THE MAMMALIAN GENERA
ARCTORYCTES AND CRYPTORYCTES

FROM THE OLIGOCENE AND MIOCENE
OF NORTH AMERICA

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INTRODUCTION

At the time of our previous work on *Arctoryctes* and associated vertebrates (Turnbull and Reed, 1960) we had on hand, as it turns out, only eight bones of the forelimb of *Arctoryctes* with which to work. Descriptions of those Chadronian materials from Nebraska, which were published in that work, soon brought to our attention a number of additional examples of the peculiar knobbed metacarpals from several other localities. Craig Black (Carnegie Museum) observed our specimens and recalled having seen in the Split Rock local fauna many metacarpals similar to the ones we have described. One of us (Reed) discovered dozens of the knobbed metacarpals in association with humeri of *Arctoryctes* in an Orellan collection belonging to E. C. Galbreath (Southern Illinois University). Indeed, since our publication of 1960 many new specimens of *Arctoryctes* and *Cryptoryctes* have appeared. Six additional humeri of *C. kayi* have been located in the Carnegie Museum collection and two others in the collection of the United States National Museum. R. W. Fields and his field parties from the University of Montana have collected two more humeri of *C. kayi*, one at Pipestone Springs and the other from a nearby, almost contemporaneous bed. From J. R. MacDonald (then of the South Dakota School of Mines) has come a nearly complete humerus of *Arctoryctes* from the Crazy Johnson member of the Chadron formation of South Dakota. J. R. Hough (Long Island University) and James Hopson (University of Chicago) collected a humerus of *Arctoryctes* from the Orellan, Lower Brule formation of North Dakota. Peter Robinson (University of Colorado Museum) in working over the Orellan materials from the Mellinger locality in Colorado, discovered some 15 or more specimens, including knobbed metacarpals and two humeri of *Arctoryctes*. In Galbreath's material from the Cedar Creek member of the Orellan Brule formation of Colorado are at least 50 specimens of knobbed

metacarpals in addition to the three humeri of *Arctoryctes* previously published, and perhaps an additional dozen more fragmentary humeral scraps. From the Arikareean Rosebud beds of South Dakota, through J. R. MacDonald and J. D. Bump (South Dakota School of Mines) have come 13 more humeri of *Arctoryctes terrenus*. Finally, the materials observed by Craig Black turned out to be the best and most numerous of the metacarpal (and also antebrachial, carpal, and phalangeal) materials to date. They are from the Split Rock local fauna (Hemingfordian) of Wyoming, and associated are 15 very fragmentary though clearly recognizable pieces of humeri of the *Arctoryctes—Cryptoryctes* type. These Split Rock specimens belong to two collections (Amherst College and Chicago Natural History Museum)[1] which Black, K. M. Reed and others had sorted over in connection with their own special projects. The materials from each of these localities are discussed in the text. Grateful acknowledgment is made to all of those persons just named, and to A. E. Wood (Amherst) and C. L. Gazin (United States National Museum) for their work on, or for the loan of, the materials in their charge. Their assistance and kindness in this is most appreciated. We wish also to thank D. Dwight Davis (Chicago Natural History Museum) for giving generously of his time to take the photographs that collectively make up figures 13–23, and to acknowledge other help and advice from him and from Rainer Zangerl (Chicago Natural History Museum).

It appears that we now have at hand an adequate representation of the materials presently known to exist in collections. Many of the additional materials need description, the information afforded by them needs to be presented, and a synthesis is now in order. It is the aim of this work to accomplish these ends. The now abundant, though fragmentary materials have allowed us to go significantly beyond the humeri of *Arctoryctes* and *Cryptoryctes* themselves, and (at least for *Arctoryctes*) to give the first extensive account of morphology and function of the front limb as an integrated unit.

The following abbreviations are used:

ACM=Amherst College Museum
AMNH=American Museum of Natural History
CM=Carnegie Museum
CNHM=Chicago Natural History Museum
ECG=Personal collection of E. C. Galbreath
LACM=Los Angeles County Museum

[1] We have not seen the Split Rock materials in the collection of the Royal Ontario Museum, or University of Wyoming, but these, too, doubtless contain additional specimens.

MV=Montana State University
SDSM=South Dakota School of Mines
UCM=University of Colorado Museum
UK–VP=University of Kansas, Vertebrate Paleontology
USNM=United States National Museum
YPM=Yale Peabody Museum

NATURE OF MATERIALS

The extent to which any fossil fauna is known depends upon many factors. Occasionally mere chance finds of single specimens occur. Sometimes materials are collected but not described or noted for years. In most instances the entire representation of a fauna is based solely upon its macrofaunal constituents, either because no concentration of the microfaunal segment has ever been discovered, or because of a bias in collecting. Only occasionally does the ideal situation occur, wherein collecting nets ample materials from the entire size range of the original fauna. But even given this ideal, the sample is drawn from a death assemblage which may not properly represent the once-living fauna.

With these factors in mind one can appreciate that the known Split Rock fauna approaches the ideal, for it has been collected in a balanced way. The area has been generally prospected, and the Frick Laboratory has quarried there. More recently, beginning in 1948, much ant-hill collecting has been done, and a very small amount of material has even come from mining the weathered surface of the beds.

For our immediate consideration the significant fact is that the microfauna has been so adequately sampled. This has made it possible to assemble in principle (if not actually) the entire front limb of *Arctoryctes* from thousands of near-microscopic fragments.

It should here be noted also that even with such rich microfaunal materials as these, which were in large measure gathered together by harvester ants (Galbreath, 1959; Turnbull, 1959), another kind of bias is incorporated into the sampling—a bias of the ants' making. Harvester ants, in building their mounds, "select" objects to be incorporated into the mound according to size, shape and weight. Too small or light an object does little for the protection of the mound, and may be blown or washed away. Too large or heavy an object cannot be picked up and hauled for any distance by the ants. Thus, ill-defined limits exist as regards the size of the stone, bone or tooth which can be transported to the ant hill, and it is important to recognize the existence of this bias. In particular for *Arctoryctes*, the

humerus, radius and ulna are all too large to be found as complete bones under these circumstances, although fragments of them are abundant. Thus for complete bones we must rely on the more conventional techniques of prospecting, or the more rarely employed one of mining the formation in a richly fossiliferous area. The other bones of the manus of *Arctoryctes* all fall within the upper size limits of the ant's carrying capabilities. However, we are certain that the smaller carpals and phalanges approach the lower limit of size for use as a roofing shingle for the ant mound. Accordingly, these smaller elements are decidedly less well represented in the total sample of the fauna.

In most respects the Cedar Creek and Mellinger faunas present parallel situations to this one as just described for the Split Rock fauna, except that the amount of material is not as extensive.

METHODS

Only three comments on methods are necessary, and all relate to the nature of the materials—the abundant microfaunal scraps of bone. The first of these concerns the method of deciding just which scraps to pick out from the total in order to attempt to "build our animal"; the second relates to the actual articulation of the scrap in order to make a functional unit of it; and the last to a set of working principles for associating parts of skeletons never found articulated.

The decision, as to which of all the thousands of available postcranial scraps one should sort out and work with, was not made all at once, but in steps. The historical events of repeated discoveries of the *Arctoryctes-Cyptoryctes* type of humeri set the stage. It was immediately clear that the materials to be associated with such a highly specialized kind of humerus showing fossorial adaptation would have to be equally specialized along the same lines. Thus, when it was discovered that the Arner Ranch *?Proscalops* mentioned by Hough and Alf (1956) consisted of two fragments of humeri of *Arctoryctes* in faunal association with three distinct types of highly specialized metacarpals, all admirably suited for digging (Turnbull and Reed, 1960), it became clear that one or more of these metacarpals belonged to *Arctoryctes*. Then followed the puzzling problem that one of these peculiar kinds of specialized metacarpals (our "knobbed" metacarpals) occurred in large numbers in the Split Rock fauna, without there having been any humeri of *Arctoryctes* recognized there. If this were the case, the knobbed metacarpals

could be eliminated from consideration. However, once we had the Split Rock collections in hand (less the cranial, primarily dental, scraps referred to various Insectivora, Lagomorpha, Rodentia and Carnivora, which had been sorted out earlier) we found that the Amherst and Chicago Natural History Museum collections yielded sixteen pieces of humeri clearly referable to *Arctoryctes*. In addition, as many more capitular heads of humeri are almost certainly referable to *Arctoryctes*. Thus, the probability was greatly enhanced that the *Arctoryctes-Cryptoryctes* type of humerus and the knobbed metacarpals belong together. Repeated careful scrutiny of all of the fragments netted bits of most of the remaining elements of the forelimb. The next logical step was to sort the most distinctive elements, the metacarpals, into morphologically distinct groups —and reasonably enough there turned out to be five such. Thus, by stages, and sometimes by trial and error, a logical method evolved for sorting over the scrap and picking out the proper materials.

Another method deserving of comment is that by which all of these scraps suspected of belonging together could be articulated into a functional harmonious whole limb. This was accomplished by a straightforward anatomical procedure—that of systematic examination of the joint surfaces. Particular peculiarities which would necessarily have to be matched on the joint of the adjacent articulating bone were noted, and the articulations made. This procedure served well for all but the carpals, which we have not yet been able to assemble into a functional wrist.

Finally, the following are some ideal working principles for associating parts of skeletons never found articulated:

1. The various parts suggested for association should occur in the same sites and in the same stratigraphic units (as within a local fauna); it is not sufficient to show that skulls and postcranial parts, for instance, are found somewhere in the same large areas and somewhere in the same faunal age. However, in instances where one series of skeletal parts is found over a considerable range of area and/or time, it is to be expected that the parts being suggested for association will be found over the same range of area and/or time.

2. In instances where such associated skeletal parts are found together over a considerable period of time, it is not to be expected that a neat evolutionary sequence of specialization will be found, from older to younger periods. Many lineages, and many modern taxa, show persistence of relatively unspecialized forms contemporaneous with more specialized ones.

3. It is not to be expected that all parts of disarticulated skeletons will be recovered in the same numbers as were present in the living animals, as varying conditions of preservation differentially favor preservations of different skeletal parts. There should, however, be some rough correlation, the degree varying from site to site, between cranial and post-cranial parts, between bones of the fore and hind limbs, etc. Thus, association of very rare bones and very common ones at the same site, while possibly correct, is always suspect. (Techniques of collection may actually introduce the greatest bias in the sample; unless one achieves the difficult but happy optimum of complete recovery of materials from a given site, some bias is almost inevitable.)

4. The parts being associated should be of such a size that they would have fitted into a harmonious whole in the living animal.

5. The parts being associated should, within limits dictated by the accumulated experience of comparative anatomists and vertebrate paleontologists, reflect the same habitus. As between cranial and post-cranial parts, a similarity of habitus may be difficult or impossible to judge, but within a limb, at least, the principle is clear.

6. When parts being associated are artificially fitted together, a functional morphologic unit must emerge, with all details agreeing.

7. Collecting must have been sufficiently thorough (and in this instance have included the microfauna), and morphologic and taxonomic identification sufficiently accurate, to make workable the prior six points.

HISTORY OF ARCTORYCTES AND CRYPTORYCTES

The single humerus upon which the genus *Arctoryctes* was named was first discussed by Matthew in 1906, and for almost a half-century no other specimen of this group was reported, although we now know that some specimens were collected in the meantime. The near simultaneous appearance of Galbreath's publication (1953, p. 49) and the more thorough discussion by Charles Reed (1954) stimulated interest, however, and the amount of material has steadily grown—a trend which was sharply accentuated with the interest aroused by the tentative identification of the metacarpals by Turnbull and Reed (1960). At present, two genera and three species of this group have been named, all based on humeri, and we suspect that other species of *Arctoryctes* could be named from other populations of Chadronian, Orellan, and Hemingfordian ages, if we had more complete material.

HISTORICAL SUMMARY

1. Matthew (1906) discussed, but did not name or even describe, a humerus (AMNH 12864) from the Upper Rosebud formation[1] (early Miocene) of South Dakota. He thought the animal represented a "golden mole" (Chrysochloridae), native now to South Africa, and this preliminary identification was copied in many subsequent papers.

2. Matthew (1907), without further description or discussion, named a new genus and species, *Arctoryctes terrenus*, based upon the humerus.

3. Simpson (1927) suggested that *Arctoryctes* may have belonged to the Epoicotheriidae, a North American Oligocene family of palaeanodont edentates.

4. Matthew became less convinced of the chrysochlorid affinities of *Arctoryctes;* he discussed (1928) possible relationships with the moles (Insectivora: Talpidae), and with *Apternodus*, an Oligocene insectivore of uncertain relationships, but concluded that the affinities were still undeterminable. He also stated that if *Arctoryctes* represented the humerus of *Proscalops*, then *Proscalops* must represent a distinct family.

5. Schlaikjer (1933) first figured the humerus of *Arctoryctes* and concluded that it probably belonged to *Proscalops*, which he included in the Talpidae (*sensu lato*).

6. Simpson (1937, pp. 139–140) described and figured a humerus (USNM 9777) of a fossorial mammal, similar in basic conformation to that of *Arctoryctes*, from the mid-Paleocene, Torrejonian of the Fort Union series, Montana. He compared this unnamed humerus with that of *Arctoryctes* and mentioned possible relationship with *Proscalops*, a talpid.

7. Simpson (1945, p. 53) placed *Arctoryctes* in the ?Insectivora as genus *incertae sedis*.

8. Gregory (1951, **2**, p. 692) regarded *Arctoryctes* as a mole.

9. Galbreath (1953) assigned three humeri, UK–VP 9837–9839, from the Cedar Creek, Orellan of Colorado to *?Arctoryctes*. He astutely stated that *Arctoryctes* "certainly is not talpid-like."

10. Charles Reed (1954) named the related but less specialized *Cryptoryctes kayi*, based on six humeri, CNHM, PM 1009, 1010;

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[1] Matthew may have been correct in his designation of "Upper Rosebud," but the exact horizon may be different. See, for example, the discussion by Macdonald (1957) of Matthew's usage of "Rosebud."

USNM 19102; CM 8931–8933, from the early Oligocene of Montana. Discussing *Cryptoryctes* and *Arctoryctes* together, he denied the possibility of their relationship with the Chrysochloridae or the Talpidae (as that family was then known). He discussed their possible affinities with *Apternodus* and with members of the Epoicotheriidae, and tentatively concluded that relationship with any known Oligocene edentate was probably unlikely. He refigured and discussed the Paleocene humerus described by Simpson (1937).

11. White (1954) discussed three humeri (USNM 18915 and 19024, and CM 9184) from the Chadronian of the Canyon Ferry Reservoir area, Montana, which he assigned to the Talpidae, genus and species undetermined. The first of these is a specimen of *Cryptoryctes*, and the others (which are now missing) may well be, too, for White clearly considered them all to be alike.

12. Saban (1954) mentioned possible chrysochlorid affinities for *Arctoryctes* and *Cryptoryctes*.

13. Charles Reed (1956) described *Arctoryctes galbreathi*, from the middle Oligocene of Colorado, based upon the University of Kansas specimens mentioned by Galbreath. He also included a humerus, USNM 21310, from the Orellan Toston beds, Montana. He suggested that possibly the skull of *Kentrogomphios strophenis* White, 1954, a Chadronian insectivore from Montana, could belong to the same animal as did the humerus of *Cryptoryctes kayi*.

14. White (1956, personal correspondence with Reed) stated that he had found one of the three humeri of *Cryptoryctes kayi* only a few feet from the skull of the type of *Kentrogomphios strophenis*.

15. Reed and Downs (1958) described a peculiar small humerus, LACM 1380, from the Esmeralda formation, late mid-Miocene of Nevada. This humerus seemingly is that of a lateral-thrust type of digging mammal but of a non-talpid kind.

16. During the Field Conference of the Society of Vertebrate Paleontology in 1958, Mrs. John Donohoe collected a humerus of *Cryptoryctes kayi*, MV 5813/0297, from the Oligocene site of McCarty's Mountain, Montana. It is of interest that the type specimen, a skull, of *Epoicotherium* Simpson 1927 (=*Xenotherium unicum* Douglas, 1905), also came from this site; this is the first discovery of either *Arctoryctes* or *Cryptoryctes* at a site where an epoicotheriid had also been found.

17. Saban (1958, p. 528) assigned *Arctoryctes* and *Cryptoryctes* to the Epoicotheriidae *incertae sedis*, presumably only on the basis of

the supposed similarity of these humeri to that of *Pentapassalus pearcei* Gazin, 1952, an edentate (possibly epoicotheriid, possibly metacheiromyid) from the early Eocene of Wyoming. However, Charles Reed (1954) had already discussed the reasons for his conclusion that the humerus of *Pentapassalus,* in contrast to those of *Arctoryctes* and *Cryptoryctes,* belonged to a fossorial animal using a completely different type of burrowing stroke, a difference of such a degree as to ". . . preclude close relationship."

18. Russell (1960) assigned a skull of an insectivore from Pipestone Springs, Montana, to *Micropternodus,* the type of which, a lower jaw, was also collected there (Matthew, 1903). This is the same site from which have come a great number of specimens of *Cryptoryctes kayi.* Russell thinks that *Micropternodus* may have been a burrowing animal, and that *Kentrogomphios* is a synonym of *Micropternodus.* Accordingly, he suggested that the humeri of *Cryptoryctes* might well belong to the skull of *Micropternodus,* and that all of the fossorial humeri here being considered (Paleocene to Miocene) could possibly belong with the erinaceid subfamily Geolabidinae (McKenna, 1960), along with certain other related insectivores of the Late Cretaceous and Tertiary.

19. Turnbull and Reed (1960) described two humeral fragments, CNHM, PM 3878-9, as belonging to *Arctoryctes* sp. These humeri, from the early Oligocene of Nebraska, were collected with a fragment of a radius, PM 3880, and with several separate metacarpals, PM 3887-3891. Although these metacarpals are morphologically similar to those of some small digging edentates, no identification was possible, but association with *Arctoryctes* and/or *Cryptoryctes* was suggested.

20. K. M. Reed (1961) described the Proscalopinae, a new subfamily of Oligocene and Miocene wide-skulled talpids. She suggested again that the humeri of *Arctoryctes* and *Cryptoryctes* might be those of talpids, particularly of the forms assigned to her new subfamily. If such an association were to be proved, she believes that the animals involved should constitute a new family.

21. Reed and Turnbull (this paper) attempt a reconstruction and functional analysis of the forelimb of *Arctoryctes,* although they cannot yet identify all of the bones of the carpus. The time range of *Arctoryctes* is extended into mid-Miocene (Split Rock local fauna; Wyoming), and the association of humeri of *Arctoryctes* with certain types of fossorially adapted radii, ulnae, metacarpals, and phalanges

(first suggested in 1960) is shown to occur from the Chadronian into the Hemingfordian.

They consider it nearly certain that the various species of *Arctoryctes* (including those designated but unnamed) are to be synonymized with the various species of Proscalopines. Other possible affinities are also discussed, and it is suggested that *Micropternodus* (= *Kentrogomphios*) and *Cryptoryctes* may prove to be synonyms, too, and hence that all may be allied as Proscalopines, or preferably as proscalopids.

DESCRIPTIONS AND LISTINGS

MISCELLANEOUS

A number of specimens have turned up in collections which have never been noted in the literature, and a few new specimens have been discovered. These are listed by institution and number, and with appropriate brief comments.

The first group of these contains specimens of *Cryptoryctes kayi* from Pipestone Springs and they fit into the range of the suite of materials in the hypodigm. They are as follows:

1. Recently re-located humeri, one nearly complete (CM 9806) and five less complete (lumped together under CM 2092). These have been in the Carnegie Museum collection for several years.

2. A humerus (MV 5810/0296), collected by J. L. Kay in 1958 just prior to the Field Conference of the Society of Vertebrate Paleontology.

3. Two humeri, uncatalogued, in the U. S. National Museum collections of Pipestone specimens. These have been assigned the numbers USNM 22869 and 22870.

4. A humerus discovered in 1959 by a party from Montana State University (MV 5810/0385), and another humerus fragment (MV 6008/0627) from the Easter Lily Mine locality[1] collected in 1960.

5. Two humeri collected by William and Priscilla Turnbull in June 1962 (CNHM, PM 8621 and PM 8647).

The other group of specimens is referred to *Arctoryctes*, as follows:

1. A fragment of the distal end of a humerus (CM 8752) comes from the Chadronian, Dry Creek locality, about four miles N.E. of

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[1] R. Fields has informed us that this locality lies in Jefferson County, Montana (secs. 16 and 21, T. 2 N., R. 5 W.), about 1½ miles north of the main bone pocket and that other specimens indicate a Chadronian age.

Toston, Montana.   Little can be done with this specimen beyond
tentatively referring it to *Arctoryctes* on the basis of its morphology
in the regions of the trochlear lip and the opening of the entepicon-
dylar foramen on the anterior face of the bone.   In *Cryptoryctes* there
is a broad depressed area between the lip and the opening, while in
Arctoryctes and talpids this pit is rounder and the lip and opening
are close together.   Between *Arctoryctes* and the talpids, there are
no clear-cut distinguishing features in this region.   The standard
measure "D" (see p. 135) is the only one possible for this fragmentary
specimen, and it must be estimated.   It is about 6.6 mm.

2.   A humerus of *Arctoryctes galbreathi* (SDSM 55193) from the
Crazy Johnson member of the Chadron of South Dakota, is similar
in size to the humerus (CNHM, PM 3878) of *Arctoryctes* from the
Chadron of Nebraska (Turnbull and Reed, 1960) but is more spe-
cialized in possessing a groove along the distal aspect of the teres
tubercle.   This groove indicates a medial elongation of the supra-
condyloid foramen and thus a greater development of the medial
epicondyle.   In this respect this Chadronian specimen from South
Dakota is more like the Orellan humeri assigned to *A. galbreathi*.

3.   An Orellan *A. galbreathi* (CNHM, PM 3901) was collected in
North Dakota by Jean Hough and James Hopson in the summer of
1959.   It came from the Lower Brule formation (sec. 7, T. 13 N.,
R. 97 W., Stark Co.; Fitterer's Ranch).   This specimen is a partial
humerus very similar to the type of *A. galbreathi*.

4.   Thirteen hitherto unpublished humeri (SDSM 5579, 5659,
5693, 5697, 5962, 5970, 53435, 54250, 54274, 54311, 54342, 55112, and
56104) of *A. terrenus* from the Rosebud formation of South Dakota
constitute the first addition of known specimens of this species since
the discovery of the type.   All are very similar to the type, although
not one is as complete as Matthew's original specimen; however, two
of the new specimens (SDSM 55112 and 54311) are from juvenile
specimens and show stages in the growth processes of the humerus
of *A. terrenus*.

4.   Mr. R. Alf, Webb School, Claremont, California, has located
another small batch of scrap from the Arner Ranch (sec. 26, T. 33 N.,
R. 53 W., Sioux Co., Nebraska) collection which he has presented to
us.   Accordingly, these specimens which we here assign to *Arcto-
ryctes* sp. bear CNHM catalogue numbers[1] (including those already
reported) as follows:

3 fragmentary humerii; CNHM, PM 3878-3879 and PM 8092.

2 partial radii; PM 3880 and PM 8093.

2 partial ulnae; PM 8094, 8095.

6 metacarpals, 1 metacarpal ?I; PM 8096.

       1 metacarpal ?II; PM 3887.

       3 metacarpal III; PM 3888, 3890-3891.

       1 metacarpal ?IV; PM 3889.

1 first phalanx; PM 8097.

3 terminal phalanges; PM 8098-8100.

It will be noted that the metacarpals described by us in 1960 have been assigned as to their position in the manus. This assignment is in conformity with that deduced for the Split Rock specimens (see pp. 117-118) of *Arctoryctes* sp. The first phalanx is notable in that it differs from the known Split Rock first phalanges (see p. 119) by being neither of the "squat" type nor the "long" type. Instead, its proportions are intermediate between the two. The terminal phalanges show a slightly less well-developed retroarticular process than do those from Split Rock. Otherwise these Arner Ranch specimens are similar, but smaller than their Split Rock counterparts.

The remainder of the new materials are from extensive microfaunal collections wherein large numbers of fragmentary specimens are involved.

SPLIT ROCK LOCAL FAUNA

(NW. ¼, sec. 36, T. 29 N., R. 90 W., Fremont Co., Wyoming;
Mid-Miocene)

Humerus.—Fifteen referred specimens of fragments of humeri of *Arctoryctes* sp.: CNHM, PM 8535-8537, 8579-8581, 8593, and ACM 8500-8507. In addition, the following twenty capitular heads of humeri are probably all referable to *Arctoryctes*, as all are of the proper size for that genus but not for the small mole (p. 156) that occurs as a rare member of the fauna: CNHM, PM 8582a-g, PM 8592, and ACM 8508-8519.

The fifteen fragments of the distal ends of humeri of *Arctoryctes* are quite certainly identifiable, being scraps which include the capitular head and enough of the unique lateral articular joint surface (see fig. 25, A and B, where this joint is illustrated in the Pipestone *C. kayi* and the Rosebud *A. terrenus*) or enough of the distal half of the humerus as to leave little room for doubt as to the assignment. The twenty capitular pieces are such small fragments that no posi-

tively diagnostic features are preserved, yet their size and morphology are so much in agreement with the others that we have little doubt that they also are referable to *Arctoryctes*.

Radius and ulna.—Thirty-eight referred specimens of radii: CNHM, PM 8538, 8540–8545, and 8546a and b, 8585–8588; and ACM 8520–8544 (figs. 13 and 16, A and B). 25 referred specimens of ulnae: CNHM, PM 8572–8578, 8589–8591; and ACM 8545–8550, ACM 8552–8560 (figs. 14 and 16, A and B).

Both of these elements are represented by a fair number of specimens (especially in the Amherst collection) with 38 radii and 25 ulnae having been identified. The most striking features about these bones, in comparison with their counterparts in the specialized mole *Scalopus*, are their relatively elongate and slender lines. The proximal end of the radius has a considerable lateral extension to its strong broad capitular process, which bears a well-marked articular surface for a greatly expanded joint (fig. 13, A and D). This surface articulates with a similarly expanded joint surface that is situated on the lateral epicondyle of the humerus (fig. 25, B). There is also a very marked joint on the medial side of the radius (ulnar facet) (fig 13,D) for articulation with a correspondingly well-developed (radial) articular facet on the lateral side of the ulna (fig. 14, C). The ulna has a complex and sizable olecranon process (fig. 14, A, B, and C) as would be expected of such a highly specialized burrowing animal, but it lacks the massiveness seen in *Scalopus* (fig. 15) or *Scapanus*. Too, the shafts of both bones are less stout than in these moles. However, the distal ends exhibit nearly as much of a flare, and show quite similar articular surfaces to those of *Scalopus*, although the proportions of the joint facets differ in several notable ways. Those of the ulna in *Arctoryctes* have a smaller joint for articulation with the cuboid (=ulnare), and a larger one for the lunar (=intermedium), than in *Scalopus*. The radius has its distal articulation nearly equally divided between facets for the scaphoid (=radiale) and lunar, but favoring the latter somewhat, whereas in *Scalopus* the situation is the reverse.

Carpus.—The identification and articulation of the carpals (including the separation of carpals from one another as well as the separation of those belonging to other small mammals from those of *Arctoryctes*) has proven to be an extremely difficult, uncertain and tedious undertaking. Only the scaphoid and lunar (fig. 16, A and B) have been identified and articulated with a reasonable degree of certainty. A total of thirty scaphoids have been recognized: ACM 8716a–b, 8717a–c, 8718a–b, 8719a–d, 8720, 8721a–d, 8722, 8723; and
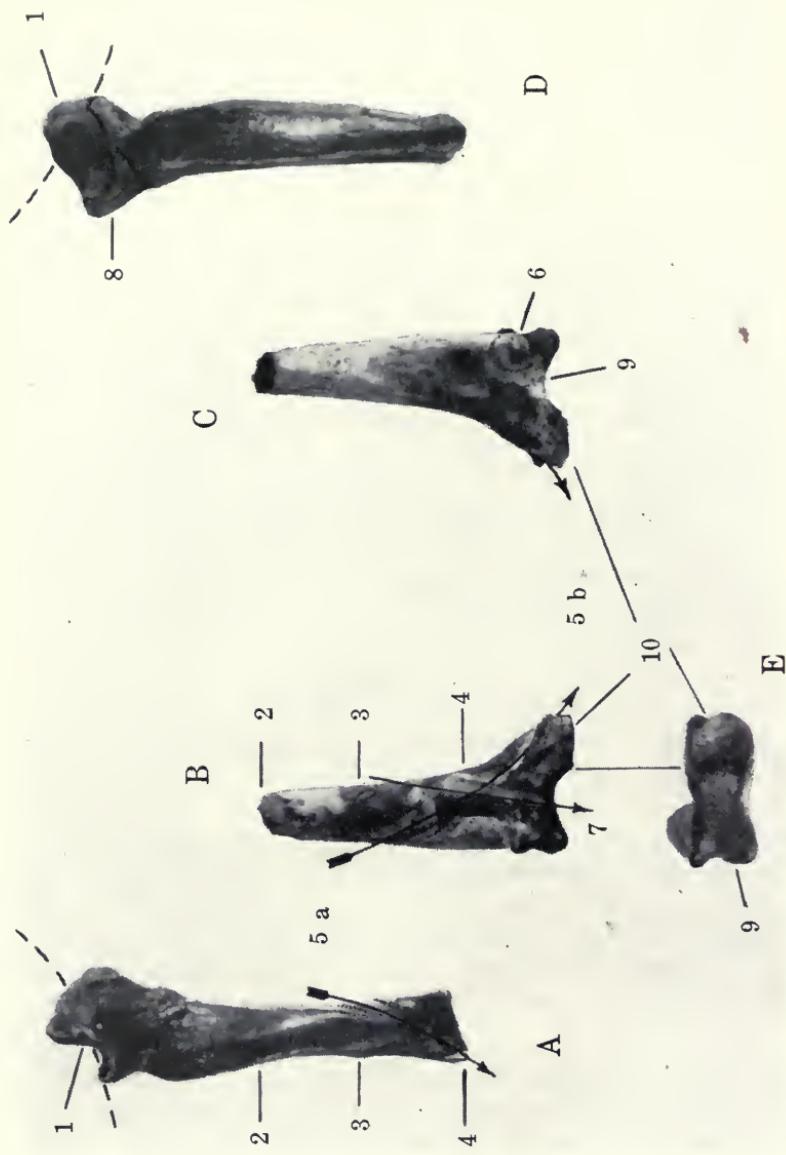
Fig. 13. Various views of two selected fragments of radii of *Arctoryctes* from the Split Rock fauna.

A, proximal 4/5 l. radius ACM 8527 in anconeal aspect; D, same in anterior aspect (ie, rotated 90° from anconeal aspect); B, distal 2/3 r. radius ACM 8528 in anconeal aspect; C, same in palmar aspect; E, same in distal aspect.

(1) lateral extension of capitular process with its additional articular surface for an important lateral joint to articulate with a similar accessory development on the humerus; (2) & (3) attachment scars of M. supinator and M. pronator radii teres; (4) terminus of ridge at edge of grooves where tendon of M. abductor pollicis longus crosses that of M. extensor carpi radialis; (5a)→ & (5b)→ groove for tendon of M. abductor pollicis longus; (6) joint facet for articulation with distal end of ulna; (7)→groove for tendon of M. extensor carpi radialis, (8) ulnar articular facet; (9) joint facet for articulation with lunar (intermedium); (10) joint facet for articulation with scaphoid (radiale). Note that the correspondence of points 2 through 5 permits a reasonable estimation of total length. Approx. ×5½.
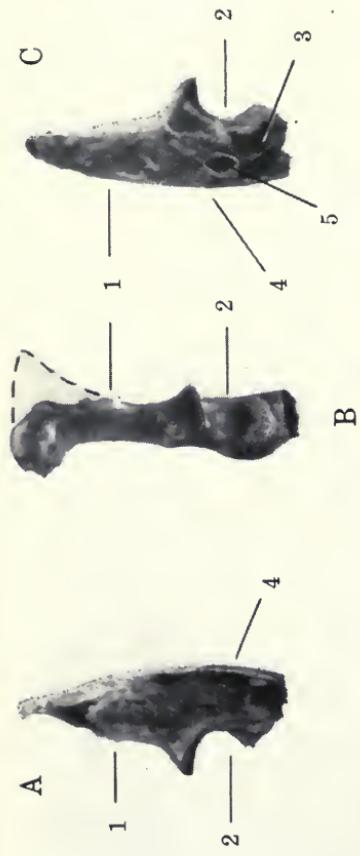
Fig. 14. Views of two fragments of ulnae of *Arctoryctes* from the Split Rock fauna. A-B-C, proximal ⅓ right ulna, ACM 8552 in palmar, anterior and dorsal aspects respectively; D-E-F, distal ⅓ left ulna, ACM 8555 in palmar, distal and dorsal aspects respectively; (1) olecranon process; (2) semilunar notch; (3) radial articulation facet; (4) posterior crest; (5) pit—possibly for a tendon attachment—adjacent to attachment region (area of origin) of M. abductor pollicis longus; (6) joint facet for articulation with distal end of radius; (7) joint facet for articulation with lunar (intermedium); (8) joint facet for articulation with cuneiform (ulnare); (9) ?joint facet for articulation with pisiforme. Approx. × 5½.

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CNHM, PM 8595–8606. The scaphoid (radiale) is readily comparable with that of *Scalopus* (fig. 15) in its general morphology, although its proportions are quite different, and its share of the distal articular surface of the radius is less than that of the scaphoid in *Scalopus*. In its plantar aspect it is more elongate, and hence far less broad than its counterpart in *Scalopus*. In dorsal aspect one can see that its distal articular surface is disrupted so as to lie at two different levels whereas in *Scalopus* the distal articular surface is essentially all in one plane.

Sixteen lunars have been recognized: ACM 8724, 8725a–b, 8726–8728, 8729a–c, 8730; and CNHM, PM 8648, 8701 and 8702a–d. The lunar (intermedium) is less recognizable since its shape and proportions deviate considerably from its homologue in *Scalopus*. The relatively larger articulation of this element with the radius in *Arctoryctes* is strikingly provided by a large hemispherical blob of bone which articulates beautifully with the facets of both the radius and the scaphoid.

Unfortunately the remainder of the carpals can only be questionably referred to *Arctoryctes*. A type of cuneiform (ulnare) (fig. 16, C and D) is thought to be that of *Arctoryctes*, but has not been satisfactorily articulated and so its referral is dubious. ACM 8731 and CNHM, PM 8654, 8703, 8704a–c, all fall into this category of specimens. The same may be said for a ?pisiform (fig. 16, E and F). ACM 8732, 8733 and CNHM, PM 8650, 8705a–c and 8706a–c constitute the presumed pisiforms. A number of distal carpals are also thought to belong to *Arctoryctes*, but again our attempts at fitting and manipulating possible articulations under low magnification have not been successful. Therefore these bones cannot be referred at this time. Fig. 16, G–J show several of these, in various comparable views. Note the consistency of the process or spine on the ?palmar side of three of these presumed distal carpals. This long process is intriguing, for it could serve as a tendon attachment which would provide a tremendous flexion leverage advantage—just the kind and degree of development that might be expected to be associated with the knobbed metacarpals such as *Arctoryctes* possessed. On the other hand, the fact that these Split Rock ?distal carpals are somewhat smaller on the average than the similar bones from the Cedar Creek materials of Galbreath, would argue against this referral because the Split Rock *Arctoryctes* is in all other respects a larger form than the Cedar Creek *A. galbreathi*. They are represented by fifty-three specimens which are catalogued under the fol-

Fig. 15. Articulated radius, ulna and proximal series of carpals of Recent mole, *Scalopus aquaticus* (CNHM 19034) for comparison with figs. 13, 14, & 16; A, palmar aspect; B, dorsal aspect; (1) scaphoid (radiale); (2) lunar (intermedium); (3) cuneiform (ulnare); (4) pisiforme. Approx. × 5½.

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lowing numbers: ACM 8734-8743; and CNHM, PM 8649, 8651-
8653, 8707-8713.

Metacarpus.—Referred materials of *Arctoryctes:* 14 specimens of
metacarpal ?I (or ?V): ACM 8561-8568; and CNHM, PM 8351-
8352; PM 8509-8511; and PM 8608.

42 specimens of metacarpal ?II (or ?IV): ACM 8569-8590; and
CNHM, PM 8361-8365; PM 8474-8488.

41 specimens of metacarpal III: ACM 8591-8617 and CNHM,
PM 8353-8355; PM 8463-8473.

55 specimens of metacarpal ?IV (or ?II): ACM 8618-8646; 8714;
and CNHM, PM 8356-8359; PM 8489-8508; and PM 8520a.

21 specimens of metacarpal ?V (or ?I): ACM 8647-8656; and
CNHM, PM 8512-8519; PM 8583-8584; and PM 8607.

9 specimens of metacarpals, indeterminate as to position because
of breakage or wear. ACM 8657-8661; and CNHM, PM 8521a-d.

The metacarpals of *Arctoryctes* with their distal knobs[1] are such
remarkable bones, and they occur in sufficient abundance, that were
it not for their small size they would probably have been discovered
long ago. To date a total of 182 of them have been recognized in the
ACM and CNHM Split Rock collections alone—metacarpals II, III,
and IV together accounting for 137 of these. Five kinds occur, all
with left- and right-handed representatives. Each kind is distinc-
tive, and the central three join with one another so beautifully and
by means of such well-defined articulation surfaces that no uncer-
tainty about their articulation is possible (figs. 17, A; and 18). Yet
since metacarpals I and V are less certainly fitted, we cannot make
a categorical statement as to which is which for either II and IV or
I and V, nor do we know left from right for any of them with cer-
tainty. For this reason it was necessary to list them all with a query
as to position within the manus, except for metacarpals III.

[1] Actually, a number of moles also have similarly knobbed metacarpals we now
discover. *Uropsilus* (*Nasilius*) has distinct knobs on metacarpals II and III, and
faint knobs on I and IV (V being missing on the specimen seen, CNHM 40923).
The presence of knobs on specimens of *Condylura* was found to be variable.
YPM 1698, CNHM 33932 and 34894 each have metacarpal V distinctly knobbed,
and IV with knobs almost as well developed as those of V, while each metacarpal
III has less distinct knobs and I and II either lack the knob or evidence but a
trace of it. In *Scalopus*, CNHM 19034, and *Scapanus*, CNHM 18832, metacarpals
I–III lack the knob, and IV shows a slight trace of a knob, perhaps more pro-
nounced in *Scalopus* than in *Scapanus*, and V has a weak, but distinct knob.
Apparently our sampling of the condition of the metacarpals of moles for our
previous paper was inadequate, and unfortunately happened to coincide with those
metacarpals that happened to lack the knobs. A different choice of metacarpal
on the same individuals would have located knobbed metacarpals. We are glad
that we have caught this error.

Both of the lateral metacarpals in the suite of three which articulate so perfectly (fig. 17, A, ?II and ?IV) show lateral articulation faceting proximally, for joining with metacarpals I and V. The difficulty is that either I or V will fit into one of them, ?II, about equally well, while neither will make a very good union with ?IV. The alternative articulations of the two possible first metacarpals (metacarpals ?I or ?V) with ?II are illustrated in fig. 17, B and C. We believe that fig. 17, B illustrates the least likely of the alternatives for the reason that the region marked "a" appears to be an articulation facet, and this facet will make a loose, but possible sort of fit to the free side of metacarpal ?IV (fig. 17, C) at the facet marked "ʇa)." If that is the case, the other facets (such as the one in articulation in fig. 17, B) must articulate with distal carpals, and they are in the proper position for doing so. Other points supporting this view are: 1) the fact that the alternative articulation shown in fig. 17, C is perhaps the better of the two; 2) when the metacarpals are arranged in this order, their distal knobs fall into an evenly graded series which is most pronounced on the side of the pollex; 3) the alignment of the prominent pulley-like glide surface for a very powerful tendon, presumably that of M. abductor pollicis longus,[1] which is consistent with the markings indicating a similar hyperdevelopment of this muscle and tendon that appear on the scaphoid and radius (figs. 13, A, B, C; 16, A, B; and 17, C). One point seems to oppose the acceptance of this view—that is, if it is true, then metacarpal V is markedly larger than I, which seems rather strange to us.[2]

One further minor anatomical point should be noted regarding the metacarpals. At the distal end of the palmar surface of most of them, just a short distance proximal to the terminus of the articular roll joint surfaces, can be seen a pair of raised areas, one medial and one lateral, which we presume to mark the location of the attachment of joint binding ligaments. In one specimen, CNHM, PM 8472, the ligament on one side ossified (a paleopathologic abnormality

[1] If this bone were a metacarpal V, then the tendon groove would have to be for M. extensor carpi ulnaris. This is a possibility of course, but we feel that it is an unlikely one for there is no correspondingly defined groove for it on the ulna such as would be expected. On the other hand there is a well-defined one for the tendon of M. abductor pollicis longus on the radius.

[2] Actually this may not be too surprising for *Uropsilus* and *Condylura* both have pollical metacarpals shorter than those of the other digits. Our surprise, no doubt, stems from a consideration of Talpa which has a pollical metacarpal that is larger than any of its other metacarpals.

which is probably indicative of an advanced age of the individual)
and it is thus preserved in part (fig. 19, A).

Phalanges.—Materials: 21 first phalanges of the "squat" type:
ACM 8662–8670 and CNHM, PM 8367a–g; PM 8369–8372; and
PM 8609. 20 first phalanges of the "long" type: ACM 8671–8679;
CNHM, PM 8366a–g; PM 8520b and PM 8522–8524.

57 second phalanges: ACM 8680–8682a–b; 8683–8687; 8688a–c;
8689–8690; 8691a–c; 8692–8694; 8695a–b; 8696a–e; and CNHM,
PM 8368a–s; 8520c; and PM 8525–8534.

128 terminal phalanges: ACM 8697a–c; 8698a–f; 8699a–j; 8700a–
i; 8701a–k; 8702a–b; 8703a–e; 8704a–d; 8705a–i; 8706a–c; 8707a–c;
8708a–c; 8709a–b; 8710a–c; 8711a–d; 8712, 8713a–g; and CNHM,
PM 8520; PM 8547a–p; PM 8548–8571 and PM 8610a and b.

Just as the other forelimb elements of *Arctoryctes* were readily
separated out from the totality of the microfaunal scrap comprising
the Split Rock collections because of distinguishing features, so also
were the phalanges. Just as the metacarpals possess the distal knobs
that so aptly characterize them, the proximal articular surface of
each first phalanx has a corresponding pit to receive the knob (fig.
19, B and C). Distally, these phalanges repeat the morphology of
the distal ends of the metacarpals to the extent that they, too, are
knobbed in the same manner. We do not know (nor have we made
a concerted attempt to discover) which first phalanges go to which
digit, but we do know that they come in two varieties which we have
called the "squat" and the "long" types. The "long" type is the
more symmetric of the two, but even it gives a skewed appearance
when viewed in dorsal aspect. On its palmar side, ligament (or ten-
don) attachment areas can be seen. These are similar to those noted
on the metacarpals. The "squat" type is quite asymmetric. It has
a completely reduced shaft, for it appears to consist of little more
than proximal and distal epiphyses, which are fused to one another
where the shaft should be.

On the proximal articular surfaces of the second phalanges of
Arctoryctes (fig. 19, D), we again see a replication of the pattern of
the main surface features of the first phalanges. There is a central
pit to accommodate the knob, in addition to the presence of the two
joint fossae on either side. Distally, they are more usual, although
they show a remarkable development of the roll joint itself, to span
an arc of about 225°. This would indicate considerable mobility at
this terminal joint.
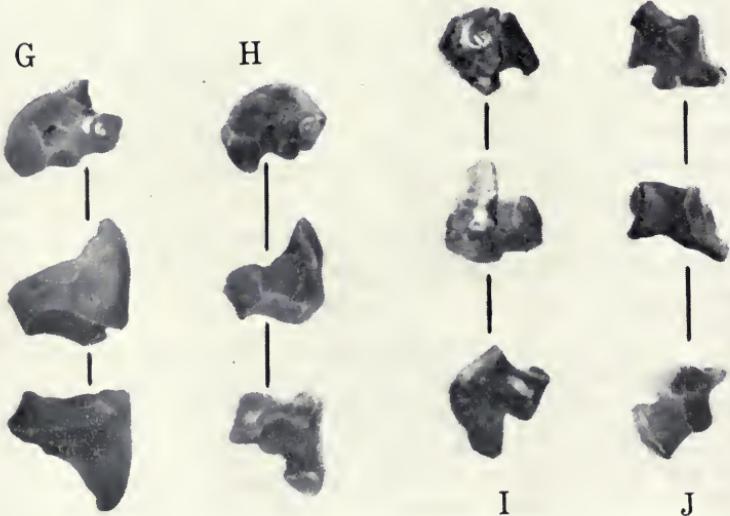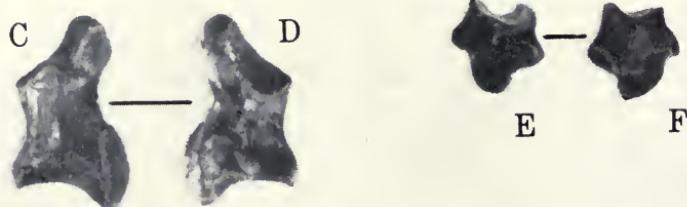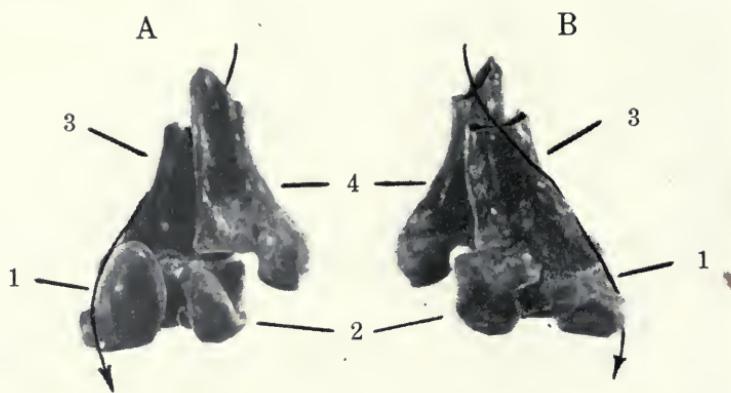
The terminal phalanges of *Arctoryctes* are proportioned very similarly to those of specialized moles, and could well be taken for such at first glance.   However, the only mole (true talpid) in the fauna is much smaller than *Arctoryctes*, and is extremely rare (only six fragments—two humeri, a partial radius, two metacarpals and a second phalanx) and hence it is unlikely that the phalanges of the two would be mistaken for one another.   Actually, close inspection reveals differences in some details between the terminal phalanges of *Arctoryctes* and those of advanced moles.   The proximal retroarticular process is more attentuated backwards than it is in *Scalopus*, and accordingly it is more slender.   The dorsal surface shows the most characteristic differences.   There one sees a median, highly arched and rounded ridge (fig. 20, A and B) instead of the cleft, or groove, which is found in all of the advanced talpids (Reed, 1951, p. 556).   Reed believed the groove to function as a strengthening mechanism between the phalanx and its claw, for he found a correlation with fossorial activity.   In *Arctoryctes* (and presumably in the *Arctoryctes–Cryptoryctes* group) apparently no such device was necessary.

It is also of interest to note that the neuro-vascular pathways as seen on the surface of the bone, are remarkably similar in the directions and routings they take, in *Scalopus* and *Arctoryctes*, differing mainly in that those of the latter are relatively larger in diameter. In both genera the pathways run on the palmar surface of the bone along both sides of the prominent attachment node of the tendon of M. flexor digitorum profundus.   They then branch proximally, within a pit, to supply the interior of the bone, and again at the level of the distal end of the tendon attachment node.   There a ventral branch swings inward somewhat, to run distally along the side of the ventral surface of the bone for the rest of its length.   The dorsal branch follows a similar pathway on the dorsal side.   In *Arctoryctes*, however, it is consistently somewhat larger than in *Scalopus* and lies nearer the central axis of the bone.   Also in *Arctoryctes* about halfway from the branching to the tip, it often enters the bone for a short

FIG 16.   A & B, articulated radius (3) (ACM 8531), ulna (4) (ACM 8546), scaphoid (1) (CNHM–PM 8599) and lunar (2) (CNHM –PM8648) of *Arctoryctes* from the Split Rock fauna in palmar and dorsal aspects respectively, arrows showing pathway (grooved) of tendon of M. abductor pollicis longus; C & D, ?cuneiform (CNHM–PM 8654), possibly belonging to *Arctoryctes* seen in two aspects; E & F, ?pisiforme (CNHM–PM 8650), possibly belonging to *Arctoryctes* seen in two apsects; G–J, ?distal carpals possibly belonging to *Arctoryctes* seen in three aspects (G=CNHM–PM 8652; H=CNHM–PM 8649; I=CNHM–PM 8651; J=CNHM–PM 8653).   Approx. × 5½.
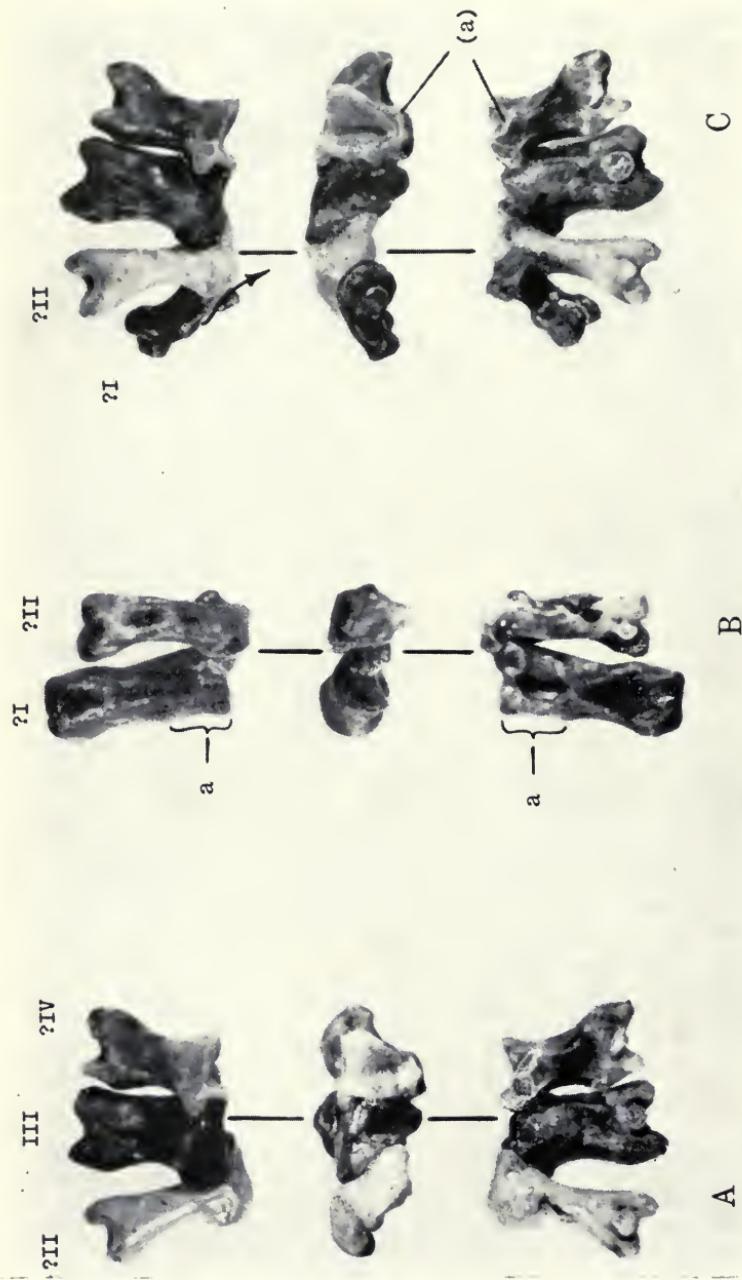
Fig. 17. Metacarpals of *Arctoryctes* from Split Rock fauna in articulation. A, The central three metacarpals which articulate with certainty, as seen in dorsal, proximal and palmar aspects. From l. to r. they are PM 8363 (?II), PM 8355 (III), and PM 8359 (?IV); B, one of two possible articulations of the remaining two kinds of metacarpals with metacarpal ?II seen in the same 3 views; "a" indicates area which may be an articulation facet. The specimens are PM 8518 on left and PM 8362 on right; C, similar views of the alternative to B. This would appear the more likely of the two. Note the tendon glide surface on the presumed pollical metacarpal, over which the tendon of M. abductor pollicis longus moves (arrow). The presumed metacarpal I, PM 8351, is on the left, and the others are the same as in A; (a) indicates the articulation facet which could accomodate "a" of B. Approx. × 5½.

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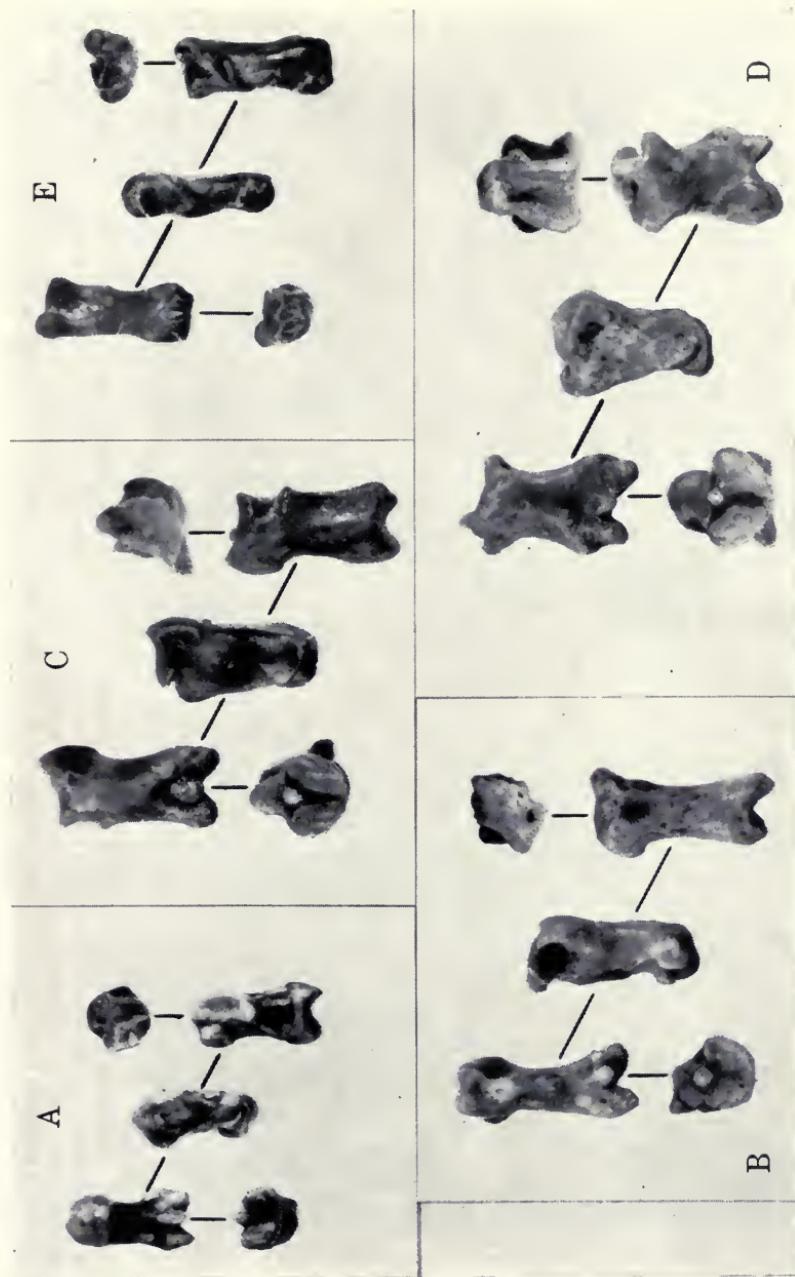
Fig. 18. The five types of *Arctoryctes* metacarpals: A, (?I) PM 8510; B, (?II) PM 8500; D, (?IV) PM 8467; and E, (?V) PM 8515. Each is shown in various aspects according to the following scheme: palmar (upper left), lateral (middle), dorsal (lower left), proximal (upper right), distal (lower left). All are from the Split Rock fauna. Approx. × 5½.

123
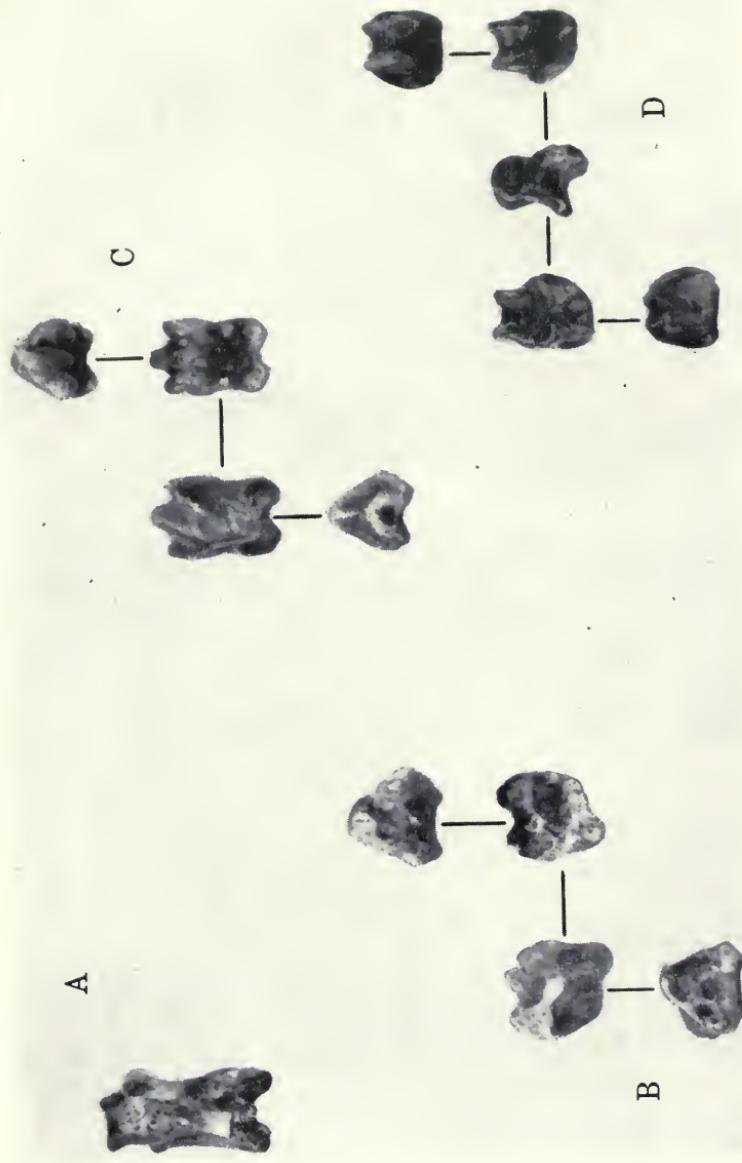
Fig. 19. A, metacarpal III of *Arctoryctes*, PM 8472, showing ossified binding ligament of joint; B, "squat" type of first phalanx of *Arctoryctes*, PM 8371 in four views according to the following scheme: dorsal (upper left), distal (upper right), palmar (lower right), and proximal (lower left); C, "long" type of first phalanx of *Arctoryctes*, PM 8522, in the same views as B; D, second phalanx of *Arctoryctes*, PM 8525, in five views (as in B & C and also in lateral aspect, center). All approx. × 5½.
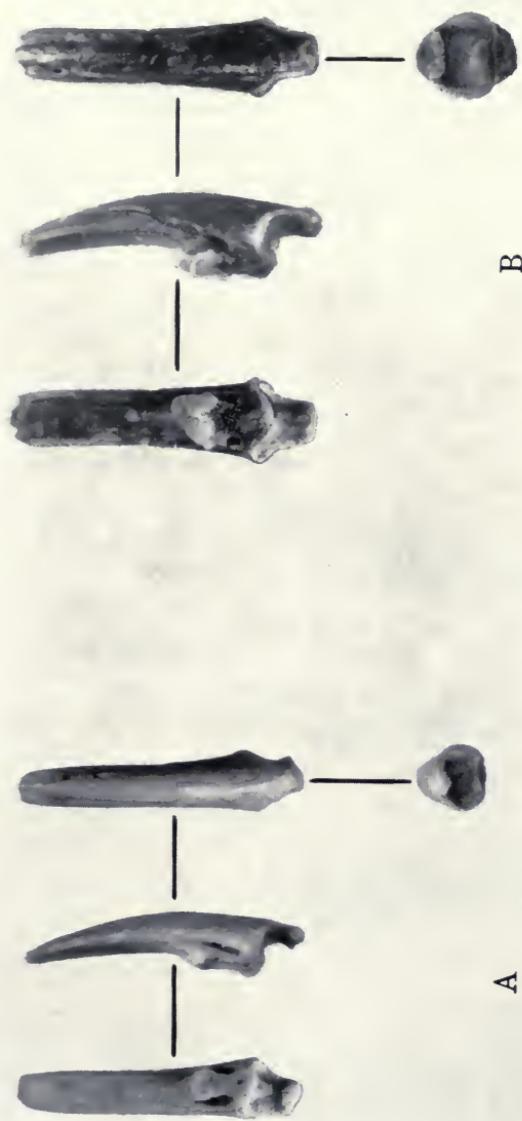
Fig. 20. Four views of two of the better terminal phalanges of *Arctoryctes*. A, PM 8553 in palmar, side, dorsal and proximal aspects; B, PM 8548 in the same four views. All approx. × 5½.

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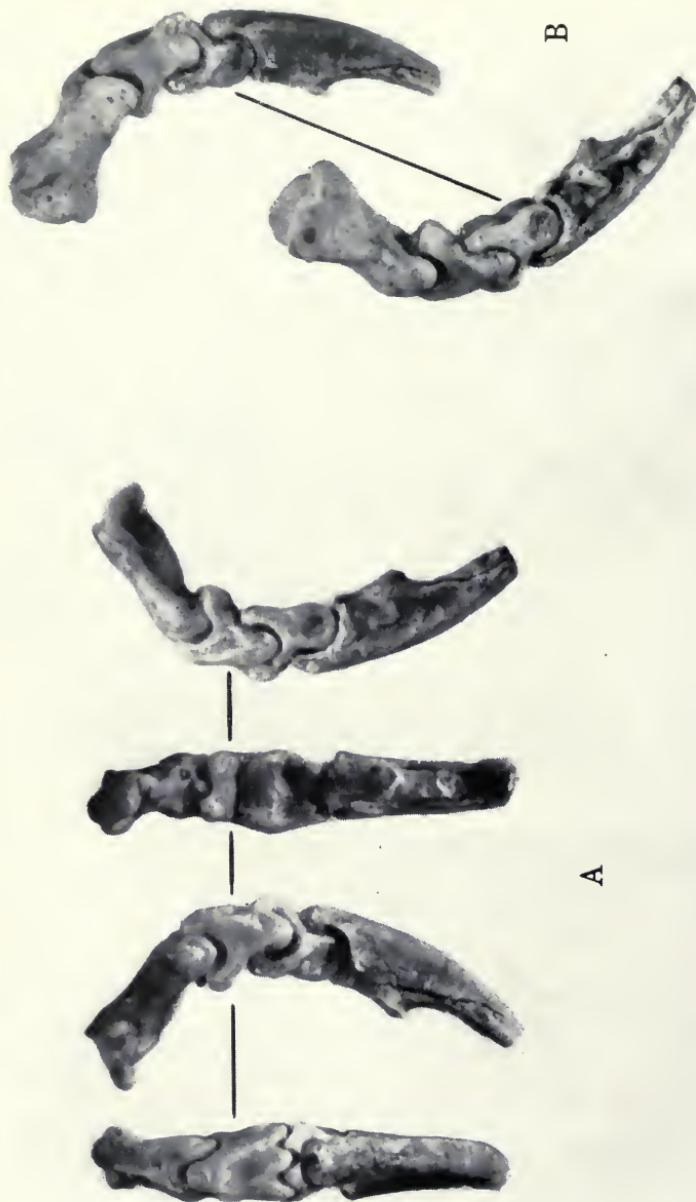
Fig. 21. A phalangeal series of *Arctoryctes* articulated in principle with several metacarpals. A, four views of the metacarpal ?II (PM 8484) in articulation with the phalangeal series comprised of a "long type" first phalanx (PM 8520b), a second phalanx (PM 8520c) and a terminal phalanx (PM 8520); B, the same phalanges articulated with another metacarpal, ?IV (PM 8520a), to emphasize the facility of making such articulations in principle. Approx. × 5½.

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distance, to emerge almost immediately with a larger diameter, having become joined with some of the internal supply. At the very tip, another such union of external and internal paths can often be seen.

Articulations in principle, for each of the types of phalanges, have been made. Fig. 21, A, illustrates one such "digit" joined to a metacarpal ?II, and fig. 21, B, to a metacarpal ?IV.

MELLINGER AND CEDAR CREEK FAUNAS

Recently Peter Robinson sorted over most of the materials from the Mellinger locality contained in the collections of various museums. He is currently gathering more materials for UCM, so that the number of specimens of *Arctoryctes* sp. from this fauna will no doubt continue to increase, and a specific assignment may become possible in the near future. Our tabulation is as up to date as we have been able to make it, and thus far, for both this fauna and for Galbreath's Cedar Creek fauna, there are far fewer specimens available than we had for the Split Rock fauna, although the Cedar Creek materials are quite abundant.

Referred specimens, *Arctoryctes* sp.: Mellinger locality: sec. 17, T. 11 N., R. 65 W., Weld County, Colorado.

YPM 15126, a nearly complete humerus.

UCM 21072, distal 3/4 humerus.

YPM 15187, a metacarpal ?IV.

UCM 21121, a metacarpal III.

UCM 21123, a "long" type first phalanx.

UCM 21119, a second phalanx.

UCM 20789–20791, three terminal phalanges.

Questionably referred to *Arctoryctes* sp.:

UCM 20792, a proximal 1/2 metacarpal.

UCM 20793, a ?cuneiform.

UCM 20794-5, two ?distal carpals comparable to the Split Rock bones as represented by fig. 16, G.

Most of these bones are illustrated in fig. 22 for comparison with those of the Split Rock and the other faunas. Little could be said that inspection of the figures would not bring out more effectively. All of the bones from the Mellinger locality are smaller except the dubiously referred ?distal carpals and have a softer appearance than their Cedar Creek equivalents (i.e., none of the surface structures are as sharp—see p. 129), and the Split Rock bones are much larger than

FIG. 22. *Arctoryctes* sp. from the Mellinger locality. A, partial left humerus in posterior and anterior aspects, (from left to right). UCM 21072; B, nearly complete, but broken, right humerus in anterior and posterior aspects (from left to right), YPM 15126. Broken humeral head and part of greater tuberosity is shown with the anterior view; C, knobbed metacarpals: YPM 15187, a metacarpal ?IV on left, and UCM 21121, a metacarpal III on right; D, a long first phalanx, UCM 21133 (bottom left), a 2nd phalanx, UCM 21119 (top left) and a distal phalanx UCM 20789 (right). Approx. × 5½.
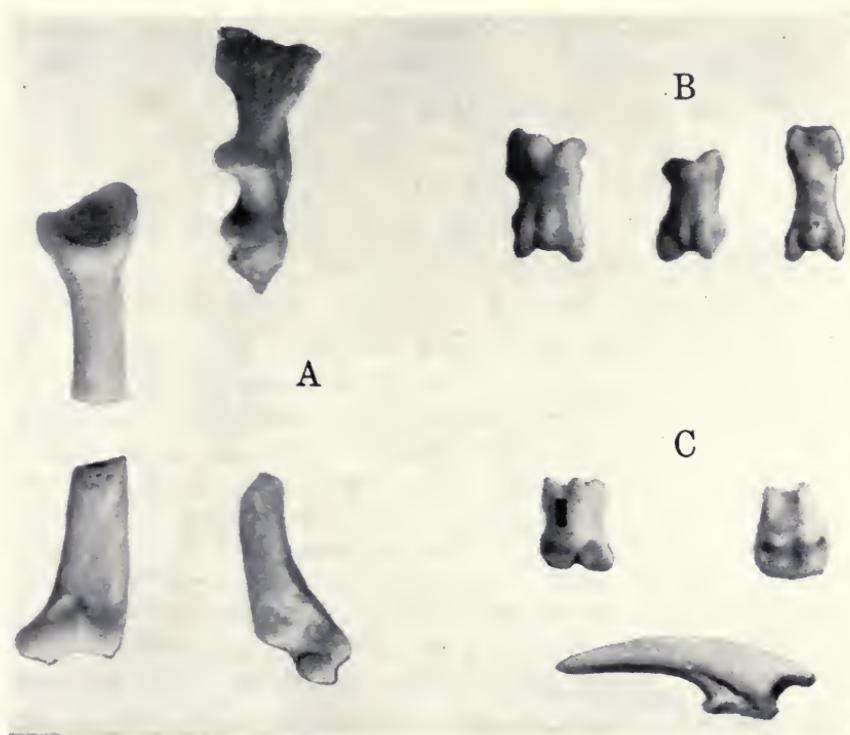
FIG. 23. *Arctoryctes galbreathi.* A, proximal (ECG–P–316) and distal (P–317) fragments of radius (left) and proximal (P–320) and distal (P–329) fragments of ulnae (right) from the Cedar Creek of Colorado; B, metacarpals ?II (P–332), ?IV (P–227) and III (P–222) from the Cedar Creek fauna (in order from left to right); C, "long" first phalanx (P–201, upper left); a second phalanx (P–213, upper right) and distal (terminal) phalanx (P–339, below) from the Cedar Creek, Colorado fauna. All approx. × 5½.

those from the Cedar Creek or Mellinger localities.   Between the Mellinger and the Cedar Creek forms, we believe that we are dealing mainly with differences of degree, and not of kind, and we interpret them to indicate local populations which are probably specifically distinct from other known near-contemporary populations of *Arctoryctes.*

Referred specimens, *A. galbreathi:* Cedar Creek fauna localities in: 1) SW¼, sec. 12, T. 11 N., R. 54 W.; 2) W½, sec. 7, T. 11 N., R. 53 W.; and 3) NE¼, sec. 3, T. 11 N., R. 54 W.; all in Logan Co., Colorado.

13 humeri (10 of them new); UK–VP 9837–9839, ECG, P 229– 231, and P 301–307, all very fragmentary except for the UK–VP specimens.

10 partial radii; ECG, P 308-317.

12 partial ulnae; ECG, P 318-329.

16 metacarpals;—7 metacarpal ?II—ECG, P 216-217,

P 224-225, and P 330-332.

6 metacarpal III—ECG, P 218-223.

3 metacarpal ?IV—ECG, P 226-228.

12 first phalanges; ECG, P 201-212.

5 second phalanges; ECG, P 213-215, P 335-336.

19 terminal phalanges; ECG, P 337-355.

These specimens from Galbreath's collection comprise the only lot of extra-humeral materials which can be referred to an already named species (as based on humeri). They are all representatives of *A. galbreathi* Reed 1956. In the other lots (Split Rock, Mellinger, and Arner Ranch), the humeri are either too poorly known from the fragments available, or the differences are of such a nature that it has in the past seemed unwise to give them names—and we continue in this view here. Fig. 23 shows a selected sample of the Cedar Creek materials for comparison with the Split Rock and Mellinger specimens. It will be noted that just as with the Split Rock specimens, the distal end of the radius has a greater articulation with the lunar than with the scaphoid, to judge by the size of the articular facets. Here for the first time we see a complete ulnar olecranon process of *Arctoryctes*. Also it is of interest that the capitular process of the radius is less well developed in Cedar Creek than in Split Rock specimens. Its lateral extension does form a lateral joint to articulate with the humerus, but the surface lacks the more distally extended portion such as is seen on the Split Rock specimens (compare with fig. 13, A and D). Otherwise, except for the smaller size, the *A. galbreathi* materials are quite like those of the *Arctoryctes* sp. from the Split Rock fauna, as the figures show.

SYNTHESIS

MEASUREMENTS OF HUMERI

(correlate with figs. 24 and 26, and Table I)

A. *Total length.*—From a line across the two most distal points (capitulum and medial edge of the pit for tendon of Musculus flexor digitorum profundus) to the most proximal point on the humerus (usually the lesser tuberosity).
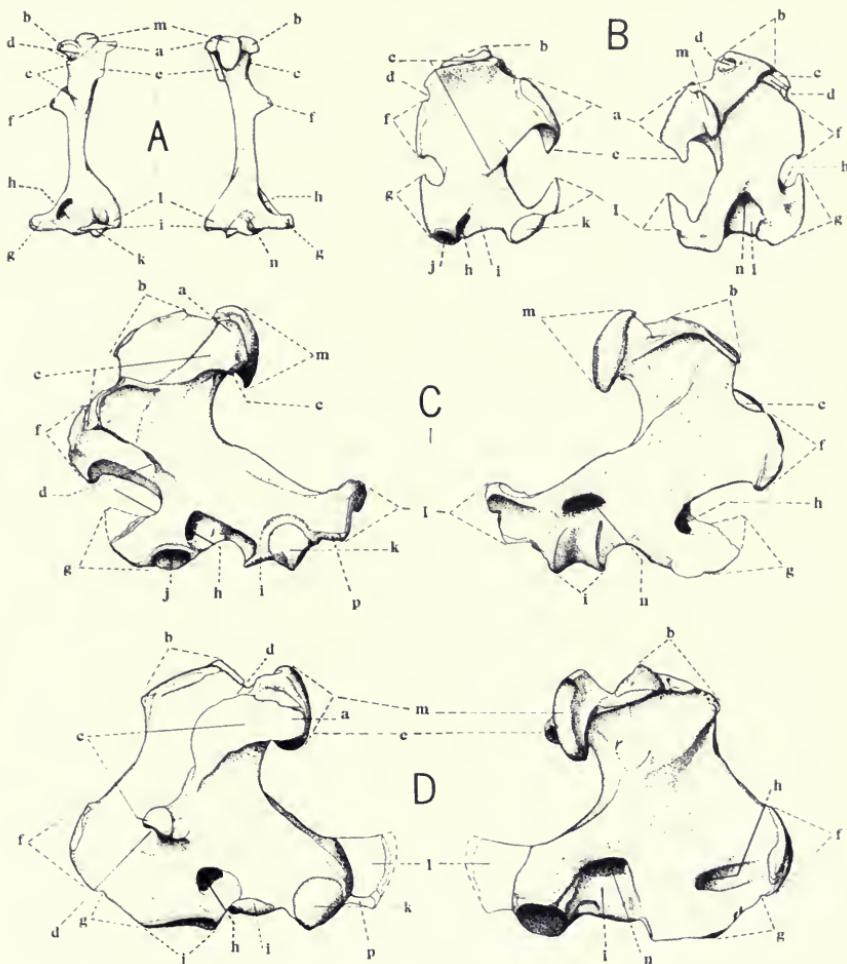
Fig. 24.   Left humeri of some talpids and arctoryctines, anterior to the right and posterior aspect to the left for each.   A, *Uropsilus soricipes;* B, *Scapanus latimanus;* C, *Cryptoryctes kayi;* D, *Arctoryctes terrenus.*   (Not to same scale.) a, greater tuberosity; b, lesser tuberosity; c, pectoral process; d, bicipital groove; e, deltoid process; f, teres tubercle; g, medial epicondyle; h, supracondyloid (ent-epicondylar) foramen; i, trochlea; j, fossa for origin of great ligament of the M. flexor digitorum profundus; k, capitulum; l, lateral epicondyle; m, head; n, ole-cranon fossa; p, humero-radial joint on lateral epicondyle of arctoryctines.

B.   *Least breadth distal to teres tubercle.*—From the deepest point of indentation on the lateral side of the shaft to the nearest medial edge, distal to the teres tubercle.   This measurement includes the median epicondyle in part (*A. galbreathi*) or entirely (*A. terrenus*), but omits it in *Cryptoryctes.*

C. *Width at the teres tubercle.*—Measured as in B, but includes the teres tubercle.

D. *Distal humeral width.*—From the lateral edge of the capitulum to the medial edge of the lip of the pit for the tendon of the M. fl. digitorum profundus. This is a measure of the distal breadth of the humerus, but is not the total breadth, since neither epicondyle is included; these, however, are so often damaged that no consistent measurement including them could be made.

E. *Proximal shaft width.*—Distance across the shaft proper, excluding the flat flange connecting the lesser tuberosity with the teres tubercle; the measurement is made as shown in fig. 26. This is the most difficult of the five measurements to duplicate from one specimen to another, and consequently ratios involving this measurement have less reliability and greater variability than any others.

HUMERAL RATIOS

Ratio 1: $\dfrac{B \quad \text{Least distal breadth}}{A \quad \text{Total length}}$

Ratio 2: $\dfrac{C \quad \text{Width at teres tubercle}}{A \quad \text{Total length}}$

Ratio 3: $\dfrac{B \quad \text{Least distal breadth}}{C \quad \text{Width at teres tubercle}}$

Ratio 4: $\dfrac{D \quad \text{Distal humeral width}}{A \quad \text{Total length}}$

Ratio 5: $\dfrac{B \quad \text{Least distal breadth}}{D \quad \text{Distal humeral width}}$

Ratio 6: $\dfrac{C \quad \text{Width at teres tubercle}}{D \quad \text{Distal humeral width}}$

Ratio 7: $\dfrac{E \quad \text{Proximal shaft width}}{A \quad \text{Total length}}$

Ratio 8: $\dfrac{E \quad \text{Proximal shaft width}}{B \quad \text{Least distal breadth}}$

Ratio 9: $\dfrac{E \quad \text{Proximal shaft width}}{C \quad \text{Width at teres tubercle}}$

Ratio 10: $\dfrac{E \quad \text{Proximal shaft width}}{D \quad \text{Distal humeral width}}$
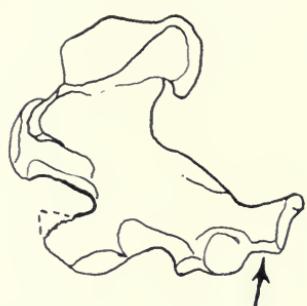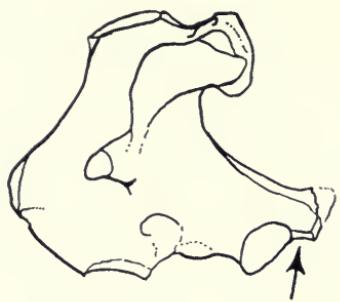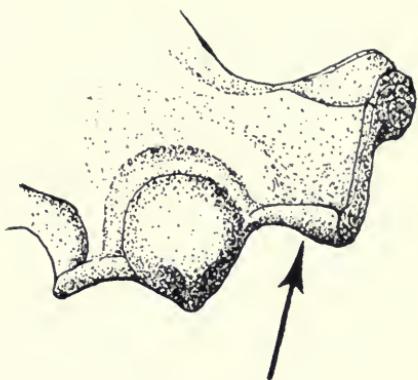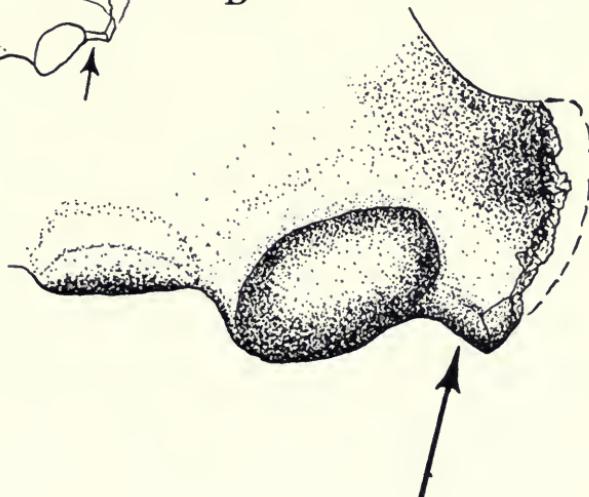
Fig. 25. A, *Cryptoryctes kayi*, left humerus, anterior aspect, showing the joint surface on the lateral epicondyle for articulation with the capitular process of the radius; B, *Arctoryctes terrenus*, the same.

Table 1.—SUMMARY OF RATIOS OF MEASUREMENTS ON HUMERI OF ARCTORYCTINES

|	Cryptoryctes kayi			Composite		Mellinger Arctoryctes		A.sp. CNHM PM3878	Arctoryctes galbreathi			Composite		A.sp. USNM 21310	Arctoryctes terrenus			Composite	
Ratio	n	Range	Mean	n	% Ratio	n	Range		n	Range	Mean	n	% Ratio		n	Range	Mean	n	% Ratio
1. B/A	5	31.5–35.7%	33.2%	16/7	33.6%	1	30.5%	—	1	47.5%	—	5/1	42.6%	64%	0	—	—	2/2	65%
2. C/A	5	56.2–62.8%	59.0%	14/7	57.5%	1	47%	—	1	63%	—	4/1	59.3%	70%	1	69%	—	6/2	71.5%
3. B/C	11	53.0–62.6%	57.8%	16/14	58.4%	1	65%	69%	4	63–75%	69.75%	5/4	72.7%	91%	2	92.5–93.5%	—	2/6	89.6%
4. D/A	3	65.7–70.4%	68.3%	9/7	70.5%	1	53.6%	—	1	68.6%	—	4/1	66%	—	2	68.5–71%	—	7/2	69.3%
5. B/D	8	44.0–50.1%	47.1%	16/9	47.7%	2	57%	—	4	60–69%	63%	5/4	65.2%	—	2	90.5–91%	—	2/7	92.5%
6. C/D	4	82.1–84.4%	83.3%	14/9	81.5%	1	88%	—	3	86.5–92.5%	90.3%	4/4	89.8%	—	4	97–104.5%	99.1%	6/7	102%
7. E/A	6	21.3–24.9%	22.7%	19/7	22.9%	1	22%	—	1	23.5%	—	5/1	25.1%	28%	2	25–25.5%	—	10/2	25.2%
8. E/B	15	57.5–76.7%	68.1%	19/16	68.2%	2	72–76%	67%	5	50–69.5%	58.5%	5/5	58.2%	43.5%	2	39–43.5%	—	10/2	39.2%
9. E/C	13	35.4–46.7%	39.9%	19/14	39.9%	1	46.5%	46%	4	37.5–48.5%	41.4%	5/4	42.3%	39.5%	4	36–40.5%	37.4%	10/6	35.1%
10. E/D	8	30.2–38.2%	33.8%	19/9	32.5%	2	41–43%	—	4	34.5–44.5%	33.1%	5/4	38.0%	—	6	34–40.5%	36.8%	10/7	36.2%

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FIG. 26. *Arctoryctes galbreathi*. Left humerus in anterior aspect, to show the measurements made on the arctoryctine humeri.

EXPLANATION OF TABLE 1

This table is standard, and needs no explanation, except for the columns marked "Composite." Each ratio in such a column was derived by taking the mean for all of the available data for one measurement for each population, and dividing that by the mean of all of the available data for the other measurement (to be used in the particular ratio) for the same population. For example, for *Arctoryctes terrenus*, Ratio 2 $(\frac{C}{A})$ could be calculated on only one humerus, as on only this one could both width at the teres tubercle (Measurement C) and total length (Measurement A) be made. In the total sample of *A. terrenus* here being studied, however, six humeri allowed Measurement C, and on two humeri Measurement A could be made; the ratio of the means of these is the "Composite" ratio, and the number of samples available for the calculation of $\frac{C}{A}$ is here expressed as $n=\frac{6}{2}$.

A composite ratio is a useful calculation where the bones available for measurement are broken, so that few of them individually allow the two measurements necessary for a ratio. Sometimes, as for Ratio 1 of *A. terrenus*, a composite ratio is all that can be calculated.

The major value of a composite ratio is that it allows an increase in the size of the measurable sample, and thus gives some measure of variability when the true ratio, as in Ratio 2 for *A. terrenus*, represents an inadequate sample (n=1). In our use of this composite ratio, in each instance we found that it fell within or extremely close to, the range of the true ratios (those taken on the same individual bones).

The measurements on the humeri of *Arctoryctes* and *Cryptoryctes*, and more particularly the ratios derived from them, verify some assumptions which had been made by observation during study of the specimens.

Ratio 2 is probably the most important to consider, as it is a measure of the relative extension of the teres tubercle medially, and thus is a rough expression of fossorial efficiency. The projecting teres tubercle can be compared to the stick thrust into a capstan; force applied to this projecting lever-arm turns the capstan on its central axis and the longer the lever the greater the mechanical advantage. Similarly, the teres tubercle (whose force is supplied by contraction of the greatly hypertrophied M. teres major, which originates on the scapula) projects medially from the humeral longitudinal axis, about which the humerus is rotated in the burrowing stroke. With the humerus held laterally or dorso-laterally, rotation alone will sweep the half-extended forearm through a considerable arc. This is the most fundamental movement in the lateral-thrust type of digging stroke, and the more specialized of the *Arctoryctes–Cryptoryctes* group had a much higher mechanical advantage, in the relatively greater length of this lever arm, than do the living moles, where Ratio 2 is about 52% (in *Scalopus aquaticus*), a figure exceeded by each of the *Arctoryctes–Cryptoryctes* group measured except the *Arctoryctes* from the Mellinger locality.

With regard to Ratio 2, the single humerus of Orellan age from Toston, Montana (USNM 21310) is similar to the Arikareean *A. terrenus*, and in this respect (as with its development of the medial epicondyle) is completely outside the range of all other Orellan *Arctoryctes*. Although such extreme specialization, as measured in the growth of the teres process and the medial epicondyle, might be thought to be an age phenomenon (we cannot study this possibility

with only one specimen from the population involved) we think it is not, and that the Montana population represented by this individual will be found to be more specialized than other Orellan groups yet known.   We think, thus, that we should remove this extremely specialized individual from *Arctoryctes galbreathi* (where it was placed by Reed, 1956), and regard it only as *Arctoryctes* sp., until further specimens are collected.

Ratio 2 for the Mellinger group is also based, unfortunately, on only a single specimen, but the relatively low ratio (coupled with the small and undeveloped metacarpals) lead to the belief that this population is the least specialized *Arctoryctes* yet known.   This population definitely is a species different from any hitherto described, but the available material does not warrant a formal description of a new species.

There remains, also, the possibility that the small sample available to us from the Mellinger locality represents a chance sampling of only a few juvenile specimens, which might explain the small size and the generally 'soft' and 'juvenile' appearance of these bones.

Thus there may have been in the Orellan different populations of *Arctoryctes* with different degrees of fossorial efficiency, a situation similar to that which exists amongst the North American Talpidae now, with *Neürotrichus*, *Condylura*, and *Scalopus* (or *Scapanus*) forming a series of increasing fossorial efficiency.

Ratio 1 is a measure of the degree of proximal and medial growth of the medial epicondyle, and of its fusion to the teres tubercle; a higher ratio is indicative of greater specialization.   The medial epicondyle serves as a point of origin for several forearm flexors, but in particular its size is to be correlated with the size of the M. pronator radii teres.   This muscle, in Recent lateral-thrust burrowers (Reed, 1951, p. 649) becomes greatly hypertrophied; unopposed, it can function as a flexor of the forearm (which action is part of the recovery stroke), but its main function during the active burrowing stroke would seem to be as a true pronator.   While it had been thought (Reed, 1951, p. 549) that supination and pronation were impossible in such specialized lateral-thrust diggers as moles, more mature consideration has modified this extreme position, and it is now believed by us that some movement of radius upon the ulna is possible.   Certainly, the large size of the M. pronator radii teres in talpids indicates a function beyond that of forearm flexion, and we suspect that the tremendous development and proximal growth of the medial epicondyle in *Arctoryctes–Cryptoryctes* is indicative of a similar hypertrophy

of the muscle in these fossils. For *Arctoryctes–Cryptoryctes*, thus, we assume forearm pronation to have been possible; such action during the digging stroke would turn the medial side of the manus up and out from its normal rest position in which it is held nearly vertically. For lateral thrust diggers this is an important function.

Visual study of a humerus of *Cryptoryctes kayi* shows that it has, in comparison with humeri of species of *Arctoryctes*, the least degree of fusion of the medial epicondyle to the teres tubercles (figs. 24, C and D, and 29), and correspondingly Ratio 1 is low in *C. kayi*. A humerus of *Arctoryctes* sp. from the Mellinger locality has as low a ratio as does *C. kayi*, indicating again that the Mellinger population is the most primitive known for *Arctoryctes*. In contrast, the humerus (USNM 21310) from the Orellan beds of Toston, Montana, hitherto included in *A. galbreathi*, is shown to fall entirely outside the proportions typical of that species and within the range of *A. terrenus*, as was also true for Ratio 2. However, in the *Arctoryctes* from Toston, the medial epicondyle and the teres tubercle had not fused completely (as they have in *A. terrenus*) and there are other minor differences; we must regard the population from Toston as a very advanced one for its time, but (as with the specimens from the Mellinger locality) forebear assigning a specific name until more specimens are known.

Ratio 4 indicates the fact, otherwise unsuspected, that *C. kayi*, *A. galbreathi*, and *A. terrenus* all had the distal end of the humerus (as here measured) approximately the same breadth, relative to humeral length. This situation indicates that these species had about the same degree of efficiency in the tightening of the tendon of the M. flexor digitorum profundus (Reed, 1951, p. 654). However, the *Arctoryctes* from the Mellinger locality, more primitive in all other respects, are also less specialized in this detail, since the distal end of the humerus is relatively narrower than in other *Arctoryctes–Cryptoryctes*.

Ratio 7 is evidence that the original shaft of the humerus proximal to the teres tubercle retains its width, relative to total length, even though the teres tubercle, the medial epicondyle, and the flange between teres tubercle and lesser tuberosity may all be broadening together, as they do so definitely in *A. terrenus*.

Ratio 3 expresses more directly and in different terms situations already explained in major part by Ratios 1 and 2. In a comparison of two populations the higher ratio indicates a relatively greater growth of the medial epicondyle in comparison with the protrusion of the teres tubercle. On this basis, as one can also see from looking

at the specimens, *C. kayi* has the least development of the medial epicondyle, and *A. terrenus* has the greatest, with the Orellan *Arctoryctes* from Montana equalling the Miocene *A. terrenus*. The Mellinger humeri, on the basis of this ratio, fit into the range of other *Arctoryctes* from the Oligocene (as they do with certain other of the ratios, also), but only because both teres tubercles and medial epicondyles are poorly developed, so that the ratio does not vary.

The remaining ratios (5, 6, 8, 9, 10) do not at this time add anything to our understanding of the functional evolution of the humerus not revealed more clearly by the ratios discussed. With larger series, these may prove valuable, and so we include them in our table.

A word remains to be said about the two fragmentary humeri of *Arctoryctes* from the Chadronian of Nebraska (Turnbull and Reed, 1960). These remain the only Chadronian humeri of *Arctoryctes* known, and, on the basis of visual inspection are somewhat less specialized than the *A. galbreathi* from the hypodigm (UK—VP 9837-9). These Chadronian humeri are more similar to those of *A. galbreathi* than are the humeri from the Orellan period of the Mellinger locality. (Unfortunately, the outline drawing used for comparison in fig. 24c of Turnbull and Reed, 1960, was based almost entirely on USNM 21310, which we now know is too specialized to be included within the normal range of variation of *A. galbreathi*.) However, until we get more Chadronian materials, we prefer to leave these specimens (CNHM, PM 3878 and 3879) from the Arner Ranch, Nebraska (Turnbull and Reed, 1960) without a specific name.

There are thus three distinctive populations of *Arctoryctes* which remain unnamed at present: 1) Chadronian, from Arner Ranch, Nebraska, more similar (on the basis of metacarpals and humeral fragments) to *A. galbreathi* than to any other known population; 2) Orellan, Mellinger locality, smallest and most primitive *Arctoryctes* known; 3) Orellan, USNM 21310 from Toston, Montana; this single specimen indicates a population almost as specialized as was *A. terrenus* from the early Miocene. Additionally, of course, there remain the mid-Miocene *Arctoryctes* from the Split Rock locality, of which the remains are too fragmentary to analyze taxonomically, but which appear to resemble *A. terrenus* closely.

FUNCTIONAL MORPHOLOGY OF THE FORELIMB IN *ARCTORYCTES* AND *CRYPTORYCTES*

The central theme of the evolutionary morphology of the members of the *Arctoryctes–Cryptoryctes* group is that they parallel the

true moles (i.e., for our present purposes: Talpidae excluding Proscalopinae) in having evolved a forelimb adapted for a lateral-thrust digging stroke (Reed, 1951; 1954), in contrast to the "rapid-scratch" and "tooth-type" burrowing behavior of other fossorial mammals (Turnbull and Reed, 1960). This pattern, and its accompanying morphological and functional correlations, has been discussed before (Reed, 1951, 1954), and need not be repeated in detail again. The present increase in available specimens of *Arctoryctes* and *Cryptoryctes* does, however, allow for clarification on some problems:

SCAPULA

We have not, unfortunately, been able to pick any scapular fragments assignable to *Arctoryctes* from the material available to us. The glenoid fossa of the scapula of *Arctoryctes* or *Cryptoryctes* must be elliptical in shape, to match the elliptical head of the humerus, but beyond that we cannot safely prognosticate. One would expect, in animals so specialized fossorially, that the scapula would be as strong and dense as in *Scapanus* (Reed, 1951, p. 536), *Scalopus*, or *Talpa*, but we have not as yet identified any pieces which we thought would have come from such a scapula.

CLAVICLE

A clavicle has not been identified as yet for *Arctoryctes* or *Cryptoryctes* (for the latter, indeed, no bones are known at present other than the humeri). Our sorting of the microfauna from Split Rock turned up two kinds of enigmatic small bones of the proper size to be clavicles. Each of these kinds of bones was somewhat slipper-shaped, with the sole of the "slipper" suggestive of a surface which could have been fitted upon the greater tuberosity of the humerus. However, since they could not both be clavicles of *Arctoryctes*, since neither of the two types of bones were like anything else we had ever seen, and since the evidence is so tenuous as yet, we do not figure these pieces, and must at present leave this most interesting problem quite unsolved.

HUMERUS

Longitudinal Axis of Rotation.—In the lateral-thrust digging-stroke, the broad humerus is held in a lateral or latero-dorsal position and is both retracted on the thorax and rotated about its own longitudinal axis. This axis of rotation (fig. 27 *f*, *g*,) passes approximately through the center of the scapular-humeral articulation and

between the capitulum and the trochlea.   In most mammals the axis can be considered as generally approximating the center of the humeral shaft, but in moles it is offset laterally and in members of the *Arctoryctes–Cryptoryctes* group this lateral displacement of head, trochlea, and capitulum (and thus of the functional axis of rotation) is extreme.   Such a lateral displacement of the longitudinal axis means that the lever arm (fig. 27, *h, i*), which rotates the humerus during the power-stroke, is in turn elongated.   (The same principle applies in consideration of the act of counter-rotation by the contraction of the M. biceps brachii; see below for more detailed discussion.)   Indeed, it is really this length of lever arm, *h, i* (and not the length C, fig. 26) which one should measure as an expression of rotatory efficiency, but on fragmentary fossils the possibility of this ideal is rarely realizable.

It is noticeable from a study of fig. 27 that *Arctoryctes* in general, and *A. terrenus* in particular, has the lever arm (*h, i*) placed more distally on the humerus (i.e., the teres tubercle is more distal on the humerus) than does *Cryptoryctes*.   The same pattern of more distal extension of the teres tubercle in the more fossorial animals is also true of the living moles; although in these latter the teres tubercle is always retained on the medial half of the humerus.   The more distal position allows a more powerful action by the Mm. teres major and latissimus dorsi of flexion of the humerus upon the thorax and gives some advantage (by placing the point of application of force nearer the resistance against the manus) to the act of rotation.

Bicipital Groove.—In all of the living moles except *Uropsilus*, the proximal part of the pectoral process has moved against and sometimes fused with the lesser tuberosity, to produce a bicipital tunnel and to divert the course of the tendon of origin in the M. biceps brachii across the proximal end of the humerus (fig. 28, B; Reed, 1951; 1954).   In *Uropsilus*, the most primitive of the living Talpidae, the pectoral process has been partially shifted toward the lesser tuberosity, although not yet abutting against it; however, the long head of the biceps passes posterior to the projecting point of the greater tuberosity (fig. 28, A) in a way that clearly foretells the more specialized evolution of this morphological complex in the more specialized moles.

The humeri of all species of the *Arctoryctes–Cryptoryctes* group lacked this unique and remarkable talpid arrangement of the bicipital tunnel; consequently, the biceps muscle lay along the front of the humerus in a more standard mammalian pattern.   However, the
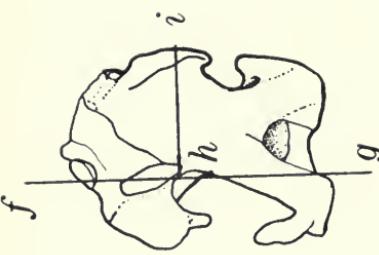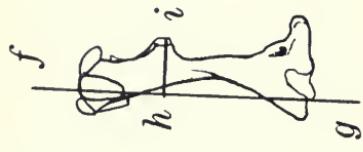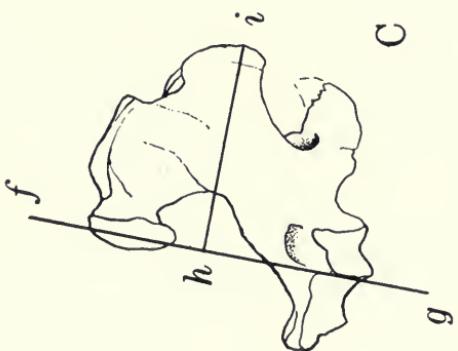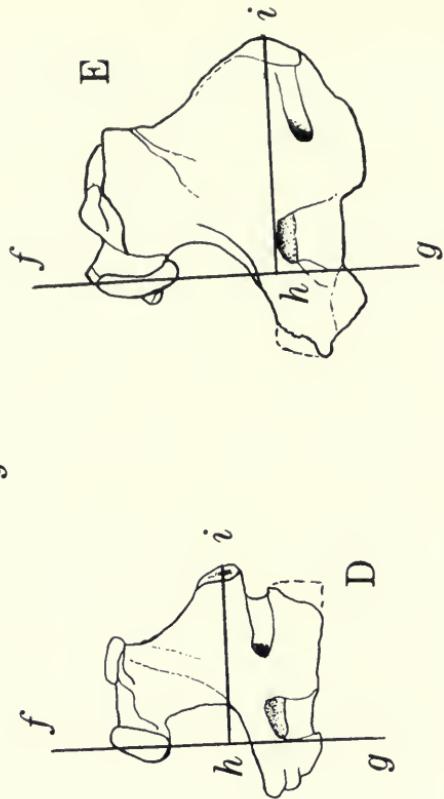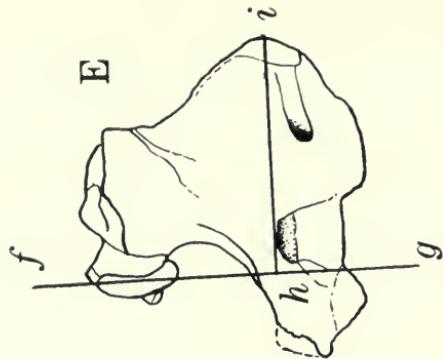
Fig. 27. Drawing to show the axis of rotation, *fg*, and the length of the rotatory lever arm, *hi*. All drawings of left humeri, posterior aspect; not to same scale. A, *Uropsilus soricipes*; B, *Scapanus latimanus*; C, *Cryptoryctes kaji*; D, *Arctoryctes galbreathi*; E, *A. terrenus*.

muscle (or its tendon) presumably passed medial to the distal end of the pectoral process (fig. 28, C, E) and must then have turned quite sharply laterad to reach its normal insertion upon the radius, since the radius articulated with the capitulum and lateral epicondyle, which were far laterad on the humerus. However, the insertion of the biceps may have been shifted distally on the radius, as it is in the more specialized moles (Reed, 1951, p. 642), so the exact angle assumed by the muscle as it bent around the pectoral process cannot be known.

Whatever the details, the muscle must have formed a pulley around the end of the pectoral process in all members of the *Arctoryctes–Cryptoryctes* group. Contraction of the M. biceps brachii would necessarily counter-rotate the humerus into its normal position as a part of the recovery stroke of the forelimb, preparatory for the next burrowing stroke. In both rotation and counter-rotation, the long axis of the humerus remains the same (fig. 28, f, g), and the relative length of the lever arm jk is thus a rough measure of the efficiency of the counter-rotating function of the biceps. (The biceps muscle also has its normal action as a flexor, during each recovery stroke while burrowing.) A more exact statement cannot be made, as too many unknown variables are present. However, the more specialized mechanism of the bicipital tunnel, as found in the true moles, probably provides a more efficient counter-rotatory device than did the simpler bending of the biceps around the distal tip of the pectoral process in individuals of the *Arctoryctes–Cryptoryctes* group.

Fusion of Teres Tubercle and Medial Epicondyle.—The humerus of *C. kayi* shows little more tendency toward fusion of these two processes than occurs in Recent specialized moles, although in *C. kayi* the teres tubercle is longer and heavier than in any mole. In *Arctoryctes*, however, one sees an evolutionary sequence of greater specialization, from the simpler type of *A. galbreathi* through a type represented by the Orellan *Arctoryctes* sp. from Toston, Montana (USNM 21310) to the complete fusion found in *A. terrenus* (fig. 29). While near-complete fusion was already accomplished in USNM 21310, by the Miocene specialization had proceeded even further; the medial epicondyle extended medially as far as or farther than did the teres tubercle, and grew proximally past the teres tubercle on the latter's anterior surface before fusing with it. This complicated process can be seen (fig. 30) in the process of happening, as it were,

A

B

C

D

E

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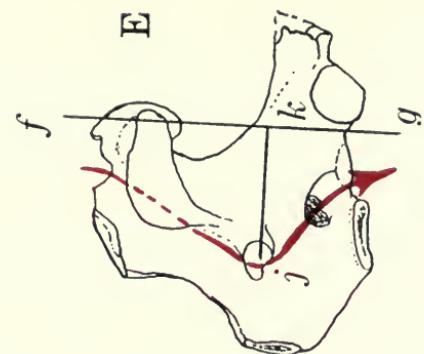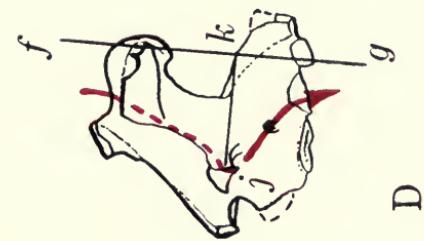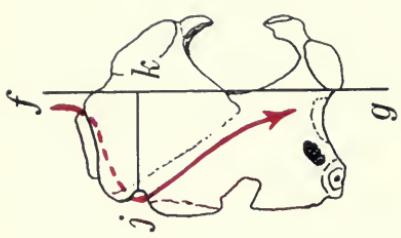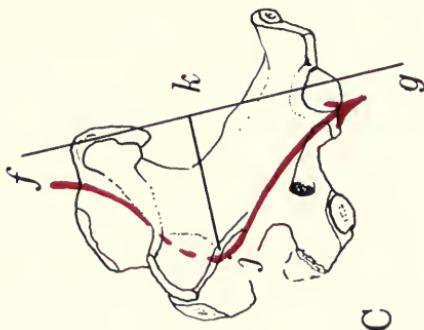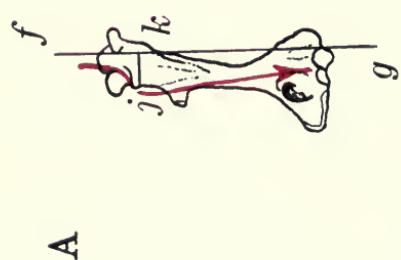
in one juvenile humerus of *A. terrenus* (SDSM 55112), but the line of fusion can be seen clearly on several of the adult specimens.

In this detail of the fusion of the medial epicondyle to the teres tubercle, *Arctoryctes* had already in the early Oligocene achieved a greater degree of specialization than has any other mammal; indeed, it seems probable that by the Paleocene (USNM 9777) such an extreme degree of specialization had already been achieved (Reed, 1954, p. 108).[1]

Humero-clavicular Joint.—The known talpids, with the exception of *Uropsilus*, have a synovial joint between the distal end of the clavicle and the greater tuberosity of the humerus (Reed, 1951). Whether such a unique morphological transformation was or was not achieved in the *Arctoryctes–Cryptoryctes* group remains a mystery. The Paleocene humerus USNM 9777 appears to have had a humero-clavicular joint, but the relationship of this form to *Arctoryctes* or to *Cryptoryctes* or to the talpids is quite uncertain. The greater tuberosity of any humerus of any specimen of *Arctoryctes* is definitely smooth, quite as if it bore an articular surface, but this area in *C. kayi* was small and often roughened, as if no such articular facet was present (fig. 31). Such a surface for a joint may have been present, however, but remained small and so the evidence for it will be obscure until such time as we find articulated or at least associated skeletal remains.

Humeral-radial Joint.—As mentioned before (p. 111) a laterally-projecting process from the head of the radius forms a joint with the distal end of the lateral epicondyle of the humerus (figs. 13 and 25); this joint, not found in moles, is present in *Cryptoryctes* and all known populations of *Arctoryctes*. Thus the humero-radial joint in *Arctoryctes* and *Cryptoryctes* was greatly strengthened, as compared to the situation in moles, in which the humeral-radial joint is little more than the typical one between capitulum and the cupped surface of the radial head (Reed, 1951).

Great Ligament of the M. Flexor Digitorum Profundus.—This ligament originates from a distinctive pit on the distal end of the humerus

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[1] Because of the presence of a well-developed distal portion to its pectoral process it would seem to be closer to the *Arctoryctes–Cryptoryctes* group than to the talpids (s.s.) and we tentatively marshal it in this manner.

Fɪɢ. 28. Left humeri, anterior aspect, to show the course of the M. biceps brachii (red arrow) in different talpids and arctoryctines. A, *Uropsilus soricipes*; B, *Scapanus latimanus*; C, *Cryptoryctes kayi*; D, *Arctoryctes galbreathi*; E, *Arctoryctes terrenus*. (Not to the same scale.)
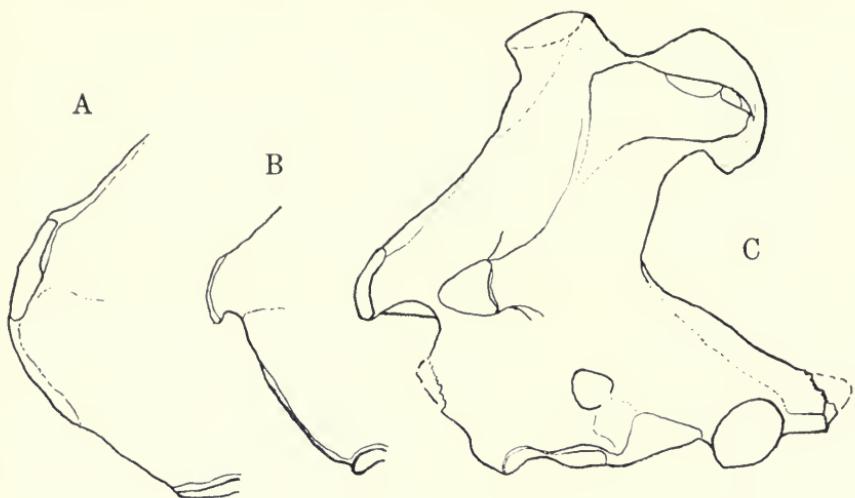
FIG. 29. Left humeri, anterior aspect. Drawings show degree of fusion between teres tubercle and medial epicondyle. A, *Arctoryctes terrenus*; B, *Arctoryctes* sp. from Toston, Montana (USNM 21310); C, *A. galbreathi*.
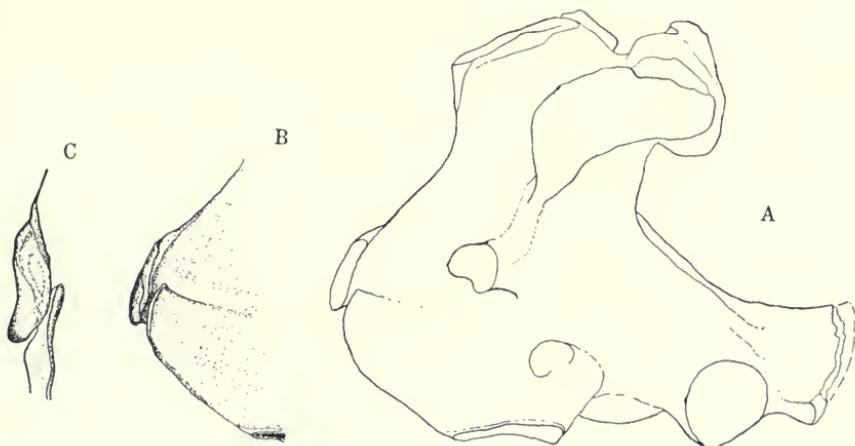
FIG. 30. *Arctoryctes terrenus*, SDSM 55112, left humerus, anterior aspect. A, outline of the whole humerus, based in part on AMNH 12864; B, detail of region of teres tubercle and medial epicondyle, showing overgrowth of the latter onto the former; C, medial edge of the teres tubercle and medial epicondyle (same as in B, but turned 90° toward the viewer).

in all living moles except *Uropsilus*. It functions as an automatic flexor of the digits when the humerus is rotated during the burrowing stroke (Reed, 1951, pp. 654–656). There is little doubt that the possession of the distinctive pit on the humeri of *Arctoryctes* and *Cryptoryctes*, correlated with all the other evidence for lateral-thrust burrowing strokes, is evidence for the presence of the same great ligament in the antebrachia of *Arctoryctes* and *Cryptoryctes*. Insertion was undoubtedly into the distal phalanges, quite as in living moles. This pit was possibly also present, and if so was very large, in the humerus USNM 9777 from the Paleocene of Montana.
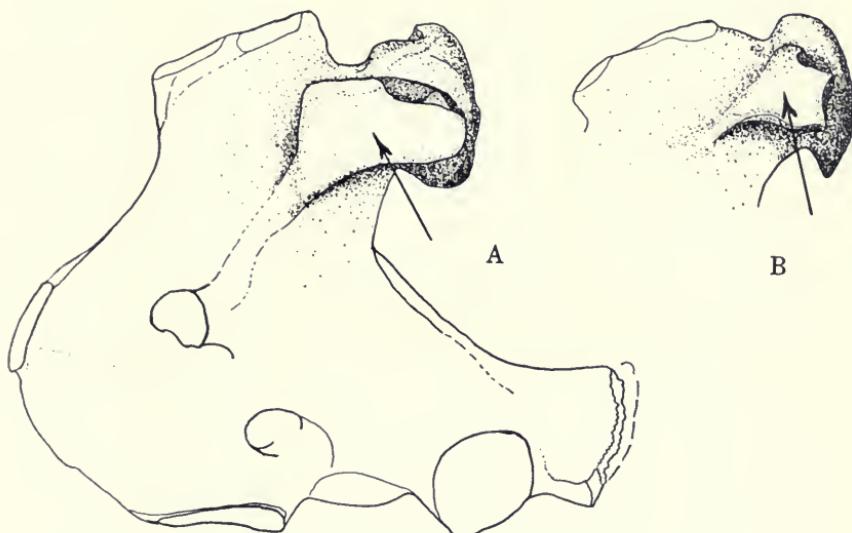
FIG. 31. A, anterior aspect of the left humerus of *Arctoryctes terrenus*, showing the greater tuberosity (black arrow) as a possible area for a synovial joint with the distal end of the clavicle; B, the same region of the humerus in *Cryptoryctes kayi*.

Pectoral Process.—In *C. kayi*, the distal end of the pectoral process is elevated into a high, rugged and elongate crest; in all individuals of all species of *Arctoryctes* it is a rather flat-topped button; and in living moles it is a barely discernible line, slightly accentuated distally. These basic differences in morphology imply a more powerful action of the muscles inserting into the pectoral process in the *Arctoryctes–Cryptoryctes* group, and particularly in *Cryptoryctes*. In the living moles, the muscles inserting here are the acromiodeltoidus

TABLE 2.—COMPARISON OF CHARACTERS OF HUMERUS OF SPECIALIZED TALPIDS, WITH THOSE OF *CRYPTORYCTES* AND *ARCTORYCTES*

Character	Specialized Talpids	Cryptoryctes	Arctoryctes
1. Greater tuberosity	Forms a synovial joint with the distal end of the clavicle	Not certain that it forms a joint with the distal end of the clavicle	
2. Lesser tuberosity	Elongated and fused to the pectoral process to form a bicipital tunnel	Elongated, but not fused to anything else	Variable as to degree of development, but in general similar to that of *Cryptoryctes*
3. Pectoral process	Fused to lesser tuberosity to form a bicipital tunnel	Strongly developed, but not in contact with lesser tuberosity	Similar to that in *C.*, but not so strongly developed
4. Bicipital groove	Is a complete tunnel, between the lesser tuberosity and the pectoral process	No tunnel formed	No tunnel formed
5. Teres tubercle	Elongated, but on proximal half of humerus; not fused to medial epicondyle	Elongated and protrudes medially; on the middle third of the humerus; not fused to medial epicondyle	Elongated and protrudes medially; is on the distal third of the humerus; in *A. galbreathi* degree of fusion to medial epicondyle is variable, but in *A. terrenus* is always completely fused

Character	Specialized Talpids	Cryptoryctes	Arctoryctes
6. Medial epicondyle	Enlarged, but never fused to teres tubercle	Enlarged, but not fused to teres tubercle	Extremely enlarged, and always fused to teres tubercle; degree of fusion variable in *A. galbreathi*, but always completely fused in *A. terrenus*
7. Supracondyloid foramen	Elongated, but not forming a groove on the posterior surface of the humerus	Elongated, but not forming a groove on the posterior surface of the humerus	Elongated and, due to enlargement of the medial epicondyle, forms a groove on the posterior surface of the humerus
8. Large fossa on the distal surface of the medial epicondyle	Present; region of origin for the great ligament of the M. flexor digitorum profundus	Present; presumably is a point of origin of the great ligament of the M. flexor digitorum profundus	
9. Lateral epicondyle	Elongate, but has no articular surface for the shaft near proximal end	Strongly developed, and has an articular surface for the radius	
10. Head	Elongated, and on the posterior surface of the shaft near proximal end	Elongated proximo-distally (as in talpids), but set far laterally on the posterior surface of the proximal end of the shaft	
11. Extension of radial-humeral joint to the lateral epicondyle	Absent	Present	Present

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and the anterior portion of the pectoralis superficialis (Reed, 1951, fig. 30). It does not seem possible that either muscle could be used in the power-stroke; the acromiodeltoideus is normally a levator and abductor of the humerus, and the pectoralis is a strong adductor as well as counter-rotator of the humerus. In this latter capacity it is an antagonist of the Mm. teres major, subscapularis, and latissimus dorsi. In living moles this counter-rotation, during the recovery stroke, is aided in large part by the contraction of the M. biceps brachii, which follows from the peculiar course of the bicipital tunnel (fig. 28, B; Reed, 1951, pp. 640–642). In the *Arctoryctes–Cryptoryctes* group the counter-rotatory action of the biceps undoubtedly remained an important factor in the succession of burrowing strokes. However, the great development of the pectoral process, upon which the main adductor muscles inserted, indicates to us that this latter muscle mass was relatively more important in counter-rotation in the *Arctoryctes–Cryptoryctes* group than in living moles (see Table 2).

ANTEBRACHIUM

The radius and ulna have been described (p. 111), and not much more of functional significance can be added. The humeral-radial joint, as mentioned above, gave great stability to the elbow, but both radius and ulna (the latter particularly) appear as rather delicate links between the rugged, broad humerus and the large hand. This situation is in marked contrast to that of a specialized mole such as *Scapanus* (Reed, 1951, p. 547) or *Scalopus* (fig. 15), where radius and ulna are short and heavy.

Unfortunately, we do not have a complete ulna, so cannot learn directly the important matter of the ratio between length of olecranon and length of the shaft. Indirectly, by aligning ulnar fragments facet for facet against a reconstructed radius, we were able to calculate that the length of the olecranon of the *Arctoryctes* from Split Rock was approximately 42% of the ulnar shaft length (Reed, 1951, p. 547). This ratio of olecranon to shaft is considerably less than the 64% of *Scapanus*, indicating a much more powerful extensor action of the triceps complex in the latter. However, the 42% ratio of *Arctoryctes* exceeds that of *Condylura* (35%) and *Neürotrichus* (27%). Since antebrachial extension is an important factor in the burrowing stroke, we can say that in this respect *Arctoryctes*, by the mid-Miocene, was as efficient, or possibly a somewhat more efficient burrower than is *Condylura*, but had not acquired the ability for the powerful forearm extension of a *Scapanus* or *Scalopus*.

The radius, as reconstructed from two overlapping pieces, was approximately 12.8 mm. long, not including the capitular process. This length compares with similar measurements of 12.4 mm. for *Condylura cristata* and 9.8 mm. for a *Scalopus aquaticus*.   Whereas the ulna of these Arctoryctes from Split Rock remains relatively delicate, and is quite similar in this respect to that of *Condylura*, the radius is relatively much heavier than is that of *Condylura*, and much more massive relative to its own ulna.   Also it is more rugose than is a radius of *Cryptoryctes* of approximately the same length.

If the humerus of an average individual of the *Arctoryctes* at Split Rock was the same size as that of the Arikareean *A. terrenus* (a supposition for which we have as yet no good evidence) the ratio of length of humerus (11.4 mm.) to length of radius (12.8 mm.) would be 89%; in *Condylura* this ratio is approximately 110%, in *Scalopus* 158%.   The similarity of radius and ulna in both general appearance and in this ratio is thus closer between *Arctoryctes* and *Condylura* than between *Arctoryctes* and the more specialized mole, and we can conclude that, in spite of the broad strong humerus and highly specialized burrowing hand, the antebrachium of *Arctoryctes* remained surprisingly long (for a lateral-thrust burrower) with the radius being more powerful than the ulna.

MANUS

We cannot be specific in statements concerning wrist and hand, lacking as we do a detailed reconstruction.   The carpus is largely missing as yet; we think we know the order of the metacarpals, but are not certain and so cannot be final in our discrimination between those from the right hand and those from the left.   We can distinguish first, second, and third phalanges from each other but cannot distinguish those belonging together in any particular digit.   Nor, for the first phalanges do we know to which digit to assign the longer ones, to which to assign the extremely short ones (which do, indeed, have the appearance of being two epiphyses fused together without a shaft).

When we turn for comparison to the hands of living moles we find few detailed analogies to the pecularities of shapes and angles of the bones in the hand of *Arctoryctes*.   Indeed, no one has made the necessary morphological study of the hand of any living mole—bone by bone, facet by facet, ligament by ligament, muscle by muscle, and tendon by tendon—which would yield an analysis of function and furnish a basis for comparisons.

We can say, for talpids in general, that the hands show a remarkable series of increasing specialization, from the long slim manus of *Uropsilus* through intermediate types such as those of *Scaptonyx* and *Neürotrichus* to the somewhat more specialized stage of *Condylura*, then *Talpa* (in which the metacarpals are still relatively long), and finally to the hands of *Scapanus* and *Scalopus*, in which the metacarpals are broader than long.

The proximal ends of the metacarpals of *Arctoryctes* are more complexly faceted and sculptured than are those of any of the living moles we have studied, and the carpal bones are obviously quite different, too. Indeed, the whole hand shows in almost every detail the evidence of a long independent—though possibly parallel—evolution with that of the moles.

It is our interpretation that the hand of the *Arctoryctes* from the Split Rock would have been proportioned approximately as is that of *Condylura*, the North American star-nosed mole. This latter is, on the ascending scale of specialization, a step below that of *Talpa* but yet is considerably broader and heavier than is the manus of *Neürotrichus*. In *Condylura* the breadth of a metacarpal is approximately one-third that of the length; in *Arctoryctes* each is usually slightly stockier, from one-third to one-half as wide as long, but in the same general size range as are those of *Condylura*. In both *Condylura* and *Arctoryctes* the first and second phalanges are relatively short and the distal phalanx is long, broad, and spade-like.

A hand of the general proportion of that of *Condylura* is not as large and heavy as we had visualized for an animal such as *Arctoryctes terrenus* when we had first studied the humerus; we had in mind reconstructing a manus for the mid-Miocene *Arctoryctes* from Split Rock something more of the proportions of that of *Scapanus* or *Scalopus*. However, a *Condylura*-like manus is in proportion to the antebrachium of *Arctoryctes*, which could not logically be expected to have supported the large heavy hand of a *Scalopus*.

SUMMARY

The forelimb of the *Arctoryctes* from the mid-Miocene at Split Rock, which animal we assume to be very similar to *A. terrenus*, operated on the same basic principle as does a living mole, but the anatomical and functional details were different.

A study of the extraordinary humerus, more specialized in appearance than that of any living mole, would lead one to expect that the remainder of the limb would also be hyper-specialized. However,

such appears not to have been the situation. True, the radius seems to have been relatively larger and more important in comparison with the ulna, and the metacarpals and the phalanges have many strange details eventually deserving of more concentrated study, but the basic pattern which emerges is that of a lateral-thrust burrowing animal near the general efficiency of *Condylura*. This mole is limited to rather soft ground and favors stream-side environments, and cannot survive in the harder ground of open fields where the more powerful and more versatile *Scapanus*, *Scalopus*, and *Talpa* are often found.

If these conclusions are valid, what appears to be the most specialized of fossorial humeri, that of *Arctoryctes*, was in an arm which in its entirety was not as specialized (at least not as efficient) as is that of an 'advanced' living talpid. We have come to believe thus that the most specialized arctoryctine humerus, even with its tremendous breadth, even with its extremely distal position of the teres tubercle, even with its fusion of teres tubercle and medial epicondyle, and even with its other strange features, was yet not much more efficient as a unit in the burrowing-organ than is the humerus of *Condylura*. But the humerus—indeed, the whole skeleton of *Condylura*—has not evolved to that more advanced degree of structural and functional complexity reached by such really specialized talpids as *Scapanus*, *Scalopus*, and *Talpa*.

Parallel evolution (if our reconstructions are valid) carried the arctoryctines and the talpids along similar paths. It appears that the talpid humerus is more 'stream-lined,' and allows for greater final efficiency of function, in contrast to the humerus of the arctoryctines, which became increasingly specialized through the Oligocene and Miocene. However, the Arctoryctine humerus and its correlated structures presumably remained 'clumsy' in action and less efficient than were (and are) such structures in corresponding evolutionary stages in talpids.

We believe that somewhere in this rather vague and speculative discussion may lie the explanation for the extinction of the arctoryctines and the continued and continuing success of the talpids.

CONCLUSION

Analyses of suggested recommendations for relationships of
Arctoryctes *and* Cryptoryctes

Since *Arctoryctes* and *Cryptoryctes* are believed by us to be closely related but divergent lineages, the skulls which have been suggested

for association should also show relationships. Unfortunately, we must state in advance that we have not as yet reached a final decision on this problem.

CHRYSOCHLORIDAE

Matthew (1906) first suggested affinities with chrysochlorids (African golden "moles") for *Arctoryctes,* and later (1913) used this suggestion as evidence for ideas he held at that time for world-wide distribution of the zalambdodont insectivores in the Tertiary. However, there is practically no point of resemblance between humeri of the *Arctoryctes–Cryptoryctes* group and those of chrysochlorids, and in 1928 Matthew abandoned this idea. Thus this original suggestion, although widely copied for many years, has now universally been rejected.

PALAEANODONT EDENTATES

Simpson (1927) first suggested a possible association between skulls of Epoicotheriidae, a family of North American palaeanodont edentates, and the one humerus of *Arctoryctes* then known. For reasons enumerated below, such an association has come to seem most improbable as time as passed, and we now consider it to be even less probable than when C. A. Reed (1954) discussed the problem. However, Saban (1958, p. 528; see point 17 in our chronology) assigned *Arctoryctes* and *Cryptoryctes* to the Epoicotheriidae *incertae sedis,* without any mention of other possibilities. In spite of the fact that the metacarpals we are here associating with *Arctoryctes* resemble in many curious details those of several small edentates, particularly those which habitually use their fore-feet for digging (Turnbull and Reed, 1960), we continue seriously to doubt any possible relationship between *Arctoryctes–Cryptoryctes* and the edentates, for the following reasons: a) the great rarity of epoicotheriid palaeanodont edentates in the early and middle Oligocene (only four specimens are known at present), and their absence from the North American record thereafter, in contrast to the numerous sites, ranging from early Oligocene to mid-Miocene, now known for *Arctoryctes* and *Cryptoryctes;* b) the relatively large number (12) of sites from which humeri of *Arctoryctes* and *Cryptoryctes* have been recovered, only one of which (McCarty's Mountain) has yielded a specimen of an edentate; c) the probability that the known humeri of the Eocene fossorial palaenodont edentates (*Metacheiromys* and *Pentapassalus*), and thus pre-

sumably of their Oligocene relatives, were used in "rapid-scratch" digging, while in contrast the humeri of *Arctoryctes* and *Cryptoryctes* were used for "lateral-thrust" digging (see Reed, 1954, for more complete explanation); d) the broad hand of *Arctoryctes*, with all metacarpals of nearly the same size (as reconstructed by us), is in agreement with the other morphological features of a lateral-thrust forelimb, in contrast to the typical hypertrophy of one of the central metacarpals (with reduction or absence of metacarpals I and/or V) in highly specialized "rapid-scratch" digging mammals, such as chrysochlorids, *Notoryctes*, and many of the small edentates.

It is thus our opinion, in the light of the above argument, that any edentate-like characteristics of the bones of the reconstructed manus here assigned to *Arctoryctes* (Turnbull and Reed, 1960; descriptions of bones, this paper) are due to convergent evolution and not to common ancestry.

TALPIDAE

K. M. Reed (1961) has re-introduced the idea that the humeri of *Arctoryctes* (Matthew, 1928) and *Cryptoryctes* may have belonged to moles (Talpidae), specifically to members of her new subfamily, the Proscalopinae. The simultaneous occurrence of some 200 teeth of a proscalopine and of numerous bones of the forelimb of an *Arctoryctes* in the Split Rock local fauna is indeed evidence for such identity. Further, the possibility that *Arctoryctes* (and perhaps also *Cryptoryctes*) possessed a humero-clavicular joint (p. 145) weakens the prior argument (C. A. Reed, 1954) that *Arctoryctes* and *Cryptoryctes* could not be related to talpids, but must have evolved their burrowing adaptation convergently. Briefly, his arguments were:

1. The presence of a bicipital tunnel in all known moles except *Uropsilus* (and the presence of the necessary pre-adaptive evolutionary antecedent in that genus) was (and is still) thought to be a fundamental factor in the evolution of the Talpidae. Since the bicipital tunnel and its associated muscle-tendon mechanism of the M. biceps brachii (p. 141) was positively correlated with increase in fossorial efficiency, it was not believed that *Arctoryctes* and *Cryptoryctes* could have evolved from an ancestor which had even an incipient bicipital tunnel. This conclusion meant that these genera could not be derived from, or belong to, the Talpidae, as that family was then understood.

2. A similar argument involved the presence of the humero-clavicular joint, which also is present in all talpids except *Uropsilus*, and is also more specialized in correlation with greater fossorial activity. However, there is less certainty now that *Arctoryctes* and *Cryptoryctes* lacked a humero-clavicular joint (p. 145) and the argument must rest until the problem can be settled.

In addition to the fundamental difference of presence or absence of the bicipital tunnel (and the possible difference of presence or absence of a humeral-clavicular joint), there are several other important differences between the talpids (as we now understand that family) and *Arctoryctes* and *Cryptoryctes*. Not one of these differences to be discussed would exclude its possessor from being a talpid, although of a type considerably variant from any known hitherto: a) more distal position of teres tubercle in *Arctoryctes* and *Cryptoryctes*, with fusion to the medial epicondyle in *A. terrenus*; b) extreme lateral displacement of the longitudinal axis of rotation of the humerus in *Arctoryctes* and *Cryptoryctes*, so that the whole configuration of the bone is different; c) presence of an accessory joint between the lateral epicondyle of the humerus and the capitular process of the radius in *Arctoryctes and Cryptoryctes*; d) greater size and strength of radius relative to the ulna in *Arctoryctes* and *Cryptoryctes*; e) the unique individual characters and combinations of characters of metacarpals and phalanges (pp. 117–127).

We continue to believe that all of the above factors, as correlated with other discussions in this paper and prior publications of one or both of us, indicate definitely that *Arctoryctes* and *Cryptoryctes* cannot have evolved from any talpid for which the forelimb skeleton is known.

If, on the other hand, one considers that the proscalopines were really sufficiently different from true talpids to have had the humeri of *Arctoryctes* and *Cryptoryctes* belong with them, as K. M. Reed suggests as a possibility, some other problems must also be considered. If one had only the Split Rock local fauna to consider, the evidence would definitely be in favor of such a hypothesis. K. M. Reed (1960) lists almost 200 cheek-teeth of a proscalopine, *Mesoscalops scopelotemos*, from the Split Rock; if the proscalopines were true talpids we would expect to find dozens, at least, of identifiable post-cranial bones of moles. Instead, we found in the material examined by us only six identifiable fragments of a true talpid (ACM 8750–8752; and CNHM, PM 8360, 8617–8618) mentioned on p. 110, in-

dicating the presence of a tiny mole at about a *Neürotrichus* or *Scaptonyx* stage of evolution. We found none of the typical talpid clavicles, radial heads, ulnar olecranon pieces, or bifid distal phalanges (metacarpals and first and second phalanges would not necessarily be so specialized as to be identifiable). In contrast to this nearly complete lack of talpid material, we found numerous recognizable fragments of most of these same bones for *Arctoryctes* (as we are here assigning these bones): 15 certainly identifiable humeral fragments (plus 20 smaller pieces, most of which are thought to be from *Arctoryctes*=total of 35), 34 pieces of radii, 24 ulnar pieces, 173 metacarpals, 34 first phalanges, 56 second phalanges, and 126 third phalanges.

If we had only the Split Rock collections to consider, the proposed association of proscalopine skulls with forelimb bones of *Arctoryctes* would neatly satisfy the requirements of our "working principles" (p. 103) as these apply to a single site. However, of the 14 sites, other than Split Rock, where *Arctoryctes* and/or *Cryptoryctes* have been found, no proscalopine has been reported from 12 of them (Table 3).[1] Is it possible that the technique of near-complete collection, as practiced at Split Rock, would yet turn up proscalopines at these 12 localities? The only answer is to try, which will take some time and considerable effort.

Both *Arctoryctes* (*A. galbreathi;* 13 humeri and other forelimb elements—see p. 129) and two proscalopines (a skull and jaws of *Proscalops miocaenus* and a partial mandible of *Oligoscalops whitmanensis*) are known from the Cedar Creek (Orellan) member of the White River formation, Logan County, Colorado. As at Split Rock, a humerus of a true mole (Scalopine) has also been found at Cedar Creek (Galbreath, 1953, p. 49), so again there exists the possibility of skeletal association of the proscalopine with a known talpid humerus. Whether or not other talpid bones can be identified from the collections made at Cedar Creek we do not know, since we have not examined these.

If, as mentioned before, we were to consider only Split Rock, the large numbers of *Mesoscalops scopelotemos* cheek-teeth and of postcranial fragments of *Arctoryctes* sp. found there, coupled with the paucity of true talpid skeletal parts, strongly support the suggestion of Matthew, and more recently of K. M. Reed, that *Arctoryctes* belongs with the proscalopines. Actually the key to the identity may

[1] Or eleven, if the "Lower Rosebud" specimen of *Proscalops secundus* Matthew, 1909, should prove to be from a locality or horizon from which the "Rosebud" *A. terrenus* have been collected.

TABLE 3.—Listing of the various sites which have yielded Arctoryctines, and of some of the associated species which have been considered as possibly to be synonymized with them. The table also lists the number of Arctoryctine humeri known from each locality, as well as the total of other front limb bones to come from these same sites.

SITE	AGE	SPECIES	NO. OF SPECIMENS		POSSIBLY RELATED ASSOCIATED SPECIES	REFERENCES
			Humeri	Other forelimb bones		
LACM no. 1380 Nevada	Miocene Hemingfordian	Unnamed gen. and sp.	1			C. A. Reed & Downs, 1958.
Split Rock fauna Wyoming	Miocene Hemingfordian	Arctoryctes sp. (possibly A. terrenus)	15 large & 20 small fragments = 35†	500	*Mesoscalops scopelotemos; Metechinus marslandensis; indet. prim. true talpid (see p. 156).	K. M. Reed, 1960; This work.
Wounded Knee fauna; Upper Rosebud fm.; So. Dakota	Miocene Arikareean	Arctoryctes terrenus	14	**	possible *Proscalops secundus (see K. M. Reed, 1961, p. 477, footnote).	Matthew, 1909; Galbreath, 1953; K. M. Reed, 1961; Macdonald, 1951.
Cedar Creek Member, White River fm., N.E. Colorado	Oligocene Orellan	Arctoryctes galbreathi	3 + 10 fragments =13	77	Metacodon mellingeri; M. magnus; Ankylodon progressus; A. annectens; ?Geolabis rynchaeus; *Oligoscalops whitmanensis; *Proscalops miocaenus; indet. scalopine.	Galbreath, 1953; C. A. Reed, 1956; K. M. Reed, 1961.
Fitterer's Ranch, etc., No. Dakota	Oligocene Orellan	Arctoryctes galbreathi	1			
Toston Beds, Montana	Oligocene Orellan	Arctoryctes galbreathi	1			C. A. Reed, 1956; Kay, Fields & Orr, 1958.
Mellinger loc., Colorado	Oligocene Orellan	Arctoryctes sp.	2		Metacodon mellingeri; Ankylodon annectens	Patterson & McGrew, 1937.
McCarty's Mountain, Montana	Oligocene ?Chadronian	Cryptoryctes kayi	1		Apternodus mediaevus (?Micropternodus in CM Collection no. 1097) Epoicotherium unicum	Simpson, 1927; Kay, Fields & Orr, 1958

SITE	AGE	SPECIES	NO. OF SPECIMENS		POSSIBLY RELATED ASSOCIATED SPECIES	REFERENCES
			Humeri	Other forelimb bones		
Crazy Johnson Member-SDSM no. 55193	Oligocene Chadronian	*Arctoryctes ?galbreathi*	1			
CM no. 8752 near Toston, Montana	Oligocene Chadronian	*Arctoryctes ?galbreathi*	1		*Micropternodus* in CM Collection no. 9576)	
Arner Ranch, Nebraska	Oligocene Chadronian	*Arctoryctes* sp.	3	18	*Apternodus* sp.; *Metacodon* sp.; *Clinopternodus?*; *Proterix?*	Hough & Alf, 1956; Turnbull & Reed, 1960.
Canyon Ferry, Montana	Oligocene Chadronian	*Cryptoryctes kayi*	2		*Apternodus mediaevus*; *Micropternodus* (*Kentrogomphius*)	White, 1954; C. A. Reed, 1956; Russell, 1960.
Little Pipestone, Montana	Oligocene Chadronian	*Cryptoryctes kayi*	5		*Apternodus mediaevus*	Kay, Fields & Orr, 1958.
Pipestone Springs, Montana (includes Easter Lily mine)	Oligocene Chadronian	*Cryptoryctes kayi*	14	††	*Apternodus mediaevus*; *Geolabis*, *Micropternodus borealis*	C. A. Reed, 1954; Kay, Fields & Orr, 1958; McKenna, 1960; Russell, 1960.
Crazy Mt'n. Field, Montana (Gidley Quarry)	Paleocene Torrejonian	Unnamed gen. & sp.	1		?Possibly *Eudaemonema* (or even *Aphronorus* or *Gelastops*)	Simpson, 1937; C. A. Reed, 1954.

* Dental or cranial materials now thought to belong with Arctoryctines.

† Since this was written, Craig Black has made another large collection at the Split Rock locality for Carnegie Museum. He reports that a "remarkably complete" humerus of *Arctoryctes* has shown up in this lot.

** The Lower Miocene beds (Gehring equivalent) of 66 Mountain, near Goshen Hole, Wyoming have recently yielded three knobbed metacarpals and a single terminal phalange of *Arctoryctes* thanks to Craig Black's careful scrutiny.

†† One metacarpal has recently turned up in a washed sieve sample of matrix from Pipestone Springs, Montana. It is not one of the "knobbed" sort, but is of the "keeled" type, comparable to the Arner Ranch specimen PM 3886 described by us in 1960.

well be that here the sampling of the total fauna approaches more nearly the ideal than does any other fauna which is known to contain either an arctoryctine or a proscalopine.

If further intensive collecting at several critical sites adds confirmation to the occurrence of proscalopine skulls and arctoryctine forelimbs, we would—as K. M. Reed points out—have the logical association of talpid-like, but aberrant, skulls and talpid-like, but equally aberrant, post-cranial bones. In such a case we, too, concur in thinking that the individuals of such a group should be placed in a family separate from the Talpidae. A new family would be needed for we do not think the complex of the forelimb to be derivable from any known talpid, since the humerus of *Uropsilus* is already too specialized toward the evolutionary development of a bicipital tunnel to have furnished an ancestral type for a group of specialized lateral-thrust burrowers which were never to have a bicipital tunnel. The talpid bicipital tunnel is formed by a specialization of the proximal part of the pectoral process growing against the lesser tuberosity. The pectoral process of the *Arctoryctes-Cryptoryctes* group is specialized, too, but more distally, and no approximation of any part of it to the lesser tuberosity ever occurs (fig. 28, C–E).

If the *Arctoryctes-Cryptoryctes* group is synonymized with the proscalopines, as at present we believe to be the most probable relationship, we think the common ancestor with the Talpidae must have been from an evolutionary type more primitive than *Uropsilus*. The basic evolutionary feature which must have been possessed by this common ancestor was a tendency toward lateral-thrust digging. The associated morphological specializations may have been most meager—merely a slight hypertrophy of the M. teres major and a more distal location of the teres tubercle and pectoral process on the shaft of the humerus (fig. 32, B) than is typical for most small cursorial mammals. The cranial, and especially dental, characters which hitherto led investigators to put the proscalopines into the Talpidae would have been retained by both groups while the forelimb morphology followed divergent but remarkably parallel evolutionary pathways (figs. 32 and 33).

OTHER SUGGESTED RELATIONSHIPS

The association of the humeri of *Arctoryctes* and skulls of *Apternodus,* a small, possibly fossorial insectivore of uncertain relation-

ships[1] has been considered by various authors. The idea of this possible association with members of the *Arctoryctes–Cryptoryctes* group was strengthened when *Cryptoryctes* was first described, because the types of both *Apternodus* and *Cryptoryctes* were from the same site (Pipestone Springs, Montana), and either *Arctoryctes* or *Cryptoryctes* have since been collected at several sites with *Apternodus* (Table 3). However, we now find much more convincing the presently-described association of arctoryctine limb bones and proscalopine crania and/or teeth, as at Split Rock and Cedar Creek. We believe that acceptance of this association for *Arctoryctes* must necessarily rule out consideration of any morphological identity between *Apternodus* and *Cryptoryctes*, for the latter (due to its great similarity to *Arctoryctes*) must also be either a proscalopine or closely related to them. However, *Apternodus*—whatever it may finally be determined to be—is a zalambdodont in addition to numerous other peculiarities, and the proscalopines are definitely dilambdodont. We believe that this basic evidence of the dentition outweighs the above-mentioned coincidences of geographical and temporal association.

One other genus needs to be discussed here, *Micropternodus* (= *Kentrogomphios*), as regards possible relationships with the *Arctoryctes–Cryptoryctes* line. Russell (1960) has reviewed the history, discovery and taxonomic assignment of *Micropternodus*. In doing so he included forms which are, or have at one time been, suggested as being allied to it. In concluding his review of the relationships he states, "In spite of its mole-like adaptations, such as a long, flattened snout with its peculiar anterior protuberances and the dilambdodont pattern common in moles, I do not believe that *Micropternodus* is very closely related to the talpids. The character and position of its hypocone, the distinct cusps of the upper molars and the subdivided stylar cusps exclude it from any moles known to me." The hypocone argument is the only one that needs discussion, for the other points do not hold for the first talpids that we checked, *Talpa caeca* and *T. europaea*[2] (and we have gone no further in this). Since at the time Russell worked on *Micropternodus*, K. M. Reed's subfamily Proscalopinae had not been named, and the animals in it were

[1] See McKenna, 1960, p. 159; McDowell, 1958, for recent discussions of relationships of *Apternodus*.

[2] In *T. caeca* (CNHM 35943) the mesostylar cusp of M^2 is deeply bifid, and this specimen is quite typical in this respect. For *T. europaea*, Stein (1951, p. 338) gives a detailed report showing the frequency of bifid mesostyles of M^2, M^3, or both in that species.
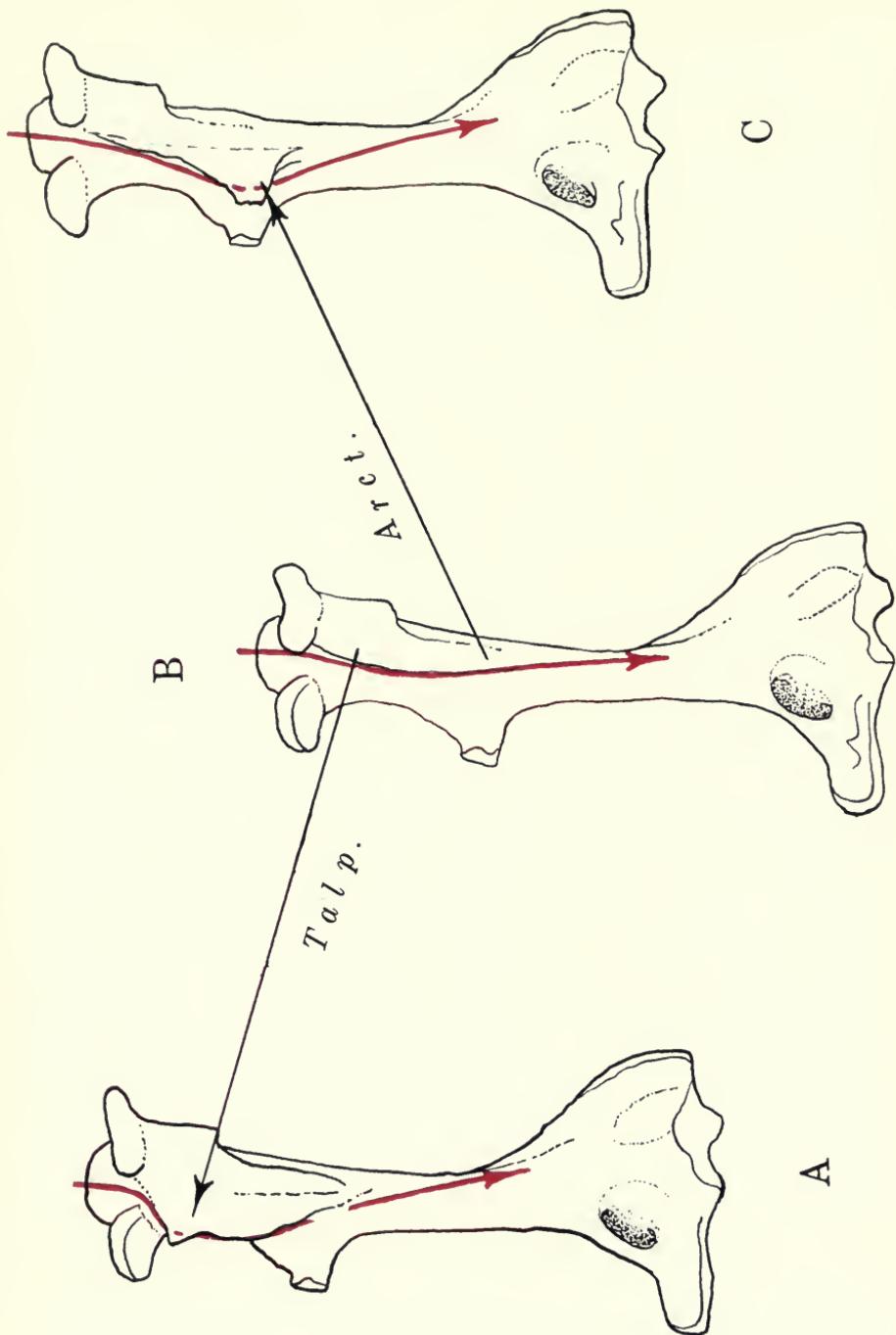
little known, it is not surprising that his point about the hypocone was made.   However, some of the Proscalopines do have a very considerable development of the hypocone—one that approaches nearly to that of *Micropternodus* actually so that while the argument may hold for moles (Talpidae) generally,[1] it does not hold for the proscalopines.   Further, the presence of hypocones in *Uropsilus* and other generalized moles is another bit of evidence in support of the concept that *Uropsilus*, the most primitive living talpid, is at a morphologic level nearly comparable to that which must have marked the division point between talpids (s.s.) and proscalopines.   As regards locomotor adaptation, the humerus of *Uropsilus* is very generalized, although showing somewhat the talpid specialization (fig. 32).   Thus in both dental and locomotor adaptive levels, *Uropsilus* shows a generalized ancestral pattern.   The considerable canine development of *Micropternodus* would seemingly rule it out from synonymy with any presently known proscalopine, but would not prevent a close relationship with that group.   In fact, within the Talpidae, some have rather large canines, although most do not.   In any event, the new near-certain synonymy of the arctoryctines and the proscalopines, and the dental and general similarities of *Micropternodus* to known members of the latter group, strongly suggests that all may be allied (fig. 33).

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[1] In the primitive mole *Uropsilus*, the upper molars have a good hypocone developed.   This can be seen on any of over 100 specimens from 9 localities in Szechwan, China, from 6 specimens from 2 localities in Yunan, China and from a single specimen from Kachin Prov., Burma, in the CNHM collection.   In *Uropsilus* the hypocone occupies most of the space (lingually) between adjacent molars, in contrast to conditions in other moles in which open triangular areas exist.   Traces of hypocones are encountered in most individuals of *Scaptonyx*, too, and *Neurotrichus* has a weak hypocone on M^{1-2}.   Rarely an individual of *Talpa* will show a trace of a hypocone, but none were found on any other genus of mole examined.

FIG. 32.   Left humeri, anterior aspect. A, *Uropsilus* (Recent), the most primitive known talpid, showing evolutionary specialization of the proximal end of the pectoral process; B, humerus of the hypothetical ancestor of Talpidae and Arctoryctines, with an unspecialized pectoral process, showing the different parts which underwent specialization in each of the groups; C, hypothetical primitive Arctoryctine, showing evolutionary specialization of the distal end of the pectoral process.   (In each, the course of the M. biceps brachii is shown by the elongate red arrow.)
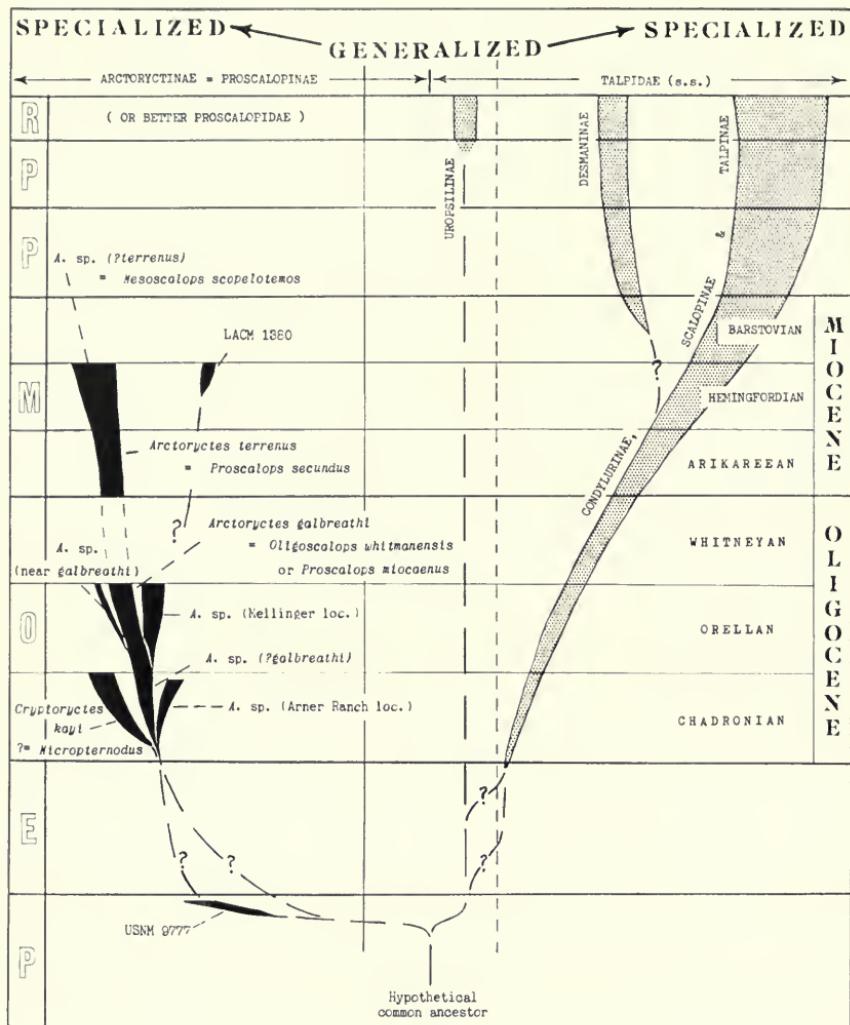
Addendum No. 1

As this paper was going to press, another humerus referrable to *Arctoryctes* has come to us from Peter Robinson, University of Colorado Museum, Boulder, Colorado. Specimen UCM 22144 is a left humerus, found imbedded in matrix, and subsequently prepared free on its anterior surface. Its fragile condition makes further preparation unwise. The specimen was collected by J. Clark and K. Kietzke in August, 1961, from the Brule formation, Pole Slide beds, *"Protoceros* ss," at NW ¼, sec. 33, T. 43 N., R. 44 W., Sheep Mountain Table, South Dakota. It is the first Whitneyan *Arctoryctes* known to us. The bone is nearly complete in anterior aspect, lacking only the greater tuberosity and the distal end of the pectoral process. The anterior surface of the lesser tuberosity has suffered minor abrasion. One feature, rarely preserved in *Arctoryctes*, but well preserved in this specimen is the complete lateral epicondyle.

The degree of fusion of the teres tubercle and the medial epicondyle is as advanced as in *A. terrenus,* and the specimen compares well with the Miocene specimens of *A. terrenus* from South Dakota, falling within the size range of variation for the measures B, D, and E and the proximal breadth measure. It is about 10% below the range for measures A and C and for greatest breadth (teres tubercle—

Fig. 33. Tentative phylogenetic tree (very schematic for Talpidae) showing the possible relationships of Arctoryctinae=Proscalopinae (or preferably Proscalopidae) to the Talpidae (s.s.) as interpreted here. It is based upon kind and degree of development (generalized to specialized) of front limbs in Arctoryctines and Talpids, and upon dental features, mainly hypocone development in Proscalopines and Talpids according to the following scheme:

SPECIALIZED ←——— ARCTORYCTINES	GENERALIZED ———→	SPECIALIZED TALPIDS
development distally	(1) weak development pectoral process of humerus	development proximally
strong knobbing on metacarpals and proximal phalanges	(2) lack of knobbing of metacarpals	unknobbed, partially or weakly knobbed metacarpals
non-bifed terminal phalanges	(3) biffing of terminal phalanges	bifed terminal phalanges
strong hypocone development	(4) modest hypocone development	strong tendency for loss of hypocone

NOTE: There is now a Whitneyan representative of the Arctoryctinae lineage. Details concerning it have been given in Addendum No. 1.

SUMMARY TABLE OF HUMERAL MEASUREMENTS OF VARIOUS ARCTORYCTES SPECIES

Measures Specimen	A Total length	Greatest breadth teres tub. lat. epi.	B Min. width distal teres tub.	C Breadth at teres tub.	D Distance lat. edge capit. =med. edge pit of tendon M. flex. dig. prof.	Distal width	Proximal width	E Min. shaft width prox. teres tub.
A. terrenus								
N^1	3(+)	2(+)	7	8	10	1(+)	4	11
Mean	11.4	14.5	6.5	8.2	8.3	13.2	6.5	2.9
UCM 22144	10.4	12.7	5.9	7.3	7.5	10.3	6.1	2.8
A. galbreathi	2	2	4	3	3	2	1	4
	8.8	9.5	4.0	5.5	6.0	7.9	4.8	2.3
A. sp.	1	(+)	4	2	2(+)	(+)		4
	8.2	7.7	2.9	4.2	4.5	5.9	..	1.6

[1] The values of N indicate the maximum number of specimens for which it was possible to take the measure indicated. The (+) symbol indicates that other more fragmentary pieces which tended to confirm the values given were present. In the case of A. sp. in two instances such chips provided the basis for an estimate value which has been entered in the table.

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lat. epicondyle) and distal breadth measures as well.   Thus it would appear to be referrable to *A. terrenus*, but is the smallest individual in over-all proportions, as may be seen from the summary table.

Addendum No. 2

The Stirton and Rensberger 1964 work, "Occurrence of the insectivore genus *Micropternodus* in the John Day formation of Central Oregon" (Bull. So. Calif. Acad. Sc., **63**, pt. 2, pp. 57–80), arrived while this was in galley.   Certainly we should now expect to find Arctoryctine fore-limb elements in that formation also if our notions about the synonomy are correct.   This additional point should be kept in mind especially when using Table 3 and fig. 33.

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