to that of *Ornithomimus* (YPM 542) but larger and more perfectly rounded in its distal articular surface. It is quite unlike the astragalus of *Allosaurus.*

The main body of the astragalus has the shape of an asymmetrical cylinder which is constricted at mid-length and unequally expanded at both ends (in anterior or distal view). The articular facets for the tibia occupy its upper posterior aspect. Cross sections taken at almost any point through the astragalus "cylinder" would show an almost perfectly circular section ranging from a little more than 155° to about 180° of arc. The anterior and posterior margins of this broad, rounded, articular surface are sharply defined by a distinct transverse ridge at the base of the ascending process and by the posterior limit of the astragalus. The latter feature, together with the apparent form (in AMNH 3015) of the inferior part of the posterior tibia surface immediately above the astragalus, strongly suggests that the tibia contributed to the posterior part of this articular facet. If so, the total arc of the proximal surface may have been as much as 270°, which would have permitted an unusual degree of extension and flexion. The distal surfaces of the American Museum tibia are not well preserved, but a perpendicular to the apparent upper posterior limit of this surface trends caudally at about 30° below the horizontal when the tibia shaft is

---

[5] Gilmore referred this specimen (USNM 4734) to *Antrodemus valens,* but, as noted in Footnote 2, p. 16, I consider that species as indeterminate—a *nomen dubium.* This specimen was identified as *Allosaurus fragilis* by Marsh (1896).

oriented vertically. A similar perpendicular at the highest anterior point trends anteriorly at about 50° above the horizontal. The encompassed arc approximates 200°, the largest fraction of which (140°) faces forward and clearly must have provided for unusual extension of the foot.

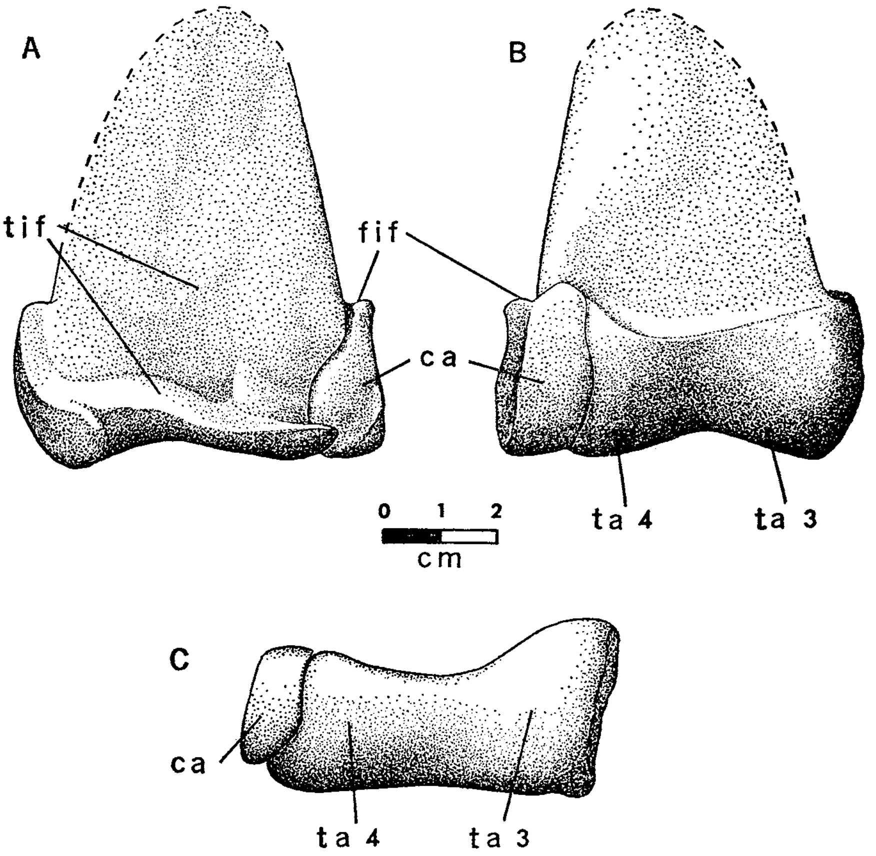


FIG. 68. Left astragalus and calcaneum (reversed) of *Deinonychus antirrhopus* (YPM 5226) in posterior (A), anterior (B) and distal (C) views. Abbreviations: ca—calcaneum; fif—fibular facet; ta 3—articular surface for tarsal III; ta 4—articular surface for tarsal IV; tif—tibial facets.

The internal expansion of the astragalus is considerably larger than the lateral expansion, but the latter is supplemented externally by the calcaneum. With the calcaneum in place, lateral and internal expansions of this joint surface are approximately equal, although not symmetrical. The constricted or narrow-waisted design of this articular surface is best likened to the ginglymoid or saddle-like distal surfaces of phalanges. It permitted a great deal of flexion and extension, but tended to restrict movement to a single plane. The opposing surface, constructed by tarsals III and IV, probably had the obverse form, although this cannot clearly be shown with the existing materials. We can conclude that the tarsus permitted considerable hinge-like movement of the foot, but probably little, if any, transverse adduction or abduction.

The ascending astragalar process is quite long—a thin blade reaching more than 50 mm up the anterior surface of the tibia. It is triangular in outline, tapering upward, and surprisingly thin (2 mm or less at most points). Its posterior surface is nearly flat and quite smooth. Distally it meets a narrow wedge-shaped shelf at a near 90° angle. This is the surface of contact with the distal extremity of the tibia. The internal surface of the astragalus is semicircular in outline, broadly convex, but with a shallow central concavity that is irregularly pitted. The counterpart of the latter is formed by the external surface of the calcaneum, and the two together are suggestive of the collateral ligament fossae of phalanges.

Calcaneum

This is a small, semicircular, button-like bone tightly appressed (if not coalesced) to the external end of the astragalus "cylinder" (Fig. 68). It completes the outer end of the mesotarsal joint articulating against tarsal IV. A thin dorsal lip, situated lateral to the main mass of the calcaneum, butted against the distal end of the fibula, and a broad triangular posterior surface contacted the external anterior part of the tibia extremity.

The external surface is roughly semicircular in outline and gently concave and has been likened above to the collateral ligament fossa of a phalanx. The calcaneum is preserved in its normal position against the astragalus in AMNH 3015 and YPM 5226, but an isolated calcaneum (YPM 5225) found at the Yale site indicates that the coalescing of these elements may not be complete. The calcaneum is larger and broader (transversely) and more semicircular in shape than that of *Ornithomimus* (YPM 542), which is quadrangular. However, the latter has a larger, more robust facet for the fibula. The calcaneum of *Allosaurus* is much larger relatively, is triangular, and contributes less to the anterior part of the mesotarsal joint surface.

Tarsal III

Of the five examples available of this bone, one was found in articulation with the right pes in AMNH 3015 and another was slightly displaced against the left pes in YPM 5205. These finds, together with the distal surfaces, clearly establish this bone as tarsal III, the medial element in the distal row of tarsals (Fig. 69A–C). Except for a rectangular notch at the anterior internal corner, tarsal III could be described as subrectangular in shape and strongly compressed. Maximum thickness is along the sharply convex posterior edge. Anteriorly, it wedges to a thin anterior edge. Passing from front to back, the proximal surface is increasingly convex, so in external or internal view it is wedge-shaped, tapering forward and becoming thicker and strongly rounded posteriorly. This curvature is the counterpart of the astragalus "cylinder." Because of the shorter fore-aft internal dimension, tarsal III is more rounded internally than it is externally. The external edge is straight, but rugose, indicating sutural or ligamentous union with tarsal IV.

Whereas the proximal surface is smooth and broadly rounded, the distal surface is gently concave and moderately rough. A fore-aft ridge divides it

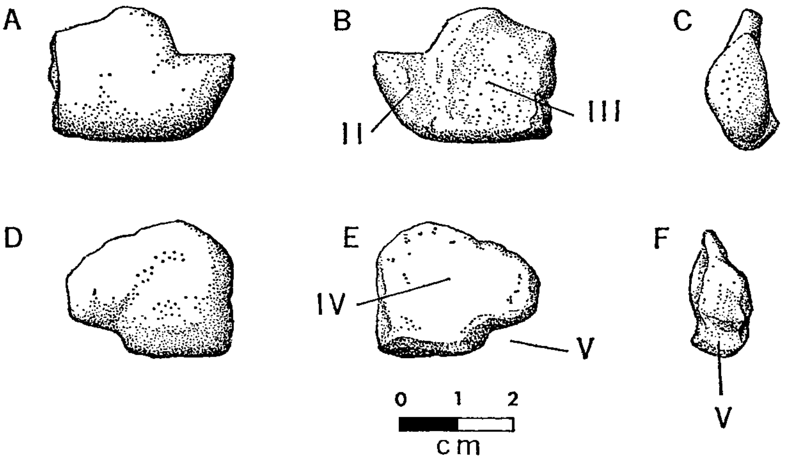


FIG. 69. Distal tarsals of *Deinonychus antirrhopus* (YPM 5207). Both elements drawn in reverse from right tarsus. Tarsal III in proximal (A), distal (B) and medial (C) views. Tarsal IV in proximal (D), distal (E) and lateral (F) views. In all views, anterior is up and posterior is down. II, III, IV and V—articular facets for respective metatarsals.

into a small, irregular, internal concavity (beneath the bulbous inner projection) for contact with metatarsal II, and a larger, nearly rectangular surface for metatarsal III. The latter caps the posterior two thirds of the proximal surface of metatarsal III, but only the posterior third of metatarsal II proximal surface is so covered. Apparently both of these bones contributed to the inferior surface of the mesotarsal joint.

Tarsal IV

This bone (Fig. 69D–F) was found articulated in proper position in the right pes of AMNH 3015. It is similar to the preceding bone except that it is thinner, slightly less convex proximally, and less concave distally. The greatest convexity is along the posterior border, as in tarsal III. The external posterior corner is notched, marking the position of the fifth metatarsal. The internal edge corresponds to and articulates with the external edge of tarsal III. There is no division of the distal surface, but as in tarsal III it is of moderately rough texture. It articulates only with metatarsal IV, although it may have had contact with metatarsal V. It caps all but the anterior edge of the metatarsal proximal surface.

These two tarsals appear to have been tightly bound together, probably by ligaments, in a plane which passed between digits III and IV. They appear to have been firmly fixed on the proximal extremities of the three principal metatarsals and functioned as part of the pes (Fig. 70). The gently convex anterior half of their combined proximal surface, together with the concavity in front of this, formed by the anterior parts of the metatarsal proximal surfaces, probably functioned as the normal weight-bearing surface of the mesotarsal joint. The more strongly convex posterior surface permitted the final phases of flexion at the tarsus at the end of each stride.

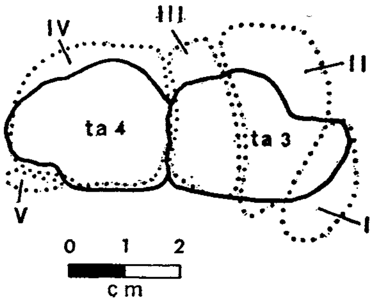


FIG. 70. Outline of the distal tarsals (solid lines) in *Deinonychus antirrhopus* and their relationships with the metatarsals (outlined by dotted lines). Abbreviations: ta 3—tarsal III; ta 4—tarsal IV; I, II, III, IV, V—the five metatarsals.

PES

The pes is basically tridactyl in structure, although a reduced hallux, as well as a remnant of metatarsal V, are present. However, the foot functioned as a didactyl structure in walking. Digit II is highly specialized for a non-locomotory, predatory function and quite probably did not contact the ground at all under normal circumstances (Fig. 71). The structural weight-bearing axis of the foot has been incompletely shifted from digit III to a position between III and IV. This is reflected in a number of features, but particularly in the equal lengths of digits III and IV (Fig. 73) and the distinctly shorter length of digit II, the trenchant form of the second ungual (Figs. 74 and 75) and the junction of tarsals III and IV coinciding with that of metatarsals III and IV (Fig. 70).

The unusual structure of the pes is an important clue to understanding the habits and nature of this strange animal. It is also considered to be of unusual taxonomic significance, as is discussed in the section on the affinities of *Deinonychus.*

Metatarsus

As shown in Figs. 73–75, the metatarsus of *Deinonychus* consists of six bones, three large, stout elements (II, III and IV), a long splint-like fifth, and a divided first. All are represented in the Yale collections and all but the first are present in the American Museum specimen. With the exception of the bone here interpreted as the proximal end of metatarsal I, all were found articulated, either in YPM 5205 or in AMNH 3015. The metatarsus is of normal theropod design, but is unusually short, measuring less than 50 percent of tibia length.

The first digit has been reduced and directed back and inward. The metatarsal is divided into distal and proximal halves (Fig. 72); the intervening part of the shaft failed to ossify and was probably cartilaginous. The distal portion consists of a slightly curved bone, oval in section distally, but flattened and tapered proximally. The flattened upper end fitted against a small depression on the posteromedial surface of the shaft of metatarsal II, slightly above mid-length. From this attachment, it curves down and posteromedially. The distal end is expanded into a triangular head with a deep bisecting

FIG. 71. Left pes of *Deinonychus antirrhopus*, YPM 5205, holotype.

groove—an incipient ginglymoid facet. The groove is oriented at about 45° to the fore-aft plane of the pes, indicating that in the flexed position the first digit reached forward and inward, whereas in the extended state it reached back and outward to a position behind the principal metatarsals. A deep oval fossa is present on the outside at the distal end next to metatarsal II, indicating the existence of a very strong collateral ligament on the external side of the joint with the first phalanx. The absence of a comparable internal collateral ligament probably is correlated with the position of this joint—alongside the medial surface of the second metatarsal near its mid-length. At this location, there is little possibility of dislocating the proximal phalanx outward against metatarsal II, hence little need for a strong internal collateral ligament. The opposite dislocation (inward away from metatarsal II) would

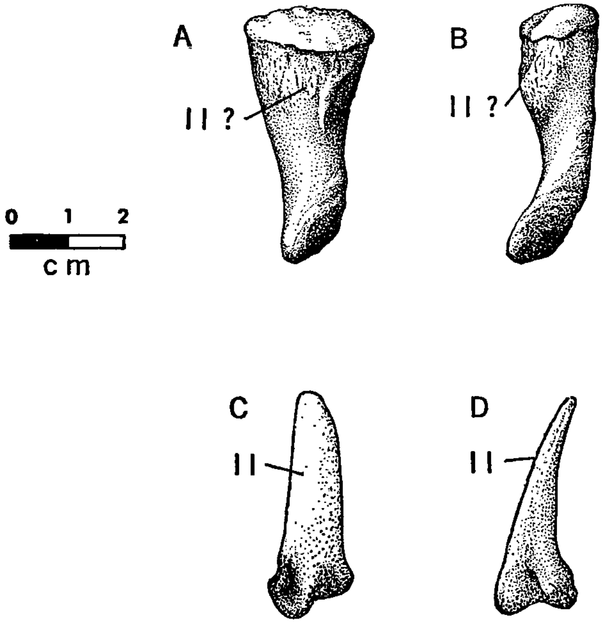


FIG. 72. Metatarsal I of *Deinonychus antirrhopus.* A) B) probable proximal half of the first metatarsal (YPM 5240) in lateral and posterior views; C) and D) the distal half of metatarsal I (YPM 5217) in lateral and posterior views. Abbreviations: II—articular contact with metatarsal II; II?—possible scar of articular contact with metatarsal II.

have been more probable, however, and thus required a resisting external ligament.

A single example (YPM 5240) is available of what I consider to be the proximal end of the first metatarsal (Fig. 72A and B). This bone was found associated with elements of left and right feet and a right manus, but was not in articulation. Its identity must remain in doubt, but it resembles very closely the proximal end of metatarsal I in *Allosaurus* as shown by Osborn (1899: Fig. 4a). It is approximately the right size, but is more robust than I would have expected for this element.

Like the distal half, this bone is curved slightly, and the proximal end is expanded into an oval, convex, articular surface. The upper part of the shaft is oval in section, striated internally and rugose externally. The latter may mark the site of ligaments which joined this to the upper posterior part of the second metatarsal. Except for this latter feature, there is no scar, facet, or other indication of direct contact with metatarsal II.

The bone tapers distally, but retains its oval cross section, and terminates quite abruptly in an oblique, convex surface that is slightly rough in texture, perhaps indicative of a cartilaginous extension to the distal half described above.

Metatarsals II, III and IV are long and rather stout (Figs. 73 and 75). The third is the longest, although it is only a little longer than IV, and is straight shafted. Both metatarsals II and IV curve away from the median metatarsal distally. Proximally, the three elements are tightly appressed together, as shown by large flat appositional facets on all three. As a consequence of the close apposition of the metatarsals, III is moderately compressed transversely at its upper end, although not wedge-shaped as in *Ornithomimus*. The proximal end is still stout and contributes significantly to the tarsal-metatarsal joint. Whereas II and IV have near uniform shafts throughout their length, III is stouter in its distal half, as a result of transverse compression proximally between the adjacent metatarsals. The shafts of II and IV are oval in section, that of III is rectangular.

Proximally the ends of all three main metatarsals are expanded into large, flat to slightly concave, articular surfaces. That of IV is the largest in area and the only one to show significant concavity. It is nearly square in outline. The proximal surface of III is a slightly convex, narrow, fore-aft rectangle. That

TABLE 11. Measurements (in millimeters) of the pes of *Deinonychus antirrhopus*

	AMNH 3015 Left	AMNH 3015 Right	YPM 5205 Left	YPM 5207 Right	YPM 5217 Left
TARSAL III					
Length (proximo-distal)	—	9.2	11.6	11.3	7.8
Transverse width	25.0	27.0	32.0	32.7	24.7
Antero-posterior width	24.0	22.3	24.9	23.8	18.7
					YPM 5223 Left
TARSAL IV					
Length (proximo-distal)	8.0	7.9	—	8.6	6.0
Transverse width	27.4	27.0	—	29.0	23.6
Antero-posterior width	20.0	18.2	—	23.7	17.0
			YPM 5240 Left	YPM 5217 Right	
METATARSAL I					
Length (proximal half)	—	—	45.5	—	—
Proximal transverse width	—	—	22.0	—	—
Length (distal half)	—	—	40.0	39.1	—
Distal transverse width	—	—	14.6	15.2	—
			YPM 5205 Left		
METATARSAL II					
Length	—	129.0	134.0	—	—
Distal transverse width	21.4	21.4	21.8	—	—
Proximal transverse width	21.1	20.5	18.6	—	—
METATARSAL III					
Length	—	151.0*	150.0*	150.5	—
Distal transverse width	24.1	24.0	24.3	22.4	—
Proximal transverse width	15.0	15.1	—	15.1	—

TABLE 11. (continued)

METATARSAL IV						
Length	134.0	134.0*	141.0	—	—	
Distal transverse width	21.5	25.5	21.0	—	—	
Proximal transverse width	25.3	28.5	28.0	—	—	
			YPM 5217 Left			
METATARSAL V						
Length	—	>34.0	53.3?	69.1	—	
Distal transverse width	—	—	5.6	4.9	—	
Proximal transverse width	—	11.0	10.8	10.7	—	
			YPM 5205 Left	YPM 5207 Right	YPM 5217 Left	YPM 5217 Right
PHALANGES						
I^1 Length	—	—	32.9	33.1	—	—
Distal transverse width	—	—	11.8	11.5	—	—
Proximal transverse width	—	—	16.2	16.3	14.4	—
				YPM 5205 Right		
I^2 Length along outer curve	—	—	>47.0	—	>41.0	—
Facet height	—	—	20.8*	20.2	15.7	—
Proximal transverse width	8.5	—	9.5	9.1	8.8	—
II^1 Length	—	37.7	43.5	—	43.3	42.8
Distal transverse width	19.6	19.8	19.5	—	19.8	18.6
Proximal transverse width	—	25.2	23.0	—	22.2	21.6
II^2 Length	41.0	42.2	49.6	44.8†	—	—
Distal transverse width	12.8	13.4	14.0	15.0	—	—
Proximal transverse width	17.7	17.7	19.0	24.3	—	—
						YPM 5218 Right
II^3 Length along outer curve	—	>85.0	>122.0	—	—	>112.0
Facet height	27.8	27.5	35.0*	—	—	31.0*
Proximal transverse width	11.2	11.9	12.4	—	—	11.9
III^1 Length	52.0	52.5	59.5	59.4	—	—
Distal transverse width	19.0	19.5	20.0	20.1	19.8	—
Proximal transverse width	24.4	23.6	26.7	25.5	—	—

TABLE 11. (continued)

					YPM 5207 Right		
III²	Length	33.0	30.1	39.9	39.0	—	—
	Distal transverse width	17.0	16.8	18.2	18.0	—	—
	Proximal transverse width	18.6	18.5	20.8	21.4	—	—
III³	Length	28.0	25.9	37.6	37.4	35.4	—
	Distal transverse width	15.4	15.0	14.2	14.8	12.8	—
	Proximal transverse width	16.5	16.4	18.2	18.5	11.2	—
					YPM 5205 Right		
III⁴	Length along outer curve	—	>50.0	>67.0	>50.0	65.5	—
	Facet height	—	19.0*	24.0	23.9	21.2	—
	Proximal transverse width	—	12.5	12.9	13.3	11.9	—
IV¹	Length	44.7	44.7	49.0	50.0	46.5	46.6
	Distal transverse width	18.4	18.9	19.3	20.1	18.2	18.3
	Proximal transverse width	—	19.9	22.3	21.5	18.1	20.2
IV²	Length	35.0	35.9	34.7	36.0	33.6	36.9
	Distal transverse width	17.4	19.2	18.5	18.5	17.5	17.0
	Proximal transverse width	19.1	20.0	20.0	19.8	18.4	18.4
IV³	Length	—	32.2	30.3*	30.6	—	27.8
	Distal transverse width	15.0	14.7	16.0	16.4	17.3*	15.1
	Proximal transverse width	—	18.0	17.3	18.6	—	16.3
					YPM 5205 Right		
IV⁴	Length	26.3	25.0*	28.7	28.5	28.0	—
	Distal transverse width	13.6	—	12.9	13.3	11.5	—
	Proximal transverse width	14.2	14.0	15.2	16.0	14.4	—
IV⁵	Length along outer curve	—	>42.0	>55.0	>54.0	56.0	>40.0
	Facet height	17.0*	—	20.1	19.8	18.6	18.8
	Proximal transverse width	9.5	—	11.6	12.0	10.9	10.9

† Fractured during life.
* = approximate.

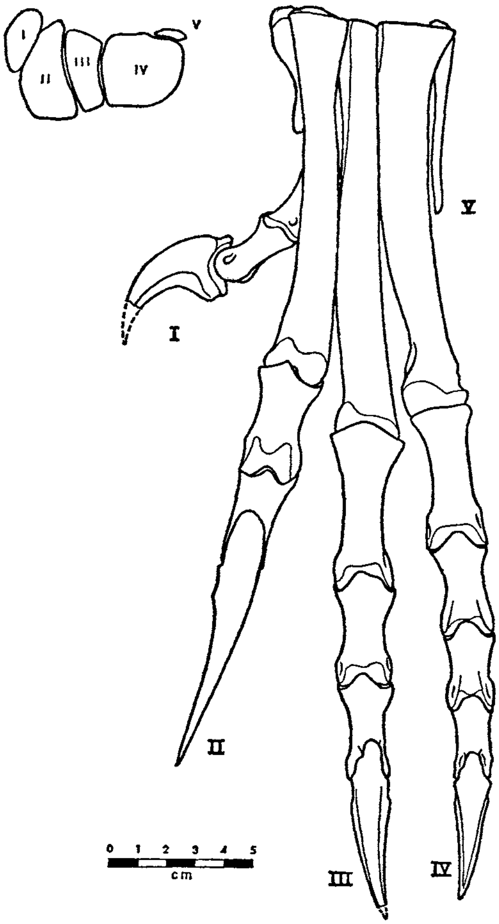


FIG. 73. Left pes of *Deinonychus antirrhopus* (YPM 5205) in dorsal (anterior) aspect. The proximal end of the metatarsus is outlined at upper left.

of II is semicircular in outline and nearly planar. All three surfaces are finely textured and lack the smooth, "highly finished" surfaces characteristic of the more distal articular facets of the foot.

The distal ends of all three metatarsals are well-formed and distinctive. That of II is unusual in that it is a deeply grooved, strongly asymmetrical ginglymus, the medial condyle of which is much smaller than the lateral. Both condyles extend well onto the ventral (posterior) surface of the shaft, indicative of considerable freedom of flexion. A large, deep, external, collateral ligament fossa is present, but the medial fossa is represented only by a faint depression. A plausible explanation for this parallels that suggested for the similar condition of the first metatarsal. A large lateral ligament here would resist displacement of the digit away (inward) from the median (III) digit. (Metatarsal III has subequal collateral fossae and IV has one internally, or next to III, but not externally).

Metatarsal III also has a deeply grooved distal articular surface but in this instance it forms a nearly symmetrical ginglymus. The collateral ligament fossae are subequal. Metatarsal IV, however, has a broadly rounded (transversely and longitudinally) distal articular facet, quite unlike the extremities of II and III, without the slightest suggestion of a fore-aft groove.

Aside from their somewhat shorter relative lengths, the metatarsals appear to be of normal theropod construction, and in the absence of phalanges certain peculiarities in their morphology might not be noticed. First of all, the deeply grooved distal facet of metatarsal II is extraordinary. Excluding the few exceptions that I have noted in a following section, this condition is not known in any other theropod. Its development is a critical factor in the remarkable specialization of the second digit. Second, metatarsals II and IV are not subequal in length, the usual condition in most theropods, but instead metatarsal IV is nearly as long as III. Third, the metatarsus displays other evidence that the structural axis of the foot passed between metatarsals III and IV, rather than along III as in most theropods. The evidence is: the disparity in the sizes of the appositional scars on either side of metatarsal III, a very large and long scar for metatarsal II, but a very short and small scar for metatarsal IV; and the junction of the subequal tarsal III and tarsal IV situated directly above the contact of metatarsal III and IV, as shown in Figure 70. Metatarsals II and III were tightly bound together and in contact for more than half their length. (YPM 5217, a nearly perfect third metatarsal shows a long flat inner surface that extends over more than 75% of its length, and in metatarsal II of YPM 5205 the counterpart scar extends almost to the distal extremity.) Metatarsal IV diverged more widely from III and contacted the latter only proximally. The very pronounced asymmetry of the distal facet of II is probably related to the extensive contact of the second and third metatarsals. The divergence of III and IV clearly broadened the weight-bearing part of the foot. The tight apposition of II and III probably provided reinforcement of digit II.

The fifth metatarsal is preserved in place in the right pes of AMNH 3015, and several isolated fifth metatarsals were recovered at the Yale site. This bone has been reduced to a long but narrow splinter. It tapers distally to an irregular extremity. Proximally it is slightly expanded transversely, but compressed fore and aft. The proximal end is strongly convex and the extent of its articular surface is well shown by texture and a faint, bordering ridge. The bone was situated along the posterior face of the fourth metatarsal shaft and articulated with that bone at the posterior-external margin of its proximal facet. A distinct concave notch exists at this point. The proximal end of V is flattened anteriorly for this contact.

Phalanges

The phalangeal formula of the pes is 2–3–4–5–0, (Figs. 73 and 75), the same as in most other theropods. The proximal phalanges are the longest elements, as usual, in digits III and IV, but not in digit II where the ungual is twice as long as the other phalanges. The articular facets of all phalangeal elements are well-formed and highly finished. With the exception of the proximal surface of the first phalanx of digit IV, all proximal phalangeal facets feature prominent lateral and medial concavities separated by a strong vertical ridge. The distal facets are all strongly grooved, nearly symmetrical, ginglymoid articulations.

In all phalanges except those of II, the ginglymus is bounded on both sides by very deep, subequal, collateral ligament fossae. In the penultimate phalanges these fossae are situated well above the geometric center of the ginglymus arc, a condition which is correlated with the lower limit of extension characteristic of the ungual as compared with more proximal phalanges. In the latter, the collateral ligament fossae are almost precisely at the geometric center of the articular arc.

The phalanges of III and IV are normal in form and provided the usual ranges of extension and flexion at all joints. In all instances, the amount of flexion possible (50°) appears about twice as great as the degree of extension (25°), the precise arcs of rotation varying slightly from one joint to another. The unguals of digits III and IV are also of normal design, being slightly curved, strongly tapered bones with well defined, ridged articular facets. Both are quite robust and triangular in cross section, the ventral surface being broad and flat, as compared with a narrow and curved dorsal section. Strong grooves mark both lateral and medial surfaces. A massive, but not elongate, flexor tubercle is present at the proximal limit of the ventral surface immediately distal to the articular facet. The dorsal profile is slightly prolonged proximally at the upper limit of the articular surface for attachment of extensor ligaments.

Digit one presents comparable phalanges except that the ungual is relatively shorter and deeper and is oval rather than triangular in section. These differences undoubtedly are related to the fact that this digit probably was not used in walking and could not touch the ground under most circumstances.

Digit II differs from the other digits in the enormous size and scimitar shape of the ungual and in the very large radius of curvature and peculiar form of the articular facets at all joints. The phalangeal articulations have been highly specialized so that the distal joint is for flexion only and the proximal interphalangeal joint is for extension only.

As noted earlier, the distal extremity of metatarsal II is deeply grooved

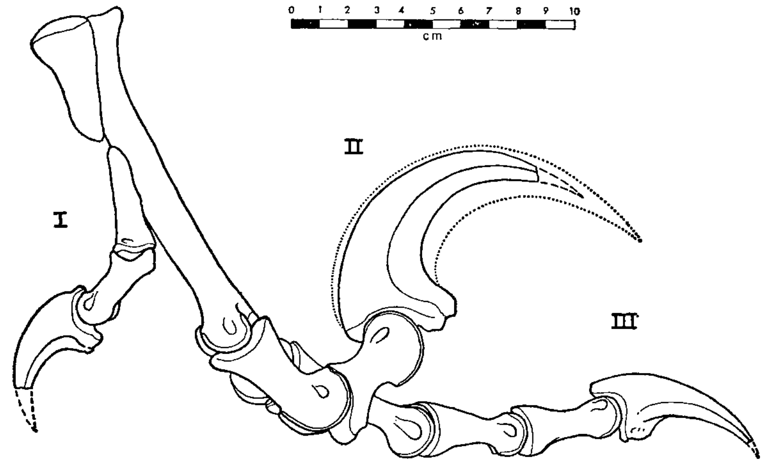


FIG. 74. Left pes of *Deinonychus antirrhopus* (YPM 5205) in internal aspect. Notice the extreme contrast in the form of the second and third unguals. The dotted line represents a conservative estimate of the size and shape of the horny claw carried by the ungual.

(Fig. 75). Accordingly, the proximal surface of the first phalanx is strongly ridged. These features are as prominently developed here as at any joint on the other digits. To the best of my knowledge, this is unique to *Deinonychus* and related forms. Undoubtly, this joint provided the usual flexion and extension of the proximal phalanx but allowed little or no lateral or medial movement. As closely as I can measure it, the plane of flexion at this joint diverged approximately 25° from the axis of metatarsal III, partly a result of the medial deflection of the distal end of the second metatarsal, but also resulting from the pronounced asymmetry of the distal facet of that metatarsal (Figs. 73, 75).

The distal end of the first phalanx of II is distinctive in that the ginglymoid facet is divided by an extremely deep groove. Moreover, this groove is not rounded in dorsal profile but is triangular, i.e., the groove is very narrow at the bottom, and both side walls of the groove are convex transversely as well as longitudinally. The proximal ridge of the second phalanx is correspondingly sharp-crested and not rounded in cross section and the flanks of this ridge are concave both transversely and longitudinally. The unusual form of this ginglymus appears to have established absolutely perfect planar motion at this joint—only pure flexion and extension with no adduction or abduction or twisting of the second phalanx against the first.

Another unusual feature is the extreme development of the ginglymus well above the dorsal surface of the shaft, extending far proximally in its dorsal development, rather than ventrally as in most instances. This extension of the upper limits of the distal facet greatly increased the radius of curvature and provided an unusual degree of extension, whereas the restriction of the inferior limits of these surfaces reduced the amount of flexion possible, as shown in Figure 76. The enlarged radius of curvature of these articular facets probably strengthened these joints as well as changing the movements possible.

The proximal end of the second phalanx is extended ventrally into a very robust proximal projection or "heel." The articular facet extends over the length of this ventral heel, so that the ventral limit of the facet reaches far proximal to the dorsal limit. As shown in Figures 75 and 76, when in articulation with the proximal phalanx, this heel extends far beneath the distal end of the adjacent bone. Quite probably, this structure was the attachment site of a powerful flexor muscle, but notice that flexion was also limited by this process. On the other hand, this joint permitted perhaps as much as 90° of extension, a unique adaptation to provide considerable planar extension, apparently to elevate the ungual well off the ground, or at least to separate it widely from the adjacent digits. The proximal heel may have been developed to increase the leverage of flexors that attached in this region and which probably served to resist the tendency for the distal phalanges to be "extended" whenever the claw was applied against the flesh of a victim.

The distal end of the second phalanx bears a very large and very deeply grooved ginglymoid articular facet with an unusually large radius of curvature. Again, the groove is triangular in cross section—sharply defined at the base and broad above. The facet arc is nearly circular and passes through approximately 180°. Unlike the previous ginglymus, however, the present one is extended ventrally, reaching far proximally in its ventral limit, but is not excessively developed in its dorsal limits. The collateral ligament fossae, which are relatively

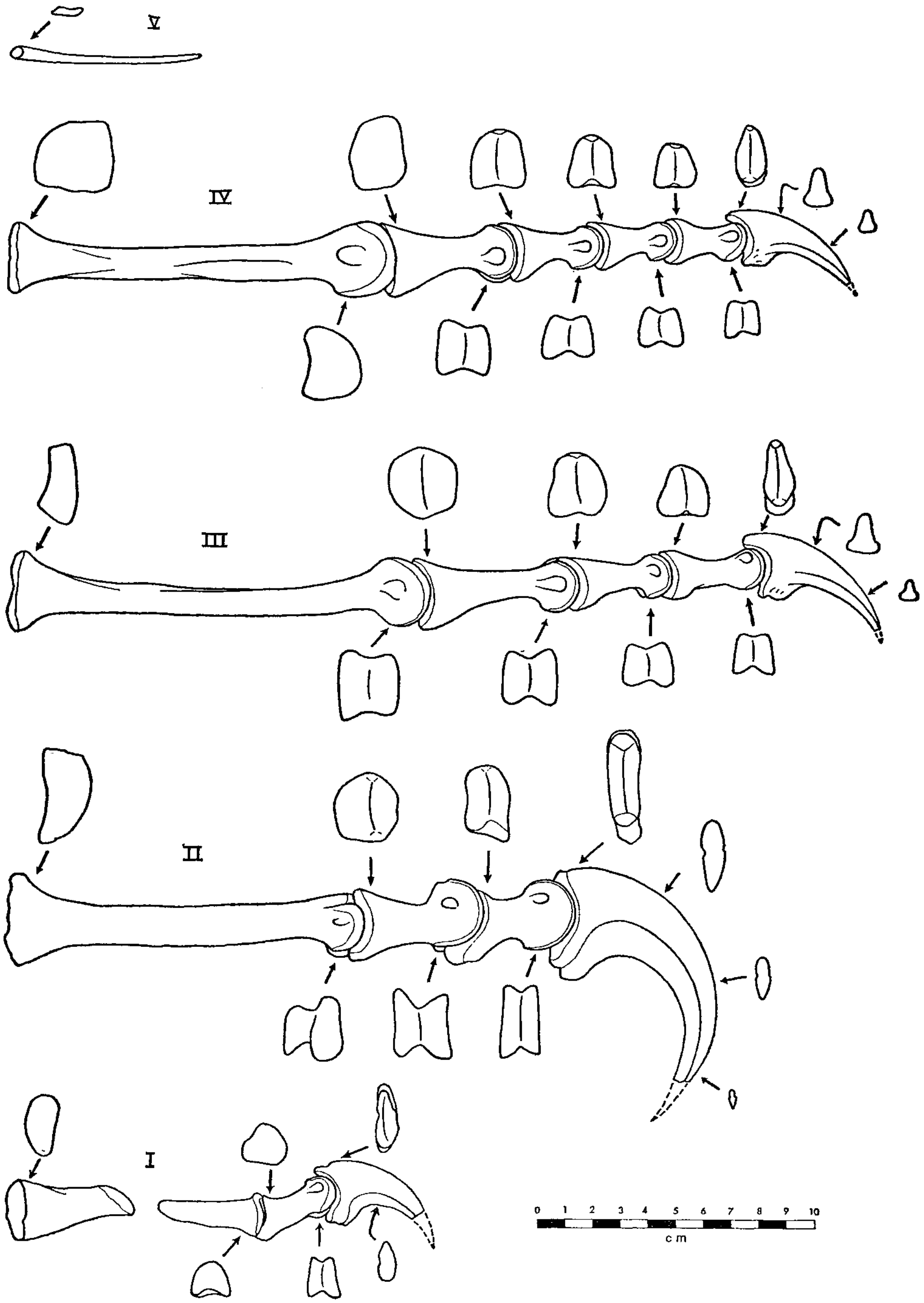


FIG. 75. The digits of the left pes of *Deinonychus antirrhopus* (based largely on YPM 5205) in medial aspect. Outlines of the proximal extremities of each element occur above each digit, outlines of distal extremities are below. Notice the differences in the articular facets and cross sections between ungual II and unguals III and IV.

small but extremely deep, are accentrically located, well above the center of the ginglymus arc. The positions of these fossae and the ventral extension of the articular surface permitted considerable flexion, but very little, if any, extension (Fig. 76). The three joints of digit II are highly specialized to a condition that has not previously been noticed among theropods. Following recognition of this condition in *Deinonychus,* owing to the remarkable preservation of the Yale material, nearly identical specializations have been found in several other species (Fig. 80). These are discussed in a following section.

The ungual of digit II is the most impressive of all the foot elements, and therefore deserves more detailed comments. The ungual closely resembles the strongly recurved, laterally compressed and trenchant claws of the manus, but it is much larger, more strongly recurved and more trenchant—almost bladelike (compare Figs. 74, 75 and 77 with Fig. 63). Originally, in fact, I thought it to be a manus claw (it was found several inches away from the rest of the foot—YPM 5205—in the Yale quarry) because it was so much larger and very different in form from the unguals found in articulation in pes digits III and IV. However, the articular facet is much too large for any phalanx of the manus and it articulates perfectly with the penultimate phalanx of the second pedal digit found in articulation. Subsequent finds have verified this relationship.

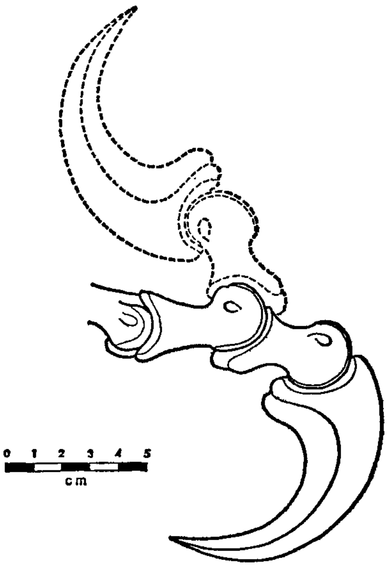


FIG. 76. Medial outline of the second digit of the pes of *Deinonychus antirrhopus* (YPM 5205) showing maximum flexion (solid lines) and the unusual degree of extension (dashed lines) possible at the two distal joints. Extension is achieved largely between the first and second phalanges and flexion largely between the second and third phalanges. Extreme extension appears to have been an adaptation to elevate the digit off the ground and thus protect the claw from damage while walking.

The ungual articular facet is a deep, nearly circular curve in lateral view and a parallel-sided, narrow rectangle in proximal view. This facet is bisected by a very strong, sharp-crested, vertical ridge which fits "like a cast in a mold" into the distal facet of the second phalanx. Its form provided perfect planar rotation (flexion) of the ungual through an arc of 90° or more. Figure 76 illustrates the maximum degrees of flexion and extension permitted by these joints.

An additional feature that seems to be distinctive of *Deinonychus* and closely related forms and that distinguishes this second ungual from similar trenchant and strongly recurved claws of other theropods (whether of manus or pes) is its abrupt curvature relative to the chord of the articular facet (the line connecting upper and lower extremities of the articular facet when viewed laterally). This abrupt curvature is most apparent when comparable unguals are oriented in identical positions, as for example in Figure 77a-e, where the articular facet chord is oriented vertically. As shown in Figure 77a, the ungual of *Deinonychus* curves through a far greater arc (160°) than do any of the other examples, including the claws of the manus of *Deinonychus,* yet it features the shortest ungual extension (e) perpendicular to the articular facet chord. The ratio of ungual extension to height (h) is much less (.45)

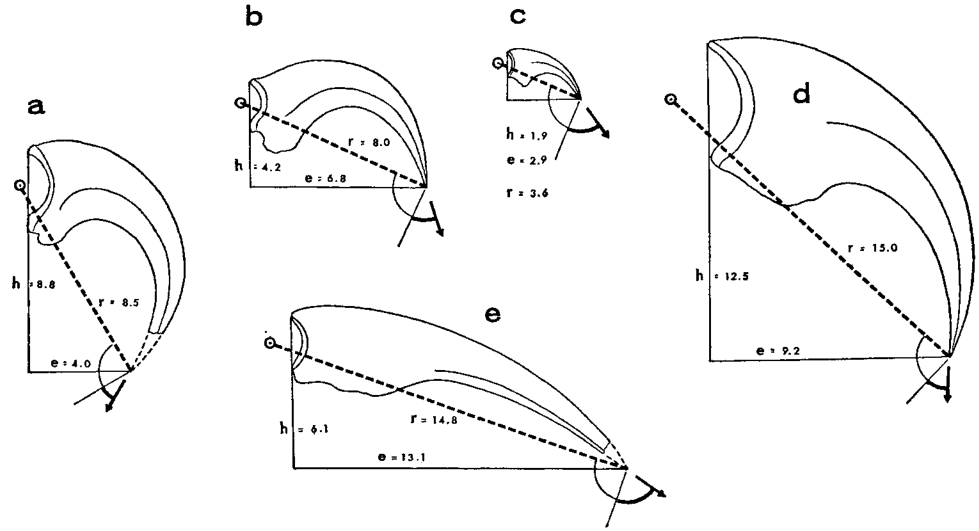


FIG. 77. Comparison of the second pedal ungual of *Deinonychus* (a) with raptorial type manus unguals of *Deinonychus* (b), *Ornitholestes* (c) and *Allosaurus* (d), all drawn in simple profile, one third natural size. The second ungual of the manus of *Ornithomimus* (e) is included to provide comparison with a straight, non-raptorial ungual form. To facilitate comparison, all have the chord of the articular facet arc oriented vertically. This chord has been extended (h) to meet a perpendicular (e) from the ungual extremity. The differences in ungual form are obvious; these may also be expressed by the ratio of height (h) to extension (e). The radius (r) of ungual rotation (flexion) has been drawn (heavy dashed line) from the center of rotation to the extremity of each ungual. These radii may also be considered as ungual lever arms. The arrows indicate the projected trace of the inner cutting edge of each ungual. Notice the contrast in arrow orientation relative to the vertical chord of the articular facet. See text for further discussion. All linear dimensions are in centimeters.

a = *Deinonychus antirrhopus,* pes digit II, YPM 5205
b = *Deinonychus antirrhopus,* manus digit II, YPM 5206
c = *Ornitholestes hermanni,* manus digit III, AMNH 587
d = *Allosaurus fragilis,* manus digit I, USNM 4734
e = *Ornithomimus sedens,* manus digit II, USNM 4736

in the second digit of the pes in *Deinonychus* than it is in unguals of the manus in *Deinonychus* (1.62), *Ornitholestes* (1.52) or *Allosaurus* (.73). This relationship is also evident in the much steeper orientation of the radius of ungual flexion (r) drawn from the center of rotation to the tip of the ungual (Fig. 77a-e). The second manus ungual of *Ornithomimus sedens* is included in Figure 77 (e) to illustrate the opposite extreme of ungual form.

The functional significance of this extreme curvature is not entirely understood, but the condition appears to be correlated with the orientation of the extremity and the cutting edge (inferior distal curvature) relative to both the articular facet and the lever arm (r) of the ungual. Compare the attitudes of the five arrows indicating the axis of each cutting edge at the extremity in Figure 77. It is obvious, I think, that the attitude of a claw extremity is *the* critical factor in its design. The fact that the extremity of the present ungual is actually directed backward toward the articular facet chord, and the cutting edge faces backward rather than downward, suggests that retraction or a backward phase to the stroke may have been as important as flexion during use of this structure. Application of this claw probably involved an initial downward stroke produced by flexion from the fully extended position (Fig. 76) probably at all three digit joints and perhaps also by flexion at the mesotarsal joint and the knee. This may have been continued as a downward and backward stroke (retraction) produced by the flexors of the lower limb and the femoral retractors. Hypothetical as this picture is, it provides the best explanation for the unusual position of the ungual extremity relative to the articular facet and the unusual degree of curvature.

The actual arc through which the *Deinonychus* claw moved during use was produced by movements at several joints. It is not possible to reconstruct which joints flexed (and to what extent), which were fixed and which extended. Nor is it possible to determine the sequence of joint actions or the instant of particular joint action during the offensive stroke. Therefore, it is not possible to determine the precise angular relationships between the piercing talon and the surface under attack. However, we can evaluate the relationships of the two distal segments of this weapon system. The point about which the ungual rotated during flexion against the adjacent phalanx is known and the arc of ungual flexion can therefore be determined. That arc probably exceeded 90° and its radius was at least 80 mm. The radius of rotation of the horny claw probably exceeded 100 mm.

The radius of ungual rotation also represents the ungual lever arm. The dashed lines (r) of Figures 77 and 78 represent the lever arms of the various unguals illustrated, connecting the fulcrum of each to the ungual extremity. Considering the unguals alone, the maximum force that can be applied by the ungual as it pivots about its fulcrum acts perpendicular to this lever arm (tangential to the arc of ungual flexion). In Figure 77a-e, it is evident that the extremity of the *Deinonychus* pedal ungual deviates from the perpendicular by a smaller angle than do the extremities of the other unguals illustrated. In other words, the ungual shape in *Deinonychus* very nearly coincides with the axis of maximum force and thus is designed for maximum penetration. Figure 78 illustrates these features in greater detail. The same four raptorial unguals of Figure 77 are shown here, but they have been drawn so that all ungual levers

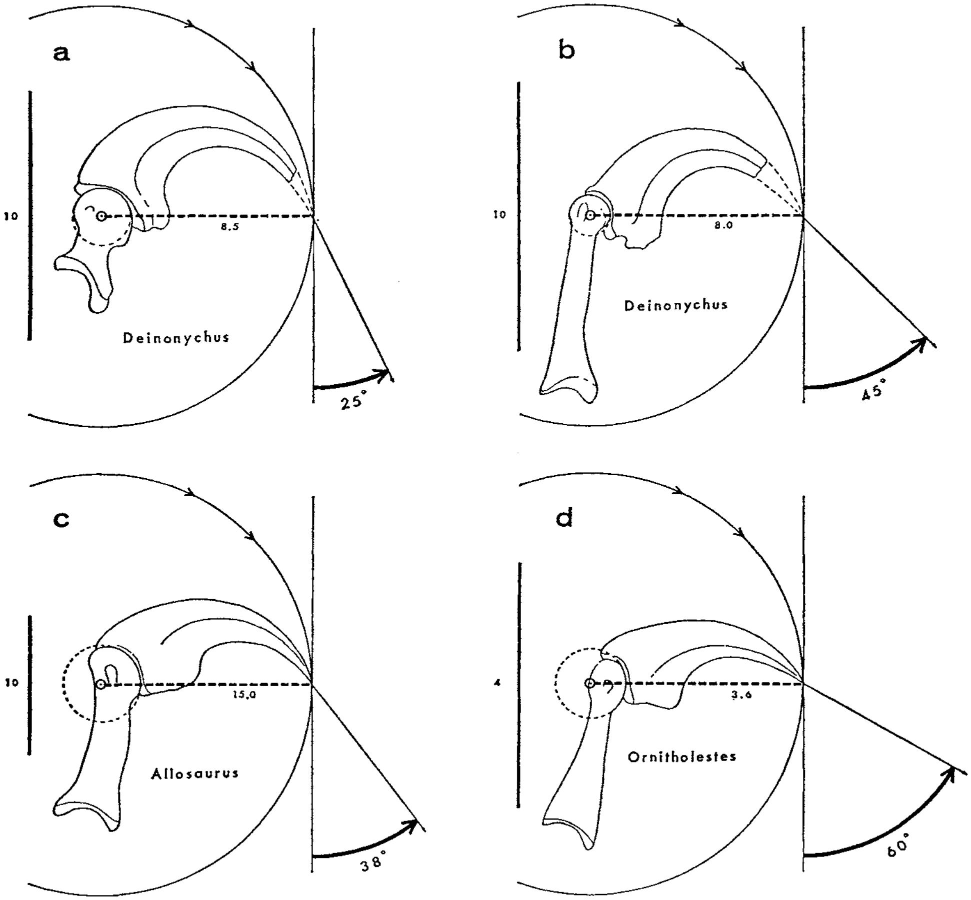


FIG. 78. Comparison of ungual form and mechanics of the second pedal ungual of *Deinonychus* (a) with the second manual ungual of *Deinonychus* (b), the first manual ungual of *Allosaurus* (c) and the third manual ungual of *Ornitholestes* (d). All unguals are drawn to unit length so the ungual lever arms or radii of flexion (heavy dashed lines) are equal. The vertical lines to the left of each give the true scale in centimeters. The small dashed-line circles represent projections of the curvature of the articular facets on the penultimate phalanges. Notice the comparatively small angle between the cutting edge of the ungual and the arc of rotation of the *Deinonychus* pes claw (a) as compared with the others. See text for further discussion. All linear dimensions are in centimeters.
a = *Deinonychus antirrhopus*, pes digit II, YPM 5205.
b = *Deinonychus antirrhopus*, manus digit II, YPM 5206.
c = *Allosaurus fragilis*, manus digit I, USNM 4734.
d = *Ornitholestes hermanni*, manus digit III, AMNH 587.

are equal. The actual length of each lever arm is given in centimeters and the scale for each is shown by the heavy vertical lines. The cutting edge of the *Deinonychus* pedal ungual (Fig. 78a) forms a very small angle (25°) with the arc of flexion. A comparable or smaller angle must have existed with respect to the horny claw. Contrast this small angle with the much larger angle of attack of the other theropod unguals (Fig. 78c and d) and that of the second manus ungual of *Deinonychus* (Fig. 78b). It would appear that selection has shifted the angle of attack to more nearly coincide with the arc of attack of the claw, thereby providing maximum cutting power and at the same time reducing the resistance component (which here acts along the tangent line perpendicular to the lever arm). There can be little doubt that the claw of *Deinonchus* was well adapted for deep penetration and effective slashing or cutting.

The ungual itself appears disproportionately large, relative to the other bones of the foot, but the horny claw must have added another 25 or 50 percent to its length. My own observations of the claws and unguals in a number of variously aged crocodilians, lizards and birds of prey indicate that the claw is rarely less than 25 percent longer (and sometimes is as much as 50 percent longer) than its supporting ungual. For *Deinonychus* this would mean a claw of more than 120 mm length, or nearly three times as large as the claws of a full-grown lion. A very conservative reconstruction of this claw has been outlined in Figure 74.

FUNCTIONAL SIGNIFICANCE OF THE PES

In my opinion, the foot of *Deinonychus* is perhaps the most revealing bit of anatomical evidence pertaining to dinosaurian habits and capabilities to be discovered in many decades. Grandiose statements of this kind are, of course, easily rejected, but the functional implications of the pes of *Deinonychus* are not so easily discarded—especially in view of the other remarkable adaptations of this animal. *Deinonychus* must have been anything but "reptilian" in its behavior, responses and way of life. It must have been a fleet-footed, highly predaceous, extremely agile and very active animal, sensitive to many stimuli and quick in its responses. These in turn indicate an unusual level of activity for a reptile and suggest an unusually high metabolic rate. The evidence for these lie chiefly, but not entirely, in the pes.

Deinonychus was an obligatory biped, yet the standard tridactyl theropod pes has been modified to a didactyl foot bearing a highly specialized *offensive* or predatory structure—a large sickle-clawed second toe. Stance and locomotion, the primary functions of the pes, especially in bipeds, were transferred entirely to the two remaining outer digits (III and IV). The second digit lost these usual pedal functions and became adapted exclusively for predation.

The nature of the sickle-shaped second ungual clearly establishes that this digit had little, if anything, to do with locomotion and that its primary function was to cut or slash. This is substantiated by the unique proximal interphalangeal articulation which provided extreme extension, whereby the claw could be elevated well above the ground, by the expanded distal ginglymus which permitted a sweeping 90° arc of flexion for the claw (Fig. 76), and by the unusual form of the ungual.

It is quite clear that this solitary, trenchant and strongly recurved claw was not designed for grasping (the claws of the other digits are distinctly not raptorial), nor does it appear to be suited for digging. The only obvious alternative function is one of cutting or slashing. But this alternative function requires extraordinary responses of equilibration and agility, for the claws could not have been used in this fashion as long as *both feet were on the ground.* Use of these claws was entirely dependent upon the animal's agility and its ability to stand on one leg—even while subduing its prey. The full retractile powers (power stroke) of the femur and lower leg provided more than adequate slicing power for this device.

5. HABITS OF *DEINONYCHUS*

From the skeletal remains now known to us, adult specimens of *Deinonychus antirrhopus* can be described as standing slightly more than one meter high at the head, measuring not more than 2.5 m in length in normal posture, but reaching somewhat over 3 m from snout to tail tip when stretched full length. Judging from the relative robustness of tibia and dorsal vertebrae, live weight may have ranged from 60 to 75 kg. The animal was a flesh-eater (the sharp, serrated dentition leaves no doubt about that) and almost certainly a predator.

In posture, *Deinonychus* was a biped, and the anatomy of the fore limb and manus establishes beyond doubt that it was an obligatory biped (Fig. 79). The fore limbs could not have been used for locomotion and probably were not used even for momentary quadrupedal stance. The vertebral column contains several interesting features that indicate a quite different posture than has usually been suggested in the past for theropodous dinosaurs. The neural spines of the dorsal vertebrae bear very prominent anterior and posterior scars that exactly duplicate scars on the thoracic vertebral spines of large ratites such as the extinct moa (*Dinornis*) and the modern ostrich, emu and cassowary. In the living ratites these bony scars are the sites of attachment of robust and very strong interspinous ligaments. Ratites normally maintain the dorsal vertebral series in a nearly horizontal attitude and robust interspinous ligaments are required as strong anti-tension fibers to resist the force of gravity and prevent the thoracic column from sagging. The striking similarity of these scars in ratites and *Deinonychus* is strong evidence of a similar horizontal attitude for the dorsal vertebrae and trunk region in the latter, rather than the traditional inclined attitude that has been illustrated for theropods so many times in recent years. The cervical vertebrae of *Deinonychus* seem to confirm this horizontal posture. These are sharply angled or wedge-shaped with the anterior face of the centrum well above and not quite parallel to the posterior face. The result is a pronounced, natural curve of the neck, quite similar to, but not as long as that in living ratites. Such curvature of the neck would be inconsistent with a sloping thoracic column, but is entirely consistent with a horizontal trunk.

Regarding locomotion, the hind limbs of *Deinonychus* appear to have been powerful limbs for moderately, but not unusually, fast running. The absence of a femur in present collections leaves this as an incompletely documented hypothesis because we cannot determine the exact ratio of fore limb to hind limb (the usual parameter of bipedality) or the ratio of propodial to epipodial (the usual index of cursorial ability). However, elongation of the metapodials

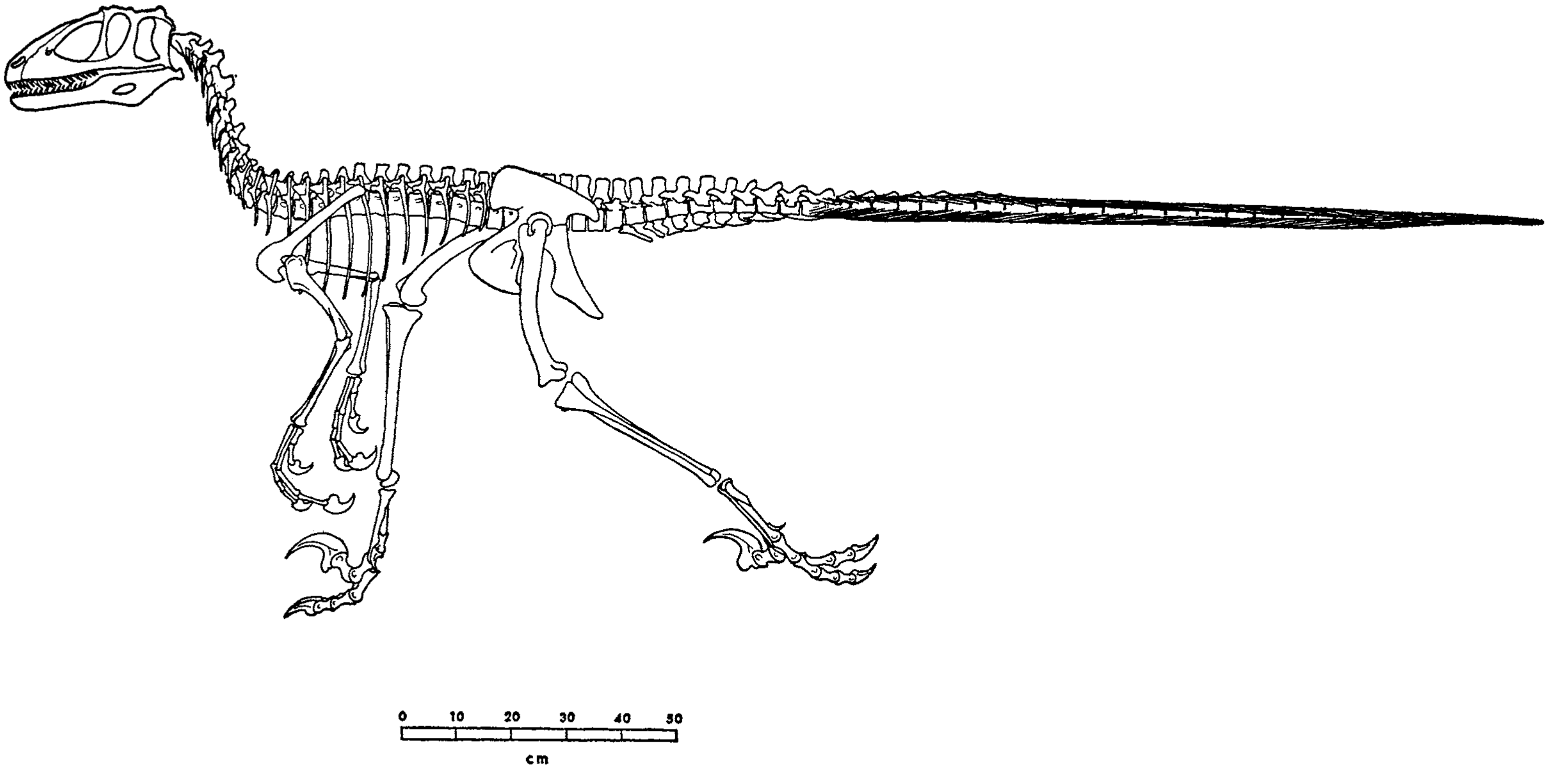


FIG. 79. Reconstruction of the skeleton of *Deinonychus antirrhopus* based on the hypodigm. Femur length is conjectural. The horizontal attitude of the dorsal series is patterned after the natural posture of the vertebral column in large ratites *(Struthio,* etc.). Supporting evidences are the enlarged interspinal ligament scars on dorsal neural spines (Fig. 34) and the natural curve of the cervical series (Fig. 31). Reconstruction by R. T. Bakker.

is a well-established index of fleet-footedness—witness the long epipodials and metapodials of antelope, deer, the cheetah and most fast-running ground birds. On this evidence, *Ornithomimus altus* with a tibia 115 percent as long as the femur and a metatarsus equal to 70 percent of tibia length has been considered very fleet of foot. *Ornitholestes,* though, has a tibia that is shorter than the femur by 15 percent, yet has a metatarsus that relatively is the longest of all theropods—75 percent of tibia length. These contrasting examples raise major doubts about extrapolating femur length from the relative lengths of metatarsus and tibia. The significant fact, however, is that the metatarsus of *Deinonychus* is the shortest, relative to tibia length, of any presently known theropod; it equals only 48 percent of tibia length. What this means is not clear, but it suggests that *Deinonychus* may not have been as fleet-footed as were many other theropods. More will be said of this peculiarity below.

The dentition of *Deinonychus* establishes that the basic diet was one of flesh. Although this animal may have been a carrion feeder, there is a significant body of evidence that indicates it was a very active predator. First, there are the long fore limbs with long hands bearing large, trenchant and raptorial claws. Second, the humerus and radius and ulna appear to have been capable of considerable abduction-adduction and the fore arm perhaps was capable of some pronation-supination. Third, the articular facets of the carpus clearly provided very precise abduction-adduction (up to 95°) and some 45° of pronation-supination of the manus. There can be little doubt that the hands and fore limbs of *Deinonychus* were well-adapted for grasping and holding. Such capabilities strongly suggest predation rather than scavenging. Add to this the highly specialized, sickle-like talon on the inner toe—a four- or five-inch-long weapon that could only have been used for cutting or slashing. Finally, consider the unusual anatomy of the caudal vertebrae that seems explicable only as a balancing adaptation—a dynamic stabilizer. When all these features are considered together, we have a rather convincing picture, I think, of *Deinonychus* as an active and very agile predator. It appears that this animal caught and held its prey in its fore hands and disemboweled it with the large pedal talons. This of course would require that *Deinonychus* stand, at least momentarily, on one foot while it ripped the victim's flesh with the claw of the opposite foot. It is of special interest here that both the ostrich and the cassowary are capable of inflicting serious injury with the large claw on the inner toe. Gilliard (1958) has noted that the cassowary can easily sever an arm or disembowel a man with its long sharp claws on the inner toes. The ostrich prefers to run, but when forced to fight slashes out with powerful kicks capable of ripping open man or lion (Austin, 1962).

Returning for a moment to the unusually short metatarsus of *Deinonychus,* I am tempted to relate this condition to the specialized second pedal digit. It is quite reasonable to suppose that a structure of this design requires more than ordinary force. Elongation of the distal limb components increases the length of the stride, but reduces the total force that can be exerted at the extremity because the resistance lever arm (total limb length) is several times as long as the applied force lever arm (that fraction of femur length between the acetabulum and the insertion of the femoral retractors). On these grounds we can suppose that femur length in *Deinonychus* exceeded tibia length. In any case, there seem to be sound mechanical reasons for equating the relatively short metatarsus of *Deinonychus* with non-locomotory activities. An interesting point that seems to substantiate this is that among the large living ratites only the cassowary bears a specialized offensive claw on the foot and the cassowary also has the shortest tarso-metatarsus relative to tibia length, although it is not as reduced as that of *Deinonychus* (Table 12).

The modified tail of *Deinonychus* appears to have been the critical stabilizing mechanism as predator and prey struggled. The large size of the ungual of the second toe (which was perhaps only half the size of the actual claw) suggests that *Deinonychus* may not have limited its predation to small animals, but may have attacked animals its own size or even several times larger than itself, for the pedal claw clearly was designed for deep penetration. This perhaps explains the unusually large skull and jaws. The above supposition does not seem so unreasonable when we recall that at least three and perhaps four or five individuals are represented among the *Deinonychus* remains collected from just a small area at the Yale site. These remains were associated with fragments of only one other species—a moderate-sized ornithopod that weighed perhaps five or six times as much as *Deinonychus.* The multiple remains of the latter suggest that *Deinonychus* may have been gregarious and hunted in packs.

The only specific evidence pertaining to the possible prey of this little carnivore are the fragmentary remains of the medium-sized ornithopod found in the Yale *Deinonychus* quarry. We cannot be certain that these remains are those of predator and prey, but we can be sure that they were not washed together by stream action. The close association of extremely delicate skull and postcranial remains with absolutely no indication of water action, abrasion, or normal chemical decomposition, all preserved in a fine-grained clay stone, indicate that these animals died together at or close to that spot. The fauna of the Cloverly Formation has not as yet been described, but it is presently under study (Ostrom, MS). Major tetrapods identified to date include small and moderate-sized ornithopods, small sauropods, a medium-sized nodosaur, large and small theropods, crocodilians and turtles. The medium-sized ornithopod is by far the most common element in the known fauna and (in view of its association in the Yale quarry) appears to be the most likely candidate as *Deinonychus* prey. An additional interesting fact that can hardly be explained as coincidental is that *Deinonychus*-type teeth (but nothing else) have been found associated with skeletons of this same ornithopod at 14 other sites in the Cloverly Formation.

6. AFFINITIES OF *DEINONYCHUS*

It should be evident from the preceding discussion that *Deinonychus* is distinguished by several unusual features. These are unusual in part because they have not previously been recognized in other taxa. Consequently, the relationships and phyletic position of *Deinonychus* are not easily established. In fact, I am unable to place this taxon in either of the conventional theropod infraorders—Coelurosauria or Carnosauria—with absolute certainty. For this reason, the infraordinal rank was intentionally omitted from the systematic summary at the beginning of the section on systematics.

The following points illustrate the problem. Of 35 *non*-carnosaurian traits listed by Romer (1956) as typical of coelurosaurs, 20 are characteristic of *Deinonychus.* Of 36 *non*-coelurosaurian traits ascribed to carnosaurs, 13 are true of *Deinonychus.* Eleven traits cited by Romer as characteristic of both infraorders are present in *Deinonychus.* From these tallies, *Deinonychus* would appear to be more coelurosaurian than carnosaurian, but the most significant point is that *Deinonychus* features both carnosaurian and coelurosaurian characters that are otherwise not generally recognized in representatives of the other infraorder. In addition to these there are a number of characters that are not known in either group.

A selection of 20 different anatomical ratios were determined for the present materials and for four other taxa from each infraorder. Representing the Carnosauria were *Allosaurus, Gorgosaurus, Albertosaurus* and *Tyrannosaurus.* The Coelurosauria included *Ornithomimus, Ornitholestes, Compsognathus* and *Coelophysis.* These taxa were selected because a) there seems to be no disagreement among paleontologists as to which infraorder each belongs and b) all are represented by reasonably good and complete skeletal remains so that most of the 20 ratios could be determined. These 20 ratios are listed in Table 12.

In some instances the ratio ranges of the coelurosaurs overlapped or coincided with the ratio spread of the carnosaurs, as, for example, in the ratio of manus to pes length. In the four carnosaurs the manus ranged from 25 percent to 70 percent of pes length, whereas in the coelurosaurs it ranged from 40 percent to 70 percent. The range common to both (i.e., 40 to 70%) is nondiscriminate and might be considered as the generalized theropod range and had the ratio in *Deinonychus* fallen within that range it would have been so classified. If, however, it fell within the range exclusively carnosaurian (i.e., 25 to 40%) it would have been counted as a carnosaurian condition. In

TABLE 12. Selected anatomic ratios in some theropods and Recent ratites

	Allosaurus USNM 4734	*Gorgosaurus* (Parks, 1928)	*Albertosaurus* (Parks, 1928)	*Tyrannosaurus* AMNH 5027	*Deinonychus*	*Ornitholestes* AMNH 619	*Ornithomimus* AMNH 5339	*Coelophysis* AMNH 7224	*Compsognathus* YPM 1781 (cast)	*Struthio* (YPMOC 4347)	*Dromaius* (YPMOC 2126)	*Casuarius* (YPMOC 4351)
Femur/Tibia	1.21	1.05	1.05	1.25	—	1.22	.88	1.00	—	.46	.52	.57
Metatarsus/Tibia	.51	.60	.60	.60?	.48 D	.73	.68	.56	.61	.95	.96	.85
Radius/Humerus	.71	.48	.45	—	.76 D	.71	.74	.67	.43			
Ulna/Tibia	.38	.18	.17	—	.57 Co	.70	.43	.41	.31			
Humerus/Tibia	.45	.32	.31	.32	.70 Co	.80	.57	.59	.57*			
Fore limb/Hind limb	.42	.26*	.22*	—	.70† D	.66	.51	.45	—			
Manus/Pes	.70	.28	.28	.20*	.92 D	.70	.52	.41	.47			
Pes/Tibia	1.17	.83	.85*	—	1.00 Ca	.66	.91	.95	.94			
Pes/Skull length	.98	.97	—	—	1.00 Ca	.52	.40	.86*	.81			
Manus/Skull length	.63	.31*	—	.33*	.93 Co	.66	1.31	.66*	.60*			
Manus/Humerus + Radius	.77	.62*	.67	—	.75 Ca	—	.58	.47	.45*			
Skull length/Fore limb	.63	1.25	—	1.20	.45 Co	.43	.28	.71	.57*			
Manus I-1/Manus I-2	.82	1.14	—	—	.83 Th	.58	1.46	.78	—			
Manus II-2/Manus II-3	.86	1.27	—	—	.95 Ca	1.25	1.17	1.18	—			
Manus III-3/Manus III-4	.83	—	—	—	1.00 Co	.86	.95	1.15	—			
Manus I-2/Digit I	.88	.61	—	—	.80 Ca	.71	.38	.42	—			
Manus II-3/Digit II	.40	.29*	—	—	.37 Ca	.28	.36	.32	—			
Pes II-3/Digit II	.73	.42	—	—	1.18 D	.61*	.42	.43	.46			
Pes III-4/Digit III	.35	.26	—	—	.48 D	.34*	.33	.31	.29			
Pes IV-5/Digit IV	.44	.36	—	—	.41 Th	.25*	.50	.54	.25			
Skull width/Skull length	.47	.40	—	.47	.34 Co	.35	.40?	.32	—			

Co = A "coelurosaurian" ratio.
Ca = A "carnosaurian" ratio.
D = A "*Deinonychus*" ratio.
Th = A generalized "theropod" ratio.

† Based on assumed femur length = tibia length.
* Approximate ratio.

the present example, the *Deinonychus* ratio of manus to pes falls well outside both ranges; the manus equals an extraordinary 92 percent of pes length. This was counted as a *Deinonychus* character. The final tally of the 20 ratios measured was: six coelurosaurian, six carnosaurian, six *Deinonychus* and two generalized theropod. This substantiates my previous assessment of Romer's list of carnosaurian and coelurosaurian characters as applied to *Deinonychus.*

A simple solution would be to adopt the majority category and place *Deinonychus* in the Coelurosauria, but such action would obscure the most important point—that many of the presumed carnosaurian and coelurosaurian traits are not exclusive. To abandon these characters and refrain from using them in a definitive systematic manner only avoids the main issue. Do the infraorders Carnosauria and Coelurosauria really represent natural categories? Looking at *Deinonychus* again, in skull morphology it seems more carnosaurian than coelurosaurian; the mandible, however, is distinctly coelurosaurian. The manus is definitely coelurosaurian, but the foot, excluding the second digit, is distinctly carnosaurian. The cervicals and dorsals are carnosaurian, but the caudals appear to be coelurosaurian. The pelvis seems to fit neither category. For these reasons, I am not able to classify *Deinonychus* as either coelurosaur or carnosaur and I presently have strong reservations about the validity of these two categories.

Although I have not been able to examine the type specimens of even a majority of theropod species, I have compared the present material with a considerable number of specimens, both type and other. To date, the only distinctive *Deinonychus* characters[6] that I have recognized in any other theropod are the tendency of the pes toward didactyly and the specialization of the second pedal digit into an offensive structure. Both these features are clearly present in specimens of *Velociraptor mongoliensis* (AMNH 5618), *Saurornithoides mongoliensis* (AMNH 5616), *Stenonychosaurus inequalis* (NMC 8539) and *Dromaeosaurus albertensis* (AMNH 5356) (Figs. 80 and 81).

Matthew and Brown (1922) established the subfamily Dromaeosaurinae for reception of the small theropod species, *Dromaeosaurus albertensis,* from the Oldman (Belly River) Formation of Alberta. The type (and only) specimen consisted of an incomplete skull, mandibles, teeth and a few foot bones. The authors noted certain similarities to *Deinodon* and provisionally assigned their new subfamily to the family Deinodontidae (= Tyrannosauridae of recent authors). At the same time, Matthew and Brown referred several other species to this subfamily: *Laelaps explanatus* Cope, 1876a; *Laelaps falculus* Cope, 1876a; *Laelaps cristatus* Cope, 1876b; *Laelaps laevifrons* Cope, 1876b; *Zapsalis abradens* Cope, 1876b; and *Coelurus gracilis* Marsh, 1888; all but *Z. abradens* were referred to the genus *Dromaeosaurus.* Gilmore (1924), in comparing another small "Belly River" theropod with the type of *Dromaeosaurus,* apapparently accepted this new subfamily and its provisional assignment to the Deinodontidae, but he removed *Coelurus gracilis* Marsh (*Dromaeosaurus gracilis*) to his new species *Chirostenotes pergracilis.* Gilmore (1933) again

---

[6] After this report had gone to press, D. A. Russell showed me a radiale, associated with *Stenonychosaurus* remains from the Oldman Formation that, although smaller, does not differ in any significant way from that of *Deinonychus.* Thus, the Canadian genus probably had a similarly specialized carpus.

acknowledged the Dromaeosaurinae (including it in the Deinodontidae) and referred to it a number of indeterminate dinosaurian bones from the Iren Dabasu Formation of Mongolia. However, he qualified this assignment (p. 39) by stating that "reference of these specimens to the subfamily Dromaeosaurinae has no special significance further than to denote small, agile, light-limbed carnivores; they might equally well be assigned to the Coeluridae or Compsognathidae, except that both these families chiefly contain much older Jurassic representatives and the rest of the fauna shows a closer affinity to Upper Cretaceous forms." Except for a recent citation by Kuhn (1966), which placed the Dromaeosaurinae in the Deinondontidae, Matthew and Brown's subfamily has received only infrequent notice and apparently has not been generally accepted. There has in fact been a general avoidance of the subfamily rank within the Theropoda by nearly all students over the past half century or more. This, at least in part, is attributable to poor samples and inadequate anatomical data, but it must also be charged to a general tendency to overemphasize the taxonomic significance of minor anatomic features.

The apparent rejection of Matthew and Brown's subfamily is understandable, in view of the fragmentary nature of the type and the very brief and inadequate description that established both the species and the subfamily. Until now the Dromaeosaurinae has been impossible to define, let alone assign to a higher category. This deficiency has been corrected by Colbert and Russell's (1969) thorough analysis of *Dromaeosaurus,* and by the present material, which provides significant new evidence relevant to this matter. On the basis of the following evidence, I concur with Colbert and Russell's decision to elevate Matthew and Brown's Dromaeosaurinae to family rank. The following taxa are assigned to this family:

- *Deinonychus antirrhopus* Ostrom, 1969
- *Dromaeosaurus albertensis* Matthew and Brown, 1922
- *Saurornithoides*[7] *mongoliensis* Osborn, 1924
- *Stenonychosaurus inequalis* Sternberg, 1932
- *Velociraptor mongoliensis* Osborn, 1924

Dromaeosauridae *incertae sedis*

- *Chirostenotes pergracilis* Gilmore, 1924
- *Laelaps explanatus* Cope, 1876a

---

[7] Confusion still exists regarding the name *Saurornithoides,* owing to misplaced footnote symbols in Nopcsa (1928). Recognizing Sauvage's error in referring a theropod caudal centrum from the Jurassic of Portugal to *Iguanodon prestwichii* (Sauvage, 1897, p. 33 and Pl. VIII, figs. 7-10), Nopcsa intended to rename this as *Teinurosaurus.* The footnote mark, however, was erroneously placed adjacent to *Saurornithoides.* Nopcsa (1929) corrected this error in his addendum (p. 201): "[F]ootnote 1 does not refer to *Saurornithoides* (line 19 from below) but to *Teinurosaurus* (last line of text)", the former being only a citation of Osborn's 1924 taxon and the latter his intended new name for the centrum mentioned by Sauvage. Huene (1932), apparently unaware of Nopcsa's 1929 correction and believing that Nopcsa had intended to rename Sauvage's centrum "*Saurornithoides*", realized this name was preoccupied (Osborn, 1924) and renamed the same vertebra *Caudocoelus sauvagei.* Nopcsa's name *Teinurosaurus* has clear priority over Huene's *Caudocoelus,* but since Nopcsa failed to provide a specific name, *Teinurosaurus* is not valid. Regardless, *Saurornithoides* has been proposed only once (Osborn, 1924) and thus is not a synonym of either *Teinurosaurus* (Nopcsa, 1928) or *Caudocoelus* (Huene, 1932).

COMPARISON OF DEINONYCHUS AND CERTAIN OTHER THEROPODS

Among the elements preserved in the type of *Dromaeosaurus* are several foot bones and fragments that Matthew and Brown (1922: p. 384) found to be "very different from those of either *Deinodon* [*Albertosaurus* or *Gorgosaurus*] or *Struthiomimus* [*Ornithomimus*], but so fragmentary that they are not positively identifiable, and no generic characters can be based upon them."

It is fortunate indeed that these foot elements were preserved, for they are the principal evidences for allying *Dromaeosaurus* and *Deinonychus.* It has been recorded elsewhere in this report that the bones of the pes of *Deinonychus* are unusual in a number of features. These unusual pedal characters are unmistakably duplicated in the few fragments of the *Dromaeosaurus* type. Neither Matthew and Brown (1922) nor Gilmore (1924) could assign these fragments with certainty to either the manus or pes (let alone to a specific digit). To equate these pedal features and postulate phyletic affinities on the bases of a few fragmentary phalangeal bones is to invite challenge. Yet, as I have attempted to show in the description of these elements, the specialized nature of the foot of *Deinonychus* is so distinctive that even fragments of the second digit are recognizable and diagnostic. The inability of earlier students to identify the few foot elements among the remains of the type of *Dromaeosaurus* is attributable to this unusual character of the foot and to the fact that a complete, articulated foot of this kind had not been recognized then. It is only now, with the discovery of *Deinonychus,* that this strange pes can be completely reconstructed.

Although Matthew and Brown stated that the several foot bones of the *Dromaeosaurus* type specimen are "so fragmentary that they are not positively identifiable, and no generic characters can be based upon them," they did devote several paragraphs to them and acknowledged their unusual nature (1922: p. 385): "The comparison of these bones with the complete manus and pes of *Struthiomimus* and *Deinodon* shows clearly that *Dromaeosaurus* differs greatly in the construction of manus or pes, and suggests a less [sic] degree of specialization and reduction of the digits in manus or pes."

Because of the overall significance of these identifications in relating *Deinonychus* and *Dromaeosaurus,* Table 13 compares Matthew and Brown's identifications with mine and with the specific elements of *Deinonychus* upon which my identifications are based. The *Deinonychus* numbers listed below YPM 5205 are specimen field numbers which were applied to all foot elements prior to their removal in the quarry.

Matthew and Brown did not say so, but we may surmise (in view of Gilmore's comments a decade later) that the apparent association of three metapodials with ginglymoid extremities in the *Dromaeosaurus* type is what confused matters. This metatarsal condition in a theropod pes was first reported by me (Ostrom, 1969). In most theropods the distal extremities of the second and fourth metatarsals are *not* grooved, but are broadly convex. Usually only metatarsal III develops a ginglymoid facet, although a faint

TABLE 13. Identification of *Dromaeosaurus* and *Deinonychus* foot bones

Dromaeosaurus albertensis (AMNH 5356)		*Deinonychus antirrhopus*
Matthew and Brown, 1922	This report	YPM 5205
(1) Metapodial compared with metacarpal II of *Struthiomimus* with deep ginglymoid groove. Metatarsal IV?	Metatarsal II	#64-55
(2) Smaller metapodial	Metatarsal I	#66-47
(3) Three phalanges close fitting. Suggested they go with (1). Thus (1) and (3) are digit IV of pes.	First phalanx of II Second phalanx of III Third phalanx of IV	#64-53 #64-24 #64-25
(4) Another phalanx "distinct in details" from the others.	Second phalanx of II	#64-60
(5) Another phalanx with basined head related to smaller metapodial (2). Phalanx of I	First phalanx of I	#64-62
(6) Another phalanx, much larger than others. "Possibly, but not probably, this is a median metapodial."	Metatarsal III	#64-57
	The other *Dromaeosaurus* fragments pertain to:	
	First phalanx of III	#64-54
	Ungual of III	#64-20
	Second phalanx of IV	#64-26

ginglymus may be present on metatarsal I. Consequently, we can appreciate Matthew and Brown's summary statement (1922: p. 385) quoted above.

Indisputable correlation of phalanges is extremely difficult, but, as Figure 80 illustrates, at least two of the *Dromaeosaurus* phalanges correspond so perfectly to the unusual form of the first and second elements of digit II in *Deinonychus* that there can be no doubt of their identity. The proximal phalanx is modified to permit extreme extension, and the ventroproximal "heel" of the second phalanx clearly limited flexion—precisely as in *Deinonychus*. The grooved distal extremity of an element that almost certainly is the second metatarsal parallels that condition in *Deinonychus* and provides further support of the close affinities suggested here between these taxa. In this connection, Gilmore's comments (1924: p. 2) are especially noteworthy: "After a careful comparison [of *Dromaeosaurus* foot elements] with the specimen here under consideration [*Chirostenotes pergracilis*] I share to some extent his [Matthew's] doubt as to whether they pertain to the fore or hind foot. From analogy it would appear that one of the metapodials of *Dromaeosaurus* certainly belongs to the manus. Reference is made to 'the distal half of a metapodial slightly larger than the mc II of *Struthiomimus*'[8] which has a deeply grooved ginglymoid distal facet and a very distinct lateral appression surface [distal end of metatarsal II]. *If this bone does not pertain to the manus, it represents a style of distal articulation the like of which has never before been known, so far as I*

---

[8] Matthew and Brown, 1922, p. 384.

can discover, in the metatarsals of a carnivorous dinosaur" (my italics). Gilmore goes on to suggest that this fragment and the "three closely fitting phalanges" may belong to the third digit of the manus, and compares their relative shortness with the manual phalanges in *Ceratosaurus.* He does note, however, that this latter feature is suggestive of the pes.

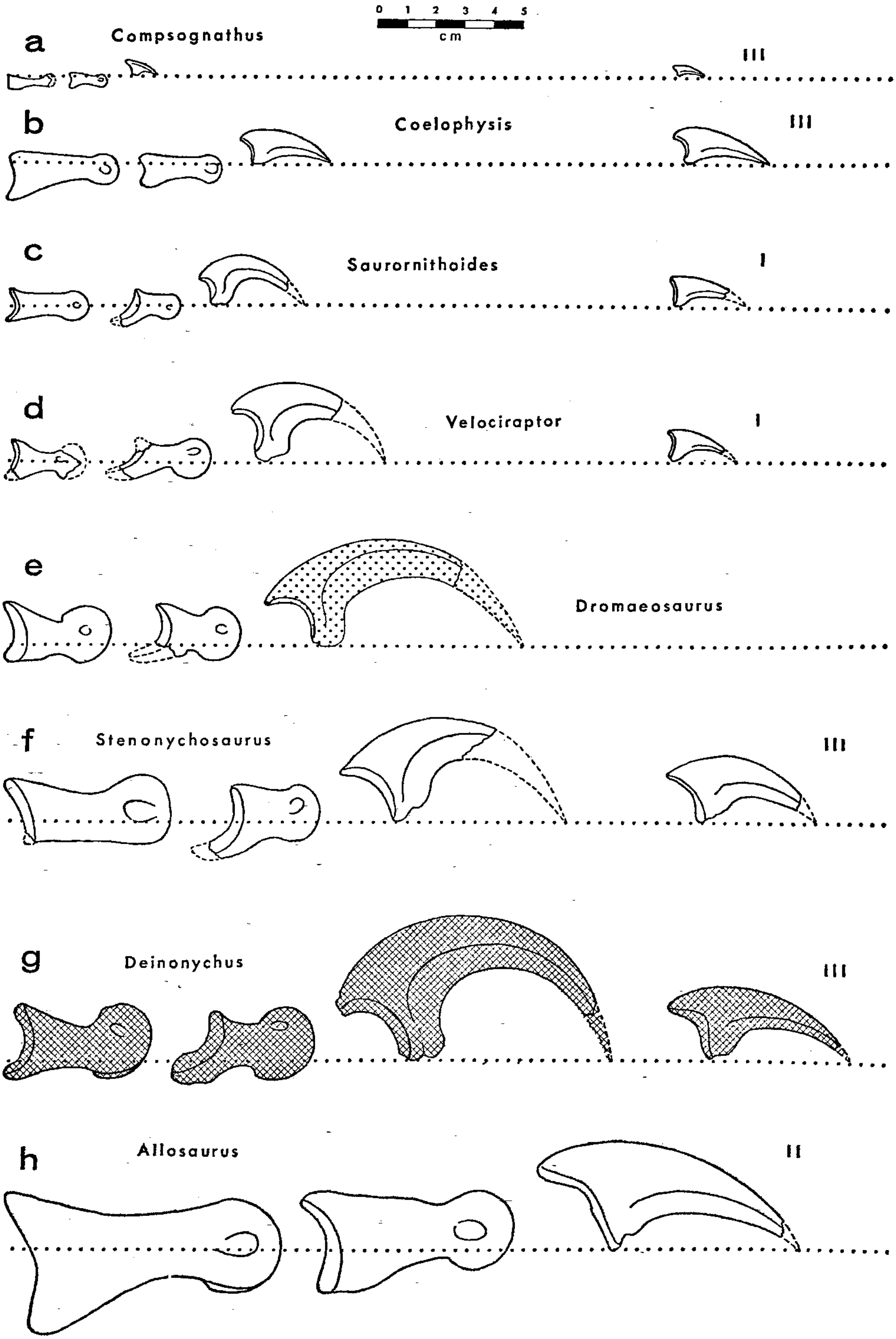
The ungual of the second digit is not represented among the *Dromaeosaurus* foot elements, but the unusual nature of the second phalanx and the other bones of the second digit clearly indicate the existence of a *Deinonychus*-type pedal claw in *Dromaeosaurus.* Such an ungual has been illustrated for *Dromaeosaurus* in Figure 80 (coarse stipple), based on an isolated ungual (NMC 12240) from the Oldman Formation. Although this ungual cannot be referred with certainty to *Dromaeosaurus* at the present time, several factors suggest that it may well belong to this genus. First, the phalanges indicate such a claw; second, the ungual in question is not only sharply recurved and extremely trenchant, but it also has a very deep (high) and narrow, parallel-sided, articular facet precisely like that of *Deinonychus* and unlike the facets of most manus unguals; third, the flexor tubercle is relatively small (as in *Deinonychus)* in contrast with the much more prominent tubercles of typical manus unguals; fourth, and most significant, this ungual fits the second phalanx of *Dromaeosaurus* perfectly. Locality and stratigraphic data are not precise for either specimen, but both are from the Oldman Formation, and a *Dromaeosaurus* assignment is not at all unreasonable for this peculiar ungual.

In addition to *Dromaeosaurus,* the *Deinonychus*-type specialization of the second pedal digit is present in the type specimens of *Saurornithoides mongoliensis* (AMNH 6516), *Stenonychosaurus inequalis* (NMC 8539), and in *Velociraptor mongoliensis* (AMNH 6518). Other specimens featuring this specialization have also been recognized recently by D. A. Russell (personal communication) in the collections of the National Museum of Canada. All are from the Oldman Formation and appear to be referable to either *Dromaeosaurus* or *Stenonychosaurus.* E. H. Colbert has also discovered an isolated phalanx (AMNH 6572) in the American Museum collections from the Iren Dabasu Formation of Mongolia which compares almost exactly with the proximal phalanx of digit II of *Deinonychus,* but is perhaps 20 percent larger. Thus, a sixth species, presently undefinable, apparently is referable to this family. In connection with this last item, it is of particular interest that Gilmore, in his 1933 report on the Iren Dabasu fauna, mentioned the existence of small dinosaurian foot bones and other elements under the Dromaeosaurinae and related these to *Velociraptor* and *Saurornithoides!* Gilmore did not intend this as a firm assignment; nevertheless, I am impressed with his intuition.

It is evident that a number of small to medium-sized carnivorous dinosaurs, all of which seem to have possessed a peculiar *Deinonychus*-type of specialization of the second pedal digit, existed in the Cretaceous faunas of both North America and Asia. It seems probable that other examples will be discovered from other strata and other continents. Before considering these matters, though, a brief comparison of the foot structure in relevant taxa is in order.

A) *Dromaeosaurus albertensis* Matthew and Brown, 1922 (Type: AMNH 5356), Oldman Formation, Alberta, Canada.

Pes represented by eleven fragmentary or complete foot bones, including


0 1 2 3 4 5
cm
a
Compsognathus
III
b
Coelophysis
III
c
Saurornithoides
I
d
Velociraptor
I
e
Dromaeosaurus
f
Stenonychosaurus
III
g
Deinonychus
III
h
Allosaurus
II

part or all of metatarsals I, II and III, first phalanx of digit I, phalanges 1 and 2 of digit II, phalanx 2 and fragments of 1 and 4 of digit III, and phalanges 2 and 3 of digit IV. The elements of the second digit are indistinguishable from those of *Deinonychus,* save for their smaller size. Other elements of the pes appear normal.

B) *Velociraptor mongoliensis* Osborn, 1924 (Type: AMNH 6515; 6518), Djadochta Formation, Shabarakh Usu, Mongolia. The type specimen (AMNH 6515) consists of a skull and mandibles and an incomplete manus. An associated specimen (AMNH 6518) consists of a nearly complete right pes, including all five metatarsals, a tarsal (IV?), all phalanges of digits I and II, and two incomplete phalanges of both III and IV. The digital formula probably was 2–3–4–5–0. The first metatarsal appears to have been incomplete proximally, as in *Deinonychus* and apparently in *Dromaeosaurus,* and also *Allosaurus* and others. The fifth metatarsal is splint-like and apparently shifted posteriorly behind the fourth metatarsal.

Of particular importance is the character of the second digit bones of the pes: 1) the grooved distal ginglymus of the second metatarsal; 2) the elevated ginglymus of the first phalanx; 3) the proximal heel and the ventrally extended ginglymus of the second phalanx. Finally, there is the surprisingly large, strongly recurved and laterally compressed ungual, a much more sharply curved ungual than would ordinarily be expected on the pes. In all features, the second digit of *Velociraptor* compares very closely with that of *Deinonychus,* as is shown in Figure 80.

C) *Saurornithoides mongoliensis* Osborn, 1924 (Type: AMNH 6516), Djadochta Formation, Shabarakh Usu, Mongolia. The type consists of a skull, jaws, and an associated partial skeleton including parts of the pelvis, hind limb and pes. The latter consists of fragmentary or nearly complete metatarsals of the first four digits (the distal extremity of the second is not complete, unfortunately), three nearly complete phalanges of II and III, and a proximal and partial second phalanx of digit IV. There is no evidence of a fifth metatarsal. The pes digital formula appears to have been the usual 2–3–4–5–0, but the two external digits remain in doubt. The nearly complete second digit closely resembles that of *Deinonychus,* particularly in the development of the large ventral proximal extension (heel) of the second phalanx and the over-sized, strongly recurved and trenchant ungual.

D) *Stenonychosaurus inequalis* Sternberg, 1932 (Type: NMC 8539), Oldman Formation, Alberta, Canada. The type specimen consists of a nearly complete

FIG. 80. Comparison of the phalanges and unguals of the second digit of the pes in several theropods. The "extra" unguals at the right in all except (e) and (h) are from an adjacent digit, as marked. Notice the greater curvature of the second ungual in all except *Compsognathus, Coelophysis* and *Allosaurus.* Notice also the enlarged proximal "heel" on all penultimate phalanges *except* those of (a), (b) and (h). Notice further the elevated distal articular condyles of the first phalanx of all *except* (a), (b) and (h). See text for further discussion. The stippling in (e) indicates that this ungual is not positively referable to *Dromaeosaurus.* a) *Compsognathus longiceps,* YPM 1781 (cast); b) *Coelophysis longicollis,* AMNH 7224; c) *Saurornithoides mongoliensis,* AMNH 6516; d) *Velociraptor mongoliensis,* AMNH 6518; e) *Dromaeosaurus albertensis,* AMNH 5356 (Ungual = *Dromaeosaurus?,* NMC 12240); f) *Stenonychosaurus inequalis,* NMC 8539; *Deinonychus antirrhopus,* YPM 5205; h) *Allosaurus fragilis?,* YPM 4944. Restoration of the ungual of *Stenonychosaurus* is based on referred material (NMC 12340 and 1650).

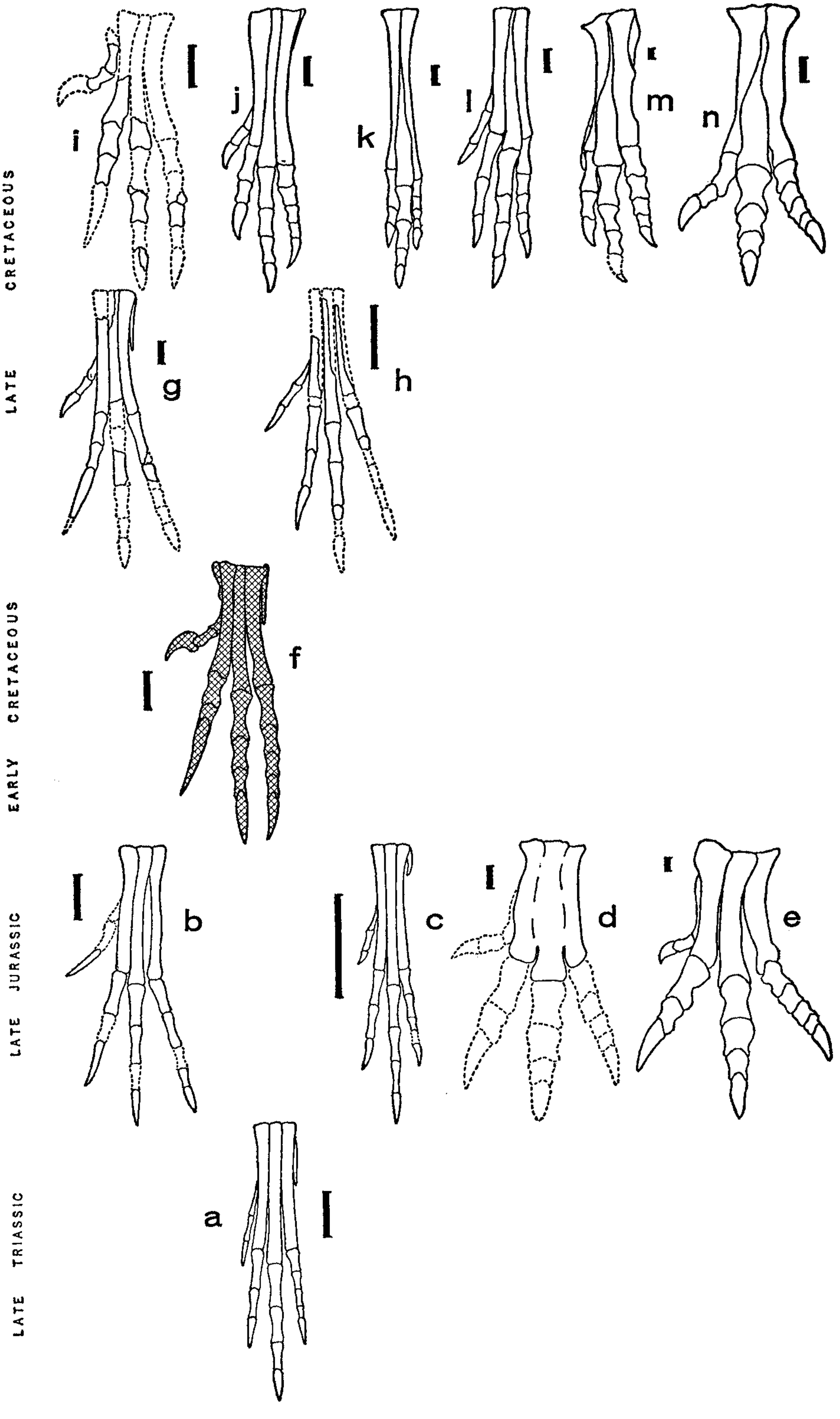
left pes, astragalus and tibia fragment, fragments of a left manus, and some caudal vertebrae. A distinctive feature of the pes is the elongated metatarsus, which may include a pinched median metatarsal, according to Russell (personal communication). The third and fourth digits are normal, and reduced first and fifth metatarsals are present. The incomplete second ungual is distinctly larger than those of III and IV (even without the missing portions), and the two phalanges feature the *Deinonychus* specialties. The ventral proximal extension (heel) of the second phalanx is particularly well developed. Additional specimens (NMC 1650, 12340) confirm these pedal conditions (Russell, pers. comm.).

Comparison of the morphology of the second digit and the metatarsus of these specimens (Figs. 80 and 81) indicates that dromaeosaurids may be separable into two distinct types (perhaps worthy of subfamily distinction). Considering the second digit first, in *Deinonychus, Dromaeosaurus* and *Velociraptor,* the two phalanges are subequal in length, the distal facet of the proximal phalanx extends significantly below the shaft as well as far above it, and the distal facet of the penultimate phalanx extends well above the shaft. Also the unguals are very strongly recurved and of disproportionate size. In *Saurornithoides* and *Stenonychosaurus* the proximal phalanx is considerably longer than the penultimate phalanx, the distal facet of the proximal phalanx does not extend appreciably below the ventral shaft surface, and the distal facet of the penultimate phalanx does not extend significantly above its shaft. Also, although the ungual is distinctly larger than adjacent pedal unguals, they are not as large or as strongly recurved in *Saurornithoides* and *Stenonychosaurus* as they are in *Deinonychus, Dromaeosaurus* (?) and *Velociraptor.*

Turning to the metatarsus, that of *Deinonychus* is of medium length, with three subequal, robust metatarsals. Metatarsal III is not pinched proximally and the second metatarsal is deeply, although asymmetrically, grooved distally. The metatarsus of *Velociraptor* appears to be comparable in all of these features. The metatarsus of *Dromaeosaurus* is very fragmentary, but as noted previously, the second metatarsal is deeply grooved distally. The metatarsus of *Saurornithoides* is also incomplete, particularly in the proximal portions and the distal extremity of metatarsal II. Thus we do not know the length of the metatarsus, the nature of the distal facet of metatarsal II, or whether the proximal end of metatarsal III was pinched. In *Stenonychosaurus,* however, the metatarsus is relatively much longer than in *Deinonychus,* the third metatarsal is strongly pinched between II and IV proximally, and the distal articular facet of metatarsal II is only slightly grooved (Fig. 81).

On the basis of this evidence, I believe that *Deinonychus, Dromaeosaurus*

FIG. 81. Comparison of the pes in various theropods, all drawn to unit length. The heavy vertical lines equal 4 cm. a) *Coelophysis longicollis,* b) *Ornitholestes hermanni,* c) *Compsognathus longiceps,* d) *Ceratosaurus nasicornis,* (from Gilmore, 1920), e) *Allosaurus fragilis*(?), (from Gilmore, 1920), f) *Deinonychus antirrhopus,* g) *Velociraptor mongoliensis,* h) *Saurornithoides mongoliensis,* i) *Dromaeosaurus albertensis,* j) *Stenonychosaurus inequalis,* k) *Struthiomimus altus,* (from Osborn, 1917), l) *Macrophalangia canadensis,* (from Sternberg, 1935), m) *Gorgosaurus libratus,* (from Lambe, 1917), n) *Tarbosaurus efremovi,* (from Maleev, 1955). Notice the subequal lengths of digits III and IV in *Ornitholestes* (b) and the dromaeosaurids (f, g, h, i and j).


LATE CRETACEOUS
EARLY CRETACEOUS
LATE JURASSIC
LATE TRIASSIC
a
b
c
d
e
f
g
h
i
j
k
l
m
n

and *Velociraptor* are closely related. *Saurornithoides* and *Stenonychosaurus* appear to be closely related to each other, but somewhat less closely related to the other taxa. Future discoveries may establish that the five species here assigned to the Dromaeosauridae should be referred to two distinct subfamilies, but until existing specimens have been thoroughly studied or new evidence is found, any formal proposal to this effect is premature, in my opinion.

With the exception of *Stenonychosaurus,* reasonably well preserved cranial material is available of all the taxa herein referred to the Dromaeosauridae. Only the briefest descriptions of these materials had been published at the time the present paper was submitted. Colbert and Russell (1969), however, have made a detailed analysis of *Dromaeosaurus* which will be most valuable in further assessment of the relationships between that taxon and other dromaeosaurids. An urgent need still exists, however, for similar analyses of the crania of *Velociraptor* and *Saurornithoides.*

At first glance there appear to be few similarities between the skulls of *Dromaeosaurus, Deinonychus, Saurornithoides* and *Velociraptor* (compare figs. 1 and 3 of Osborn, 1924, and fig. 1 of Matthew and Brown, 1922, with Fig. 4 of this report). *Deinonychus* and *Dromaeosaurus* are rather similar in having moderately deep skulls, whereas *Velociraptor* and *Saurornithoides* have relatively long, low skulls. Height to length ratios of the four skulls are as follows: *Dromaeosaurus,* .40; *Deinonychus,* .34; *Velociraptor,* .29; *Saurornithoides,* .24. These compare with .32 in *Coelophysis,* .35 in *Ornitholestes,* .40 in *Gorgosaurus* and .47 in *Allosaurus* and *Tyrannosaurus.* Personally, I do not think these skull proportions have any real taxonomic significance, but rather correlate with absolute size.

Premax-maxillary and dentary tooth counts may have specific or perhaps even generic significance. Tooth counts are as follows in the taxa in question: *Dromaeosaurus* $\frac{4+9\text{[9]}}{11}$; *Deinonychus* $\frac{4+15}{16}$; *Velociraptor* $\frac{(3-4)+(10-11?)}{15}$; *Saurornithoides* $\frac{4?+(15-16?)}{?}$. These compare with $\frac{(4-5?+(21-22?)}{25}$ in *Coelophysis,* $\frac{4+(9-10)}{12}$ in *Ornitholestes,* $\frac{5+17}{15}$ in *Allosaurus,* $\frac{4+13}{14}$ in *Gorgosaurus* and $\frac{4+12}{14}$ in *Tyrannosaurus.* There is some evidence that the general trend among theropods was a reduction in dental counts, but it is obvious that tooth size relative to total tooth row length is the critical factor. Aside from tooth shape, both size and spacing, and tooth row length are key features in predation and feeding and we can assume that both are sensitive to the selective pressures imposed by particular kinds of food and methods of obtaining and eating it. Thus, how an animal feeds and what it feeds on must be related to the above differences in dental formulae. Whereas the primitive *Coelophysis* has many small teeth in a very long tooth row (approximating 75% of basal skull length), *Ornitholestes* has few relatively large teeth in a short tooth row (40% of basal skull length). I do not think we have sufficient data to consider the latter as necessarily advanced or progressive. Within the Dromaeosauridae, *Deinonychus* has relatively large teeth in a long row (55% of estimated skull length). *Dromaeosaurus* has similarly large teeth, but in a shorter tooth row (less than 50% of basal skull length). The tooth row

---

[9] Matthew and Brown (1922) list ?3+9/10 but I counted four left premaxillary teeth and eleven alveoli in the dentary, as did Colbert and Russell (1969).

of *Saurornithoides* appears to be very short (40%), but the teeth are quite small and more closely spaced than in most other theropods. In *Velociraptor* the teeth can be judged as moderate in size and the tooth row of average (50%) length. Among dromaeosaurids, and theropods in general, there seems to be no particularly consistency in upper versus lower tooth row counts, but as a rule the premax-maxillary count is the higher of the two.

Tooth form among theropods is perhaps even less reliable than is dental formula as a taxonomic criterion. The dromaeosaurids, however, may be the exception. All dromaeosaurid teeth appear to be laterally compressed, acutely tapered, recurved and serrated both fore and aft (except possibly in *Saurornithoides*). But, as was noted earlier, all teeth of *Deinonychus* are peculiar in the disparity of denticle size between anterior and posterior serrations. To date, after examining hundreds of specimens including type specimens and other definitely assignable material, I have found this condition only in *Deinonychus antirrhopus*, *Velociraptor mongoliensis*, and *Laelaps explanatus* (Cope, 1876). This condition may have existed in *Saurornithoides*, but the abraded state of all observable teeth in that specimen preclude any interpretation. If anterior serrations are present, they clearly must be much smaller than the unusually large denticles of the posterior serrations (Table 2). It would be very important corroborative evidence for the systematic assignments made here if this condition were found in *Saurornithoides*, although it is already evident from *Dromaeosaurus* that this condition is not true for all dromaeosaurids. Thus, the mandibular teeth, none of which are visible as the specimen now stands, should be exposed by further preparation if at all feasible. *Dromaeosaurus* shows little, if any, discrepancy in denticle size between anterior and posterior serrations. In fact, *Dromaeosaurus* teeth are not distinctive in any respect, as far as I can see, being rather standard, medium-sized, theropod-type teeth.

Premaxillary teeth in three of the four present species tend to be triangular in cross section with the anterior serrations situated on the medial side of the crown and the posterior serrations at the rear. The U-shape, characteristic of *Gorgosaurus* and *Tyrannosaurus* and apparently also of *Allosaurus*, is present in *Dromaeosaurus*, but not in the other taxa.

The taxa here assigned to the Dromaeosauridae appear to possess the following cranial features in common.

1) Marginal teeth all sub-isodont with no great disparity in tooth size or shape along the maxillary or dentary series.

2) Premaxillary teeth all markedly asymmetrical, but not U-shaped in section (*Dromaeosaurus* is an exception).

3) Interdental plates are absent.

4) Nasals are narrow and parallel-sided.

5) Inferior process of premaxilla excludes maxilla from inferior border of the external nares (*Saurornithoides* may be an exception).

6) Preorbital bar is very slender (*Dromaeosaurus* may be an exception).

7) Second antorbital fenestra is small (*Saurornithoides* appears to have a rather large second antorbital fenestra).

8) Large, subcircular orbits.

9) Peterygoids extremely narrow anterior to basipterygoid notch and do

not meet in the mid-line (condition unknown in *Velociraptor* and *Saurornithoides*).

10) Ectopterygoids are complex and deeply pocketed posteroventrally (condition unknown in *Velociraptor* and *Saurornithoides*).

11) Mandible is very shallow (moderately shallow in *Dromaeosaurus*).

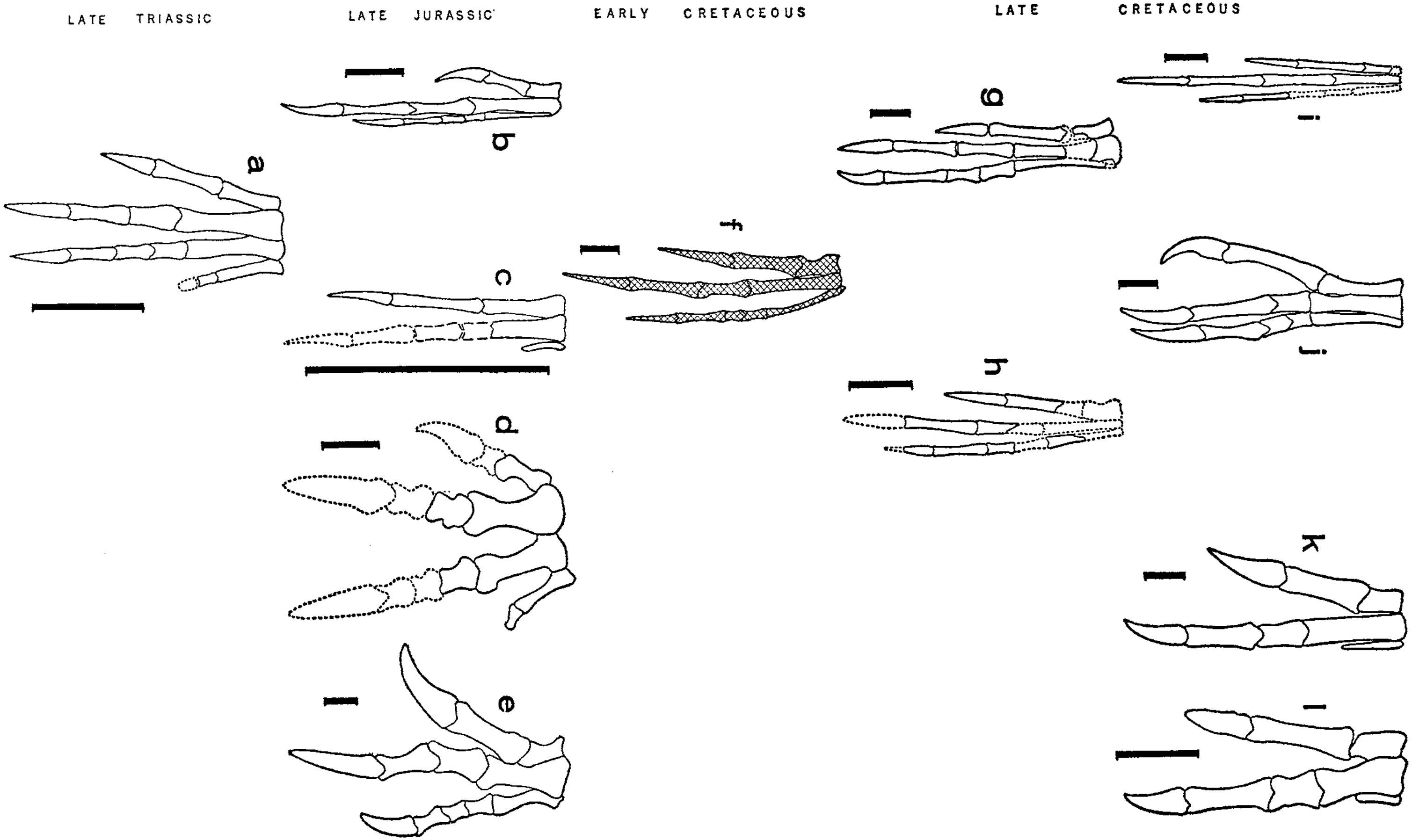
12) Presence of a large external mandibular fossa (possibly not in *Dromaeosaurus*).

Dromaeosaurus and *Deinonychus,* in addition to their relatively larger and deeper skulls, are similar in the undepressed muzzle, the greater depth of the maxillae, and the absence of even a shallow external depression or concavity in the maxilla containing the antorbital fenestrae. *Velociraptor* and *Saurornithoides* are more similar to each other in the smaller size and lower design of the skull, the depressed muzzle and the lower, longer maxillae with large, shallow, external depressions.

Chirostenotes pergracilis (Gilmore, 1924), from the Oldman Formation of Alberta, may one day prove to belong to the Dromaeosauridae, but existing evidence is not conclusive. Gilmore (1924), Sternberg (1932), Romer (1956), Rozhdestvensky and Tatarinov (1964) and Charig (1967) placed *Chirostenotes* in the Coeluridae. Romer (1945, 1966) and Lapparent and Lavocat (1955) considered it an ornithomimid and Nopcsa (1928) referred it to the Compsognathidae. As shown in Figure 82, the slender proportions and relative lengths of the digits in *Chirostenotes* are much more like those of *Ornitholestes* and *Deinonychus* than of any other theropod. The chief differences from *Deinonychus* are: slightly less curvature of the unguals, smaller flexor tubercles on the unguals, ungual I is smaller than ungual II, and the first metacarpal (at least the distal half) is much more slender and less robust than its equivalent in *Deinonychus.*

The type of *Chirostenotes* (NMC 2367) consists of incomplete, but articulated, left and right manus. Left manus: I—ungual and incomplete proximal phalanx; II—distal extremity of metacarpal and all three phalanges; III—ungual and penultimate phalanx. Right manus: I—distal extremity of metacarpal and the first and second phalanges; III—third and fourth phalanges. The relative lengths of the digits are preserved in the type (Gilmore, 1924: pl.1), as are the probable relative positions of the first and second metacarpal extremities. Sternberg (1932: p. 100) noted the similarity between certain phalanges of *Velociraptor* and *Chirostenotes* and suggested that *Velociraptor* "might well be regarded as ancestral to *Chirostenotes.*" Gilmore (1924: p. 6) remarked that the manus of *Chirostenotes* is intermediate between that of *Ornitholestes* and *Struthiomimus* (= *Ornithomimus*) without explicitly stating such a phyletic relationship. But Gilmore erred, in my opinion, in his inter-

FIG. 82. Comparison of the manus in various theropods, all drawn to unit length. The heavy vertical lines equal 4 cm. a) *Coelophysis longicollis,* b) *Ornitholestes hermanni,* (from Osborn, 1917), c) *Compsognathus longiceps,* d) *Ceratosaurus nasicornis,* (from Gilmore, 1920), e) *Allosaurus fragilis,* (from Gilmore, 1920), f) *Deinonychus antirrhopus,* g) *Oviraptor philoceratops.* h) *Velociraptor mongoliensis,* i) *Chirostenotes pergracilis,* (from Gilmore, 1924), j) *Struthiomimus altus,* (from Osborn, 1917), k) *Gorgosaurus libratus,* (from Lambe, 1917), l) *Tarbosaurus efremovi,* (from Maleev, 1955). (The elements outlined by long dashes in C are based on impressions [negatives], those in dotted lines are reconstructed from isolated phalanges slightly removed from the manus.)


LATE TRIASSIC
LATE JURASSIC
EARLY CRETACEOUS
LATE CRETACEOUS
a
b
c
d
e
f
g
h
i
j
k
l

pretation of "the elongation of mc I . . . [which] approaches the proportions found in *Struthiomimus.*" Neither the first nor the second metacarpal of *Chirostenotes* is complete, so their relative lengths are not known. However, the positions of the distal extremities of these two elements, as preserved in the articulated right manus of the type specimen, and seemingly substantiated by the left manus, clearly indicates that the first and second metacarpals were not subequal in length as in *Ornithomimus,* but were probably of quite disparate lengths, as in all other theropods. Thus, I see no evidence for equating *Chirostenotes* with ornithomimids, as Gilmore implied and Romer, and Lapparent and Lavocat later proposed.

I suggest that *Chirostenotes,* on the basis of present evidence, is best allied with the Dromaeosauridae, but until further evidence is available, it is perhaps best assigned to Dromaeosauridae *incertae sedis.*

Improbable though it may seem, there is the distinct possibility that the only known specimen of *Chirostenotes* belongs to one of the other theropods from the Oldman Formation. Suggestive but inconclusive evidence of this is the fact that the manus of *Chirostenotes* and the skull and reconstructed foot of *Dromaeosaurus* have approximately the same relative proportions to each other as do the manus, skull and foot of *Deinonychus.* On the basis of these extrapolations we must recognize the possibility that *Chirostenotes pergracilis* is referable to *Dromaeosaurus albertensis.*

The several other species referred to *Dromaeosaurus* by Matthew and Brown (1922: p. 376 and 378), (i.e. *Laelaps explanatus,* AMNH 3958; *L. falculus,* AMNH 3959; *L. cristatus,* AMNH 3954; *L. laevifrons,* AMNH 3961; *Coelurus gracilis,* USNM 4973) are based on inadequate material and cannot definitely be assigned to any family. All of the *Laelaps* species are based on isolated teeth. Only those of *Laelaps explanatus* show significant disparity of denticle sizes of anterior versus posterior serrations, as has been noted in *Deinonychus* and *Velociraptor.* The uniform size of anterior and posterior serrations in *Dromaeosaurus* teeth would seem to rule out reference of *L. explanatus* to *Dromaeosaurus,* so I consider it Dromaeosauridae *incertae sedis.* Marsh's species *Coelurus gracilis,* based on a solitary broken ungual from the Arundel Formation of Maryland closely resembles the first manual ungual of *Deinonychus,* but it is less than one third as large. The specimen is totally inadequate and cannot be assigned with certainty to any taxon.

Concerning the systematic position of the Dromaeosauridae, I have already noted that I cannot presently place this family in either the Carnosauria or Coelurosauria with any degree of confidence. The fact that other students have not always agreed on the affinities of the several dromaeosaurid genera reinforces my reservations. For example: *Dromaeosaurus* has been considered a coelurosaur by Charig (1967), Huene (1932, 1956), Romer (1956, 1966), and Rozhdestvensky and Tatarinov (1964), but a carnosaur by Matthew and Brown (1922), Nopcsa (1928), Russell (1935) and Zittel (1932). *Velociraptor* and *Saurornithoides* have been considered as coelurosaurs by everyone except Lapparent and Lavocat (1955) who referred both genera to the Megalosauridae. The several species that I have here referred to the Dromaeosauridae, insofar as they are known, appear to represent a natural group of closely related taxa. Collectively they possess a number of anatomical features characteristic of both theropod infraorders, in addition to a number of characters that are not presently known in either carnosaurs or coelurosaurs. Colbert and Russell (1969) have given an excellent summary of these characters and have arrived at the same conclusion—that the Dromaeosauridae cannot be placed in either the Carnosauria or Coelurosauria. They have resolved this dilemma by proposing a new infraorder, Deinonychosauria, for reception of the Dromaeosauridae. Their proposal is a reasonable solution, but does it clarify the question of carnosaurs versus coelurosaurs? Do these categories really represent natural or meaningful entities? This is the question to which the three of us hope to address ourselves in the near future.

ORIGIN OF THE DROMAEOSAURIDAE

Although there are a number of features in which they differ, *Deinonychus* and later dromaeosaurids appear to be most easily derived from *Ornitholestes* of the Late Jurassic Morrison Formation of Wyoming. The principal evidence for this is in the foot and hand.

A complete foot of *Ornitholestes* is not known, but on the basis of the type (AMNH 619) we can presume it had the normal theropod digital formula (2–3–4–5–0). The proximal phalanx of digit I, the penultimate phalanges of II and III, and the third phalanx of IV are missing in that specimen. However, as I have illustrated in Figure 81b, digit IV must have been appreciably longer than II and may well have equaled the median digit, as in *Deinonychus*. This is in sharp contrast to the subequal lengths of the second and fourth digits that is otherwise universally characteristic of non-dromaeosaurid theropods, as is shown in Figure 81. The pes of *Ornitholestes* may well have been functionally didactyl and borne a modified second digit, but this cannot be established on existing material. Another significant feature of *Ornitholestes* is the distinctly larger size of the second ungual compared with those of III and IV. Unfortunately this ungual is not well enough preserved to reveal more than its approximate size. Moreover, the penultimate phalanx is unknown, so it cannot be determined whether, or to what degree, the second digit resembled that of *Deinonychus*. The pes of *Ornitholestes* is clearly more similar to the dromaeosaurid condition than is that of any other well-known Jurassic theropod (Fig. 81).

The manus of *Ornitholestes* has been reconstructed by Osborn (1917) from the type and a second specimen (AMNH 587) (Fig. 82b). Except for what appears to be a tiny splinter of metacarpal IV and the relatively shorter length of the first digit, it is remarkably similar to that of *Deinonychus*. The proportions and relative robustness of each of the digits and the form of the unguals are comparable in both species. This is particularly true for the very slender, even delicate, construction of digit III in each. The very slender third digit, in fact, appears to have been characteristic of *Ornitholestes* and dromaeosaurids, but not of other theropods. The shorter length of digit I in *Ornitholestes* may be an error. Osborn reconstructed I from a second specimen (AMNH 587) and II and III from the type. Thus, the manus of *Ornitholestes*

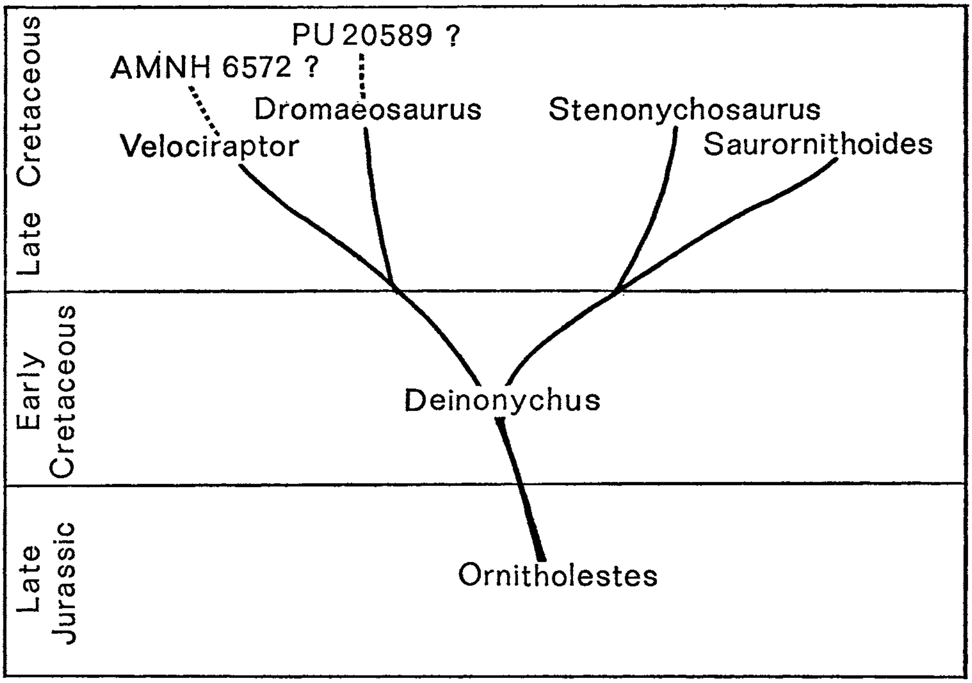


FIG. 83. Suggested phylogeny of the Dromaeosauridae.

and *Deinonychus* may be even more similar than I have illustrated in Figure 82b and f. Only *Velociraptor* (Fig. 82h) and possibly *Chirostenotes* (Fig. 82i), among the species[10] represented in that figure, bear comparable resemblances to *Deinonychus* in the proportions and construction of the manus.

Ornitholestes differs from *Deinonychus* in its long, tapered ischium; long, slender pubis; a long and low anterior process of the ilium; relatively greater length of dorsal centra; the unusually short mandibular tooth row; enlarged premaxillary teeth; a robust preorbital bar with extensive contact with the maxilla and jugal; the absence of anterior serrations on the teeth; the apparent absence of a surangular foramen and an external mandibular fenestra; and the apparent absence of hyposphene-hypantrum articulations in the dorsal vertebrae. The list undoubtedly could be made longer, but it is sufficiently clear from these that there are major differences between these two taxa. Nevertheless, I consider *Ornitholestes* as very close, if not actually ancestral, to *Deinonychus* and later dromaeosaurids.

---

[10] I have reconstructed the manus of *Compsognathus* (Fig. 82c) differently from previous authors (e.g., Huene, 1926, fig. 56) on the bases of a superb cast in the Peabody Museum collections, photographs of the original specimen and Nopcsa's interpretation (1930, pl. 18). The usual reconstruction is a tridactyl manus with an unreduced third digit. In my opinion, there is a distinct possibility that the third digit was reduced, perhaps to the extent of a vestigial metacarpal. The third metacarpal of the right manus appears to be a very short, thin, splint-like element. Whereas all the phalanges of I and II are represented, either articulated or slightly removed, there is no evidence of any phalanges of a size appropriate to the dimensions of the splint-like metacarpal III. Also, only four unguals are preserved, presumably the left and right unguals of digits I and II.

ADDENDUM

When this report was in page proof, I received from Dr. Eugene Gaffney an isolated fragment of a phalanx (PU 20589) which he had found in the Princeton University collections. The fragment is virtually identical to the proximal end of the second phalanx of pedal digit II of *Deinonychus,* except that the proximal "heel" is as long as that of *Deinonychus* whereas in all other dimensions the fragment is about one third smaller. The specimen was collected in 1947 from probable "Lance" strata at Polecat Dome near the middle of Sec. 31, T. 57 N., R. 98 W., Park County, Wyoming. Because this fragment almost certainly represents a seventh species (undefinable at present) of dromaeosaurid, and because it extends the range of the family into probable Maestrichtian time, it is especially important and warrants inclusion in this report.

LITERATURE CITED

Austin, Oliver L., Jr. 1962. Birds of the world. Paul Hamlyn, London, 317 p.

Bock, Walter J. 1960. Secondary articulation of the avian mandible. The Auk **77:** 19–55.

Brown, Barnum. 1941. The last of the dinosaurs. Nat. Hist. **48:** 290–295.

Charig, Allan. 1967. Family Coeluridae, p. 714. *In* W. B. Harland et al. (ed.) The fossil record. Geological Society, London.

Colbert, Edwin H., and Dale A. Russell. 1969. The small Cretaceous dinosaur *Dromaeosaurus.* Amer. Mus. Novitates, no. 2380:1–49.

Cope, Edward Drinker. 1876a. Descriptions of some vertebrate remains from the Fort Union beds of Montana. Proc. Acad. Nat. Sci. Philadelphia **28:** 248–261.

——— 1876b. On some extinct reptiles and Batrachia from the Judith River and Fox Hills beds of Montana. Proc. Acad. Nat. Sci. Philadelphia **28:** 340–359.

Gilliard, E. T. 1958. Living birds of the world. Doubleday, Garden City, N.Y. 400 p.

Gilmore, Charles W. 1920. Osteology of the carnivorus Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus (Allosaurus)* and *Ceratosaurus.* Bull. U.S. Nat. Mus. **110:** 1–159.

——— 1924. A new coelurid dinosaur from the Belly River Cretaceous of Alberta. Bull. Can. Geol. Surv., Dept. of Mines, **38:** 1–12.

——— 1933. On the dinosaurian fauna of the Iren Dabasu Formation. Bull. Amer. Mus. Nat. Hist. **67:** 23–78.

Gregory, William K. 1918. Note on the origin and evolution of certain adaptations for forward locomotion in the pectoral and pelvic girdles of reptiles and mammals, p. 515–527. *In* William K. Gregory and Charles L. Camp. Studies in comparative myology and osteology No. 3, part 3. Bull. Amer. Mus. Nat. Hist. 38.

Gregory, William L., and Charles L. Camp. 1918. A comparison of the muscle areas of the pelvis of *Alligator, Struthio* and *Ornitholestes,* p. 515. Studies in comparative myology and osteology No. 3, part 2. Bull. Amer. Mus. Nat. Hist. 38.

Huene, Friedrich von. 1926. The carnivorous Saurischia in the Jura and Cretaceous Formations principally in Europe. Rev. Mus. de La Plata, Univ. Nat. de La Plata **29:** 35–167.

——— 1932. Die fossile Reptile-Ordnung Saurischia, ihre Entwicklung und Geschichte. Mon. Geol. Paläontol. **(1), 4:** 1–361.

——— 1956. Paläontologie und Phylogenie der Niederen Tetrapoden. Gustav Fischer, Jena. 716 p.

Kuhn, Oskar. 1966. Die Reptilien. Krailling, Munich. 154 p.

Lakjer, Tage. 1926. Studien uber die Trigeminus-Versorgte Kaumuskulatur der Sauropsiden. C. A. Reitzel. Copenhagen. 153 p.

Lambe, Lawrence. M. 1917. The Cretaceous theropodous dinosaur *Gorgosaurus.* Mem. Can. Geol. Surv., Dept. of Mines, **100:** 1–84.

Lapparent, Albert, and René Lavocat. 1955. Dinosauriens, p. 785–962. *In* Jean Piveteau et al [ed.] Traité de Paléontologie. V. Masson et C^{ie}, Paris.

Leidy, Joseph. 1870. [Remarks on *Antrodemus valens*]. Proc. Acad. Nat. Sci. Philadelphia **22:** 3–4.

Luther, Alexander. 1914. Über die vom N. trigeminus versorgte muskulatur der Amphibien. Acta Soc. Sci. Fennicae. **44:7:1** 1–151.

Maleev, E. A. 1955. New carnivorous dinosaurs from the Upper Cretaceous of Mongolia [in Russian]. C. R. Acad. Sci. U.R.S.S. **104:** 779–783.

Marsh, Othniel C. 1877. Notice of new dinosaurian reptiles from the Jurassic formation. Amer. Jour. Sci. **(3)14:** 514–516.

——— 1881. Principal characters of American Jurassic dinosaurs, pt. V. Amer. Jour. Sci. **(3)21:** 417–423.

——— 1888. Notice of a new genus of Sauropoda and other new dinosaurs from the Potomac Formation. Amer. Jour. Sci. **(3)35:** 89–94.

——— 1896. Dinosaurs of North America. Sixteenth Ann. Rept. U.S. Geol. Survey: 133–415.

Matthew, William D., and Barnum Brown. 1922. The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. Bull. Amer. Mus. Nat. Hist. **46:** 367–385.

Miller, Malcolm E., George C. Christensen, and Howard E. Evans. 1964. Anatomy of the dog. W. B. Saunders, Philadelphia. 941 p.

Moberly, Ralph, Jr. 1960. Morrison, Cloverly, and Sykes Mountain Formations, northern Bighorn Basin, Wyoming and Montana. Bull. Geol. Soc. Amer. **71:** 1137–1176.

Nopcsa, Franz von. 1903. Neues über *Compsognathus.* Neven Jahrb. Min. Geol. Pal. **16:** 476–494.

——— 1928. The genera of reptiles. Palaeobiologica **1:** 163–188.

——— 1929. Addendum. *In* Sexual differences in ornithopodous dinosaurs. Palaeobiologica **2:** 187–201.

Osborn, Henry Fairfield. 1899. Fore and hind limbs of carnivorous and herbivorous dinosaurs from the Jurassic of Wyoming. Dinosaur contribution No. 3. Bull. Amer. Mus. Nat. Hist. **12:** 161–172.

——— 1903. *Ornitholestes hermanni,* a new compsognathid dinosaur from the Upper Jurassic. Bull. Amer. Mus. Nat. Hist. **19:** 281–296.

——— 1906. *Tyrannosaurus,* Upper Cretaceous carnivorous dinosaur (second communication). Bull. Amer. Mus. Nat. Hist. **22:** 281–296.

——— 1917. Skeletal adaptations of *Ornitholestes, Struthiomimus, Tyrannosaurus.* Bull. Amer. Mus. Nat. Hist. **35:** 733–771.

——— 1924. Three new Theropoda, *Protoceratops* zone, central Mongolia. Amer. Mus. Novitates, no. **144:** 1–12.

Ostrom, John H. 1969. A new theropod dinosaur from the Lower Cretaceous of Montana. Postilla (Peabody Mus. Nat. Hist.), no. 128: 1–17.

——— (MS). Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana.

Parks, William A. 1928. *Albertosaurus arctunguis,* a new species of theropodous dinosaur from the Edmonton Formation of Alberta. Univ. Toronto Studies, Geol. Ser. **25:** 3–42.

——— 1933. New species of dinosaurs and turtles from the Upper Cretaceous formations of Alberta. Univ. Toronto Press, Geol. Ser. **34:** 1–33.

Romer, Alfred S. 1923a. Crocodilian pelvic muscles and their avian and reptilian homologues. Bull. Amer. Mus. Nat. Hist. **48:** 533–552.

——— 1923b. The pelvic musculature of saurischian dinosaurs. Bull. Amer. Mus. Nat. Hist. **48:** 605–617.

——— 1945. Vertebrate Paleontology. Second edition. Univ. Chicago Press, Chicago. 687 p.

——— 1956. Osteology of the reptiles. Univ. Chicago Press, Chicago. 772 p.

——— 1966. Vertebrate paleontology. Third edition. Univ. Chicago Press, Chicago. 468 p.

Rozhdestvensky, A. K., and L. P. Tatarinov. 1964. Order Saurischia, p. 529–552. *In* J. A. Orlov, [ed.] Osnovy paleontologii [Fundamentals of paleontology], (Moscow) 12.

Russell, Loris S. 1935. Fauna of the upper Milk River beds, southern Alberta. Trans. Roy. Soc. Canada **29:** 115–127.

Sauvage, H. E. 1897–98. Vertebrés fossiles du Portugal. Dir. des Traveaux Géol. du Portugal. 46 p.

Slijper, E. J. 1946. Comparative biologic anatomical investigations on the vertebral column and spinal musculature of mammals. Verhand. der Koninklijke Neder. Akad. van Wetenschappen, afd. Natur. **42:** 1–128.

Sternberg, Charles M. 1932. Two new theropod dinosaurs from the Belly River Formation of Alberta. Canadian Field Naturalist **46:** 99–105.

Stovall, J. W., and Wann Langston. 1950. *Acrocanthosaurus atokensis,* a new genus and species of Lower Cretaceous Theropoda from Oklahoma. Amer. Midland Nat. **43:** 696–728.

Walker, A. D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. Phil. Trans. Roy. Soc. London. (B) **248:** 53–134.

Zittel, Karl von. 1932. Text-book of palaeontology. Second English edition, revised and edited by C. R. Eastman and A. Smith Woodward. Macmillan & Co., London. 2 vols. 464 p.