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Morphological trends in the molars of fossil rodents from the Fayum Depression, Egypt

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While many of the mammalian taxa from the Fayum of Egypt, such as the primates and hyraxes, have been well-studied, little is known about the rodents. Species described to date have all been referred to the endemic family Phiomyidae. Many rodent species from this family have been named and their importance to biogeography addressed, but what this fauna can reveal about the palaeoenvironment of the Fayum has yet to be determined. The study of palaeoenvironmental trends begins with a general examination of species diversity and morphology of the specific rodent lineages. A statistical analysis of available molar measurements of Fayum rodents estimates general size and shape trends and changes in rodent diversity through the stratigraphic sequence of the Fayum. This analysis finds stability in species diversity and an increase in the average body size of taxa using molar length as an estimate of body size. The body size pattern of the rodents is similar to the pattern found among the Fayum primates. Analysis of molar length and width has been performed to test whether these variables could discriminate accurately between taxa. If molars that are too worn to be identified by cusp pattern can be identified confidently based on length and width, more specimens could be included in future analyses and a more accurate depiction of the small mammal fauna attained. Length is significantly different between most of the species, and several species can be identified by length and width alone. Length and width relationships were consistent for species within the same genus.

Keywords: evolutionary trends, Fayum, palaeoenvironment, molar morphology.

INTRODUCTION

The Fayum Depression of Egypt has long been known for its wealth of primate fossils and its importance in the study of biogeography during the late Eocene and early Oligocene. Among the qualities that separate the Fayum from other localities of this period are the great diversity of species, excellent fossil preservation, and large number of fossils that many of its quarries produce. One of the most common mammalian groups recovered in the deposits of the Fayum are the rodents. These mammals gain importance for they can be used as palaeoenvironmental indicators. The rodents of the Fayum, however, have yet to be studied for what they may reveal about environmental changes throughout the Fayum stratigraphic sequence. Such an analysis first requires an assessment of general changes in species diversity and variation to determine if appreciable differences exist between rodent faunas from successive stratigraphic layers. This preliminary study of the Fayum rodents, therefore, seeks to determine if variation in the rodent fauna is sufficient to warrant a further investigation.

The excellent preservation of fossils found in the Fayum has produced a highly varied rodent fauna having substantial sample sizes for many species. The rodent fauna is composed of seven genera and 13 species (Table 1) ranging from the latest Eocene to early Oligocene in age (Holroyd 1994). These taxa are diagnosed principally based on molar cusp patterns, but many species also have distinctive overall molar morphologies. If these morphological features differ sufficiently, those fossil specimens currently too worn to be identified confidently by cusp patterns may be identified by measuring their overall size and shape. The use of overall molar morphology may allow us to estimate the species identification of more fossil specimens and ultimately provide a better understanding of the relative abundance of the various species. As any environmental data that can be gathered from the rodent fauna will depend not only on the presence or absence of various taxa but on their relative abundance, the identification of as many molars (i.e. different individuals) as possible is desirable.

The following research tests the degree of variation present in the molars of Fayum rodents through time and across taxonomic classification, and assesses the degree that size and shape of molars are appropriate for classifying species. Trends in size and shape are analysed for consistency within species and genera, and through lineages, using length and width of the lower first (M_1) and second (M_2) molars to test for differences between various taxa. Lastly, the relative diversity of taxa and morphological trends through the stratigraphic sequence are discussed.

MATERIALS AND METHODS

The Fayum Depression lies in Egypt on the eastern edge of the Sahara Desert. The site has been collected for fossils since the latter part of the 19th century, and has produced a large variety of late Eocene and Oligocene fossils of land mammals (Simons & Rasmussen 1995, and references cited there). These fossils are found in the Birket Qarun, Qasr el Sagha, and Jebel Qatrani formations. The Widen el Faras Basalt caps the Jebel Qatrani formation, and has been dated to *c.* 25–27 million years, although some debate occurs over these dates (Kappelman *et al.* 1992; Prothero & Berggren 1992; Seiffert *et al.* 2005; Seiffert 2006). Specimens studied here have been recovered at various stratigraphic levels within the Jebel Qatrani Formation. The geologically younger quarries (M, I, G, V,

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Table 1. Mean length and width data with standard deviations f**or each rod**ent species

Species	M1					M2					
	n	L	S.D.	W	S.D.	*n*	L	S.D.	W	S.D.	Location
Phiomys andrewsi	11	1.44	0.09	1.22	0.06	8	1.22	0.06	1.41	0.09	B, E
Phiomys stellae	2	1.40	–	1.20	–	2	1.30	0.14	1.25	0.07	I
Phiomys troctatus	11	1.63	0.10	1.51	0.07	8	1.69	0.08	1.51	0.08	I, M
Acritophiomys adaios	27	1.83	0.90	1.53	0.10	26	1.91	0.11	1.69	0.12	A, B, E
Acritophiomys bowni	4	2.05	0.06	1.73	0.06	5	2.10	0.12	1.96	0.09	L-41
Acritophiomys woodi	22	1.66	0.08	1.47	0.07	19	1.77	0.09	1.66	0.06	L-41
Metaphiomys beadnelli	27	2.61	0.13	2.09	0.08	27	2.87	0.15	2.55	0.09	V, I, M, P
*Metaphiomys schaubi**	7	2.44	0.09	2.17	0.08	4	2.48	0.10	2.40	0.17	G, V, L-12
Gharbalamys simonsi	11	3.36	0.11	3.19	0.19	15	3.55	0.25	3.39	0.29	I, M
Gaudeamus aegypticus	16	1.71	0.11	1.63	0.12	18	1.81	0.21	1.81	0.18	E
Gaudeamus hylaeus	8	2.00	0.09	1.94	0.11	11	2.06	0.16	2.07	0.09	L-41
Elwynomys lavocati	14	1.06	0.05	0.99	0.06	14	1.04	0.05	1.01	0.06	L-41, E

Data from Holroyd (1994), * = not recognized in Holroyd (1994). *Phiocricetomys minutus* and *Phiomys paraphiomyoides* (found at quarries G,V, I, and M) are not listed due to lack of sufficient material for this analysis.

and P) are thought to date to approximately 30–31 mya (Seiffert 2006). The older quarries (L-41, A, B, and E) are dated to the early Oligocene, approximately 33–34 mya (Seiffert 2006). In general, the palaeoenvironment during the time of sediment deposition was a heavily forested tropical landscape with meandering streams (Bown & Kraus 1988).

All the Fayum rodents in this study belong in the superfamily Thryonomyoidea and the infraorder Phiomorpha. The Thryonomyoidea have hysticognathous mandibles and hystricomorphous attachments for the masseteric muscle (Nowak 1991). The Phiomorphs differ from the caviomorphs mainly in biogeographic ranges and the two are likely sister taxa (Lavocat 1973). Whereas some disagreement exists over the taxonomy of the Fayum rodents (see Wood 1968; Holryod 1994), the diagnoses of Holryod (1994) are followed here.

Several ancestor/descendent relationships are probable within the Fayum rodents (Wood 1968; Holroyd 1994). *Phiomys andrewsi* is suggested as the probable ancestor for later taxa including *Gaudeamus* spp., *Metaphiomys* spp., and *Phiomys lavocati* (Wood 1968). *Phiomys andrewsi* itself ranges from the late Eocene through the early Oligocene. *Metaphiomys schaubi,* a proposed descendant of *P. andrewsi,* also is suggested to be the ancestor of *M. beadnelli* (Wood 1968). Holroyd (1994), however, considers the two *Metaphiomys* species to be synonymous.

Of the 13 known species, two are not represented in this analysis due to the absence of either the M_1 or M_2 in any available specimen (*Phiomys paraphiomyoides* and *Phiocricetomys minutus*). *Metaphiomys beadnelli* (*sensu* Holryod) specimens are subdivided into *M. beadnelli* and *M. schaubi* following Wood (1968). All measurements in this analysis are from Holroyd (1994), and consist of the length and width of the M_1 and M_2. While measurements are available for other molars, these molars were selected as they demonstrated the largest sample sizes.

Descriptive statistics, regression, discriminant analysis, and several ratios are used to examine how molar length and shape (defined as the relationship between the length and width variables) vary between taxa. All measurements are transformed to natural logarithms before analysis to linearize allometric relationships and to make variation relative to tooth size rather than absolute. Multiple analysis of variance (MANOVA) tests for significant length differences between the molars of different species. A correlation matrix indicates that molar length and width are highly correlated (all measurements >0.95), making analysis of covariance (ANCOVA) inappropriate. Analysis of variance (ANOVA), therefore, is used to test for differences between molar length-to-width ratios between species and pairwise *post hoc* Bonferroni/Dunn tests are performed on length-to-width ratios to determine what species are responsible for any significant results from the ANOVAs. An α of 0.05 is used for all statistical procedures except for the multiple pairwise tests, where the α is adjusted in accordance with the Bonferroni correction (Sokal & Rohlf 1995). Lastly, discriminant analysis (DA) is used to explore the suitability of the M_1 and M_2 measurements to distinguish between the different species when both molars are present. Statistical tests are run on Minitab 5.2 software.

RESULTS

No overlap occurs in length and little overlap in width in the M_1 or M_2 of *Gharbalamys simonsi* and *Elwynomys lavocati* with any of the other species analysed (Table 1; Fig. 1A,B). Length against width plots for both molars reveal distinct clusters for several species, although substantial overlap occurs for many (Fig. 1A,B). Length and width plots for *Metaphiomys beadnelli* and *Phiomys andrewsi* also represent distinct groups for both molars. Simple regression lines for the M_1 length and width grouped by species are positively sloped, with the exception of *M. beadnelli* where molar width actually decreases with length (Fig. 2). Regression lines for the M_2 are all positive, although the line for *M. beadnelli* is very shallow, and molar width increases only slightly with increased length (Fig. 3). All species exhibit M_1 molars that are either equally long relative to width or longer than they are wide. Length ratios (Table 2) show that the molars of all species have longer M_1 than M_2 molars except *Elwynomys lavocati* and *Phiomys stellae,* both of which have slightly longer M_2 molars. MANOVA for M_1 and M_2 lengths and widths

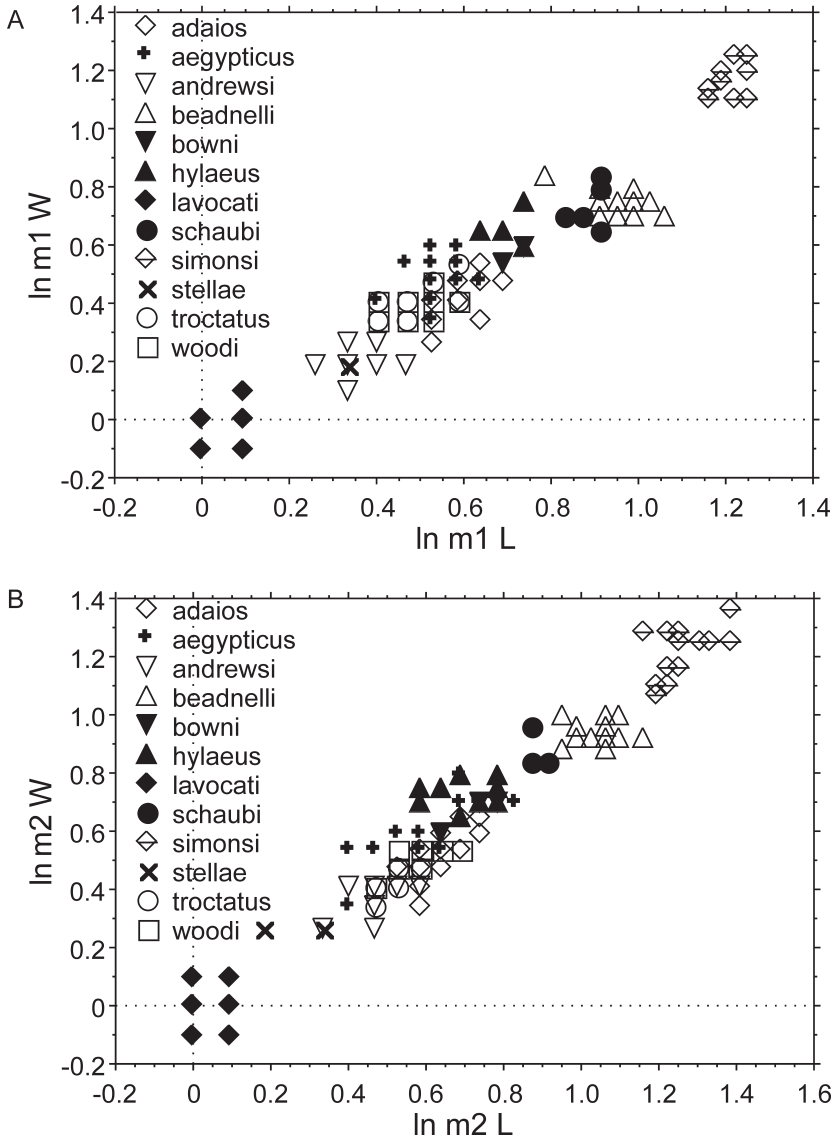


Figure 1. Plots of natural log length and width for (**A**) M_1 and (**B**) M_2 (data from Holroyd 1994).

returns significant results (d.f. = 94, $P < 0.001$).

Length-to-width ratios of M_1 molars fall roughly into two groups, with several species ranging from 1.05–1.08 and the remainder ranging from 1.16–1.25 (Table 2). These groups, however, vary within the genera morphologically such that species of the same genera exhibited differently shaped molars. Length-to-width ratios for the M_2 molars are less variable than M_1 ratios, with ratio values ranging from 0.99 to 1.13. ANOVA results for M_1 length-to-width ratios are significant ($P < 0.001$), with *post hoc* Bonferroni/Dunn tests finding 21 of 66 pairwise tests significant (Table 3). An ANOVA for the M_2 length-to-width ratios is also significant ($P < 0.001$), but Bonferroni/Dunn tests find only 10 of 66 pairwise tests significant (Table 3).

Discriminant analysis correctly identifies species with an overall 86% accuracy rate using length and width of the M_1 and M_2. *Acritophiomys bowni, Elwynomys lavocati, Gharbalamys simonsi, Metaphiomys schaubi, Phiomys stellae,* and *P. andrewsi* are each discriminated without error (100%). *Metaphiomys beadnelli* (94%), *Gaudeamus hylaeus* (85%), *A. woodi* (82%), and *P. troctatus* (75%) also are identified effectively, whereas *G. aegypticus* (63%) and *A. adaios*

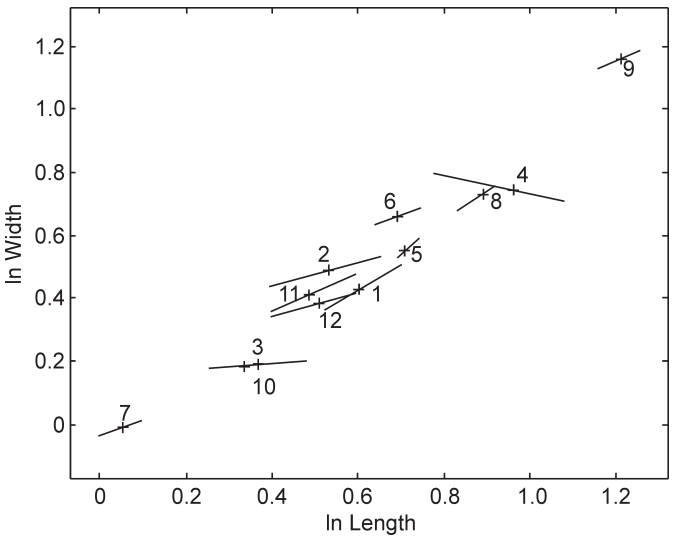


Figure 2. Regression lines and centroids for the M_1 molars of the 12 Fayum rodent species analysed (data from Holroyd 1994). 1 = *Acritophiomys adaios*, 2 = *Gaudeamus aegypticus*, 3 = *Phiomys andrewsi*, 4 = *Metaphiomys beadnelli*, 5 = *A. bowni*, 6 = *Gaudeamus hylaeus*, 7 = *Elwynomys lavocati*, 8 = *M. schaubi*, 9 = *Gharbalamys simonsi*, 10 = *P. stellae*, 11 = *P. troctatus*, 12 = *A. woodi*.

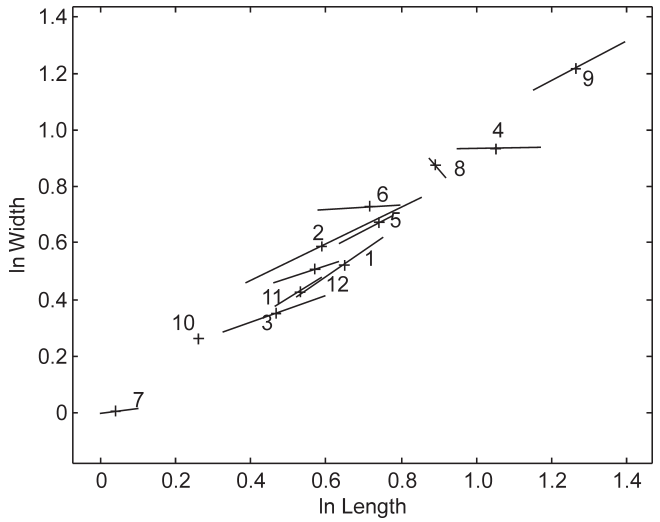


Figure 3. Regression lines and centroids for the M_2 molars of the 12 Fayum rodent species analysed (data from Holroyd 1994). 1 = *Acritophiomys adaios*, 2 = *Gaudeamus aegypticus*, 3 = *Phiomys andrewsi*, 4 = *Metaphiomys beadnelli*, 5 = *A. bowni*, 6 = *Gaudeamus hylaeus*, 7 = *Elwynomys lavocati*, 8 = *M. schaubi*, 9 = *Gharbalamys simonsi*, 10 = *P. stellae*, 11 = *P. troctatus*, 12 = *A. woodi*.

(60%) are discriminated least accurately. While those specimens of *G. aegypticus* that are not identified correctly are assigned to a variety of taxa, those of *A. adaios* incorrectly identified are all assigned to other species of the same genus (*Acritophiomys*).

DISCUSSION

Species identification

Statistical results indicate significant differences in molar size (as defined by length) and shape (as defined by the relationship of length to width) for many of the species studied. Several species, particularly *Elwynomys lacovati* and *Gharbalamys simonsi,* clearly are discernible from the other rodent species on size alone, having no overlap in M_1 or M_2 length (Fig. 1). In general, molars associated with the largest and smallest taxa are discriminated most reliably, whereas those of more intermediate sized taxa overlap and are recognized less easily. Results of the MANOVA and DA, however, suggest that many of the Fayum rodents can be diagnosed reliably based on simple length and width measurements, particularly when both M_1 and M_2 are present. That many of the pairwise tests of length-to-width ratios for both molars were significant likewise suggests that molar shape is sufficient to diagnose several of the species tested. This consistency of particular sizes and shapes of molars within many of the taxa shows that molars showing high rates of occlusal wear may be identified at the species level based on general molar morphology. The ability to identify more specimens using size and shape will allow a more detailed description of the rodent fauna and ultimately a better understanding of the palaeoenvironment. Our preliminary results using only length and width variables suggest that the use of more variables to more finely define molar shape may allow a more confident assessment of species and better separation of those taxa that were not identifiable reliably in this analysis.

Table 2. Mean length and width ratios for each rodent species.

Species	M_1L/M_2L	M_1L/M_1W	M_2L/M_2W
Phiomys andrewsi	0.90	1.20	1.12
Phiomys stellae	1.08	1.17	1.00
Phiomys troctatus	0.94	1.08	1.11
Acritophiomys adaios	0.96	1.19	1.13
Acritophiomys bowni	0.94	1.17	1.07
Acritophiomys woodi	0.94	1.13	1.06
Metaphiomys beadnelli	0.93	1.25	1.13
*Metaphiomys schaubi**	0.99	1.18	1.02
Gharbalamys simonsi	0.94	1.06	1.05
Gaudeamus aegypticus	0.99	1.05	1.00
Gaudeamus hylaeus	0.98	1.05	0.99
Elwynomys lavocati	1.02	1.07	1.04

Raw data from Holroyd (1994), * = not recognized in Holroyd (1994).

Variability

Size and shape variability within the rodent taxa of the Fayum is low. Length and width standard deviations are all less than one, with all species but *Gaudeamus hylaeus* with less than 0.3 (Table 1). Such limited variation is surprising in fossil species, as values under two standard deviations are suggested to be consistent with variation found in modern subspecies (Lande 1986). The low standard deviations, however, could be an artifact of

Table 3. Results of Fisher's *post hoc* pairwise tests for M_1 and M_2 length-to-width ratios.

	P. andrewsi	*P. stellae*	*P. troctatus*	*A. adaios*	*A. bowni*	*A. woodi*	*M. beadnelli*	*M. schaubi**	*G. simonsi*	*G. aegypticus*	*G. hylaeus*	*E. lavocati*
P. andrewsi		n	n	n	n	n	n	n	n	**s**	s	n
P. stellae	n		n	n	n	n	n	n	n	n	n	n
P. troctatus	s	n		n	n	n	n	n	n	s	s	n
A. adaios	n	n	s		n	n	n	n	s	s	s	s
A. bowni	n	n	n	n		n	n	n	n	n	n	n
A. woodi	n	n	n	s	n		n	n	n	n	n	n
M. beadnelli	n	n	s	n	n	s		n	n	s	s	n
*M. schaubi**	n	n	n	n	n	n	n		n	n	n	n
G. simonsi	s	n	n	s	n	n	s	n		n	n	n
G. aegypticus	s	n	n	s	n	s	s	s	n		n	n
G. hylaeus	s	n	n	s	n	s	s	s	n	n		n
E. lavocati	s	n	n	s	n	n	s	n	n	n	n	

Significant results are indicated by 's', and insignificant results by 'n'. Shaded rows are for tests on the ratios of the M_2, and unshaded rows are for tests on the ratios of the M_1. *See Table 2 for explanation.

discriminating molar measurements to the nearest 0.1 mm on such small specimens. That some true species may currently be categorized incorrectly into multiple species is also a possibility, although other morphological analyses suggest that this is unlikely (Holroyd 1994). Nevertheless, even if the actual variation were twice that indicated, the taxa studied here would be surprisingly homogeneous in terms of interspecific molar morphology. Low variability in these fossil rodent species may indicate that the samples represent short temporal durations.

Using molar length as proxy for size suggests that the rodent fauna was increasing in overall body size through time. The earlier species (those lowest in the stratigraphic sequence), represented by specimens from quarries L-41, A, B, and E, have an average combined length of the M_1 and M_2 of 3.35 mm. Those species from the more recent dating quarries of I, M, G, V, and P average 5.22 mm (36% larger). This difference, however, may be the result of differential preservation, as quarry L-41 often has superior preservation to any of the stratigraphically higher quarries. While small taxa are found in the younger quarries, only a few specimens represent the smallest species (such as *Phiocricetomys minutus* and specimens placed in the genus *Phiomys*). Given the relative rarity of small fossils in these more recent quarries, a preservation bias favoring larger taxa is likely. Increased size through time, however, is a common trait in many mammalian lineages (MacFadden 1986; Cope 1896) and also is found in the primate fauna from the Fayum.

Examining size change within particular lineages also supports a trend for increased size. *Phiomys andrewsi* is suggested as the ancestor of *M. schaubi,* with *M. schaubi* ancestral to *M. beadnellii* (Wood 1968). The *P. andrewsi*/*M. schaubi*/*M. beadnelli* lineage shows increasing size for both the M_1 and the M_2 through time (Table 1; Fig. 4). While the lack of absolute dates precludes a quantitative estimate of evolutionary rates, a qualitative examination, nevertheless, is possible. The rate of change appears rapid in the earlier stages of the lineage (Fig. 4). An apparently rapid rate of size increase occurs between *P. andrewsi* from localities B and E and its presumed descendent *M. beadnelli* (*sensu* Holroyd) from the quarries G and V (37% increase in combined M_1 and M_2 length). While the amount of sediment deposition between quarries G and V is similar to the amount of sediment deposition between quarries M and I, there is a much more modest increase in size between the *M. beadnelli* specimens from those quarries (11% increase in size). Quarries I and M are very nearly the same age, based on their close stratigraphic locations and similar faunas (Bown & Kraus 1988), and very little difference in size exists in the *M. beadnelli* specimens from them. A substantial thickness of sediment exists between quarries G and V and quarry I, however, and there could also have been a period of nondeposition suggesting that the slowing rate of change in the *P. andrewsi*/*M. schaubi*/*M. beadnelli* lineage is real. This overall pattern indicates that either a much greater amount of time separates quarries B and E from quarries G and V than separates quarries G and V from quarries M and I, or that the rate of size increase slows through time.

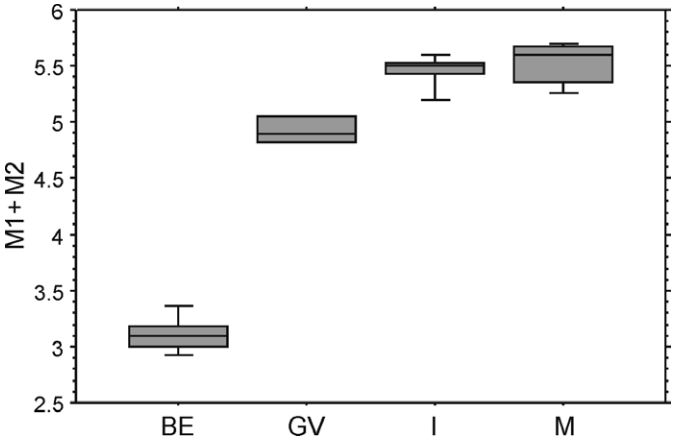


Figure 4. Cumulative lengths of M_1 and M_2 of *Phiomys andrewsi* from localities B and E, and *Metaphiomys beadnelli* (*sensu* Holroyd) from the sequentially dated quarries G, V, I, and M (data from Holroyd 1994).

The three species of *Acritophiomys* also are found at multiple quarries, with *A. woodi* and *A. bowni* found at quarry L-41 and *A. adaios* from the more recent quarries of A, B, and E. If *A. bowni* is viewed as the ancestor to *A. adaios,* a decrease in size is indicated. If *A. woodi* is viewed as the ancestor to *A. adaios,* an increase in size is indicated (Table 1). As the true relationships between these taxa are unclear, no trend in body size can be suggested. However, specimens of *A. adaios* from the lower quarries of A and B can be compared to *A. adaios* specimens from the stratigraphically higher quarry E. Unfortunately, 22 of the 27 *A. adaios* M_1 specimens are from quarry E, limiting the utility in examining changes in the lineage. A combined sample of quarry A and B specimens compared to specimens from quarry E finds no notable differences between the two groups in molar length, although the small sample size from quarries A and B likely affects this outcome.

Species diversity

Relative stability appears to exist in species diversity at the Fayum through time. The earlier quarries of L-41, A, B, and E contain four genera and seven different species. The more recent quarries of M, I, G, V, and P contain four genera and six species. While a preservation bias may exist that favors the older quarries, small and delicate species (such as the primate *Afrotarsius chatrathii* and the rodent *Phiocricetomys minutus*) have been recovered from these latter stratigraphically higher quarries. Sampling at these more recent quarries, however, has been carried out for roughly twice as long as on the older quarries. Also, it is likely that new species of rodents have been discovered at quarry L-41 since the last study of the rodent fauna in the early 1990s. But, given available data, the apparent stability in species diversity may indicate little change in the environment inhabited by these taxa. Normally, the introduction of new predators, removal or addition of new competitors, or dramatic changes in resources may be expected to have caused an increase or decrease in species diversity. As many of the earlier rodent taxa are arboreal (Holroyd 1994), they likely inhabited similar niches as did the primates from these quarries. Since the primates from more recent quarries are, on the whole, larger than those

from older quarries, it might be anticipated that niche space would have been opened for rodents to occupy. It does not appear that new rodent species migrated in from Asia to fill postulated emptied niches, nor does it appear that a radiation of endemic rodents took place.

The apparent diversity of the rodent fauna may be influenced by taxonomic approaches, as many of the younger species were described long before and by different researchers than the new taxa from the stratigraphically lower quarries, particularly taxa from the single most productive of these quarries, L-41. Little disagreement exists, however, between the various researchers regarding taxonomy. An exception is Wood's (1968) belief that *Metaphiomys schaubi* from quarries G and V is a species separate from *M. beadnelli,* while Holroyd (1994) places both of them in *M. beadnelli.* Molar size and shape data, presented in this study, indicate substantial morphological differences between *M. schaubi* and *M. beadnelli* and support distinct species in accordance with Wood (1968). While the nature of the differences separating the taxa is primarily size (generally a poor character for separating taxa), the relationship between molar length and width variables also is different (Figs 2 & 3).

SUMMARY

This analysis revealed significant size and shape differences between molars of many of the Fayum rodent species. Statistical analyses indicated that the differences in overall M_1 and M_2 morphology allow accurate recognition of many of the different species, particularly when both molars are present. These differences in molar morphology should allow many mandibles with worn molars to be accurately identified, thereby allowing a more complete picture of the small mammal fauna. Overall increases in molar length through time for the rodent fauna suggests a trend toward increased body size, although little change in the overall diversity of species occurred. While little variation within taxa existed and homogeneity within genera was found, size and shape differences within the *Metaphiomys* genus supports the presence of two species.

This preliminary study was focused on molar dimensions, species diversity, and molar morphological trends of the rodent fauna of the Fayum examined throughout the stratigraphic sequence. These rodents were found to be a dynamic group, exhibiting distinct temporal trends in size and diversity. The results suggest that a more detailed study of the Fayum rodents, defining molar morphology and expanding the analysis to include incisors, may provide useful data in the future. More specimens should be diagnosable and thereby provide as accurate an estimate of relative species abundance as possible. As the relative abundance of rodent taxa associated with particular strata is better defined, biostratigraphic correlations will be possible. A comparison of the Fayum rodents with modern, closely related rodents may also help better understand the Fayum flora. Comparisons of the diet of modern rodents of similar size, having similar molar morphology, and exhibiting similar dental microwear patterns as the Fayum rodents, could provide proxy data for inferring plant types present in the Fayum. Such an analysis holds the potential to reveal changes in the environment and could tell us more about the evolutionary forces acting in the late Eocene and early Oligocene of north Africa. Such a study is relevant not only to the rodents but also to the many other taxa, including anthropoid primates, that are preserved in the deposits of the Fayum.

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