Taxeopody in the carpus and tarsus of Oligocene Pliohyracidae (Mammalia: Hyracoidea) and the phyletic position of Hyraxes

(mammalian systematics/Paenungulata/Proboscidea/Perissodactyla/vertebrate paleontology)

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ABSTRACT   Recent hyracoids and elephants share a taxeopode arrangement of tarsal and carpal bones, a condition in which bones are aligned with minimal interlocking between adjacent elements. Taxeopody has often been interpreted as a synapomorphy reflecting a close phyletic link between Hyracoidea and Proboscidea, but recently it has been suggested [Fischer, M. S. (1986) *Cour. Forschungsinst. Senckenberg* 84, 1–132] that hyracoid taxeopody is an independent acquisition resulting from selection favoring increased midcarpal and midtarsal rotation and that Hyracoidea is actually allied with Perissodactyla. As a test of this hypothesis, isolated carpal and tarsal bones of primitive Oligocene hyracoids from the Fayum, Egypt, have been examined to determine whether these indicate a taxeopode or diplarthral carpus and tarsus. Four complete astragali from the Fayum, representing at least three taxa, show a single, slightly convex articular surface on the head for articulation with the navicular and lack a facet for the cuboid. Two complete magna representing two species have a single proximal facet for articulation with the lunar, and they lack a facet for the scaphoid. Thus, both the carpus and tarsus of Fayum hyracoids are taxeopode. Taxeopody in hyracoids cannot be attributed to selection for carpal and tarsal rotation in climbers because the Oligocene, Miocene, and Recent species show great diversity in body size and probably locomotor specializations, despite relative uniformity of structure in the carpus and tarsus. The shared taxeopody of hyracoids and proboscideans, along with other osteological characters and similarities in hemoglobin, eye lens proteins, and other molecules, all suggest that Hyracoidea belongs within Paenungulata.

Modern hyraxes (family Procaviidae) have a taxeopode, or serial, arrangement of the carpal and tarsal bones (1–4). In this arrangement, podial elements are aligned proximo-distally with minimal interlocking between the proximal and distal rows of elements, thus providing relatively smooth and uninterrupted midtarsal and midcarpal joints, as illustrated elsewhere (1, 3, 4). In the carpus, taxeopody is especially evident in the proximal magnum and the distal lunar, which fit together by a single, flat articular surface and do not interlock with medial and lateral elements (although the slightly broader lunar may contact the centrale and unciform, especially during rotation). Similarly, in the tarsus, the distal articulation of the astragalus (= talus) is exclusively with the navicular, and the distal articulation of the calcaneus is strictly with the cuboid. Taxeopody is found in Hyracoidea, Proboscidea, species of *Phenacodus* and *Meniscotherium*, and with significant variations in some other extinct ungulate groups (1, 5).

Most ungulate taxa, including Perissodactyla, share a diplarthral, or alternating, arrangement of the carpals and tarsals, in which podial bones from the proximal and distal rows interlock in a zig-zag fashion (1, 3, 4). Thus, the lunar shares distal articulation with both the magnum and the unciform, and the magnum articulates proximo-medially with the scaphoid. In the tarsus, the astragalus articulates with both the navicular and the cuboid.

The taxeopody of Hyracoidea and Proboscidea has been interpreted as an indication of phyletic relationship between the two orders (1, 4, 6, 7). However, this view has been challenged, most recently, by Fischer (8, 9), who concluded that taxeopody has been acquired independently in Hyracoidea and Proboscidea. Since the feet of desmostylians are diplarthral (10), and because Fischer accepted the conclusion that desmostylians are the sister group of Proboscidea (11), Fischer therefore concluded that the taxeopody of Proboscidea and Hyracoidea evolved convergently. The independent acquisition of taxeopody in Hyracoidea was accounted for by postulating that modern hyracoids evolved from a cursorial, unguligrade ancestor that had lost all rotational movement in the lower arm, wrist joint, and ankle joint and that when hyraxes became climbers the new requirements for rotation were attained by the evolution of taxeopody and the consequent ability to generate twisting movements at the mid-tarsal and mid-carpal joints (8). Fischer's analysis of this and other morphological features led him to revive the idea that hyracoids are phylogenetically related to Perissodactyla (8, 9).

In order to test these phylogenetic and functional hypotheses, it is desirable to understand the tarsal and carpal structure of primitive hyracoids. The earliest known hyracoids belonging to the subfamilies Geniohyinae and Saghatheriinae of the extinct family Pliohyracidae come from the Eocene of Algeria, but no podial elements have been described (12–15). Slightly younger pliohyracids closely related to and often congeneric with the Algerian taxa are abundant at early Oligocene sites in the Fayum, Egypt, where more than eight genera are represented (15–18). To date, podial elements from the Fayum have been mentioned only briefly (19). The earliest previously described hyracoid foot elements date back only to the early Miocene. Tarsal bones of *Megalohyrax championi*, a tapir-sized pliohyracid from East Africa, indicate that this species had a cursorially adapted and fully taxeopode foot (8, 20). To date, carpal bones that could help in assessing hyracoid taxeopody are not known before the Pliocene. Taxeopody is evident in the carpus of *Procavia transvaalensis*, a Plio-Pleistocene species closely related to extant *Procavia capensis* (21).

Podial specimens of Oligocene hyracoids were collected from the Jebel Qatrani Formation of Fayum Province, Egypt, during recent expeditions to the Fayum led by one of us (E.L.S., Duke University) in cooperation with the Egyptian Geological Survey. These podial elements include diagnostic specimens that can be used to assess whether Oligocene

Abbreviation: DPC, Duke Primate Center.

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hyracoids had a taxeopode or diplarthral structure of both the carpus and tarsus. The purpose of this report is to describe these podial elements, to determine if the Oligocene hyracoids had taxeopode or diplarthral tarsus and carpus, and to discuss the functional and systematic significance of the finds.

MATERIALS AND METHODS

The Jebel Qatrani Formation consists of continental sediments deposited as sand bars and overbank deposits by a series of rivers during the early to middle Oligocene; the bottom of the section may be late Eocene (18, 22, 23). The stratigraphic positions of hyracoid localities are distributed in four major faunal units representing distinct temporal intervals (18, 23). Fossils described here are catalogued in the collections of the Duke Primate Center (DPC).

Dental remains of hyracoids are abundant and diverse in the Fayum fossil quarries, with single quarries yielding up to six genera of hyracoids, with significant overlap in size among species. Thus, the confident allocation of podial elements to specific genera or species is impossible; rough allocations are made on the basis of size and the relative abundance of hyracoid taxa at particular quarries.

The specimens included in the analysis are the following: DPC 3383, left astragalus, quarry M; DPC 3481, right calcaneus, quarry V; DPC 4515, left astragalus, quarry M; DPC 6065, right magnum (= capitate), quarry M; DPC 6361a, left navicular, quarry L-41; DPC 6361b, left triquetrum (= cuneiform), quarry L-41; DPC 6375, right astragalus, quarry I; DPC 7553, right magnum, quarry L-41; DPC 7665, left astragalus, quarry L-41.

The most useful elements in our sample for distinguishing between taxeopody and diplarthry are the astragalus and the magnum. In taxeopody, the astragalus has a single distal articulation with navicular, but none with the cuboid, and the magnum has a single articular surface with the lunar, and none with the scaphoid. In diplarthry, the astragalus has a double distal articulation, with one facet for the navicular and another for the cuboid, whereas the magnum has two distinct proximal facets, one with the lunar and one with the scaphoid.

RESULTS

Astragalus. The four astragali (DPC 3383, 4515, 6375, 7665) represent at least three different taxa, based on structure and size. All four are significantly larger than astragali of Recent hyracoids. The smallest of these, DPC 6375, can be referred to a species of either *Thyrohyrax* or *Saghatherium*, which are the only two small genera known from quarry L-41. The largest specimen, DPC 4515, is from quarry M where teeth and jaws of *Magalohyrax eocaenus* are common. DPC 3383 and 6375 are smaller than DPC 4515 and may belong to *Pachyhyrax crassidentatus*, a common species from quarries I and M with teeth that are smaller than those of *M. eocaenus*. It is possible, however, that any of these three latter astragali belong to another, less common genus, such as *Titanohyrax* or *Bunohyrax*.

All specimens show the deep, rounded articular fossa for the medial malleolus of the tibia that is characteristic of Hyracoidea [and which is also present in primitive proboscideans (14)]. The structure of the condylar surface and the distinctive spiral articulation for the fibular malleolus also serve to confidently identify these elements as hyracoid (Fig. 1).

There are notable morphological differences among the specimens. In the smallest species the head and neck are offset markedly to the medial side, forming a deep, square-cut notch between the anterior border of the tibial condyle and the lateral border of the neck, as in modern Procaviidae (Fig. 1*d*). In the largest species the head and neck project almost directly distal to the condyle and lack the square notch
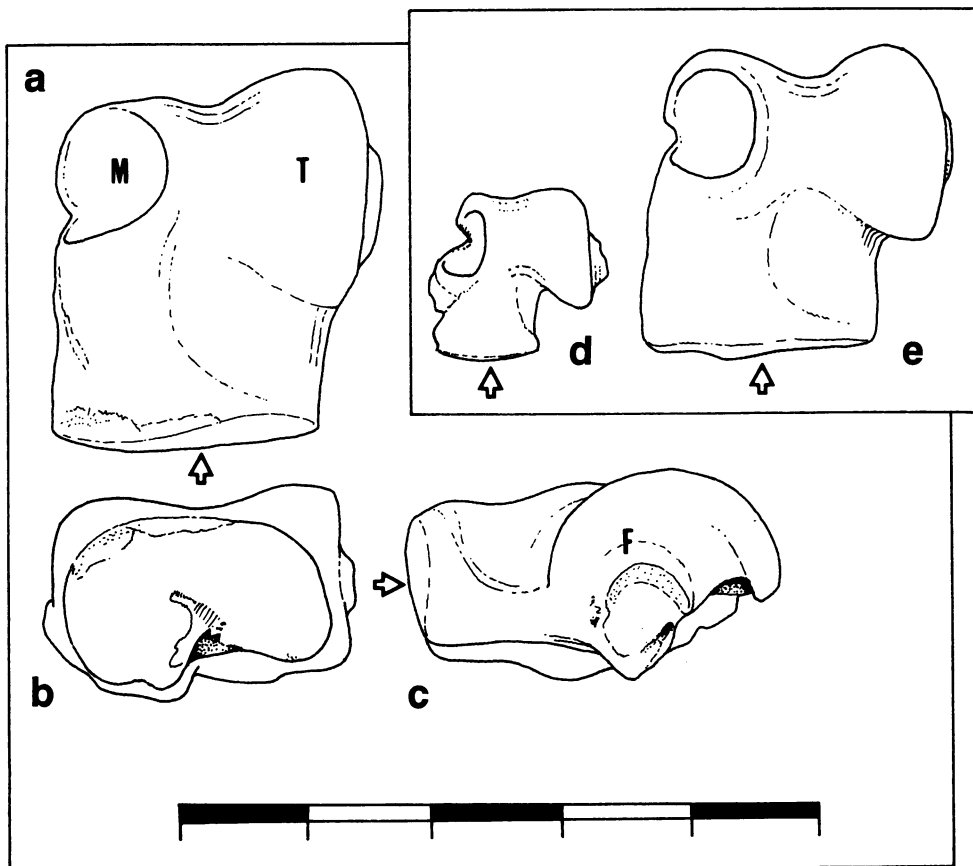

Fig. 1. Astragali of Oligocene hyracoids. A large specimen (DPC 4515) in dorsal (*a*), distal (*b*), and lateral (*c*) aspects shows a single distal articulation for the navicular, indicated by arrows in all drawings but *b*, and no facet for the cuboid. Astragali of smaller Oligocene taxa are also taxeopode, despite differences in size and proportions (*d*, DPC 7665; *e*, DPC 6375, a right astragalus reversed for comparison; both in dorsal aspect, and all drawn to same scale). F, articulation with fibula; M, fossa for medial malleolus of tibia; T, condyle for articulation with tibia. (Bar scale subdivisions = 1 cm.)

(Fig. 1a). DPC 3383 and 6375 are intermediate in size and also in the degree to which the head and neck are offset to the medial side (Fig. 1e). These varying degrees of medial offset may be an allometric or functional correlate of differences in body mass.

The head of the astragalus shows a single articular surface for the navicular (Fig. 1). This surface is broad with an inferior groove or notch that gives it a rounded semilunar shape in distal view (Fig. 1b). There is no facet for articulation with the cuboid. This is true even of the large specimens lacking the medial offset of the astragalar neck. Thus, all specimens indicate a taxeopode arrangement of the tarsus.

Magnum. One magnum comes from a relatively large species at quarry M; the other is from a medium-sized species at quarry L-41. The former is probably referrable to *M. eocaenus* (or a species of *Pachyhyrax* or *Titanohyrax*), whereas, the latter may belong to any of several medium-sized taxa at L-41. These specimens differ markedly from the magnum of anthracotheres, the only other Fayum ungulates in that size range.

In both specimens, the distal articulation with the third metacarpal is a concave surface, deeper than it is wide and narrowing ventrally. On the medial surface are three well-defined articular facets, for the second metacarpal, the trapezoid, and the carpi centrale (Fig. 2a). The lateral side articulates only with the unciform and bears deep scars for ligamental attachments. In all of these features, and also in general shape, the Fayum magnum resembles closely the condition seen in modern procaviids, which is especially notable because of the size difference. In proportions, the Fayum magna are relatively longer and shallower than those of procaviids.

The magnum's proximal articular surface is a single, smooth, strongly convex articulation with the lunar (Fig. 2 a–c). There are no articular facets for the scaphoid or the triquetrum. In ungulates with a diplarthral carpus, the proximal magnum bears two distinct articular surfaces forming a dihedral angle. The Fayum fossils therefore establish the occurrence of a taxeopode arrangement of the carpus in at least two Fayum hyracoids.

Other Podial Elements. The navicular from the Fayum (DPC 6361a), representing a large species, is a relatively flat, disk-like structure, as in modern hyracoids. The proximal facet for the astragalus is concave (Fig. 2 d and e). The distal surface has two distinct facets for the cuneiforms and an extended ventral process (with the distal portion broken off). As in modern hyracoids there is a slightly concave facet for articulation with the cuboid on the ventrolateral surface (Fig. 2e). In DPC 6361a, this facet is relatively smaller than in modern species. Unlike modern hyracoids, DPC 6361a also bears an additional small but well-defined facet between this cuboid facet and the ventral rim of the astragalar facet (Fig. 2 d and e). The face of this small facet is oriented ventrally and somewhat proximally, suggesting that it is a point of articulation with the calcaneus.

In modern hyracoids, the navicular and calcaneus closely approach each other at this point but do not form a bony articulation. In proboscideans, an articulation does occur here between navicular and calcaneus. In perissodactyls and other diplarthral ungulates, the cuboid articulates with the astragalus, which precludes articulation between the navicular and the calcaneus. Thus, in the relationship between navicular and calcaneus the Fayum hyracoid differs from that of living species but resembles that of proboscideans, not perissodactyls.

The triquetrum from the Fayum (DPC 6361b), also representing a large species, has a large, saddle-shaped proximal surface for the ulna, a flat ventral facet for the pisiform, and a concave distal facet for the unciform. On the medial side near the distal end lies a wedge-shaped facet for articulation with the lunar. The Fayum triquetrum differs from that of modern hyracoids in being relatively longer and narrower, but in articular pattern it is very similar to those of procaviids.

The calcaneus from the Fayum (DPC 3481) shows an obliquely oriented posterior astragalar facet that is elongated and hemicylindrical, a distinctive feature of living species. The sustentaculum is very broad, perhaps correlated with its large size. Unfortunately, on this specimen and others that are even more fragmentary the distal portion of the bone is missing so articular facets cannot be discerned; in observable
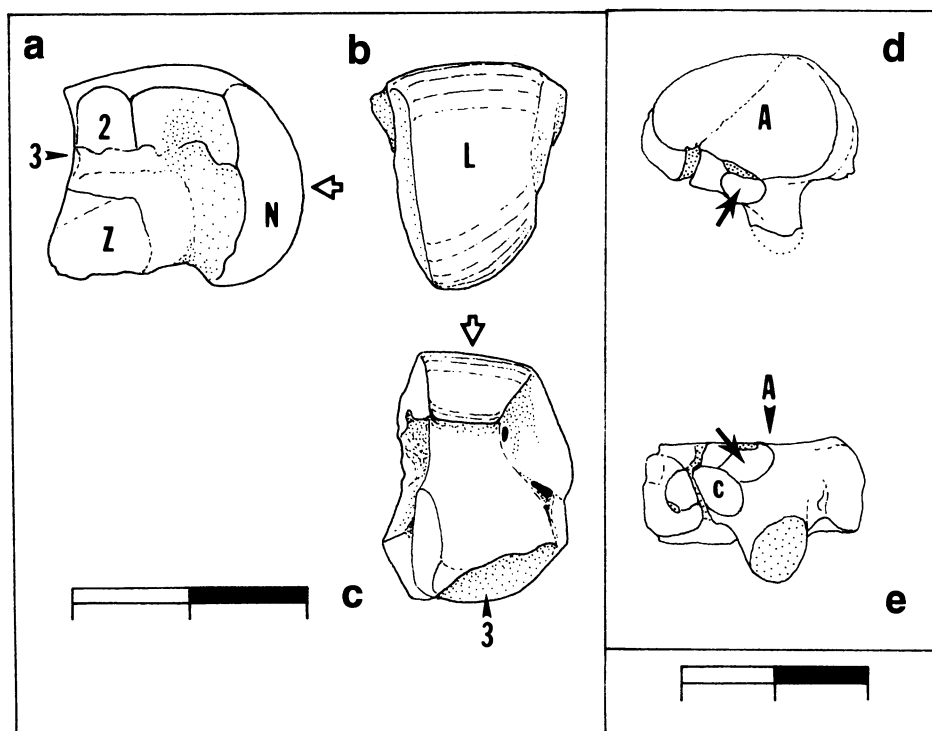

FIG. 2. Foot and wrist bones of Oligocene hyracoids. (*Left*) A fossil right magnum (DPC 6065) in medial (a), proximal (b), and ventral (c) aspects showing the single convex condyle for articulation with the lunar indicated by arrows in a and c and by L in b. Additional symbols: 2, facet for second metacarpal; 3, facet for third metacarpal; N, facet for carpi centrale; Z, facet for trapezoid. (*Right*) A fossil left navicular (DPC 6361a) in proximal (d) and ventral (e) aspects showing the large, slightly convex articulation for the astragalus (A), the small ventrolateral facet for articulation with the cuboid (C) that is split by a crack in the fossil, and the smaller proximoventral facet for articulation with the calcaneus (arrow). (Bar scale subdivisions = 1 cm.)

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details, the Fayum calcaneus closely resembles those of modern procaviids.

The morphology of all of the Fayum podial elements supports the general conclusion that Oligocene hyrax feet were structured very much like those of modern hyracoids but that they differed in some details that may be related in part to size differences and possibly also to locomotor specializations. There is no evidence that primitive pliohyracid feet depart from a taxeopode pattern in ways that resemble diplarthral perissodactyls.

DISCUSSION

The astragali recovered from the Fayum indicate conclusively that the tarsus of primitive pliohyracids was taxeopode, as in proboscideans and procaviid hyracoids. In those tarsal elements that have been recovered, the articular pattern seen in pliohyracids does not differ substantially from the procaviid arrangement except for the navicular, which has distinct facets for both the cuboid and possibly the calcaneus that are lacking in Recent hyracoids. This is a resemblance to proboscideans and is very different from the diplarthral arrangement of perissodactyls in which the cuboid articulates with the astragalus. The astragali of hyracoids also share an exclusive similarity to primitive proboscideans such as *Numidotherium* and *Palaeomastodon* in the deep, round fossa for the medial malleolus of the tibia (14). In the carpus, the two magnum specimens recovered from the Fayum prove that at least two species of pliohyracids showed carpal taxeopody. The magnum is one of the two carpal bones that are most useful for defining the taxeopode pattern (1).

The similarity between the feet of pliohyracids and procaviids is notable despite the great size diversity evident among the Oligocene taxa (15, 17). Given the size differences and the variation observed in some postcranial characters, such as the position of the astragalar neck relative to the condyle, it seems likely that the locomotion of Fayum hyracoids was not uniform. In any case, the large body size of most taxa excludes the possibility that these were agile climbers of trees or rocks, as are the small, living hyracoids. The early Miocene pliohyracid from East Africa, *M. championi*, was a large-bodied cursorial species with a taxeopode tarsus (8, 20). Thus, taxeopody is not associated with a particular locomotor specialization but instead occurs among all known hyracoids and proboscideans, from the largest graviportal elephantids to small arboreal *Dendrohyrax dorsalis*.

The hypothesis that hyracoid taxeopody evolved secondarily from a diplarthral ancestor and in parallel with proboscideans because of selection for enhanced mid-tarsal and mid-carpal rotation (8), perhaps for climbing, finds no support in the data presented here. This hypothesis does not explain why elephants and hyracoids, which do not have similar functional requirements, have similar foot structure. Nor does it explain why *M. championi*, which is cursorial like many perissodactyls, does not have perissodactyl-like feet. The fossil evidence shows that typical taxeopody was well established in the earliest known radiation of pliohyracid hyracoids and has been consistently present in the order from the Oligocene to the present. We cannot definitively exclude the possibility that yet older hyracoids will have diplarthral feet. However, proponents of the hypothesis that taxeopody evolved to allow increased midtarsal and midcarpal rotation in climbers must now posit that this occurred well before the early Oligocene and that it was then retained in all later species despite differing functional requirements.

A more likely hypothesis is that carpal and tarsal taxeopody is a synapomorphy linking hyracoids and proboscideans. We cannot absolutely rule out the possibility of evolutionary convergence or of incorrectly determined character polarity; other authors have accepted ungulate taxeopody as

a derived condition (4, 7, 9). However, this phylogenetic hypothesis is supported by independent morphological (4, 7) and biochemical data (7, 24–26), including squamosal overlap of the mastoid (4), amino acid sequences of eye lens α-crystallins (24), and α- and β-hemoglobins (25); but see criticisms by Fischer (8, 9).

Hyracoidea and Proboscidea first appear together in the Eocene of Africa, where perissodactyls are absent. Although hyracoids do exhibit some morphological resemblances to perissodactyls (8), most of these are likely to be convergent (4). The molars of some hyracoids resemble those of certain ceratomorph perissodactyls (4), but primitive hyracoids have quadrituburcular, bunodont molars unlike those of perissodactyls proving that dental resemblances between the two orders are convergent (15). The fossil evidence suggests that hyracoids, like some of the South American ungulates such as litopterns, have evolved perissodactyl-like traits convergently while isolated on their respective island continents during the early Tertiary. The true phylogenetic affinities of Hyracoidea appear to lie with Proboscidea. This is best reflected by classifying both orders in Simpson's Superorder Paenungulata (6) (minus the Pantodonta, Dinocerata, and Pyrotheria, whose inclusion Simpson admitted was "frankly hypothetical").

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