Relationships of Endemic African Mammals and Their Fossil Relatives Based on Morphological and Molecular Evidence

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Analyses of anatomical and DNA sequence data run on a parallel supercomputer that include fossil taxa support the inclusion of tenrecs and golden moles in the Afrotheria, an endemic African clade of placental mammals. According to weighting schemes of morphological and molecular data that maximize congruence, extinct members of the afrotherian crown group include embirithopods, Plesiorycteropus, desmostylians, and the “condylarths” Hyopsodus, Meniscotherium, and possibly Phenacodus. By influencing the optimization of anatomical characters, molecular data have a large influence on the relationships of several extinct taxa. The inclusion of fossils and morphological data increases support for an elephant-sea cow clade within Paenungulata and identifies ancient, northern elements of a clade whose living members in contrast suggest an historically Gondwanan distribution. In addition, maximally congruent topologies support the position of Afrotheria as well-nested, not basal, within Placentalia. This pattern does not accord with the recent hypothesis that the divergence of placental mammals co-occurred with the tectonic separation of Africa and South America.

KEY WORDS: tenrecs; golden moles; Afrotheria; Lipotyphla; Insectivora; Placentalia; phylogeny; fossils.

INTRODUCTION

One of the more drastic rearrangements to the mammalian evolutionary tree in recent years concerns the African mammalian families Tenrecidae (tenrecs) and Chrysochloridae (golden moles). In the nineteenth and early twentieth centuries zoologists commonly regarded these animals as part of a paraphyletic assemblage from which other placental orders were believed to have evolved (Wyss, 1987). For most of the twentieth century, tenrecs and golden moles were considered to be part of the “Lipotyphla,” along with shrews, hedgehogs, moles, and solenodons (Butler, 1988). Recently (e.g., Stanhope et al., 1998; Emerson et al., 1999; Mouchaty et al., 2000; Madsen et al., 2001; Murphy et al., 2001a,b; Arnason et al., 2002; Douady et al., 2002a,b; Malia et al., 2002), a wide array of DNA sequence data has been interpreted to support a close relationship between African insectivorans and elephants, sea

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cows, hyraxes, elephant shrews, and aardvarks, a clade known as the Afrotheria (Stanhope
et al., 1998). Sequence-based studies that sample mostly nuclear DNA (e.g., Murphy et al.,
2001a,b) have argued for the position of Afrotheria near the base of the placental radiation,
whereas those based on mitochondrial proteins (e.g., Mouchaty et al., 2000; Arnason et al.,
2002) favor an Afrotheria nested well within Placentalia. All sequence-based studies support
an Afrotheria with an extant core consisting of elephants, sea cows, and hyraxes, a group
known since 1945 as the Paenungulata (Simpson, 1945). The inclusion of golden moles and
tenrecs in a clade with paenungulates is novel, particularly given the anatomical similarities
of the former two groups with insectivoran mammals from northern continents (Butler,
1988; MacPhee and Novacek, 1993; Asher, 1999).

Articles published to date in support of Afrotheria have been restricted to the use of
sequence data for living taxa, despite the fact that living African mammals, and mammals
generally, are taxonomically depauperate in comparison with their past diversity (McKenna
and Bell, 1997). In addition, most recent molecular analyses of Afrotheria have not explored
issues regarding molecular sequence homology (Lee, 2001; Asher, 2003; but see Douady
et al., 2003) and have been limited to a relatively narrow range of assumptions regarding
the relative influence of certain molecular character transformations (Wheeler, 1995). The
availability of large collections of skeletal data, online repositories of sequence data, and
access to a parallel supercomputing cluster (Giribet et al., 2001; Janies and Wheeler, 2001),
enables us in this paper to examine in detail the question of African mammal phylogeny.
Specifically, we ask whether or not tenrecs and golden moles are more closely related to
other African taxa than to groups such as hedgehogs, shrews, and moles by using both mor-
phological and molecular data, by sampling extinct taxa, and by implementing optimization
alignment (Wheeler, 1996) and sensitivity analysis (Wheeler, 1995) on a predefined series
of molecular and morphological character transformation weights. To distinguish among
competing topologies, we use parsimony and congruence among data partitions as measured
by the Incongruence Length Difference (ILD) index (Wheeler, 1995) and a new, topological
index (Fig. 1) as optimality criteria.

**MATERIALS AND METHODS**

**Taxon and Character Sampling**

We constructed a matrix representing morphological and, where possible, genetic di-
versity of 60 taxa (2 extant marsupials, 47 extant, and 11 extinct eutherians). The data
comprise 433 morphological character states distributed across 196 characters and approx-
imately 17 kilobases distributed across 22 genes (Table I). Extant taxa were selected based
on the degree to which each was represented by the 22 genes used in Murphy et al. (2001b),
most of which were in turn first published by Madsen et al. (2001) and Murphy et al.
(2001a). At the low end of the genetic sample (besides fossils) are *Tenrec* and *Tarsius*,
represented by 6 and 14 (respectively) out of 22 genes (Table I). *Nycteris* follows with 16,
and the remaining 46 extant taxa are sampled for 17 genes or more. Terminal taxa are rep-
resented at the level of the genus; in several cases we used multiple species to code a given
genus (Table II). The extinct taxa examined in this study are *Arsinoitherium*, *Anagale*,
*Hyopsodus*, *Leptictis*, *Meniscotherium*, *Moeritherium*, *Palaeoparadoxia*, *Phenacodus*,
*Plesiorycteropus*, *Ukhaatherium*, and *Zalambdalestes* (see Table II for specimens examined
and references). All but the last two were included based on previous hypotheses of their