

Analysis of function in the absence of extant functional homologues: a case study using mesotheriid notoungulates (Mammalia)

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Abstract.—We use two approaches to test hypotheses regarding function in a group of extinct mammals (Family Mesotheriidae, Order Notoungulata) that lack any close extant relatives: a principle-derived paradigm method and empirically derived analog method. Metric and discrete morphological traits of mesotheriid postcranial elements are found to be consistent with the morphology predicted by a modified version of Hildebrand's paradigm for scratch diggers. Ratios of in-force to out-force lever arms based on skeletal elements indicate that the mesotheriids examined had limbs modified for high out-forces (i.e., they were "low geared"), consistent with the digging hypothesis. Other mesotheriid characters, such as cleft ungual phalanges, a curved olecranon, and a highly modified pelvis (with extra vertebrae incorporated into the sacrum and fusion between the ischium and the axial skeleton) are regarded as being functionally significant for digging and also occur in a variety of extant diggers. Analog methods indicate that mesotheriids share numerous traits common to a variety of extant diggers. Principal component analyses of postcranial elements indicate that mesotheriids consistently share morphometric space with larger extant fossorial mammals: armadillo, anteaters, wombats, and badger. Likewise, discriminant function analyses categorized mesotheriids as fossorial, though imperfectly analogous to the extant diggers analyzed. Thus, both theory-driven and empirically derived methods of estimating function in these extinct taxa support a digging hypothesis for the mesotheriids examined. Adaptations for digging in both the forelimb and sacropelvic functional complexes of mesotheriids provide independent support for the fossorial hypothesis.

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Accepted: 27 September 2006

Introduction

Functional reconstruction of life in the past is challenging, especially for extinct taxa that lack extant functional homologues. To be confident in functional interpretations for such taxa, any proposed hypothesis must somehow be tested. In this work, we provide an example that uses principles from functional morphology to predict the morphology for a given behavioral complex and then test that prediction by empirically derived means. In this case, a modified version of the "scratch digging" paradigm (*sensu* Hildebrand 1974, 1985) is used to predict morphological patterns in a mammal that habitually digs (see "Methods"). Comparing morphologies of the putative fossorial fossil taxa and a variety of unrelated extant mammals in order to find close functional analogs tests the hypothesis de-

rived from the paradigm method. Theory-driven and empirically derived hypotheses serve as at least quasi-independent tests for one another (Rudwick 1964). Likewise, functional hypotheses based on metric variables (lengths of elements, and ratios of these lengths) may be compared with those based upon discrete (presence-absence) morphological characters. When both types of data are compatible with the hypothetical function, then confidence in the hypothesis is much greater.

Our example here is from the extinct, endemic, South American notoungulates (Order Notoungulata Roth, 1904) and includes three taxa in the family Mesotheriidae Alston, 1876. Mesotheriids were rabbit- to mostly sheep-sized notoungulates distinguished by their ever-growing, gliriform, chisel-like incisors,