Locomotion in Moles (Insectivora, Proscalopidae) from the Middle Tertiary of North America

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take place with a much thinner layer. The low dielectric constant observed on Terra Ishtar suggests that a large amount of low-density material is present in the highlands, to a depth of at least tens of centimeters. The observed wind speeds are probably sufficient to remove the weathering products into the lowland regions, but this is subject to experimental verification. Most sediment transport will occur during short, rare intervals of higher wind speeds. Large grains released by disaggregation of primary igneous rocks will be much harder to transport. Such large, relatively immobile grains would include quartz from granite weathering.

Of course, we cannot be sure which reactions, if any, actually occur and buffer the gas composition of the Venus lower atmosphere, but some type of chemical weathering can occur at any altitude. However, if Venus does have the surface igneous assemblages observed on the earth, the moon, and in meteorites, it is certain that chemical weathering will be more effective at higher altitudes, for any reasonable atmospheric H_2O mole fraction. Since Venus has very few mountains high enough for vigorous chemical weathering, such effects are probably confined to Maxwell and the top of Aphrodite. Future experiments will shed more light on the subject of chemical weathering on Venus by performing in situ chemical analyses with the same precision performed on Mars by the Viking landers. Specifically, the Ca/Si, Fe/Si, Mg/Si, and S/Si ratios in the soil and the atmospheric abundances of H_2O, HF, HCl, COS, SO_2, H_2S, and CO must be measured. Such analyses could be performed by x-ray fluorescence and gas chromatography–mass spectrometry on board a surface lander.

At present we are able to describe only one plausible geochemical transport process on Venus. Previous assumptions of gross chemical equilibrium between the lower atmosphere and surface of Venus are probably best justified by the existence of such a mechanism combined with the high surface temperatures and pressures. These assumptions lead us to the suggestion that the topography, radar properties, and lower atmosphere composition are interrelated.

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Locomotion in Moles (Insectivora, Proscalopidae) from the Middle Tertiary of North America

Abstract. *The locomotion of proscalopid moles, an extinct group restricted to North America, differed from that of other animals. Analysis of a newly discovered and relatively complete and articulated skeleton shows that the digging technique of proscalopids involved a combination of motions that has not been observed in modern fossorial insectivores. The many anatomical peculiarities of proscalopids are related to their specialized digging technique and justify their assignment to a new family of insectivores, the Proscalopidae.*

Proscalopids, a group of moles known only from the Oligocene and Miocene of North America, had a specialized skeletal morphology that was different from any Recent mammal. The scarcity of fossil remains, however, has limited the inferences that could be made about the evolutionary history and the function of the specializations of these mammals. Only isolated teeth, bones of the forelimb, and some cranial elements had been reported (*1, 2*), and only recently was it shown that the bones belonged to the same type of animal (*3, 4*). The breadth and unusual shape of the humerus led early investigators to suggest that it was adapted for digging, and proscalopids have been classified in the same family as the fossorial golden moles (Chrysochloridae) (*5, 6*), palaeanodont edentates (Epoicotheriidae) (*7*), and true moles (Talpidae). Although some investigators suggested that proscalopids represented a distinct family of insectivores (*1, 8*), most have regarded them as talpids (*1, 3, 4*).

A nearly complete and partially articulated skull and skeleton of a proscalopid (genus *Mesoscalops*) was found in the siltstones of the Miocene Deep River Formation (probably of Hemingfordian age) of western Montana (*9*). Analysis of this skeleton has revealed that proscalopids differ more from other small mammals than has been recognized, in both gross anatomy and mode of locomotion. The digging stroke in proscalopids may resemble that of modern chrysochlorids more than that of talpids (*1*). The many differences preclude a family-level relation between proscalopids and talpids.

Anatomically, the proscalopids are a peculiar blend of specializations, some of which are found in golden moles and fewer in true moles. For example, the short skull of proscalopids is most similar to that of chrysochlorids (*8*) in the prominent shelves that extend toward the side from the snout, the deep basicranium, and the prominent nuchal crest. The nuchal crest often extends onto the top of the posterior portion of the zygomatic arch, which is continuous with a broadened flange that covers the squamosal region. Talpids lack all of these features but resemble proscalopids in dental characteristics, particularly in the W-shaped ectoloph of the molars. The robust cervical vertebrae of proscalopids have unusually large neural spines, and vertebrae two through five are fused. The neural spines on thoracic vertebrae two to five (Fig. 1A) are much higher than those in either golden or true moles. A prominent fossa (*f* in Fig. 1A) covers the anterior surface of the spines in the proscalopid.

Because many of these features are found in modern animals that use the head in digging, such as chrysochlorids

(*10*) and fossorial rodents (*11*), a similar digging action is postulated for proscalopids. Talpids, lacking such specializations, do not use the head in digging (*12, 13*). In the modern analogs, the lateral rostrum flanges support a tough, cartilaginous nose pad that protects the anterior part of the rostrum against abrasion. The short rostrum and deep basicranium effectively increase the upward force that the head can apply by providing a more efficient lever for upward motion. The muscles that run between the head, neck, and back supply input force to the head. Attachment points for these muscles, including the nuchal crest, squamosal flange, neural spines, and scapular spine, are hypertrophied, suggesting great potential for applying force. If modern analogs provide a valid approximation (*10, 14*), the muscles involved were probably the biventer cervicis (running from the cervical vertebrae to the posterior part of the skull), splenius capitis (cervical vertebrae to posterior skull), rhomboideus (posterior skull and cervical vertebrae to scapular spine), trapezius anticus (posterior skull to scapular spine), and cleidooccipitalis (clavicle to posterior skull). Large neural spines on the thoracic vertebrae would provide an attachment area for hypertrophied muscles used to extend the head and neck (portions of the multifidus spinae complex), and the fused cervical vertebrae would provide a rigid base to counteract the upward force at the rostrum.

The scapula (*s* in Fig. 1B) and the clavicles of the new skeleton resemble the upper portion of the arm of the golden moles. The scapula in both forms is elongate with a remarkably enlarged scapular spine. In chrysochlorids, this spine serves as an attachment point for muscles that lift the head (*10*) and fix the scapula during movement of the humerus. In talpids, especially the most fossorial forms, the scapular spine is reduced to increase efficiency in lateral-thrust digging (*13*), which involves pushing dirt laterally away from the body. Chrysochlorids, in contrast, use their limbs for scratch-digging (*10, 15*), the manner in which dogs dig. The scapula of proscalopids shows adaptations more suited to the motion involved in scratch-digging. The long, straight clavicle of proscalopids, similar to that in chrysochlorids, substantiates this conclusion. The clavicle articulates to the manubrium (*e* in Fig. 1A) and acromion process of the scapula. In fossorial talpids, the clavicle is short, stout, and articulates to the humerus rather than the acromion, thus absorbing some of the stress imposed by lateral-thrust digging.

That proscalopids were not true scratch-diggers, however, is indicated by the structure of the humerus. It has been recognized (*1*) that rotation of the humerus was probably as important in the power stroke as retraction. A major part of the rotational force was apparently provided by muscles that ran between the posterior surface of the scapular spine and the elongate lateral epicondyle (*ss* and *le* in Fig. 1B), which would act as an efficient (long) input lever to the axis of rotation (Fig. 2). The importance of these muscles (possibly the infraspinatus or spinodeltoideus, or both) and their mechanical advantage, was not recognized before because neither the scapula nor lateral epicondyle has commonly been preserved in proscalopids. Acting in concert with these muscles was the teres major, which ran between the teres fossa on the scapula and the teres tubercle (*tt* in Fig. 1B). The hypertrophied teres tubercle provided a long input lever for rotation, as well as an increased attachment area for the teres major. Efficient counterrotation was possible when the biceps brachii contracted because the pectoral process was located so far mediad of the head (*1*). Rotation is characteristic of a talpid-like stroke (*16*), but in fossorial talpids rotation is accomplished almost exclusively by the teres major (*13*). Talpids lack the hypertrophied lateral epicondyle and associated musculature that was important to proscalopids for digging.

The proscalopid digging stroke apparently also differed from that of talpids in that it required more true retraction. As in chrysochlorids, in which retraction is the main motion in digging (*10*), the teres major inserts on the distal half of the humerus, thus providing a long input lever (*re* in Fig. 2). In talpids, true retraction is not important in the power stroke, and the teres major inserts on the proxi-

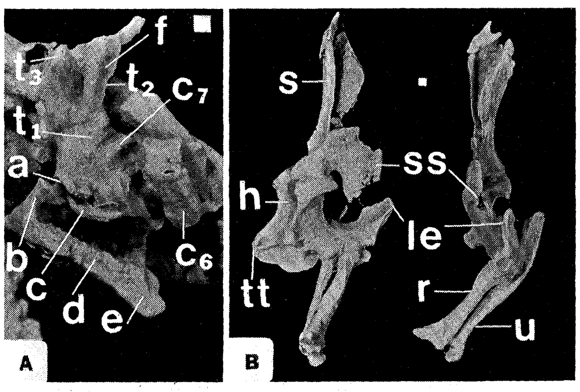

Fig. 1. (A) Posterior cervical vertebrae, anterior thoracic vertebrae, and manubrium of the proscalopid *Mesoscalops*. Abbreviations: *a*, articulation for the first rib; *b*, first rib (fused to manubrium); *c*, transverse process of C_7; *d*, manubrium; *e*, articular surface for proximal end of clavicle; *f*, fossa on neural spine of t_2; C_6 and C_7, cervical vertebrae; and t_1, t_2. and t_3, thoracic vertebrae. The body of t_1 has been crushed over the body of t_2. (B) Anterior (left) and lateral (right) views of the left front leg of *Mesoscalops*. The proximal third of the scapula and much of the scapular spine are missing; they are, however, complete in the right scapula (not shown). Abbreviations: *s*, scapula; *ss*, scapular spine; *tt*, teres tubercle; *le*, lateral epicondyle; *h*, humerus, *r*, radius; and *u*, ulna. White squares represent 1 mm.

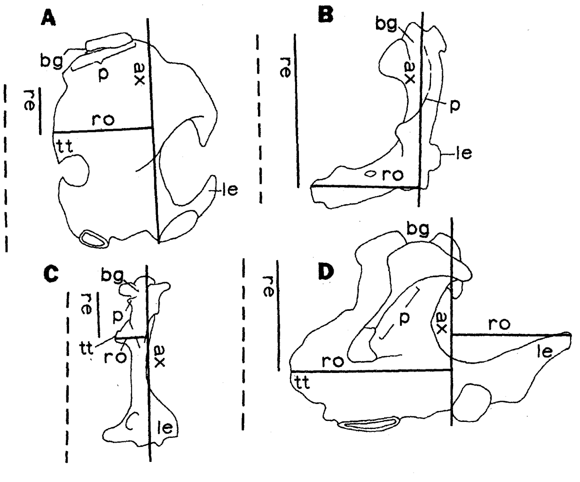

Fig. 2. Diagram of the lever arms for rotation and retraction of the left humerus, anterior view, in (A) *Scapanus*, an advanced talpid; (B) *Chrysochloris*, a chrysochlorid; (C) the generalized talpid *Uropsilus*; and (D) the proscalopid *Mesoscalops*. Abbreviations: *ax*, axis of rotation; *bg*, bicipital groove (closed into a tunnel in advanced talpids); *le*, lateral epicondyle; *p*, pectoral process; *re*, input lever for retraction by teres major; *ro*, major input levers used for rotation; and *tt*, teres tubercle. In order to illustrate relative lengths of input levers the humeri are scaled so that the output levers for retraction, represented by the vertical dotted lines, are equal for each taxon. In chrysochlorids, the major function of the elongate median epicondyle is to increase attachment area for the latissimus dorsi and teres major, which mainly retract the humerus during the power stroke. Rotation occurs in the recovery stroke (*10*).

mal part of the humerus. The digging stroke of proscalopids apparently required more retraction than that of talpids and more rotation than that of chrysochlorids. The broad glenoid fossa on the scapula, which would allow a considerable range of movement, also indicates that this was the case. The glenoid fossae of golden moles and true moles are narrow, confining the humerus mainly to retractional and rotational movements, respectively. The broad hand of proscalopids, although known only from fragmentary material, apparently resembled that of talpids more than that of chrysochlorids (*1, 9*).

The morphologic features of proscalopids indicate that their digging stroke combined an upward thrust of the head with a downward, posterior, and lateral movement of the hand. The stroke differed from that of chrysochlorids in that it allowed greater rotation of the humerus so that dirt could be moved laterally and because the hand could be used as a broad scoop. It differed from the stroke of talpids because the head was apparently thrust upward to displace dirt, and the humeri were retracted to apply counteracting downward forces at each of the hands. Such an arrangement would provide two directions of force so that the animal would be braced in the burrow as dirt was displaced in a third direction (*17*). The lateral orientation of thrust at the hands must have been less than that in talpids because the more laterally that this thrust is directed, the less the forelimbs would be capable of countering the upward movement of the head.

These differences between proscalopids and true moles suggest that the evolutionary history of the two groups is more distinct than has generally been recognized (*1, 3*). The fossorial specializations, rather than indicating affinities between the groups, indicate that proscalopids used a fundamentally different type of digging than true moles. Except for the broad hand, morphology associated with digging in proscalopids is confined to that group (that is, the humerus and vertebrae) or resembles that in chrysochlorids (that is, the skull, scapula, and clavicle). Similarities to chrysochlorids are probably due to evolution converging toward the use of the head in burrowing, because the zalambdodont dentition of golden moles is so different from the dilambdodont molars in proscalopids. Features not correlated with burrowing, such as the W-shaped ectoloph and complete zygomatic arch, may indicate that proscalopids are related to talpids at the superfamily level. The separate tibia and fibula of proscalopids suggest that these insectivores diverged from a form more primitive than any talpid, because in all talpids these bones are fused. It is unlikely that the morphology of the proscalopid humerus was derived from any known talpid because the pectoral process of even the most generalized true mole (*p* in Fig. 2C) has migrated toward the lesser tuberosity (*1*). In more advanced talpids these two structures meet to form the bicipital tunnel (Fig. 2A), a characteristic talpid feature that is absent in proscalopids. Furthermore, the earliest proscalopids (Chadronian) have specializations that are common to the group, and they appear on a different continent than the early talpids, which were confined to Europe and Asia until the middle Miocene (*3*). For these reasons, I concur with those who have suggested that the Proscalopidae represent a distinct family of insectivores (*1, 8*).

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Area-Perimeter Relation for Rain and Cloud Areas

Abstract. *Following Mandelbrot's theory of fractals, the area-perimeter relation is used to investigate the geometry of satellite- and radar-determined cloud and rain areas between 1 and* 1.2×10^6 *square kilometers. The data are well fit by a formula in which the perimeter is given approximately by the square root of the area raised to the power D* ($P \sim \sqrt{A}^D$), *where D is interpreted as the fractal dimension of the perimeter. It is concluded that rain and cloud perimeters are fractals—they have no characteristic horizontal length scale between 1 and 1000 kilometers.*

The diversity of cloud sizes and shapes is well known. No two clouds are alike, and while some can be measured in meters, others are as large as continents. Yet the "cloudlike" appearance of these shapes is seen even in the horizontal projections of clouds familiar to meteorologists in black-and-white satellite photographs. Similarly, rain areas as depicted by radar exhibit characteristic shapes that can help meteorologists to distinguish rainy regions from ground clutter (noise). Until recently, these simple geometric facts about clouds (and the associated rain areas) could not be incorporated directly into any theory, because of the lack of an appropriate geometric framework. However, since the publication of Mandelbrot's work on fractals (*1*), this situation has changed, and there are now simple methods for analyzing and modeling such shapes. In this report, we present the results of one such technique based on the area-perimeter relation, which indicates a remarkable constancy of the horizontal shapes of tropical clouds and rain areas over a range spanning six orders of magnitude in area. These findings lend support to the idea, first enunciated more than 50 years ago (*2*), that the outer limit of atmospheric turbulence may not be "attained within the atmosphere." This would mean that there is no special or preferred horizontal length scale for atmospheric processes, except scales of the order of the size of the earth. Shapes with structure at all scales, with no characteristic length, are known as fractals (*1*). Within the size range studied ($1\ \mathrm{km}^2$ to $1.2 \times 10^6\ \mathrm{km}^2$), cloud and rain areas are therefore fractals.

Mandelbrot (*1*) proposed using area-perimeter relations to investigate the structure of planar shapes. In the present study, the shapes considered are derived from digitized cloud and rain pictures on an approximately rectangular grid. These pictures define the projection of cloud and rain regions on the earth's

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