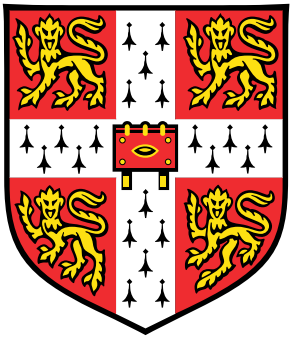
What's in a Tooth? Signals of Ecogeography and Phylogeny in the Dentition of Macaques (Cercopithecidae: *Macaca*)



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Two roads diverged in a yellow wood,
And sorry I could not travel both
And be one traveler, long I stood
And looked down one as far as I could
To where it bent in the undergrowth;

Then took the other, as just as fair,
And having perhaps the better claim,
Because it was grassy and wanted wear;
Though as for that the passing there
Had worn them really about the same,

And both that morning equally lay
In leaves no step had trodden black.
Oh, I kept the first for another day!
Yet knowing how way leads on to way,
I doubted if I should ever come back.

I shall be telling this with a sigh
Somewhere ages and ages hence:
Two roads diverged in a wood, and I-
I took the one less traveled by,
And that has made all the difference.

– Robert Frost, The Road Not Taken

Declaration

I hereby declare that except where specific reference is made to the work of others, the contents of this dissertation are original and have not been submitted in whole or in part for consideration for any other degree or qualification in this, or any other University. This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration, except where specifically indicated in the text. This dissertation contains less than 80,000 words excluding appendices, bibliography, footnotes, tables and equations and has less than 150 figures.

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Abstract

Introduction The aim of the present work was to investigate the impact of the varying environmental conditions on the taxonomic and phenotypic diversification of a geographically widespread and ecologically successful Old World primate genus, the macaques (Cercopithecidae: *Macaca*). To this end, the relationship between geography, ecology, phylogeny, and phenotypic variation among macaques was investigated. Constraints to phenotypic variation – and thus evolution – were also analysed in the form of observed amounts of phenotypic variation and patterns of phenotypic integration.

Materials and Methods A total of 72 standard linear measurements of teeth and associated cranial and mandibular structures were taken for a total sample of 744 specimens from 13 species of macaques. Climate and ecological data were collated from the literature. Univariate and multivariate statistics were employed for the analysis. Patterns of variation, covariation, and allometry were analysed in the dentition, both within and between species. The ecogeographical analysis was carried out by means of two-block partial least squares and a type of multivariate regression, both in a phylogenetic framework. Phylogenetic signal was tested for by means of Blomberg's *K*.

Main Results Macaque teeth differ in their variability. All teeth covary with each other, although correlations are strongest within tooth classes. Size was a strong contributing factor to dental integration, as evinced by lower correlations between teeth once allometric effects were removed. Integration patterns also showed modularity between the anterior and the posterior dentition. Between-species variation in overall craniodental size was associated with temperature, latitude, and body size. Species also varied, albeit to a lesser degree, along an antero-posterior contrast in relative tooth size. Larger anterior were found to be associated with frugivory and tropical ecology, whereas a larger posterior dentition was linked to a more folivorous diet and temperate environments. The latter pattern was largely a function of phylogenetic relatedness. Phylogenetic signal was generally strong in the dentition, although it was substantially greater in the anterior teeth (incisors and canines) than in the posterior teeth (premolars and molars).

Conclusion Macaques show adaptive differentiation in body size in response to temperature along a latitudinal cline, corroborating the presence of the Bergmann effect in macaques. There was no conclusive support for further adaptive differentiation, despite an association between relative tooth size and diet. Allometry appears to channel evolutionary divergence of macaques along a line of least evolutionary resistance, and developmental modularity allows for partly uncoupled evolution of the anterior and posterior dentition. Future research should be aimed at broadening the taxonomic scope to include craniodental variation of the African papionins and cercopithecins in order to put the observed macaque patterns in a broader evolutionary context.

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Chapter 1

Introduction

The central aim of evolutionary biology is to reconstruct and explain the tree of life. Once a tree or phylogeny is constructed, for any group of organisms, effort is directed at understanding the role of natural selection and non-adaptive processes in driving the evolution of phenotypic variants, the effect of the biotic and abiotic environment in mediating these causal mechanisms, and the influence of genotypic and ontogenetic constraints on the potential for evolutionary change. This thesis explores the process of evolution by investigating patterns of phenotypic and environmental variation in a primate radiation in a novel, multifaceted manner. Using the dentition as an integrated phenotype under selection, this work is primarily aimed at investigating the relationship between the ecogeographical environment and the production of between-species phenotypic variation in macaques (Cercopithecidae: *Macaca*). Macaques, despite being a well-known and successful primate group, have been comparatively under-studied for their phenotypic diversification in relation to their taxonomic diversity and the numerous environments and habitats they occupy. I aim to address this gap in our understanding of macaque evolution by investigating evolutionary patterns in the macaque dental phenotype. As part of this endeavor, I explore the influence of internal constraints to the phenotype, environmental conditions, and phylogeny, to consider several distinct but interacting factors that all contribute to the produced variation, in order to ultimately infer the role of adaptive and nonadaptive processes in phenotypic evolution across a widespread primate genus.

Derived in a comparative framework and based on a canalised phenotype, observed phenotype-environment patterns are expected to be mainly of evolutionary origin and can therefore be used to explore the role of natural selection, neutral processes such as genetic drift, and historical contingency. I will also explore relevant intrinsic (developmental) factors that constrain explanations of obtained ecomorphological and macroecological relationships. Adaptive radiations are particularly interesting for the study of adaptive evolution because

they represent groups of closely related taxa that have speciated and differentiated phenotypically as a result of the exploitation of different ecological niches. Macaques (genus *Macaca*) are an ecologically diverse Old World monkey radiation that present an ideal opportunity to analyse macroecological relationships within the framework of evolutionary ecology and geography right at the species level, and allow us to hone in on the evolutionary mechanisms at work by studying within-species patterns.

This chapter will proceed to present a relevant theoretical background to this study (Section 1.1), focusing on those aspects of evolutionary theory that form the basis for the questions and hypotheses of the present work. Furthermore, in Section 1.2 the theoretical and analytical framework and research questions are made explicit.

1.1 Background

Charles Darwin devoted his life to explaining the variation in flora and fauna that he observed. He wished to understand how and why the variation among life forms had arisen and how variation within them eventually gave rise to the large-scale pattern that is Earth's biodiversity. He discovered that populations and species have the ability to change their phenotype over time by adapting to their environment. He was keenly aware that the phenotypic variation between individuals meant that some will do better in the struggle for survival and yield more offspring. Darwin also realised that only when this variation is heritable it is passed on to successive generations. He described this mechanism of adaptive change through time as evolution by natural selection (Darwin, 1859). Modifications across generations may eventually give rise to lineage-splitting and speciation. This branching process also leads to closely related life forms to be more similar to each other than distantly related life forms, and subsequent evolutionary change takes place by adding further modifications to the ancestral phenotype. Darwin thus identified the key role of adaptation through the process of natural selection and phylogeny through the process of ancestral inheritance in evolution.

1.1.1 Evolution: Process and Pattern

The classic definition of evolution is "descent with modification", given by Darwin (1859). It refers both to the process of change and the pattern of variation that it produces on a larger scale (Gingerich, 2001). An important reason why patterns are widely investigated in evolutionary biology is to study the outcomes of evolution and to infer underlying processes (e.g., Eldredge, 1971; Endler, 1986; Harvey and Pagel, 1991; Losos, 2009; Simpson, 1953). Evolution is difficult to observe in real time due to long species generation times, the small

scale at which variation is produced during the observer's lifetime, or the lack of control over the mechanisms and conditions of the evolutionary process in natural populations. Phenotypic patterns that are visible across taxa are often interpreted to reflect adaptation and are thus argued to demonstrate the role of natural selection (Schluter, 2000). The functional significance of a phenotypic trait is consequently treated to be the reason why it evolved in the first place (Gould and Lewontin, 1979; Pianka, 1978). Extinct taxa lived and died at a time and place that is inaccessible to us. In order to reconstruct and explain the evolutionary histories of specific fossil groups we turn to the fossil record to provide us with a glimpse – albeit an imperfect one – into the past by laying out the patterns of variation in time and space. However, in order to correctly attribute process to pattern we need to understand the relationship between the two.

Evolutionary processes can be understood as the mechanisms of evolutionary change, and evolutionary patterns as the outcomes of these processes (Foley, 1999). However, the scale at which they are observed and studied differs. Patterns may refer to the large-scale branching pattern as a result of speciation, extinction, and phylogenetic relationships, or to the origin and change of phenotypic forms; often one reflects the other. A pattern is thus commonly used to describe a biological phenomenon above species level (although theoretically one can define patterns as low as on a molecular level). The process of evolution, on the other hand, is accepted to be a population-level process (though not exclusively, according to some scholars; Futuyma, 2013; Jablonski, 2008. Darwin stressed genetic inheritance as the mechanism for the transmission of variation but in his time little was known about how this worked on a molecular level. In the early 20th century, R.A. Fisher made a series of monumental contributions towards our understanding of the genetic mechanism behind the process of natural selection, by elucidating that selection is able to shift a population's phenotype through the alteration of the population frequency of genes (or more properly alleles) that underlie the phenotypic variation (Fisher, 1918, 1930; Fisher et al., 1932). In doing so, he co-founded the field of population genetics. In population genetics, evolution is defined as the change in allele frequency within a population across generations. This process of change in the allelic distribution is also called microevolution, and importantly may include neutral processes (e.g., genetic drift and gene flow) in addition to natural selection. The large-scale phenotypic patterns visible above the species level are referred to as macroevolution (Hendry and Kinnison, 2001).

Micro- and macroevolution

For the most part, the relationship between microevolution and macroevolution represents the relationship between process and pattern. Macroevolution is often regarded as an extrap-

olation of microevolution: the microevolutionary outcomes repeated over geological time. However, since the inception of the terms micro- and macroevolution by Filipchenko in the 1920's (Hendry and Kinnison, 2001), heated debate has existed over whether evolution that occurs within and between populations (microevolution) can in fact explain all evolutionary variation that exists between species or higher-level taxa (macroevolution). Although some large-scale patterns go unexplained by microevolutionary mechanisms of population genetics, and there is some support for processes operating at or above the species level (multi-level selection; Jablonski, 2008, 2010), most theoretical and empirical research have shown that microevolutionary processes are compatible with macroevolutionary patterns (see the *Genetica* issue, 2001, volume 112-113, devoted to a review of this topic).

There are four main recognised mechanisms of microevolutionary change: natural selection (with sexual selection as a special case), gene flow, genetic drift, and mutation (Futuyma, 1998). The process of natural selection acts on the phenotype (e.g., a particular trait or a whole organism), but alters the underlying gene frequencies present in a population by favouring genotypes with the highest associated fitness (or highest inclusive fitness, *sensu* Hamilton (1964)). Selection can be stabilising, trimming phenotypic extremes and favouring the phenotypic mean; it can be directional, pushing a population towards one extreme of the phenotypic distribution; and it can be divergent (or disruptive), driving a population to move towards either of the two phenotypic extremes, but in both cases away from the mean phenotype (Pianka, 1978). The process of natural selection thus always favours a particular direction (even if it is to stay within a defined range). Gene flow simply refers to the process of migration; a change in allele frequencies because individuals leave or enter the population (Futuyma, 2013). Genetic drift is the random process of changes in allele frequencies due to chance (Wright, 1931). Although genetic drift occurs in all populations, its effect in terms of evolutionary change strongly depends on the effective population size (N_e), with small and isolated populations being more susceptible to drift (Futuyma, 2013; Hamilton, 2009). Lastly, genetic mutation is the formation of new alleles and the ultimate source of new genetic variation. Natural selection is the only process responsible for adaptive evolution. Genetic drift, gene flow, and mutation, on the other hand, are neutral processes, leading to non-adaptive evolution when the power of selection is comparatively weak.

The role of variation in microevolution A biological system's ability to vary is fundamental for evolution. Natural selection requires the existence of phenotypic variation and it requires part of this variation to be genetic so that modifications may be made to future generations. This ability to vary is an important aspect of *evolvability*: the ability to respond to selection (Hansen and Houle, 2008). There are several components that control a pheno-

type's variability, so-called variational properties, and they are fundamental to the evolution of the phenotype by natural selection (Hansen, 2011; Wagner and Altenberg, 1996). These properties include, among others, genetic variance, canalisation, phenotypic plasticity, and morphological integration (Debat and David, 2001; Willmore et al., 2007), and they structure phenotypic expression during the developmental stages (Maynard Smith et al., 1985; Müller, 2007). Variational properties can limit, enhance, or bias the direction of phenotypic variation and therefore help shape phenotypic evolution (Rolian, 2014; Wagner and Altenberg, 1996).

Adaptive radiations

We can observe how the history of life has unfolded on a macroevolutionary scale by studying the patterns that describe the evolution of specific lineages, or focus on specific large-scale trends that can yield insight into the process of evolution more generally. Of great value to the study of evolution are adaptive radiations, events of often rapid cladogenesis concomitant with adaptive diversification. A popular assumption in evolutionary biology has been that adaptive radiation is the primary mechanism behind the taxonomic and adaptive diversity on earth (Darwin, 1859; Huxley, 1942; Simpson, 1953). Adaptive radiations therefore exist and can be identified at different levels in the tree of life, with some nested within others (e.g., birds nested within the reptiles). Some of the best-known examples of adaptive radiations are Galápagos finches, Hawaiian silverswords (plants), *Anolis* lizards, and East African cichlid fish (Gavrilets and Losos, 2009).

Held to be the epitome of adaptive evolution, adaptive radiations represent clades that proliferated from a common ancestor following the colonisation of, and subsequent adaptation to various different ecological niches, accompanied by phenotypic divergence and concomitant speciation through the process of natural selection (Schluter, 2000). The notion that natural selection, mediated by ecology, is the main driver of phenotypic and taxonomic diversification is known as the 'ecological theory' (Schluter, 2000) and dates back to naturalists such as Darwin and Wallace, before being formally incorporated into the evolutionary synthesis of neo-Darwinian theory (Simpson, 1953). Thus, underlying the taxonomic diversification in adaptive radiations is, broadly speaking, the playing out of microevolutionary processes such as competition and ecological opportunity in various environments and conditions of both sympatry and allopatry (Glor, 2010; Mayr, 1963; Rainey and Travisano, 1998; Schluter, 1994, 1996b, 2000, 2009; Simpson, 1953; Via, 2001).

In addition to the classic examples of adaptive radiations mentioned above, Malagasy primates, Old World Monkeys (Fleagle, 1999), macaques (Thierry et al., 2000), hominins (Foley, 2003; Jolly, 2001), and other groups (Elton, 2007; Fleagle, 1999), have also been cited as constituting adaptive radiations among the primates. Without formal testing, these

examples likely represent a broader and more informal usage of the adaptive radiation concept, as is not uncommon in the evolutionary biology literature. In recent years, however, some workers have promoted a more formal and narrow definition of adaptive radiation to facilitate its study and the evolutionary mechanisms and ecological conditions underpinning it, as well as to be able to quantify their importance to the evolution of biodiversity (Gavrilets and Losos, 2009; Givnish, 1997; Glor, 2010; Losos and Miles, 2002; Rundell and Price, 2009; Schluter, 2000). According to this definition, an adaptive radiation constitutes the rapid evolutionary diversification of species from a common ancestor by natural selection in response to ecological opportunity. Concomitant with the diversification of species into different ecological niches is adaptive phenotypic differentiation (Gavrilets and Losos, 2009; Givnish, 1997; Glor, 2010; Losos and Mahler, 2010; Rundell and Price, 2009; Schluter, 2000). Moreover, it is argued, the process of adaptive radiation occurs through ecological speciation, namely, associated with ecological differentiation (Rundell and Price, 2009). The same mechanisms therefore drive speciation and the phenotypic differentiation in physiology, morphology and behaviour (Rundle and Nosil, 2005; Schluter, 2000, 2001, 2009). This definition allows for sympatric speciation (Gavrilets and Losos, 2009; Schluter, 2000). Geographical speciation, by contrast, occurs in allopatric populations (Rundell and Price, 2009; Schluter, 2000). According to adaptive radiation theory, early rapid multiplication is followed by decelerating diversification rates (Gavrilets and Losos, 2009). This theory further stresses competition as the main mechanism of ecological and phenotypic divergence, and ecological opportunity as an important determinant for the ecological establishment of the radiating species (Futuyma, 2013; Losos, 1994; Schluter, 2000). Thus, adaptive radiations arise through the process of divergent selection across environments and ecological strategies (Losos, 1994; Schluter, 2001). Not all adaptive radiations may have an evolutionary ecological basis, however, but rather seem to have differentiated by means of sexual selection, contradictory to the hypothesis of ecological divergence (Futuyma, 2013).

There are some additional patterns that are typical of adaptive radiations (reviewed in Gavrilets and Losos, 2009). These include a high rate of diversification in the early stage of radiation. After this 'early burst', the rate of cladogenesis declines and later speciation events involve reduced phenotypic differentiation. Furthermore, there is a stage of radiation where differentiation and adaptation occur first in response to the macrohabitat, next the microhabitat, followed by a divergence in secondary traits pertaining to survival and reproduction. Speciation driven by ecological factors is more likely to occur in larger geographical areas (the Area Effect), and lastly, the origin of radiations appears to be linked to intermediate selection gradients that are steep enough to drive divergence, but low enough to promote successful colonisation of a new ecological niche (Gavrilets and Losos, 2009).

There are therefore also nonadaptive radiations. In contrast to adaptive radiations, these are characterised by allopatry, geographical speciation, and/or little to no niche differentiation (Rundell and Price, 2009). Members of nonadaptive radiations are also called 'allospecies' and they are said to be common (Rundell and Price, 2009). Radiations, be they adaptive or nonadaptive, defined as monophyletic groups (clades), are useful tools in evolutionary biology, because they serve as analytical units defined to study a particular part of evolutionary history, and the processes underlying it. Radiations may be identified at different taxonomic levels, and are therefore expected to vary in scale, in taxonomic, ecological, and phenotypic diversity.

1.1.2 Evolutionary Ecology

The field of evolutionary ecology is essential to the study of evolution. It integrates the study of the evolutionary changes in biodiversity over geological time with the study of how biological variation can be explained by the interactions of individuals, populations, communities and so on with their biotic (and abiotic) environment. This branch of biology investigates how ecological conditions have shaped evolutionary differences within and between lineages, as well as how evolutionary histories influence the ecological behaviour of organisms at present (Mayhew, 2006). Both research on prospective change in response to ecological conditions and the relationship between historic patterns and ecological conditions are important approaches (Losos, 1994). Evolutionary ecology is therefore at the intersection between microevolutionary processes and macroevolutionary patterns.

The dominating picture of biodiversity is the goodness of fit between organisms and their environment (e.g. Lack, 1947; Losos and Mahler, 2010; Schluter, 2000; Simpson, 1953). The evolution of adaptation can only occur through the mechanism of natural (including sexual) selection and is rooted in the ecological environment. Within the parameters of evolutionary constraints and contingency, adaptations constitute the best benefit-to-cost ratio solutions to persistent major ecological challenges. They originate and spread through the population because they yield higher reproductive fitness than less (or non-)adaptive phenotypes, leading to an increase in the frequency of the adaptive genotype in successive generations. Major ecological challenges are competition for food and mating resources, predator avoidance, and disease resistance imposed by the ecological niche and mating system (Darwin, 1859; Futuyma, 2013). Ecology underpins evolution, and this is aptly captured by G. Evelyn Hutchinson's 1965 book title 'The Ecological Theatre and the Evolutionary Play'. As environments change, the vectors of selection may change and other evolutionary processes may become more or less important, but the ecological environment will continue to provide the context in which evolution unfolds.

Ecology can influence evolutionary change within lineages (anagenesis) or between lineages (cladogenesis) (Mayhew, 2006). There is ample evidence for ecology visibly driving microevolutionary change, of which Darwin's Finches are a classic example (Grant and Grant, 2006). A widespread approach for the detection of adaptations in macroevolutionary patterns and the identification of evolutionarily relevant ecological factors is the comparative method (Harvey and Pagel, 1991). This method relies on variation between species as the source of data and seeks to identify phenotype-environment associations, which are the (presumed) signals of natural selection. When comparative analyses return such associations, they are taken to reflect systematic patterns of evolutionary origin caused by a non-random process. Phenotype-environment correlations are subsequently often interpreted as evidence for adaptation by natural selection and that this process contributed to speciation in the taxonomic group under scrutiny (Losos, 2009; Schluter, 2000) (but see objections to this kind of interpretation in the paragraph below). The branch of evolutionary biology that studies anatomy in an ecological framework in order to understand how individuals adapt to their environments over evolutionary time is called ecomorphology (van der Klaauw, 1948). Ecomorphology *sensu lato* may refer to any relationship between organismic form and ecology arising from organism-environment interactions, although the majority of ecomorphologists today take a more narrow approach in investigating the functional significance of form in relation to the ecological role of organisms, and they are therefore especially interested in the adaptive evolution of the phenotype. Within the latter scope researchers are primarily interested in patterns of functional morphology, whereas the broader definition of ecomorphology also includes the study of environmental gradients (such as the Bergmann effect, Allen's rule, and island dwarfism) and which is therefore similar to macroecology (the study of large-scale patterns in organism-environment relationships). The present work is situated in this broader definition of ecomorphology and macroecology.

An important caveat to the study of phenotype-environment correlations, as has been rightly pointed out, is that correlation is not necessarily the same as causation and that present environmental patterns in phenotypic variation cannot be assumed *de facto* to reflect the reasons for evolution (Gould and Lewontin, 1979; Losos, 2009; Pianka, 1978). There may also be other, confounding variables that are not considered in the analysis but that in fact bear more relevance to the evolutionary cause (Mitchell-Olds and Shaw, 1987). Furthermore, results from comparative analyses are at risk to be confounded by phylogeny, another non-random pattern. The evolutionary relationships between taxa need to be taken into account in any comparative analysis in order to rule out that phenotype-environment relationships are not merely the product of common ancestry and phylogenetic signal: the tendency for closely related taxa to be more similar genetically and ecologically than

distantly related taxa (Felsenstein, 1985; Harvey and Pagel, 1991). A final objection to the adaptive interpretation of phenotype-environment correlations relates to constraints on phenotypic evolution. Convergent evolution is the independent evolution of similar phenotypes in response to similar environments. The ubiquity of convergence has therefore been accepted as proof that natural selection is the dominant force in the production of biodiversity (Losos, 2009; Schluter, 2000). However, with the advance of population and quantitative genetics and evolutionary developmental biology, more has become known about how genetic and developmental systems limit the production of phenotypic variation that is subsequently available for selection (Losos, 2011a; Schwenk and Wagner, 2004). Once potential evolutionary pathways are limited and constrained, evolutionary change is channelled in certain directions and evolutionary outcomes may be similar despite differences in the selective environment.

1.1.3 Evolutionary Geography

Where evolutionary ecology looks at how the biotic environment can explain evolutionary variation between organisms, the field of evolutionary geography is aimed at understanding how spatial factors influence organismal evolution (Lahr and Foley, 1998). Also called historical biogeography, it considers the relationship between biological variation and past population range and demography, notably changes in the size and movement of populations as a result of biotic and abiotic factors (Lahr and Foley, 1998). Populations or species may vary not (only) as a result of adaptations to different environments, but rather because of differences in their past spatial distribution related to dispersal, isolation, range expansion and contraction, and concomitant evolutionary changes through gene flow, genetic drift and natural selection (Harcourt, 2012).

The significance of spatial factors lies in their influence in promoting evolutionary change, notably species formation. They represent the geographical context in which evolutionary processes take place. Factors that are relevant in this sense are those that modulate mechanisms of gene flow, genetic drift, and natural selection. The importance of a population's range, for example, lies primarily in whether it is disjunct from that of related populations and thereby establishes the necessary condition for allopatric speciation, or whether it is large enough to become fragmented in the future. Allopatric speciation, also called geographic speciation (Mayr, 1942), is the most common form of speciation and occurs when populations have split from a common ancestral population, are geographically isolated and therefore have effectively no gene flow between them, and they become reproductively and genetically isolated over time (i.e., speciation). Disjunct distributions can arise through mechanisms of long-distance dispersal and vicariance. The former describes range expansion followed

by a range contraction, yielding several fragmented daughter populations. Environmental vicariance is at work when a continuous parental population is split into daughter populations through the formation of geographical or ecological barriers, for instance as a result of climatic change or tectonic or eustatic changes (Brown and Lomolino, 1998).

Demography matters mainly with regard to population size and density. Small and isolated populations are much more strongly affected by genetic drift than populations that are larger and/or maintain gene flow with neighbouring populations (Futuyma, 2013; Wright, 1931). Genetic drift reduces the genetic variation present in a population, thereby reducing the raw material available for sorting by natural selection. As a result, drifting populations are at a higher risk to go extinct (Futuyma, 2013; Skelton and Gilmour, 1993). Populations can become isolated following vicariant events such as mountain building or the emergence of sea barriers, or following dispersal to an island. Island colonisers, or other types of founder populations, tend to be small in addition to being isolated, as are populations that have undergone genetic bottlenecks. These sorts of populations are therefore very sensitive to the effects of genetic drift, which may overpower the force of selection.

Geography thus plays a significant role in evolution by affecting the size and distribution of populations. Certain geographical conditions, notably vicariant events, reflect contingency in the time and place at which evolution is played out.

1.1.4 The 4 C's of Evolution

Species and traits represent complex phenomena that require multi-faceted explanations. To better understand any complex phenotype, it is useful to break it down into different levels of explanation. Figure 1.1 illustrates a heuristic model to understanding evolution by recognising different components – external, intrinsic, and mechanistic ones – that interact to produce evolutionary change (Foley, 1990, 1995).

Here, I refer to causes of evolutionary change as the microevolutionary processes of mutation, gene flow, genetic drift, and natural selection. The process of natural selection is defined as directly altering and determining vital rates of survival and reproductive success, or fitness. Conditions should be taken here to refer to the environmental context in which organisms live, reproduce, die, and from which causes of evolutionary change arise. Conditions therefore include factors purely extrinsic to the individual, which primarily includes the biotic environment. The abiotic environment also plays a role, but mainly by affecting biotic relationships and population demography. The environment, both ecological and geographical, is presumed to directly or indirectly influence the causes of evolution, both by creating the conditions in which evolutionary mechanisms operate (e.g. genetic drift in small, isolated populations, or natural selection in the event of climatic change),

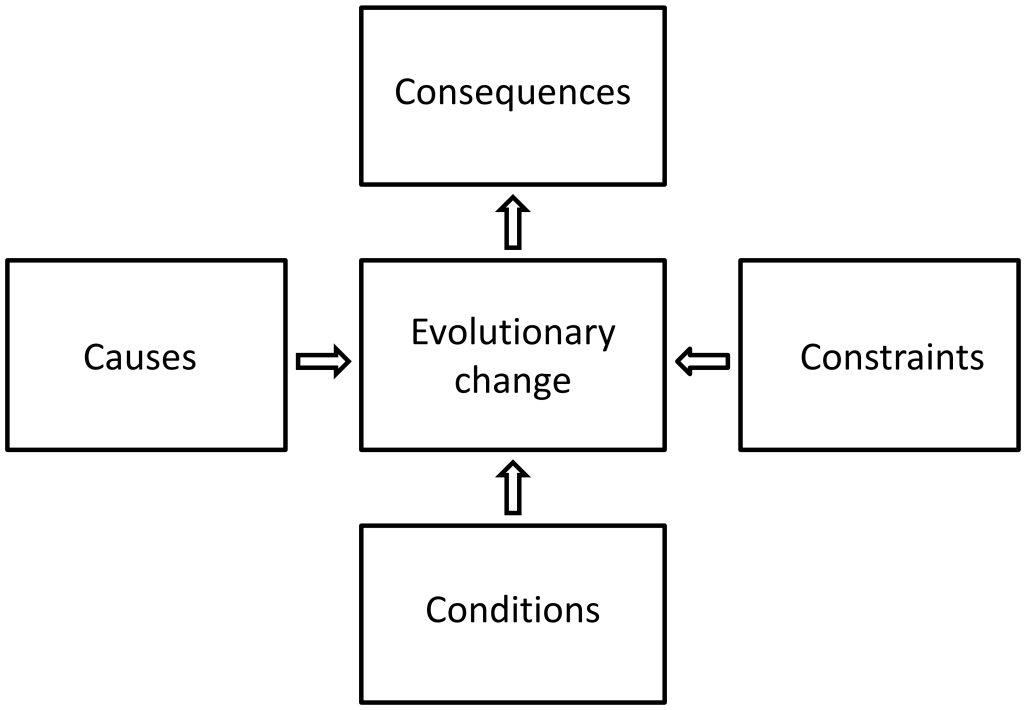


Fig. 1.1 Diagrammatic illustration of the different levels of explanation, or components, of the evolution of diversity (the 4 C's). One or several *causal mechanisms*, such as drift or natural selection, bring about the change in allelic frequency and adjust the phenotypic distribution of a trait in the population; *constraints* direct the magnitude or direction of evolutionary change; and the environmental *conditions* determine the impetus for change. Evolutionary *change* is the result of the complex interplay of these three components, and they have *consequences* for the organism, which in time will influence the conditions, causes, and constraints underlying further evolutionary change. Adapted from Foley (1995).

and by determining the nature of selection pressures (e.g., selection for larger bodies for the purpose of efficient thermoregulation in cold environments). Lastly, constraints refer mostly to variational properties, such as the amount of genetic and total variation present, the genetic, developmental, and functional structure of variation (e.g., genetic integration due to pleiotropy or linkage disequilibrium), heritability, plasticity, developmental constraints such as canalisation, and any other intrinsic factors related to evolvability that may constrain the direction and magnitude of phenotypic change (Marroig and Cheverud, 2005; Maynard Smith et al., 1985; Schluter, 1996a). Not all factors will act as a constraint per se, however. For instance, heritability is known to facilitate phenotypic change, and morphological integration can act as a facilitator as well as a constraint depending on the direction and magnitude of selection (Goswami et al., 2014; Hansen and Houle, 2008). Constraints may therefore also

be conceived of as channels. On longer time scales phylogenetic heritage may also act as a constraint, which in turn relates strongly to arguments that evolutionary change is highly contingent, and therefore not a simple and predictable playing out of ecological rules.

By using the above heuristic framework we can structure and inform theories, questions, hypotheses and consequent explanations of evolution. It also aids discussion by clarifying what part of the evolutionary process different researchers are addressing, not unlike Tinbergen's (1963) simple yet at the time much-needed delineation of complementary biological questions. The model can also be used to compare the picture that emerges from microevolutionary studies with that of macroevolution, in order to better understand what factors constrain and drive evolution on longer time scales and how they relate to more short-term evolution.

1.2 Thesis

1.2.1 Framework & Assumptions

To recap, the focus and purpose of the present work is to understand macaque diversity by examining patterns of variation in the macaque dentition and identifying the factors related to (socio)ecology, geography, and phylogeny that underpin these patterns. The primary goal is to understand the significance and the role of the ecological and geographical environment. By identifying what environmental conditions have been relevant in macaque evolution, I aim to improve our understanding of the evolutionary causes that have driven the present diversity. Differences in phenotypic starting points and genetic architecture between taxa are known to limit and/or channel potential evolutionary outcomes. Therefore I also consider patterns of integration to appreciate to what extent functional or developmental constraints have been relevant in macaque evolution. The dentition is investigated here as an ecologically salient phenotype under selection, and one that is tractable through evolutionary time.

The framework within which I will proceed to achieve the above aim includes the assumption that macroevolutionary patterns largely arise out of microevolutionary processes, that natural selection is the main force underpinning evolutionary change, and that both ecology and geography have played important roles in macaque phenotypic evolution.

As part of the scope and aim of this research, insight might also be gleaned about the transposability of microevolution to macroevolution, the relevance of particular environmental conditions for the evolutionary histories of other taxa – where parallels with macaques exist – and ostensibly also about the evolvability of the dental apparatus.

1.2.2 Macaques

Extant radiations are useful evolutionary models because they enable researchers to pose questions and frame hypotheses that are firmly situated in the framework of evolutionary theory. The total process of evolution in general and species-specific evolutionary histories must be explained by Darwinian processes. Speciose and widespread radiations can provide valuable insight into how adaptive and neutral evolutionary processes operate in varying environments and within certain phylogenetic parameters. In addition, living species can offer the resolution necessary to investigate evolutionary questions in a relatively controlled empirical manner that fossil species cannot.

The present work uses macaques (Cercopithecidae: *Macaca*) as the focus taxon. Macaques first originated in Africa and dispersed into Eurasia, becoming particularly widespread and diverse in Southeast Asia (Fa, 1989). They are marked by a wide and successful geographical dispersal, suggesting strong dispersal abilities and range expansion. Furthermore, ancestral macaques encountered a range of novel environments during their exodus out of Africa and subsequent colonisation of various parts of Eurasia (Abegg and Thierry, 2002; Fooden, 1980). Ecological versatility and the ability to thrive in various environments is particularly characteristic of the genus as a whole as well as many individual species of macaques. Macaques thus present an exciting opportunity to contrast and investigate a multitude of ecologically relevant factors owing to the marked taxonomic and ecogeographical diversity that exists between species. Moreover, macaques have been under-investigated compared to other monkeys when it comes to the study of ecomorphological patterns as a window into macaque evolution. To my knowledge, a paper published in 2014 by Ito and colleagues was the first study to investigate between-species variation in macaque craniofacial morphology specifically in relation to the environment. In doing so, they also investigated patterns of allometry, evolutionary convergence, and phylogeny (Ito et al., 2014). Their work has left much to explore about macaque diversity, however, especially with respect to a comparison of within-species and between-species patterns of variation, a more detailed and elaborate analysis of various ecogeographical variables, and tests of phylogenetic signal. This applies to macaque phenotypic variation in general, and dental variation in particular. In this thesis, I aim to respond to this gap in macaque research and conduct a more comprehensive, multivariate ecogeographical analysis, combined with an investigation of the developmental architecture underlying dental variation and covariation, including a comparison of between- and within-species variation.

As a monophyletic group of between 7-10 million years old (Arnold et al., 2010; Delson, 1980), the patterns of variation that exist between macaques are those that have arisen in a relatively short amount of time. The more inclusive the group, i.e., monophyletic groups that

exist at higher phylogenetic levels (e.g., the cercopithecids, or haplorhines, or Primates), the longer the evolutionary time scale and the more deep splits dominate the patterns of variation among the taxa. Using a comparatively young lineage like macaques, I pick up patterns of variation that have arisen more recently, in conditions that are assumed to be similar to present conditions, and these patterns are therefore more closely linked to recent speciation events rather than ancient splits. Young lineages tend to be less speciose and reduced statistical power owing to small sample sizes are problematic for phylogenetic comparative analyses; macaques, however, are relatively speciose with twenty-odd species.

Finally, observational and experimental research has unearthed a wealth of information about macaque physiology, anatomy, behaviour, and ecology (Thierry, 2004). This gives good resolution to the data. Also, in museum collections macaques are often represented by large numbers of specimens, facilitating data collection and satisfying sample size requirements. The taxonomy, species biology, ecogeography, and evolutionary history of macaques is reviewed in more detail in Chapter 2.

1.2.3 Teeth as the Exemplar Phenotype

The macaque dentition serves as the examplar phenotype under selection in the present work. The aim is to decipher what geographical, ecological and intrinsic biological variables have been important during macaque evolution, either in concert or in relative isolation of each other. Teeth are a suitable choice of phenotype for this purpose. First of all, the mammalian dentition evolved to perform one of the most important anatomical functions, namely the processing of food (Ungar, 2010). This places teeth at the direct functional interface of the individual and the individual's environment. Energy required for survival and reproduction is dependent on an animal's food intake (Lucas, 2004). Thus, selection has operated to optimise feeding efficiency by adjusting the size and shape of teeth to optimise food acquisition and mastication. As a result, dental morphology reflects the material and structural properties of food (Kay, 1975; Lucas, 2004). Teeth are thus fundamental to understanding the ecology and evolution of a taxon (Fleagle, 2013; Ungar, 2011).

In the mammalian heterodont dentition, different tooth types typically play different roles in food acquisition. The incisors are used to remove food items from their source or to modify the food source to bite-size particles as part of the process of ingestion. The molars and the premolars serve mainly to slice, shear or grind food into smaller chunks that are ready for further digestion, during the mastication process. The canines are involved in the grabbing or killing of prey in some taxa (notably felids), or it plays a non-food related role, such as fighting or social display in primates (Ungar, 2010). Due to their differing functions, different tooth classes may be subject to a suite of varying selective pressures. Ultimately,

however, individual teeth must all fit in the tooth row to form a functional whole, and thus developmental constraints are also likely to apply (Stock, 2001).

Secondly, teeth typically have high heritability estimates (Hlusko et al., 2011; Rizk et al., 2008; Townsend and Brown, 1978), which means that the observed phenotypic variation is largely determined by genetic variation. Natural selection acts on the phenotype but it is the consequent modifications to the genotype that are passed on and which determine evolutionary change. Moreover, teeth are strongly canalised, protecting their phenotypic expressions from genetic and/or environmental perturbations in realising the phenotypic *Bauplan*. Following odontogenesis, teeth also do not have the capacity to remodel in response to 'local' pressures (e.g., environmental changes associated with climate shifts or migration). Thus, due to their strong heritability and lack of plasticity after morphogenesis, teeth are expected to carry strong evolutionary signals. Dental development is discussed in more detail below.

At any stage, in any taxon, evolution is constrained by the ancestral material available for modification and thus adaptations to the same ecological challenge may end up looking phenotypically different in distant taxonomic groups (Ungar, 2010). This phenomenon is sometimes known as phylogenetic inertia, or incomplete convergence, and it is an important reason why dental morphology is widely employed in systematics. It will be necessary in this work to identify the relative contributions of adaptation versus phylogeny to the evolutionary patterns of macaque dental variation. Moreover, phylogenetic patterns can serve as a baseline against which deviations can clearly be identified as areas of adaptive evolution.

Due to their high mineral content teeth preserve exceptionally well over geological time and dominate the fossil record of many mammalian taxa. Knowledge that we acquire about ecogeographical and other biological patterns in the dental morphology of living taxa may be applied comparatively to extinct taxa in the pursuit of reconstructing and understanding the evolutionary history of fossil species (Ungar, 2011).

Finally, teeth are well-represented in museum collections, with dentitions commonly being complete for a given specimen. Teeth are also practical to measure.

Dental development

Tooth development (odontogensis) is conserved among vertebrates (Jernvall and Thesleff, 2012). The mammalian dentition forms from two types of animal tissue: the oral epithelium and the mesenchyme. Odontogenesis is initiated and finalised in three different stages, namely the bud, cap, and bell stages (in chronological order). These stages correspond to tooth initiation, cell proliferation, and tissue and shape differentiation, respectively (Hillson, 1996; Jernvall and Thesleff, 2012; Thesleff and Sharpe, 1997). First, during the bud stage,

there is thickening of the oral epithelium into a band of tissue called the dental lamina; the tooth row will ultimately form parallel to this. The dental lamina proliferates and folds into the underlying mesenchyme layer, known as invagination or 'budding'. The result is a so-called tooth bud: a group of epithelial cells at the periphery of the dental lamina that have penetrated the underlying mesenchyme. Next, in the cap stage, there is further cell proliferation, including that of the mesenchyme (sometimes called ectomesenchyme), which condenses right below the dental lamina. Meanwhile, the invaginated part of the dental lamina (the tooth bud) expands and becomes the enamel (or dental) organ, while mesenchymal cells cluster underneath it to form the dental papilla. The dental sac or follicle forms approximately around both of them. The enamel organ ultimately forms the enamel, the dental papilla the dentine and pulp, and the dental sac the cementum of the roots and supporting structures. During the bell stage the tooth buds acquire their shape through cusp patterning (morphodifferentiation, in the early bell stage) and the different tissues of enamel, dentine, pulp, and cementum are formed (histodifferentiation, in the late bell stage). Finally, the tooth mineralises and has reached its final form. Only root formation is finalised after this and the tooth erupts.

During development, the epithelium and mesenchyme (and their derived dental structures, such as the enamel knot and the dental papilla) alternate in directing tooth development by reiteratively producing signalling molecules: activators and inhibitors (Jernvall and Thesleff, 2000; Thesleff, 2003). These signalling molecules regulate gene expression, including transcription factors and signalling receptors, which in turn affect cell responses to new signals. Morphogenesis of teeth is thus regulated by complex signalling networks that are responsible for the communication between cells and tissues during tooth development (Jernvall and Thesleff, 2000; Thesleff, 2003; Thesleff and Sharpe, 1997). Signalling molecules direct not only odontogenesis of the tooth germ (i.e., bud) that produced the molecules, but also regulate the initiation and growth of subsequently developing teeth (Jernvall and Thesleff, 2000; Kavanagh et al., 2007). Their expression constitutes the developmental process by which adjacent teeth, e.g., the molar row, are coordinated in their size (Kavanagh et al., 2007). Tooth buds form in sequence and in an antero-posterior direction along the dental lamina (Thesleff and Sharpe, 1997). Until the late (or advanced) bell stage tooth buds are connected through the dental lamina tissue, which is how diffusable signalling molecules are able to mediate the development of subsequent teeth (Jernvall and Thesleff, 2000).

Variation in tooth form (size and shape) among individuals of the same species can thus arise from genetic variation or variation introduced during development. The degree of phenotypic plasticity, i.e., environmentally induced variation (Stearns, 1989), in the number, size, and shape of mammalian teeth is likely to be limited to the developmental stages:

following mineralisation, tooth crown form is fixed and does not alter throughout the tooth's lifetime, save for the effects of wear (interstitial wear, attrition, and abrasion) (Hillson, 1996). Plasticity in teeth is furthermore expected to be limited as a result of tooth development taking place inside the jaw where tooth buds are not directly exposed to the environment external to the individual. Non-genetic variation that accumulates among individuals may therefore primarily arise from influences on fluctuations in the concentration of signalling molecules and the balance between activators and inhibitors that ultimately (e.g., through cascading effects) control the onset of formation and growth rate of the different teeth (Kavanagh et al., 2007). This is an area that requires further research.

1.2.4 Research Questions and Analytical Model

Analytical model

The evolutionary role of the environment, both the resource base and the geographical context, will be explored through the study of macroecological and ecomorphological patterns. It is the phenotype-environment associations that are directly observable and describable with the data collected here. The effect of phylogeny on such associations will also be studied and taken into account. Subsequently, these patterns can and will be interpreted against relevant theoretical and empirical background. Moreover, inferences about evolutionary processes will be made based on these results.

The phenotype measured here can be represented by absolute dental trait values (linear size measurements), relative dental trait values (e.g., ratios or residuals), or dental trait variances (e.g., the variance or the coefficient of variation). Significant relationships obtained between the environment and absolute or relative tooth size are interpreted to reflect ecomorphological patterns (*sensu lato*), either as an adaptive link or as a correlated response, for example to body size. Patterns detected in dental variability are explored in the context of phenotypic integration, canalisation, and phenotypic plasticity. Therefore, whether absolute tooth size, relative size, or variance variables will be used for analysis depends on the research question at hand. Table 1.1 outlines this approach. The variables listed in this table are not exhaustive, but represent some of the main factors that will be explored in this thesis, including the type of trait value used to study it.

Research questions

In this work I am mainly interested in understanding the macroevolutionary pattern of macaque diversification, how this is related to the ecogeographical context of macaques, and what the contribution of phylogeny is to this evolutionary pattern. Since 'the environment'

Table 1.1 Model for operationalising thesis questions. Trait_{abs} refers to the absolute trait value, Trait_{rel} to the trait value relative to body size, and Trait_{var} refers to the trait variance (or another measure of variation).

	Trait_{abs}	Trait_{rel}	Trait_{var}
Integration	x	x	
Canalisation			x
Phenotypic plasticity			x
Body size	x	x	
Sexual selection	x	x	
Diet	x	x	
Habitat	x	x	
Latitude/longitude	x	x	
Climate	x	x	
Phylogeny	x	x	

refers to a number of different yet interacting abiotic and biotic factors, this question is best studied in a multivariate framework, rather than by carrying out multiple univariate analyses. The former benefits the interpretability of the results and takes into account that the dentition is an integrated structure that is likely to vary in a limited number of ways, and it takes account of how environmental variables are associated with each other in how they might influence phenotypic variation. This is followed by a separate analysis of phylogenetic signal in the macaque dentition, to investigate if different parts vary in the phylogenetic signal they carry and make inferences about constraints and processes that have been important in shaping evolutionary change in macaque dental variation.

Before analysing macroecological and phylogenetic patterns, however, it is helpful to first determine the basic patterns of variation and covariation in the macaque dentition within species, so that we may better understand the evolutionary associations between species. How much different teeth vary with respect to each other can indicate differences in developmental canalisation and plasticity. Patterns of phenotypic covariation in the dentition will be informative about how integrated teeth are with respect to each and how free they are to vary independently. Finally, body size is expected to have a strong allometric effect on macaque teeth, and this will therefore also be investigated. These aspects essentially represent constraints to the evolution of phenotypes as well as factors that constrain our interpretations about the influence of the environment in driving adaptive evolution.

1.2.5 Organisation

This dissertation will proceed to present the relevant background to macaque evolution and dispersal, and an overview of the variation in body size, ecology and spatial geography in Chapter 2. The methodology and materials used in this research are described in Chapter 3, which also includes a summary of the dental data and presents the contextual data by species that will be used in this work.

Chapters 4 through 7 present the data analyses and results. Each chapter is organised as a self-contained paper, including relevant background to the research question(s), analyses, results, and discussion. The first results chapter (Chapter 4) investigates variational properties of variability and evolvability in macaque teeth. Patterns of the phenotypic mean and variance are considered by tooth (measurement), and patterns of covariation are inspected between tooth measurements. All analyses are carried out within and between species in order to compare microevolutionary and macroevolutionary patterns and to offer mechanistic explanations for evolutionary trends further on.

The next chapter (Chapter 5) deals with allometric scaling. First, differences in allometric scaling between teeth are inspected, and compared within and between macaques. Next, I investigate whether a diet-related shift in allometric scaling of the postcanine occlusal area (PCOA) can be detected in macaques. Finally, I will address several questions with respect to sex differences in scaling in macaques. To be exact, whether sexual dimorphism in body mass increases with body size, whether patterns of sexual dimorphism are similar in the skull, the dentition, and the canine/premolar honing (CP_3) complex, and whether sex dimorphism in the CP_3 complex can be explained by body mass dimorphism alone or whether there is evidence for independent selection on the canines in macaques.

After having established the basic patterns of variation, covariation and allometric scaling in the dentition, in Chapter 6 I investigate the patterns of association between ecogeography and phenotypic variation. Spatial geography, i.e., latitude and longitude, and environment (climate, altitude, range size, and ecology) are analysed separately in their relationship to macaque (cranio)dental variation. I use a fully multivariate approach, and the phylogenetic relationships between macaques is taken into account.

The last results chapter (Chapter 7) inspects in detail the phylogenetic signal in the lengths and breadths of the various teeth in order to explore if different parts of the dentition have been subject to different constraints or evolutionary processes. This will aid the interpretation of possible adaptive and nonadaptive patterns in the macroevolutionary variation in macaque craniodental morphology and which parts of the dentition may be driving different patterns. Phylogenetic signal is tested among all macaques in the sample, as well as in the two Asian sub-lineages, separately, as a way to test for differences between clades.

I draw the different elements of the thesis together in a general discussion centred around three main questions (Chapter 8). Each main question, or topic, serves to summarise and relate the various findings made in this work to each other and place the findings in a broader evolutionary context. The discussion will touch on the shortcomings of the present research and where directions for future research exist. Finally, a concluding statement with regard to the body of work presented in this thesis will also be made in this chapter.

Chapter 2

Macaques (Cercopithecidae: *Macaca*)

2.1 Introduction

Macaques, genus *Macaca* (Lacépède, 1799), are a suitable primate taxon to test how development structures evolutionary change in closely related taxa, to investigate evolutionary correlations between ecogeography and phenotypic variation, and to appraise the relative importance of natural selection and genetic drift in creating phenotypic diversification in a young primate radiation.

Macaque evolution is characterised by adaptive radiation: macaques are among the most taxonomically and geographically diverse primate lineages. As many as twenty-four species are presently recognised and their geographical range extends from North Africa to southern and eastern Asia, making them the most widely distributed non-human primate genus. These Old World monkeys also vary in body size, allowing for the investigation of the effect of size through allometry, and they exhibit differences in their ecological and geographical distributions, social behaviour and life history strategies. Macaques have successfully diversified in, and adapted to a wide variety of environments. This makes them especially suitable as a model taxon for testing evolutionary patterns against processes of evolution in general, as well as for providing insight into the evolutionary ecological and geographical mechanisms relevant to non-human and human primate evolution in particular.

This chapter presents an overview of the relevant systematics with respect to macaque classification, evolutionary history and dispersal, current geographical distribution, and various aspects of the intrinsic (species) biology. In the light of the debate that has existed around macaque taxonomy, the classification and phylogeny of living macaque species adopted in this thesis is made explicit. Furthermore, I describe the diversity that exists in the species biology, ecology and geography of macaques.

2.2 Macaque Classification

Macaques form a monophyletic group in the tribe Papionini, subfamily Cercopithecinae (Groves, 2001). They are a taxonomically rich group. According to modern primate classification, the lineage of macaques is particularly speciose for its age with at least 20 recognised species at present, depending on lumping or splitting preferences (Arnold et al., 2010; Groves, 2001; Thierry, 2007b; Wilson and Reeder, 2005). Macaques can be divided into several sublineages, or species groups, based on their morphology as well as their genetic make-up (Delson, 1980; Fooden, 1976; Groves, 2001; Li et al., 2009). Historically, the classification of macaques has been associated with debate concerning their monophyly (Groves, 1989), the relationships between the species groups, and the taxonomic position of specific species in these groups (Fa, 1989). Molecular evidence, most notably genetic evidence, has come a long way in resolving most of this debate (e.g., Morales and Melnick, 1998; Perelman et al., 2011; Tosi et al., 2003).

2.2.1 Systematics: Taxonomy and Phylogeny

Below I will elaborate on macaque systematics with regard to the nomenclature of the genus, alpha taxonomy, and phylogenetic relationships.

Nomenclature

The genus *Macaca* is a genus in the family Cercopithecidae (Old World monkeys, Gray 1821). Old World monkeys consist of two subfamilies, the predominantly African Cercopithecinae and the predominantly Asian Colobinae. Macaques are part of the former, and within the Cercopithecinae they are situated in the tribe Papionini, together with baboons, gelada, mandrills, drills, and mangabeys (Groves, 2005; Hoelzer and Melnick, 1996). The nomenclature of the genus and many of its constituent species has changed historically (Hill, 1974; Fooden, 1976; and reviewed in Fa, 1989). Traditionally, macaques have been classified either congenerically in *Macaca* (Fooden, 1969, 1976; Groves, 1980), or divided between two genera, *Macaca* and *Cynopithecus* (Fa, 1989). The apparently derived cranial morphology of the Celebes Black Ape, *Macaca nigra*, was considered substantially different from the other macaques and as such it was accommodated in a separate genus, along with other related macaque species from Sulawesi (Fa, 1989; Hill, 1974; Pocock, 1926). However, a single genus that includes all species has become the preferred classification, and following molecular and behavioural studies of *M. nigra* (e.g., Cronin et al., 1980; Dixson, 1977) macaques are presently accepted to belong to a single genus, *Macaca* (Hoelzer and Melnick,

1996). A related systematics issue is the question of macaque monophyly, which was once debated by some (Groves, 1989), but molecular evidence has similarly corroborated the fact that all macaques descend from a common ancestor (Morales and Melnick, 1998).

Taxonomy

The number of recognised macaque species has varied historically from 11 (Ellerman and Morrison-Scott, 1966), 13 (Napier and Napier, 1967), 16 (Kellogg, 1945), to 19. The latter number resulted from a comprehensive and systematic review by Jack Fooden following extensive field research (Fooden, 1969, 1975, 1976, 1979, 1981, 1982a,b, 1986, 1988, 1996, 2000, 2006, 2007; Fooden and Aimi, 2005; Fooden and Lanyon, 1989; Fooden and Wu, 2001). Since the publication of Fooden's classification of macaques (1976) a few more taxonomic changes have taken place regarding rankings of certain (sub)species, mostly in the context of the species concept debate (Groves, 2001), as well as two recent species discoveries (Hou et al., 2016; Sinha et al., 2005). This has subsequently yielded up to as many as 24 proposed species of macaques (Groves, 2005; Thierry, 2007b), although the validity of species status is not fully resolved for all of them (discussed below). Table 2.1 lists the various taxa and their taxonomic ranking according to Fooden (1976) and Groves (2005).

Groves' publication of primate taxonomy (2001; 2005) is one of the most widely used classifications used for macaques at present. The differences that exist with this classification and that of Fooden (1976) pertain mainly to the pigtailed macaque (*M. nemestrina*) and closely related species from the Indochinese region and the Mentawai islands, namely *M. leonina*, *M. pagensis* and *M. siberu*, respectively. Fooden (1975) did not find sufficient morphological evidence for specific differentiation and as such ranked *M. n. leonina*, *M. n. nemestrina* and *M. n. pagensis* (which included *M. siberu*) as subspecies of *M. nemestrina* (see Table 2.1). However, genetic (e.g., Evans et al., 1999; Morales and Melnick, 1998; Roos et al., 2003) and morphological evidence (Gippoliti, 2001; Malaivijitnond et al., 2012) support a specific distinction between *M. leonina* and *M. nemestrina* and this revised taxonomic status as species has now been widely accepted (Eudey, 2013a,b; Roos et al., 2007). In the same vein, *M. pagensis* and *M. siberu* are now recognised to be two distinct species (Groves, 2005; Whittaker, 2013a,b).

Table 2.1 Taxonomy of macaque species.

Proposed species, authority	Common name	Taxonomy by Fooden (1976, 1980)	Taxonomy by Groves (2005)
M. arctoides, I. Geoffroy, 1831	Stumptailed macaque, or Bear macaque	*M. arctoides*	*M. arctoides*
M. assamensis, McClelland, 1839	Assam macaque	*M. assamensis*	*M. assamensis*
M. brunnescens, Matschie, 1901	Muna-Buton macaque	*M. brunnescens*	*M. ochreata brunnescens*
M. cyclopis, Swinhoe, 1862	Taiwanese macaque, or Formosan Rock macaque	*M. cyclopis*	*M. cyclopis*
M. fascicularis, Raffles, 1821	Longtailed macaque, or Crab-eating macaque	*M. fascicularis*	*M. fascicularis*
M. fuscata, Blyth, 1875	Japanese macaque	*M. fuscata*	*M. fuscata*
M. hecki, Matschie, 1901	Heck's macaque	*M. hecki*	*M. hecki*
M. leonina, Blyth, 1863	Northern pigtailed macaque	*M. nemestrina leonina*	*M. leonina*

Continued on next page

Table 2.1 – *continued*

Proposed species, authority	Common name	Taxonomy by Fooden (1976, 1980)	Taxonomy by Groves (2005)
M. leucogenys[b], Li, Zhao & Fan, 2015	White-cheeked macaque	n/a	n/a
M. maura, H.R. Schinz, 1825	Moor macaque	*M. maura*	*M. maura*
M. mulatta, Zimmermann, 1780	Rhesus macaque, or Rhesus Monkey	*M. mulatta*	*M. mulatta*
M. munzala[a], Madhusudan & Mishra, 2005	Arunachal macaque	n/a	n/a
M. nemestrina, Linnaeus, 1766	Southern pigtailed macaque	*M. nemestrina nemestrina*	*M. nemestrina*
M. nigra, Desmarest, 1822	Celebes Crested macaque, or Celebes "Ape"	*M. nigra*	*M. nigra*
M. nigrescens, Temminck, 1849	Gorontalo macaque	*M. nigrescens*	*M. nigrescens*
M. ochreata, Ogilby, 1840	Booted macaque	*M. ochreata*	*M. ochreata ochreata*

Continued on next page

Table 2.1 – *continued*

Proposed species, authority	Common name	Taxonomy by Fooden (1976, 1980)	Taxonomy by Groves (2005)
M. pagensis, Miller, 1903	Mentawai macaque	*M. nemestrina pagensis*	*M. pagensis*
M. radiata, É. Geoffroy, 1812	Bonnet macaque	*M. radiata*	*M. radiata*
M. siberu, Fuentes & Olson, 1995	Siberut macaque	*M. nemestrina pagensis*	*M. siberu*
M. sinica, Linnaeus, 1771	Toque macaque	*M. sinica*	*M. sinica*
M. silenus, Linnaeus, 1758	Liontailed macaque	*M. silenus*	*M. silenus*
M. sylvanus, Linnaeus, 1758	Barbary macaque, or Barbary "Ape"	*M. sylvanus*	*M. sylvanus*
M. thibetana, Milne-Edwards, 1870	Tibetan macaque	*M. thibetana*	
M. tonkeana, Meyer, 1899	Tonkean macaque	*M. tonkeana*	*M. tonkeana*

[a]Discovered and first proposed as a new species in 2005 (Sinha et al., 2005), and [b] in 2015 (Li et al., 2015), post Groves (2005) (see text).

A final difference between the taxonomy advocated by Fooden (1976, 1980) versus Groves (2001, 2005) regards the ranking of the Muna-Buton macaque from the islands Muna and Buton off the southeast coast of Sulawesi. Fooden (1969, 1976) recognised it as a separate species, *M. brunnescens*, on the same taxonomic level as the other Sulawesi macaques, while Groves (2001, 2005) and others (Brandon-Jones et al., 2004; Manullang and Supriatna, 2008; Riley, 2013) retain it as a subspecies of *M. ochreata* on the grounds that it lacks sufficient morphological and genetic differentiation (Brandon-Jones et al., 2004). The latter view is the approach followed here. Figure 2.1 depicts the macaques species recognised in this thesis.

A new macaque species, *M. munzala*, inhabiting the Himalaya mountains of Arunachal Pradesh, India, has been discovered and described only fairly recently (Sinha et al., 2005). The distinctiveness of this 'enigmatic macaque' from *M. assamensis* and *M. thibetana*, who it is geographically close to, has been called into question (Kumar et al., 2008b). Morphometric and molecular phylogenetic analyses indicate, however, that *M. munzala* is morphologically unique and distinct from close congeners, most notably *M. assamensis*, and that while it may be of hybrid origin as a result of male introgression, it represents a distinct genetic clade with an estimated origin around 0.48 million years ago (Chakraborty et al., 2007). A second species has been newly described even more recently: *M. leucogenys*, or the white-cheeked macaque (Hou et al., 2016; Li et al., 2015). It was first observed in Chinese Tibet and later also in northeastern India (Chetry et al., 2015; Li et al., 2015). Its distribution therefore overlaps with that of *M. mulatta*, *M. assamensis*, *M. thibetana*, and *M. munzala*. *M. leucogenys* has been distinguished from these four species, however, based on external characteristics and alarm calls (Li et al., 2015). Phylogenetically, it seems to be closely related to *M. assamensis*, *M. thibetana*, *M. radiata*, and *M. munzala* (Fan et al., 2017; Hou et al., 2016).

It is relevant at this point to refer to the existence of different species concepts and how taxonomy and systematics are in part dependent on the particular concept used. Intuitively, we think of a species as a group of interbreeding populations that are reproductively isolated from other such groups, as formulated by Ernst Mayr in the Biological Species Concept (BSC; Mayr, 1942). In reality, however, species cannot always be demarcated in this way, and indeed, different macaque species are well-known to interbreed successfully (Evans et al., 2001; Tosi et al., 2002; Watanabe and Matsumura, 1991). Other species concepts are abound (Zachos, 2016). An example is the Phylogenetic Species Concept (PSC; Cracraft, 1983; Groves, 2012), which defines a species based on diagnosability and shared ancestry and descent. (Groves, 2001) has revised primate (including macaque) taxonomy according to this species concept, and although the PSC has attracted many criticisms for being a theoretically

flawed concept as well as causing species 'inflation' (Zachos et al., 2013; Zachos and Lovari, 2013), I will nevertheless adopt Groves' 2005 taxonomy here. Firstly, the goal is not to resolve macaque systematics in this thesis. Secondly and more importantly, the present analyses benefit from a framework of a more split taxonomy that yields a greater taxonomic resolution, rather than one that restricts the level of analysis due to lumping of species at the outset. That said, as will become clear in Chapter 3, few macaque species included in the sample are the subject of debate surrounding its taxonomic status.

Taxonomic classification: this thesis The taxonomy of macaque species and subspecies employed in this thesis is the one described by Groves in Wilson & Reeder's Mammal Species of the World, third edition (2005). This taxonomy receives the most support based on current evidence (reviewed above). Moreover, it is the taxonomy that is adhered to in many molecular approaches to generating macaque phylogenies (reviewed below in section 2.2.1). The discoveries of the Arunachal macaque *M. munzala* and white-cheeked macaque *M. leucogenys* postdated the Wilson & Reeder (2005) publication, but this is irrelevant to the work presented here as no *M. munzala* and *M. leucogenys* specimens are currently identified – to my knowledge – in museum collections.

Species groups and phylogenetic relationships

Macaques can also be classified on the taxonomic level of species groups (e.g., Delson, 1980; Fooden, 1976; Groves, 2001; Li et al., 2009; Morales and Melnick, 1998; Tosi et al., 2000). Though originally defined on the basis of phenotypic patterns (Delson, 1980; Fooden, 1976; Pocock, 1926) macaque species groups are currently also recognised in a molecular phylogenetic context. Species group classification and macaque phylogenetic relationships continue to inform each other (Delson, 1980; Fooden, 1976; Hoelzer and Melnick, 1996; Perelman et al., 2011; Tosi et al., 2000, 2003) and thus they will be reviewed jointly in this section.

When revising *Macaca* systematics, Fooden (1976) identified four species groups based primarily on penile morphology and secondarily on female reproductive tract morphology, sexual swellings and copulation patterns (Fooden, 1976, 1980). The species groups defined by Fooden, listed in Table 2.2, are the *silenus-sylvanus* group, the *sinica* group, the *fascicularis* group, and the monotypic *arctoides* group. The *silenus-sylvanus* group contains 12 of the currently recognised species. Fooden (1980) proposed that this group is the result of an early dispersal in macaque evolutionary history with subsequent intermediate disappearance, as judged by the group's speciosity and disjunct geographical distribution of its constituent species. The increasingly less disjunct and wider distribution of the *sinica* and *fascicularis*

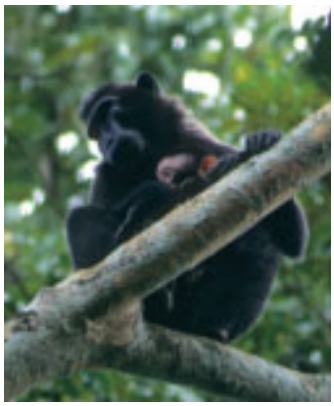
M. sylvanus

M. silenus

M. leonina

M. nemestrina

M. nigra



M. nigrescens

M. hecki

M. tonkeana

M. maura

M. ochreata

M. pagensis

M. siberu

M. sinica *M. radiata* *M. assamensis*

M. thibetana *M. munzala* *M. fascicularis*

M. arctoides *M. mulatta* *M. cyclopis*

M. fuscata

Fig. 2.1 Macaque species. Photo credits: B. Thierry (*sylvanus*, *nigra*, *tonkeana*, *thibetana*, *fascicularis*, *mulatta*), R. Seitre (*hecki*, *maura*, *sinica*, *assamensis*, *arctoides*), C. Abegg (*silenus*, *siberu*, *pagensis*, *radiata*), N. Herrenschmidt (*ochreata*), M.J. Hsu (*cyclopis*), M.D. Madhusudan (*munzala*), N. Rowe (*nigrescens*), Harrison (*leonina*), Fletcher & Baylis (*nemestrina*), J. Onsen (*fuscata*).

groups was taken as indicative of more recent respective dispersal times of the ancestral stocks of these groups. Lastly, *M. arctoides* was diagnosed to be unique in its genital morphology and tail reduction and together with its narrow distribution this was taken to be indicative of the most recent dispersal within the macaques (Fooden, 1980).

Delson (1980) essentially followed Fooden's classification of species groups but made a few changes incorporating craniodental evidence from living and fossil macaques. Firstly, most if not all of the North African and European fossil macaques from the Plio-Pleistocene are very similar in the size and morphology of their dentition to *M. sylvanus* (Delson, 1975, 1980), and together with their temporo-geographical distribution they have been argued to form a single evolving macaque lineage (Delson, 1980). Thus, *M. sylvanus* and the circum-Mediterranean fossil macaques are placed in their own species group by Delson (1980). Secondly, fossil and extant morphology suggests an affinity of *M. arctoides* to both *M. thibetana* and *M. assamensis* of the *sinica* group. The geographical distribution of *M. arctoides* is located within that of the *sinica* group. This led Delson (1980) to join *M. arctoides* with the *sinica* group, albeit as exhibiting more derived characteristics. In the tentative phylogeny that he proposed following his revised classification, Delson placed *M. sylvanus* as the African sister to an unresolved trichotomy of all other, Asian, macaques, which in turn were divided into the *silenus*, *sinica* (including *M. arctoides*) and *fascicularis* groups (Delson, 1980).

In his evaluation of the genus' taxonomy, Groves (2001) incorporated molecular studies of the taxonomic and evolutionary relationships among macaques to see if these data could recover Fooden's four species groups. Going mostly by Morales & Melnick's 1998 comprehensive genetic analysis of the mitochondrial DNA (mtDNA) of nearly all species of macaque, Groves (2001) argued for a division of species into six species groups (see Table 2.2). *M. sylvanus* would represent a presently monotypic African clade that is the sister group to all other macaques, the Asian members of Fooden's *silenus* group are split by Groves into a *nemestrina* group and a Sulawesi group, *M. fascicularis* and *M. arctoides* are grouped together to the exclusion of the rest, the *mulatta* group includes the denominate species as well as *M. fuscata* and *M. cyclopis*, and lastly the *sinica* group is proposed in exact accordance with Fooden (1976).

Studies of allozymes (blood protein alleles) have yielded species groups that correspond largely with both Fooden's (1976) and Delson's (1980) classifications (Cronin et al., 1980; Fooden and Lanyon, 1989; Melnick and Kidd, 1985), although the position of *M. arctoides* remains unclear. In the last two decades purely genetic markers have become the focus of phylogenetic reconstructions. Maternally-inherited mitochondrial DNA (mtDNA) has been analysed extensively in macaques (e.g., Hayasaka et al., 1996; Melnick et al., 1993;

Table 2.2 Taxonomy of macaque species groups according to various classifications.

Fooden (1976)	Delson (1980)	Groves (2001)	This thesis
silenus-sylvanus group	*sylvanus* group	*sylvanus* group	*sylvanus* group
M. sylvanus	*M. sylvanus*	*M. sylvanus*	*M. sylvanus*
M. silenus			
M. nemestrina	*silenus* group	*silenus* group	*silenus* group
M. nigra	*M. silenus*	*M. silenus*	*M. silenus*
M. nigrescens	*M. nemestrina*	*M. nemestrina*	*M. nemestrina*
M. hecki	*M. nigra*	*M. leonina*	*M. leonina*
M. tonkeana	*M. nigrescens*	*M. pagensis*	*M. pagensis*
M. maura	*M. hecki*		*M. siberu*
M. ochreata	*M. tonkeana*	Sulawesi group	*M. nigra*
M. brunnescens	*M. maura*	*M. nigra*	*M. nigrescens*
	M. ochreata	*M. nigrescens*	*M. hecki*
sinica group	*M. brunnescens*	*M. hecki*	*M. tonkeana*
M. sinica		*M. tonkeana*	*M. maura*
M. radiata	*sinica* group	*M. maura*	*M. ochreata*
M. assamensis	*M. sinica*	*M. ochreata*	
M. thibetana	*M. radiata*		*sinica* group
	M. assamensis	*fascicularis* group	*M. sinica*
fascicularis group	*M. thibetana*	*M. fascicularis*	*M. radiata*
M. fascicularis	*M. arctoides*	*M. arctoides*	*M. assamensis*
M. mulatta			*M. thibetana*
M. cyclopis	*fascicularis* group	*mulatta* group	*(M. munzala)*
M. fuscata	*M. fascicularis*	*M. mulatta*	
	M. mulatta	*M. cyclopis*	*fascicularis* group
arctoides group	*M. cyclopis*	*M. fuscata*	*M. fascicularis*
M. arctoides	*M. fuscata*		*M. mulatta*
		sinica group	*M. cyclopis*
		M. sinica	*M. fuscata*
		M. radiata	*M. arctoides*
		M. assamensis	
		M. thibetana	

Morales and Melnick, 1998). The consensus arising from mtDNA trees is that *M. sylvanus* is the African sister taxon to all Asian macaques, while the rest of the *silenus* group remains intact and includes the Sulawesi macaques (*sensu* Delson). Interestingly, *M. arctoides* often clusters with the *fascicularis* group (Chatterjee et al., 2009; Tosi et al., 2000). Moreover, Tosi and colleagues (2000; 2002; 2003) generated a phylogenetic tree using Y-chromosomal DNA and it was found to be broadly congruent with mtDNA-constructed phylogenies, except for the position of *M. arctoides*, which clustered with the *sinica* group (*sensu* Delson). Due to the 'uniparental' mode of inheritance of mitochondrial and Y-chromosomal DNA, the resulting topologies likely reflect sex-biases in macaque dispersal patterns, i.e. female philopatry and male obligate dispersal (Avise, 2000; Thierry, 2007b; Tosi et al., 2003). Thus, phylogenies should ideally be reconstructed using both sex-specific genetic markers and biparental autosomal genes. The few studies that included macaque autosomal DNA typically report topologies that include *M. sylvanus* as the African outgroup to the Asian lineages, and a *silenus* group *sensu* Delson (but including the now-recognised Mentawai macaques as separate species). The *sinica* and *fascicularis* clades are recovered *sensu* Delson except for the position of *M. arctoides* (Tosi et al., 2003). In fact, a combination of the genetic evidence and palaeogeographical data suggests a possible hybrid origin for this species, which would explain its ambiguous phylogenetic position (Chatterjee et al., 2009; Tosi et al., 2003).

Phylogenetic position in the Cercopithecoidea *Macaca* is a member of the tribe Papionini, together with the genera *Mandrillus* (mandrills and drills), *Cercocebus* (mangabeys), *Lophocebus* (crested mangabeys), *Papio* (baboons), and *Theropithecus* (geladas) (Hoelzer and Melnick, 1996; Raaum et al., 2005). Figure 2.2 depicts the catarrhine phylogeny and the position of macaques in it. Fossil and molecular evidence indicates that *Macaca* is the sister group to all other (African) papionins, having originated and first diversified in the Afro-European region around the Mediterranean (Delson, 1980; Raaum et al., 2005; Szalay and Delson, 1979). The skeletal and external morphology of living macaques also seems to indicate that they retain rather generalised and ancestral cercopithecine characteristics (Delson, 1980; Groves, 2000). The latter observation was reason for Groves (1989) to doubt the monophyly of the genus altogether, but molecular evidence has since resolved this and macaque monophyly has now been well established and accepted (Groves, 2001; Morales and Melnick, 1998; Raaum et al., 2005).

Macaque phylogeny: this thesis All phylogenetic trees reconstructed from particular markers, be it molecular or morphological, are in effect hypotheses about the true species phylogeny. The present work requires a phylogenetic framework on which analyses are

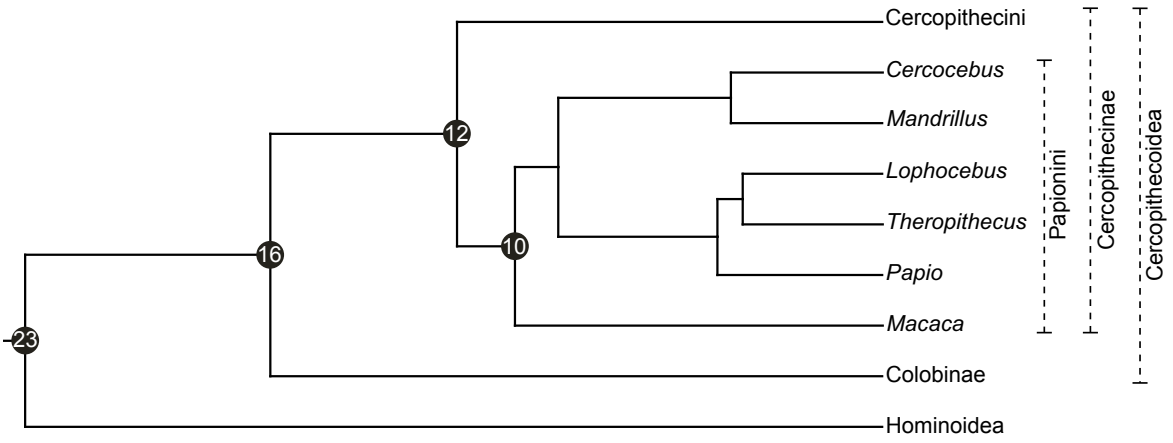


Fig. 2.2 Simplified phylogeny of Old World anthropoid (simiiform) primates (Catarrhini) and the position of the different members of the tribe Papionini, including *Macaca*, within them. Numbers at nodes are approximate divergence dates in millions of years ago (mya). (Phylogeny from Arnold et al. (2010), divergence times from Raaum et al. (2005).)

based. Arnold and colleagues (2010) provide an online, open-source database (10kTrees) of up to 10,000 Bayesian phylogenetic trees using Metropolis-coupled Markov chain Monte Carlo (MC3) algorithms for several mammalian orders, including the order Primates. Trees are generated based on a dataset derived from several mtDNA and nuclear markers and is available for nearly all species of *Macaca* (excluding *M. leucogenys* and *M. munzala*). This online source provides the possibility to download trees according to the macaque classification used in this thesis (Wilson and Reeder, 2005; see Section 2.2.1 above). Up to as many as 10,000 trees can be downloaded, ranked according to their posterior probability distributions, as well as a consensus tree. Moreover, using a relaxed molecular clock approach, this database generates both chronograms in which branch lengths represent time since divergence, and phylograms in which branch lengths are proportional to character change. Upon inspection, the trees for *Macaca* prove highly stable (the first ten trees yield an identical topology for all species; not shown) and the consensus tree corresponds to the consensus between previously published species trees (reviewed above). Therefore, the trees depicted in Figures 2.3 and 2.4 (version 2: Arnold et al. (2010)) will be used as the representation of macaque phylogeny in this thesis. Phylogenetic trees used in subsequent analyses will be pruned to the species included in the sample.

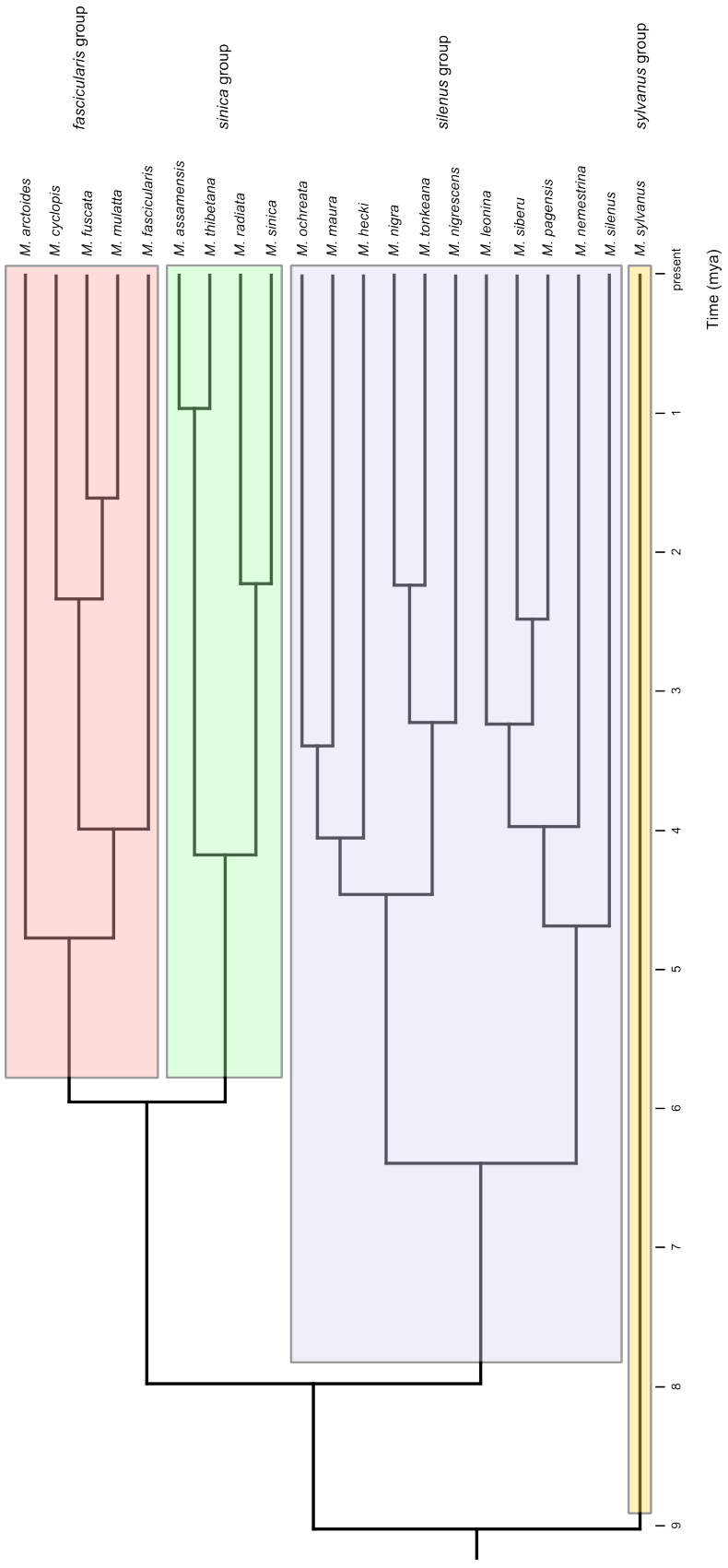


Fig. 2.3 Chronogram of macaque phylogeny (Arnold et al., 2010). Colour boxes indicate species groups as defined in this thesis. (*M. munzala* and *M. leucogenys* are not included as genetic data were not yet available for these species at the time of writing.)

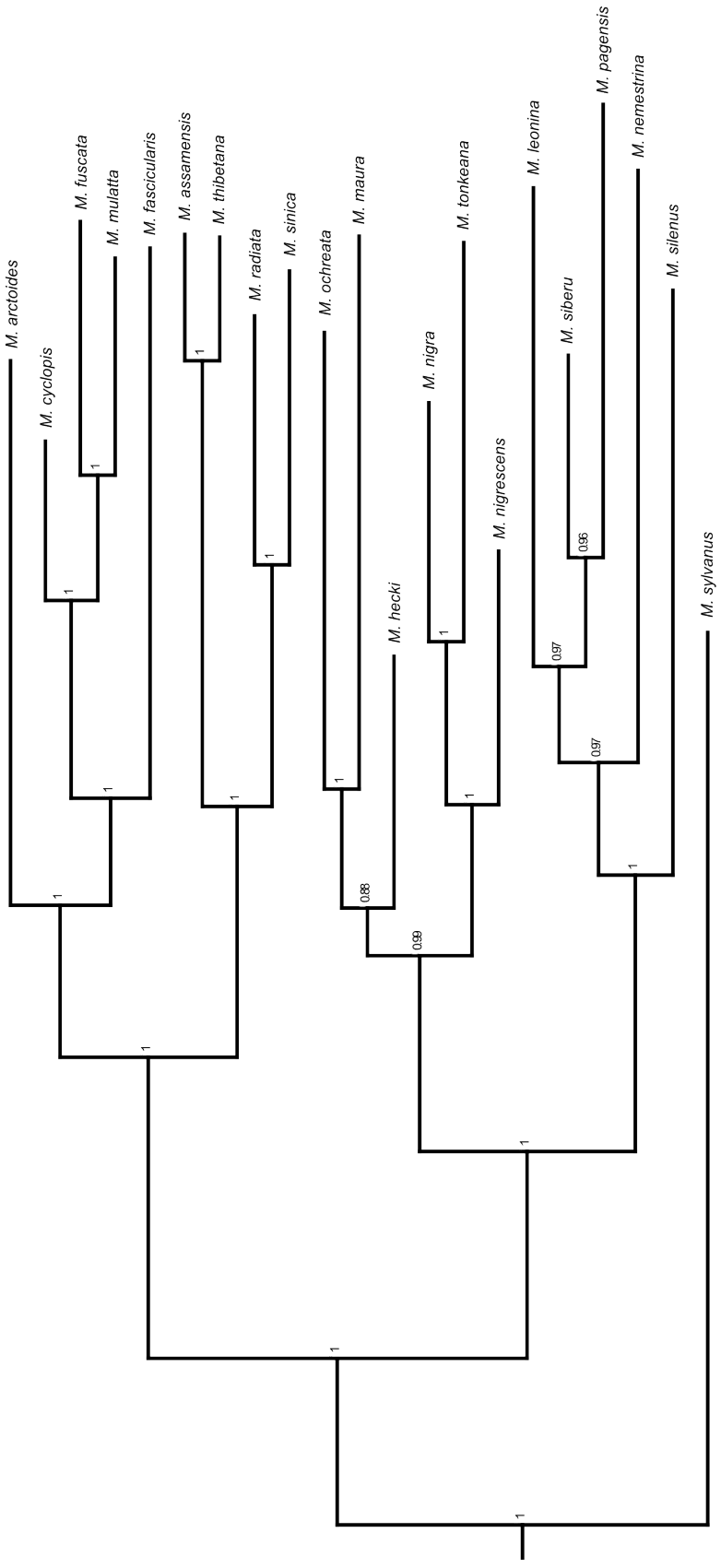


Fig. 2.4 Phylogram of macaque phylogeny (Arnold et al., 2010). Branches are proportional to the amount of character change. Clade credibility values are Bayesian posterior probabilities. All splits (internal nodes) are well resolved. (*M. munzala* and *M. leucogenys* are not included as genetic data were not yet available for these species at the time of writing.)

The classification of species groups employed in this thesis is outlined in Table 2.2. This classification is in accordance with the phylogeny used here (see especially Figure 2.3, but Figure 2.4 depicts an identical topology). This means that only monophyletic subclades within the genus are recognised as species groups (in contrast to Fooden's *sylvanus-silenus* group, which is paraphyletic - meaning that it includes the common ancestor and some but not all of its descendants). The present classification of macaques and the relationships among them is most akin to the one proposed by Delson (1980). The exception is the position of *M. arctoides*, which, is placed here in the *fascicularis* group in correspondence to the reviewed molecular evidence. A final note concerns the Sulawesi macaques, which form a monophyletic clade nested within the *silenus* group, in accordance with Groves' classification of a separate Sulawesi species group (2001). The choice of retaining the Sulawesi macaques in the *silenus* group here is to an extent arbitrary insofar as they can be regarded as a separate clade – sister to the all remaining *silenus* members – at any point in the analysis.

2.3 Distribution and Dispersal

2.3.1 Present Distribution

Macaques are an almost exclusively Asian primate lineage, occurring in tropical and subtropical Asia, on both continental land and islands. Fossil evidence indicates that during the Pleistocene macaques existed throughout northern Africa and much of Eurasia (Delson, 1980; Elton and O'Regan, 2014), where they have since gone extinct except for the sole remaining African representative of macaques, *M. sylvanus*, or the Barbary "ape" (Fa, 1989). As a group, macaques have a large geographical distribution, with the rhesus monkey (*M. mulatta*) occupying the broadest range among macaques and indeed, of all primates, second only to humans (Fooden, 2000).

Table 2.3 lists the occurrence of the various species by country or area and Figure 2.5 depicts the geographical distributions of the four species groups. *M. sylvanus* of the *sylvanus* group is the only African taxon and its relict distribution is presently confined to the Atlas Mountains of northern Morocco and Algeria and the tip of Gibraltar (see Figure 2.5a) where it is believed to have been introduced by humans (Modolo et al., 2005). The other three species groups span the Indomalaya ecozone plus the islands of Taiwan and Japan in the east. The geographical range of the *silenus* group includes the Indochinese peninsula, Malaysia and large parts of Indonesia, with *M. silenus* representing a western 'outpost' in the Western Ghats mountain range of southwest India (Figure 2.5a). The members of the *sinica* group range from peninsular India and Sri Lanka in the west to southeast China (Figure 2.5b). *M. sinica*

is the only insular species in this group. Lastly, the distribution of the *fascicularis* group is the broadest and most continuous (Figure 2.5c). *M. mulatta* spans large parts of continental southern, eastern, and some of western Asia, *M. fascicularis* covers the Indochinese and Malay peninsulas, the Philippines and the Indonesian Greater and Lesser Sunda Islands (except for Sulawesi). The remaining group members, *M. cyclopis* and *M. fuscata*, have colonised Taiwan and Japan, respectively. Notably, in part of continental and insular (i.e. Borneo and Sumatra) Southeast Asia, several macaque species have sympatric distributions, although their populations appear allopatric (Fooden, 1982a).

Latitude and island geography

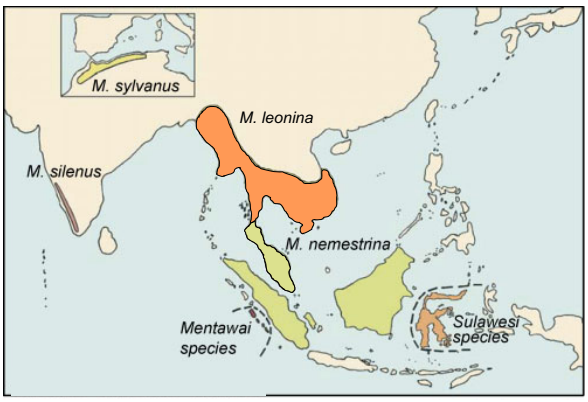
As is evident from Figure 2.5, macaques occur across a wide geographical range, both on the continent and across many islands, at both tropical and temperate latitudes. They range from approximately 20°S (*M. fascicularis*) to 40°N (*M. fuscata*) in latitude, and from roughly 70°E (*M. mulatta*) to 140°E (*M. fuscata*) in Asia, with *M. sylvanus* being found between 8°W and 6°E in northern Africa. The geographical ranges of the *silenus*, *sinica* and *fascicularis* groups broadly overlap, notably in the Indochinese peninsula where all three groups occur, dubbed macaque 'heartland' by Fooden (1982a). Within each species group species ranges are allopatric (Fooden, 1976), whereas between groups certain macaque species are sympatric (e.g., *M. fascicularis* and *M. nemestrina* on Borneo and Sumatra, and *M. mulatta*, *M. leonina*, and *M. assamensis* in the northwestern part of the Indochinese region). Populations of sympatric macaques, in turn, are mostly allopatric.

Moreover, macaque species are continentally distributed (e.g. *M. silenus*, *M. radiata*), exist on islands (e.g., Sulawesi macaques, *M. cyclopis*), or both (e.g., *M. fascicularis*). This diversity exists within species groups, as can be deduced from Figure 2.5. The islands inhabited by macaques not only differ in size, they also vary in their physiography. Some islands lie on the Asian continental shelf – the Sunda Shelf – and are separated from each other as well as from the mainland by shallow-water straits typically less than 120 meters deep, such as Borneo, Sumatra and Java (Abegg and Thierry, 2002; Fooden, 1996; Meijaard, 2003; see Figure 2.6). During the last glacial maximum 18,000 years ago (ka) and preceding glacials, land bridges would have been exposed between these continental, or shallow-water, islands and the Southeast Asian mainland due to a lowering of sea levels (Heaney, 1991; Voris, 2000). In contrast, oceanic islands, such as Sulawesi, the Philippines, and parts of Japan, have formed over oceanic plates and are separated from surrounding land masses by much deeper water straits of over 180 meters (Abegg and Thierry, 2002; Whittaker and Fernandez-Palacios, 2007). As such, these deep-water islands have rarely if ever been connected to other islands or the continental mainland (Hall, 1998). Macaques occur on both

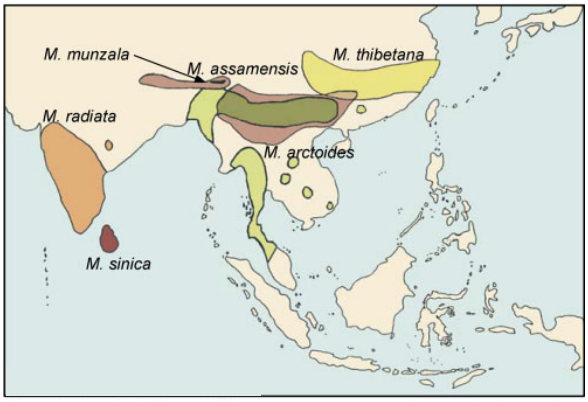
Table 2.3 Geographical distribution of the macaque species.

Species	Distribution
sylvanus group	
Barbary macaque (*M. sylvanus*)	Algeria, Morocco (and Gibraltar)
silenus group	
Liontailed macaque (*M. silenus*)	Southwest India
Northern pigtailed macaque (*M. leonina*)	Indochinese peninsula
Southern pigtailed macaque (*M. nemestrina*)	Malay peninsula, Sumatra, Borneo
Crested macaque (*M. nigra*)	North Sulawesi
Gorontalo macaque (*M. nigrescens*)	North Sulawesi
Heck's macaque (*M. hecki*)	North Sulawesi
Tonkean macaque (*M. tonkeana*)	Central Sulawesi
Moor macaque (*M. maura*)	Southwest Sulawesi
Booted macaque (*M. ochreata*)	Southeast Sulawesi
Mentawai macaque (*M. pagensis*)	Mentawai islands (except Siberut)
Siberut macaque (*M. siberu*)	Siberut Island
sinica group	
Toque macaque (*M. sinica*)	Sri Lanka
Bonnet macaque (*M. radiata*)	South and West India
Assamese macaque (*M. assamensis*)	Continental Southeast Asia
Tibetan macaque (*M. thibetana*)	East and Central China
fascicularis group	
Longtailed macaque (*M. fascicularis*)	Indochinese peninsula, Indonesia, Philippines
Stumptailed macaque (*M. arctoides*)	South China, Indochinese peninsula
Taiwanese macaque (*M. cyclopis*)	Taiwan
Japanese macaque (*M. fuscata*)	Japan

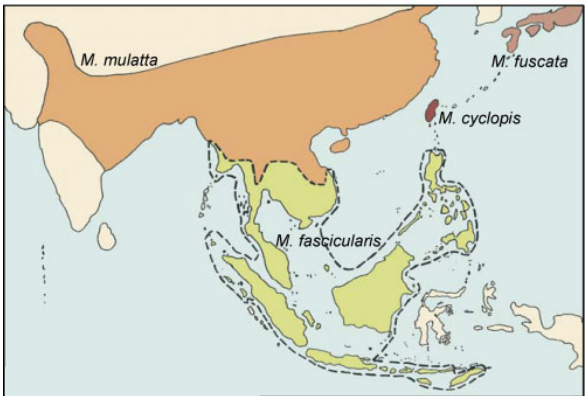
From (Fooden, 1976, 1982a; Groves, 2005).



(a) The *sylvanus* (inset) and *silenus* groups.



(b) The *sinica* group.



(c) The *fascicularis* group.

Fig. 2.5 Geographical distribution of the *Macaca* species groups. Modified from Thierry (2007b). (Note that *M. arctoides* is included in the *sinica* group here, *sensu* Delson (1980).

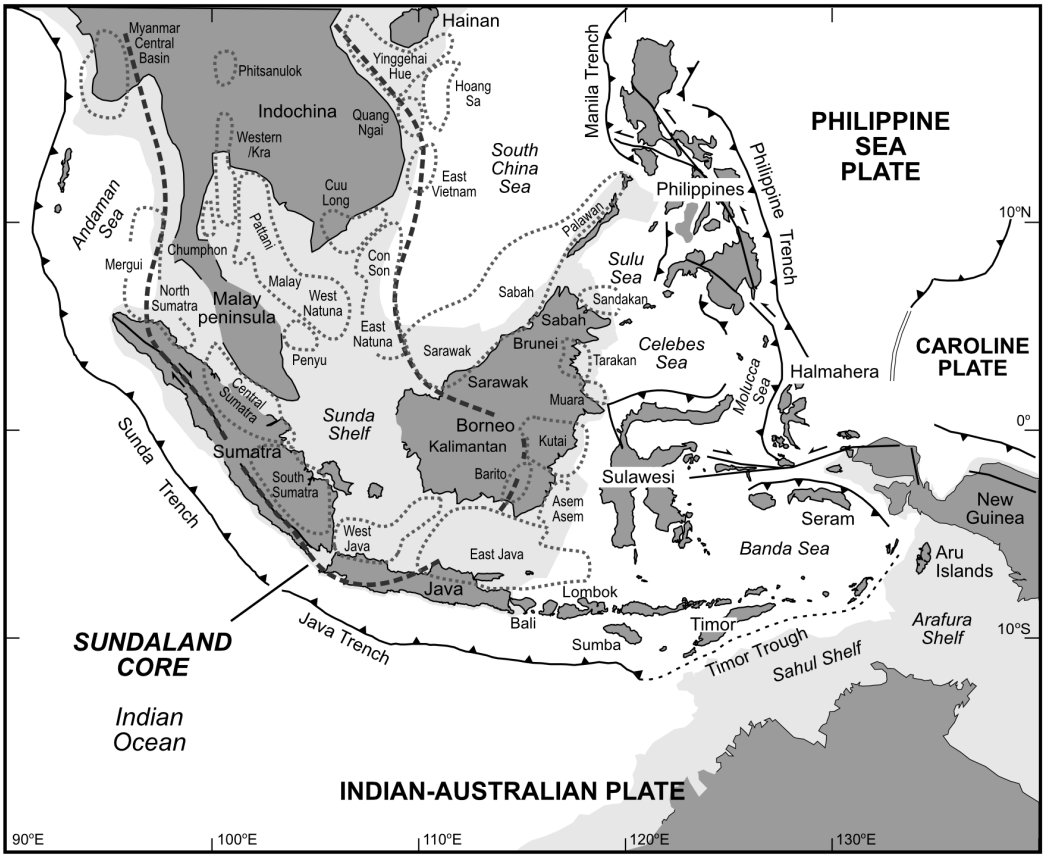


Fig. 2.6 Depiction of the landmasses (and sedimentary basins) situated on the Sunda Shelf (Sundaland), including surrounding deep-water trenches. Figure from Hall and Morley (2004) (their Figure 1).

types of islands, and presumably a variety of dispersal processes have led to this variation in distribution.

2.3.2 Evolution and Dispersal

Macaques evolved, dispersed and diversified in a relatively short period of time. Extant species are part of lineages that arose in the last five million years (Figure 2.3). A combination of processes related to competition, vicariance, migration, climatic contingencies, and resource distribution has likely given rise to the present diversity in macaque taxa and biogeography. Valuable insight may be gleaned from the palaeoclimatic and palaeogeographical background to macaque radiative evolution, as well as from the evolutionary trajectories suggested by genetic relationships. Palaeogeographical reconstructions have elucidated eustatic changes to sea levels and shifts in vegetation cover at various points in time, informing models of evolutionary dispersal by highlighting the existence of former land bridges and habitat refugia (Abegg and Thierry, 2002; Brandon-Jones, 1996; Eudey, 1980). Molecular genetic evidence offers specific windows into the temporal origins of macaques (e.g., Tosi et al., 2000, 2003; Ziegler et al., 2007), determines genetic affinity, but it can also expose historical geographical trajectories of species and populations through the study of phylogeography (Evans et al., 2003a; Kawamoto et al., 2007; Modolo et al., 2005; Rosenblum et al., 1997; Tosi and Coke, 2007).

Present zoogeography

Prior to substantive work on the molecular phylogeny of macaques, Fooden proposed the genus' major and successive waves of dispersal based on the species groupings he recognised in macaque reproductive morphology. He inferred the order of dispersal waves from present macaque zoogeography (Fooden, 1976, 1980). He posed that the *sylvanus-silenus* group (*senus* Fooden) was the first to disperse based on its highly disjunct geographical distribution. The presence of the Sulawesi and Mentawai macaques on deep-water islands that would have been inaccessible to more recent generations of macaques substantiates this assertion (Fooden, 1980). The *sinica* group shows a slightly less fragmented distribution and was therefore hypothesised to have dispersed next, displacing (ancestral) *silenus* members from areas in the process through competition (Fooden, 1976, 1980). The overwhelmingly broad and continuous geographical range of the *fascicularis* group implies that they form a lineage that evolved and dispersed last. Based on the fact that the *fascicularis* distribution is complementary, or allopatric, with that of the *sinica* group in peninsular India, Fooden

(1980) posited that the *fascicularis* members spread through competitive displacement of other macaques.

Palaeontological evidence

The fossil record indicates that the probable origin of *Macaca* was in north Africa during the Late Miocene. The split between ancestral macaques and the rest of the ancestral papionine stock represents the deepest split within the tribe Papionini (Delson, 1980; Szalay and Delson, 1979). Based on similarities in cranial morphology, it has been postulated that *Macaca* and the fossil African papionin genus *Parapapio* are sister lineages (Delson, 1980; Jablonski, 2002). The oldest fossils attributable to *Macaca* date to approximately 7 MYA (Delson, 1980; Szalay and Delson, 1979), though the taxon may be much older. The molecular phylogenetic tree in Figure 2.3 supports an origin of the crown macaques prior to 9 MYA (Arnold et al., 2010). Other published phylogenies have similarly retrieved divergence dates between extant macaques and the remaining (African) extant papionins of around 10 MYA (Liedigk et al., 2014) or older (Chatterjee et al., 2009). Next, macaque diversification started around 6-5.5 MYA in north Africa before stem macaques spread into Eurasia via northeast Africa (Delson, 1996), as evidenced by fossil remains in Egypt assigned to *Macaca lybica*.

The oldest fossil macaque from present-day Europe has been recovered in the Mediterranean Basin and date to the Ruscinian 5 MYA (Delson, 1980, 1996). Due to their strong similarity to present *M. sylvanus*, Delson assigned it subspecific status and has termed it *M. sylvanus prisca* (1980). Additional fossil macaques, *M. s. florentina* and *M. s. pliocena*, have been discovered in various European sites of Pliocene (e.g., Italy, Spain, Germany) and Pleistocene age (e.g., Great Britain, France, Czech Republic). On the basis of strong craniodental similarities, Delson assigns all European fossil macaques subspecific status to *M. sylvanus* and posits that they were all part of a single evolving lineage persisting up to as recent as 125 ka, having become extinct without major cladogenesis (1980). A notable exception is *M. majori* from the Mediterranean island of Sardinia, dated to the Pleistocene. The 100 fossil remains attributed to this taxon show a degree of morphological divergence from *M. sylvanus* that may warrant full species status (Delson, 1980; Rook and O'Higgins, 2005). There are two Eurasian papionin genera dating from the middle Pliocene to the early Pleistocene, *Paradolichopithecus* and *Procynocephalus* (Jablonski, 2002). They have been noted for their cranial affinity with *Macaca*, although postcranially they resemble terrestrial baboons (Delson, 1980; Delson et al., 2000; Jablonski, 2002). Their phylogenetic position remains unclear, but they are currently classified within the subtribe Macacina, thus recognising a closer proposed phylogenetic relationship to macaques than to other living papionins.

One of the oldest Asian fossil macaque remains have been recovered from north India in a Late Pliocene horizon (appr. 3 MYA), called *M. palaeindica* (Delson, 1980). All other well-known Asian fossil macaques date to 2 MYA or younger, but are less well known than their European congeners. Middle Pleistocene fossil macaques from Vietnam (*M. speciosa subfossilis*) and China (*M. anderssoni* and *M. jiangchuanensis*) dating to at least 1 MYA have been noted for their affinity with present *M. arctoides* and *M. thibetana*, respectively (Delson, 1980; Jablonski, 2002; Szalay and Delson, 1979). Thus, the palaeontological record seems to indicate that the macaque radiation had evolved more or less in its current form by at least 1 MYA (Delson, 1980; Jablonski, 2002).

Palaeogeographical evidence

Highly relevant to a taxon's dispersal and evolution is its past biotic and abiotic environment. This not only includes ecological competitors but also the physical geography and vegetation cover of its habitat and changes to them. Significant insights may therefore be gleaned from reconstructions of the physiography of the Southeast Asian landmasses and changes in forest cover by providing a biogeographical context to macaque evolutionary history. The climatic and eustatic changes associated with periodical glaciations and tectonic activity during the Quaternary have been invoked in explaining zoogeographical and evolutionary patterns in primates and other mammals (Brandon-Jones, 1998; Eudey, 1980; Fooden, 1975, 1976; Holloway and Hall, 1998; Jablonski et al., 2000; Meijaard, 2003).

Among macaques, the origin and dispersal of the *silenus* group in Southeast Asia has received the most attention, because it is the macaque lineage that likely most strongly experienced repeated environmental shifts arising from Pliocene and especially Quaternary oscillations in climate, landmass continuity and habitat distribution (Abegg and Thierry, 2002; Eudey, 1980; Ziegler et al., 2007). Prior to its settlement in Asia, *Macaca* was probably adapted to the seasonal habitats prevalent in North Africa and Europe. Conventionally, it has been thought that the first wave of macaque deployment occurred through a proto-*silenus* ancestor that colonised India and the Indochinese region in the Late Pliocene to Early Pleistocene (Delson, 1980; Fooden, 1975). It would have reached insular Southeast Asia during moderate cooling and drying periods that exposed the continental shelf connecting the Indonesian archipelago to the Malay peninsula, the Sunda Shelf (Figure 2.6). Lowered sea levels and corridors of remaining tropical forest presented a terrestrial path to colonise Borneo, Sumatra and other shallow-water islands in the Sunda region (Hall and Morley, 2004; Woodruff, 2003). Judging by the fact that all current *silenus* group members are encountered in evergreen forests (Fooden, 1975, 1982a), this first wave of dispersal into Asia seems to be

associated with an adaptation to tropical rainforest at a time when a largely warm and wet climate prevailed (Brandon-Jones, 1998; Heaney, 1991).

Around this time the oceanic islands of the Mentawai archipelago off the west coast of Sumatra and Sulawesi to the east of Borneo were also being stocked by macaques (Abegg and Thierry, 2002). A transitory land connection probably existed between the Mentawai islands and Sumatra, allowing not only macaques but also other mammals, including several other primate genera, to reach the islands (Abegg and Thierry, 2002). The strong level of species endemism, however, suggests that such a land connection did not exist later on in the Pleistocene, closing this region off to further dispersals (ibid.). In contrast, the biodiversity of Sulawesi is relatively impoverished and macaques are the only primates found on the island (Evans et al., 2003b). In addition, the Macassar Strait, which separates Sulawesi from neighbouring Borneo, is comparatively wide and deep and has not been connected to neighbouring Borneo or any other large island in the last 50 million years (Hall, 1998). This favours a scenario where macaques reached Sulawesi by sea rafting. Dispersal by natural rafting would have been a contingent event with incredibly low rates of success (Abegg and Thierry, 2002).

Next, evergreen forest cover was broken up during intense Quaternary glacials, forcing the ancestral *silenus* stock to retreat into refugia (Abegg and Thierry, 2002), where rainforest cover survived (Gathorne-Hardy et al., 2002; Morley, 2000). These refugia likely included the foothills of the Western Ghats mountains in southwest India, to which present *M. silenus* is confined, and peripheral islands of present-day Indonesia that would have undergone less extensive habitat changes at this time (Brandon-Jones, 1998; Morley, 2000; Woodruff, 2003). This significant climatic shift may have also contributed to the differentiation of a proto-*sinica/fascicularis* lineage (Tosi et al., 2000).

Considerably less attention has been paid to the evolutionary dispersal and differentiation of the *sinica* group and the non-*fascicularis* species of the *fascicularis* group. However, faunal migration between Sri Lanka and southern peninsular India has been possible at numerous times over the course of macaque evolution when marine transgressions frequently exposed the insular extension of the Indian tectonic plate (Rohling et al., 1998; Worldbath, 2000). The intermittent floral and faunal interchange is obvious in the similarity of biodiversity present in the Indian Western Ghats and Sri Lanka (Bossuyt et al., 2004). Glacially induced aridity and associated deforestation in northern India can account for the disjunction in the *sinica* distribution between *M. radiata* in peninsular India and *M. assamensis* and *M. thibetana* towards the northeast (Eudey, 1980; see also Figure 2.5b). Moreover, the latter two species exhibit cold adaptations, such as a large and robust body build and reduced tail length, which

suggests that they may have survived in cold climatic conditions at high latitudes during the Pleistocene (Eudey, 1980).

Members of the *fascicularis* lineage purportedly radiated during further glacial periods of the later Pleistocene and early Holocone (Abegg and Thierry, 2002). The progenitor of *M. fascicularis* in insular Southeast Asia would have invaded present-day continental islands terrestrially during climate phases when the Sunda shelf was intermittently emerged to form a continuous landmass (Abegg and Thierry, 2002; Meijaard, 2003). Concurrently, because deep-water straits were narrowed during sea lowstands, *fascicularis* progenitors would have successfully reached oceanic islands such as Nicobar, Simeulue and Lasia off northwestern Sumatra and the Philippines (Fooden, 1996). In contrast, *M. fascicularis* has seemingly not been able to colonise the oceanic islands of Mentawai and Sulawesi. Abegg and Thierry (2002) argue for a role of competition and introgression in explaining this conundrum. Once a would-be founder population successfully reaches an island it may not be able to establish itself because the area is already inhabited by ecological competitors and/or the would-be founders would be subsumed into the resident colony through interbreeding, as would have been the case on Mentawai and Sulawesi, which had both already been colonised by other macaques much earlier in time. Indeed, the oceanic islands where *M. fascicularis* is present are those where representatives of the *silenus* group are absent.

As mentioned previously, it has been postulated that the proto-*fascicularis* lineage differentiated more recently compared to the other groups on the basis of the former's wide and continuous distribution. Their dispersal and differentiation may have been, at least in part, contingent on the fragmentation in the distributions of the other macaque species groups (Eudey, 1980). Therefore, what may characterise species of the *fascicularis* group, especially *M. mulatta*, is ecological opportunism that allowed their expansion into less forested and more seasonal environments at the time of ongoing glacial cycles in the later Pleistocene. Morphological adaptations to non-tropical climates is evident in *M. mulatta*, Taiwanese *M. cyclopis*, and Japanese *M. fuscata* (Fooden, 2000; Fooden and Aimi, 2005; Fooden and Wu, 2001). Land bridges formed repeatedly between Japan and the Asian continent and between Taiwan and the mainland, which would have allowed *M. fuscata* to enter Japan as early as 500 ka (Eudey, 1980) and enabled *M. cyclopis* to reach Taiwan at various times during the last Pleistocene glaciation starting 60 ka (ibid.).

Molecular genetic evidence

The periodic nature of Pliocene and Pleistocene eustatic changes and climatic shifts, while insightful, obscures a more definitive timeline of dispersal and divergence events in the macaque lineage. An additional line of evidence comes from genetic data. Molecular genetic

data yield divergence times that are not only informative of species phylogenetic relationships, but which are also useful in providing a temporal framework for evolutionary dispersal events that is complementary to fossil and climatic data. With respect to macaques, most such analyses and evolutionary scenarios have been limited to the *silenus* group in Southeast Asia (Evans et al., 2003a; Tosi et al., 2000, 2003; Ziegler et al., 2007). Divergence dates within the macaques differ between studies, however, leading to discrepancies in the timeline of phylogenetic divergence dates coinciding with proposed environmental changes. For example, the phylogenetic tree in Figure 2.3 shows a divergence date between the African lineage (*M. sylvanus*) and Asian lineages at 8 MYA (Arnold et al., 2010). Other molecular genetic studies have found this split to be at around 11 MYA (Chatterjee et al., 2009) or 6 MYA (Liedigk et al., 2014). Ziegler et al. (2007) used evidence from the fossil record to date this branching event to 5.5 MYA and subsequently calibrated the other divergence dates based on this node. Subsequently, they put forward a scenario of the evolutionary dispersal of the *silenus* group based on their retrieved divergence dates and corresponding environmental changes. A scenario of the evolutionary dispersal of macaques based on this work (Ziegler et al., 2007) is reviewed below, but some discrepancies exist between the divergence dates amidst major climatic and eustatic events and the divergence dates retrieved by other authors and those in the phylogenetic tree in Figure 2.3.

After the aforementioned deep split between the African and Asian macaque lineages, Ziegler and colleagues (2007) found a first major split in the Asian branch of macaques at approximately 5.1 MYA based on mtDNA, between a proto-*silenus* and a proto-*sinica/ fascicularis* ancestor, following macaque dispersal from the circum-Mediterranean region into Asia around 5.5 MYA (Delson, 1980). A subsequent split evident in mtDNA occurred between the progenitors of the *sinica* and the *fascicularis* groups around approximately 4.0 MYA (Liedigk et al., 2014; Ziegler et al., 2007), which was broadly coincident with a diverging event within the ancestral *silenus* stock between an eastern lineage that led to proto-*M. nemestrina* from Borneo and the Sulawesi macaques, and a western lineage subsuming a Sumatran proto-*M. nemestrina* and the Mentawai macaques (Evans et al., 2003a; Ziegler et al., 2007). These splits occurred during a Pliocene sea level highstand in conjunction with a warmer and wetter climate (Meijaard, 2003; Woodruff, 2003).

Next, an extended cold period at the end of the Pliocene (2.7 MYA) lowered sea levels significantly, to about 100 m below present levels (BP) (Woodruff, 2003) and this may have created enough of a land bridge or a closely-spaced chain of islets for macaque progenitors to reach the Mentawai islands, where genetic data indicates that the *M. pagensis* lineage arose between 2.6 and 2.4 MYA (Ziegler et al., 2007). At around 2.3 MYA (but possibly as early as 3 MYA) the split between *M. fascicularis* and *M. mulatta* occurred somewhere in the

Indochinese region, after which *M. mulatta* dispersed west through Myanmar into India, and north and east into China (Wu et al., 2013).

The next known divergence event involved the differentiation of Sulawesi macaques around 1.9-2.0 MYA, which matches fossil and palaeogeographical estimations (Delson, 1980; Fooden, 1969). mtDNA data indicates, preceding the differentiation of the Sulawesi macaques, the possibility of either a double dispersion event to the island, one to northcentral Sulawesi and another one to southern Sulawesi, or alternatively, a single dispersal wave by a polymorphic ancestor (Evans et al., 1999, 2003a). Subsequent diversification patterns of Sulawesi macaques appears to correspond to mechanisms of allopatric speciation (Evans et al., 1999, 2003a).

Next, genetic evidence suggests there was a second colonisation event of Siberu island in the Mentawai region around 1.5-1.7 MYA by proto-*M. nemestrina* that subsequently evolved into present *M. siberu* (Roos et al., 2003; Ziegler et al., 2007). This coincided with another cold period (Meijaard, 2003) that may have briefly created a terrestrial path to Siberut Island (Worldbath, 2000). The same split, 1.5-1.7 MYA, gave rise to an ancestal *M. silenus/M. leonina* lineage that dispersed to the Malay peninsula and further north, where it diverged into the two respective lineages between 1.1-1.5 MYA, after which the ancestor to *M. silenus* became isolated in southwestern India (Ziegler et al., 2007). The evidence from mtDNA thus suggests that it was not proto-*M. silenus*, but more likely proto-*M. nemestrina* from which the members of the *silenus* group differentiated. Specifically, it was a Bornean *nemestrina*-like ancestor that dispersed to Sulawesi; not via a land bridge but probably across a shoals region in the Macassar Strait (Evans et al., 1999, 2003a; Ziegler et al., 2007).

2.4 Body Size, Ecology, Life History, and Social Organisation

2.4.1 Body Size and Tail length

Although macaques as a group are described as generic Old World monkeys (OWM) (Groves, 2001), variation in external characteristics exists between them. In fact, it is this high level of intrageneric diversity that complicates their phenotypic distinction from other OWM. Notably, macaques species vary in body size, ranging from 5 kg in *M. sinica* and *M. fascicularis* to 15 kg or more in *M. sylvanus*, *M. thibetana* and *M. fuscata* (Fa, 1989; Fooden, 1988, 2006; Fooden and Aimi, 2005; Kappeler and Pereira, 2003). This variation in body size exists irrespective of phylogenetic structuring, but rather shows evidence of a latitudinal gradient (Harcourt and Schreier, 2009; Ito et al., 2014). It is particularly evident across members of

the two species groups that span a substantial latitudinal range, namely species of the *sinica* and *fascicularis* groups (Fooden, 1988, 2006; Ito et al., 2014). The incline in species body size as a climatic adaptation to higher latitudes is known as the Bergmann effect (Harcourt and Schreier, 2009). The latitudinal cline in body size is also evident within macaque species (Albrecht, 1980; Fooden and Albrecht, 1993), dubbed Rensch's rule (Harcourt and Schreier, 2009).

All macaques are sexually dimorphic in overall size, with males being larger than females. Compared to other primates *Macaca* exhibits moderate to strong sexual dimorphism in body mass (Plavcan and van Schaik, 1997). The degree of sexual dimorphism differs between species. *M. cyclopis* and *M. mulatta* are the least sexually dimorphic, and *M. silenus* and *M. nigra* are on the most sexually dimorphic end of the spectrum (Fooden, 1975, 2006; Singh and Sinha, 2004).

Another example of size is tail length, which in macaques appears to vary from (nearly) no tail (e.g. *M. sylvanus*, *M. nigra*) to being equal to head-body length (e.g. *M. fascicularis*, *M. radiata*) (Fa, 1989; Hamada et al., 2012). As with body size, variation in tail length seems to be greater within than between species groups. Moreover, it remains unclear whether tail length evolution in macaques is characterised by independent parallel reduction or lengthening (Hamada et al., 2012). Tail length typically decreases in macaque taxa occupying high latitudes, corresponding to Allen's rule of decreasing limb length as an adaptation to cold climates (Fooden, 1980, 2006). It has been pointed out, however, that both the Bergmann effect for body size and Allen's rule for tail length in macaques are merely weakly present (Hamada et al., 2012; Harcourt and Schreier, 2009). This means that other factors have also played a role in the evolution of body size and tail length variation in macaques, be it selection or neutral evolution.

2.4.2 Diet and Habitat

Most macaques are predominantly frugivorous, although all species complement their diets with a wide variety of other food items, which may include leaves, flowers, plant stems, underground plant organs (e.g. tubers, roots), seeds, bark and other plant material, but also insects, spiders, honey, and even small invertebrates and vertebrates (e.g., Fooden, 1969, 1975, 1986, 2006; Ménard, 2004). Notably, macaques that live in urban environments or whose habitats have been disturbed by humans successfully exploit human food resources, such as cultivated crops (Ménard et al., 2014). *M. mulatta* is a prime example of this type of feeding behaviour.

There are, however, differences in the dietary ecology of macaques that cross-cut species groups, and they relate primarily to a difference in preferred habitats. As a group, macaques

occur across a broad range of habitats and environments. And while all individual taxa appear tolerant of diverse habitats, some are found more consistently in primary, broadleaf evergreen forests (e.g. *M. silenus*, *M. assamensis*, *M. arctoides*) whereas others express no such preference and exploit open, dry habitats as much as they are likely to occur in evergreen or deciduous forest (e.g. *M. fascicularis*, *M. radiata*, *M. mulatta*) (Fooden, 1982a). The distinction is especially clear between sympatric species in the macaque 'heartland', inspiring Fooden (1982a) to assign macaques to either of two ecological groups: the primary broadleaf evergreen forest, or "BE-forest", group or to the "non-BE" group, respectively.

This classification has been picked up elsewhere and has been shown to elucidate corresponding differences in life history between the two ecological groups (Ross, 1992). The non-BE macaques have been described as more opportunistic and more diverse both in terms of their habitat (Ross, 1992) and their feeding strategies (Richard et al., 1989). Richard et al. (1989) distinguished "weed" macaques from "non-weed" macaques according to the frequency and success with which species exploit human-cultivated food resources and apparently thrive on them. Non-weed macaques display a preference for and include a large portion of fruits in their diet and as such are primary feeders. Upon inspection, there is broad but incomplete overlap between the weed categories and Fooden's ecological groups. The differences between the ecological groups and weeding categories are due to macaque taxa that live in non-BE environments at high(er) latitudes but that reportedly avoid anthropogenic habitats (e.g. *M. sylvanus* and *M. cyclopis*).

Within these dual classifications of habitat and diet there is considerable variation between and within species with respect to resource exploitation. The BE-forest macaques have the most consistent preference for primary evergreen forest, including *M. silenus*, *M. nemestrina*, *M. thibetana*, and *M. arctoides* (Fooden, 1982a). Species in the non-BE group may, in addition to broadleaf forest, also be found in coastal mangroves (e.g. *M. fascicularis*, *M. mulatta*), swamp forest (e.g., *M. fascicularis*, *M. ochreata*), coniferous forest (e.g., *M. cyclopis*), scrub land (e.g. *M. sinica*), grassland (e.g., *M. maura*), cedar-oak forest (*M. sylvanus*), subalpine montane habitats (*M. fuscata*), and/or urban areas (e.g., *M. mulatta* and *M. radiata*) (e.g., Fooden, 1982a, 1986, 2006; Ménard, 2004; Riley, 2010). All macaques are semi-terrestrial, although some (e.g., *M. nemestrina*, *M. sylvanus*, and *M mulatta*) more than others (e.g. *M. silenus*, *M. sinica*, and *M. assamensis*). Some species also inhabit areas at altitudes of over 2000 meters (*M. sylvanus*, *M. nigra*), approximately 3000 meters (*M. assamensis*, *M. fuscata*), or even up to 4000 meters (*M. mulatta*) (Fooden, 2000, 2007; Fooden and Aimi, 2005; Fürtbauer et al., 2010).

2.4.3 Life History, Demography, and Social Organisation

Macaque life history, demography, and social organisation are not of special focus in this thesis and will therefore not be reviewed at length here. However, a brief mention of the variation in these parameters is meant to highlight adaptive evolution or plasticity in response to the environment.

An animal's life history refers to the suite of parameters describing an individual's timing and rate of somatic growth and reproduction (Stearns, 1992). Important life history parameters include longevity, age at first reproduction, gestation length, interbirth interval, litter size, and neonatal weight, among other traits (Harvey and Clutton-Brock, 1985; Kappeler et al., 2003). Macaques, like all primates, are characterised by slow life histories compared to other mammals (Jones, 2011; Ross, 1998), starting reproduction relatively late in life and many species producing only one infant per pregnancy. However, differences exist between species of macaque, especially in the age at first reproduction (Bercovitch and Harvey, 2004), interbirth interval (Singh et al., 2006; Wu and Lin, 1992), and breeding seasonality (Bercovitch and Harvey, 2004; Fürtbauer et al., 2010; Paul, 2004). The variation in certain life history variables in macaques corresponds not to body size but to ecological differences that result in differential selective pressures associated with environmental (un)predictability, resource distribution, and predation among others, thus providing evidence for an adaptive basis for macaque life history (Ross, 1992).

All macaques live in multi-male multi-female groups. Macaque group sizes vary depending on the environment and habitat, but mean group size is fairly stable at approximately 20-40 individuals (Ménard, 2004). Groups tend to be bigger in harsher environments (e.g. *M. fuscata* in cool forest, and *M. mulatta* in Himalayan temperate forest), and smaller where large predators are absent (e.g. some *M. fascicularis* groups in tropical rainforest) (Ménard, 2004). Group structure is characterised by female philopatry and male dispersal. Operational adult sex ratios are typically skewed towards females. In some macaques sex composition is strongly biased towards females, such as in *M. silenus* and *M. nemestrina*, whereas others have less skewed sex ratios, as in *M. sylvanus*, *M. maura*, and *M. fuscata* (Ménard, 2004). Sex ratios vary not only between but also within species, with forest populations apparently having proportionately fewer males than populations living in open habitats (e.g. *M. mulatta*). In macaques, females remain in their natal group and as a result macaque societies are organised around matrilines. Individuals form kin-biased coalitions that support each other in conflicts (Thierry, 2004). There exist notable interspecific differences with regard to patterns of aggression (e.g. intensity, retaliation) and dominance (e.g. gradient), (re)conciliatory tendencies, affiliation, nepotism, and infant handling and alloparental care, among others (Thierry, 2004; Thierry et al., 2000). There is strong empirical and statistical support that

macaque social systems reflect phylogenetic heritage (Balasubramaniam et al., 2012; Thierry et al., 2008, 2000).

Conclusion

The genus *Macaca* is taxonomically rich and geographically widely distributed for its age. Macaques occupy a range of diverse environments, marked by ecological, geographical, accompanied by at least some phenotypic differentiation. Macaques are often described as generic Old World monkeys lacking in phenotypic and ecological specialisation. However, this applies to primates in general, with only few exceptions. Moreover, variation does exist among macaques with regard to body size and associated morphological characters, ecogeographical, and other species' biology traits, and these sources of variation may therefore be investigated for signals of development, adaptation, and phylogeny.

Phenotypic adaptation to the environment through the process of natural selection is typically elucidated by cross-taxa correlations between the environment and the phenotype (Mayhew, 2006). Previous work on macaques has demonstrated a relationship between body size and tail length and latitude (e.g., Fooden, 1980, 1996, 2000; Fooden and Aimi, 2005), life history and habitat type (Ross, 1992), and habitat and ecological versatility (Fooden, 1982a; Richard et al., 1989). In contrast, the social styles of macaque species do not follow an ecological pattern but rather carry a phylogenetic signal (Thierry, 2000; Thierry et al., 2008, 2000). Furthermore, the role of contingency associated with climate change and sea level (eustatic) changes has likely facilitated the diversification of the genus *Macaca* (Abegg and Thierry, 2002; Eudey, 1980).

The traditional view of macaque evolution, especially in the Southeast Asian heartland area, has been dominated by the role of competition between ancestral populations and supposed sympatry as the dominant mode of speciation (Fooden, 1976, 1980, 1982a). However, the importance of chance events and environmental vicariance, such as climate-driven habitat contraction and the emergence of land bridges between land masses following eustatic changes, has been stressed more recently (Abegg and Thierry, 2002; Brandon-Jones, 1996, 1998; Eudey, 1980).

Chapter 3

Materials, Methods and Data

A total sample of 744 specimens comprising 13 macaque species were collected over the course of six months. This chapter first describes, in Section 3.1, the craniodental sample including the taxonomy, origin and sample sizes of the measured specimens, followed by the type of measurements, and finally a body of contextual data about the ecogeography of the species under consideration culled from published sources. Section 3.2 proceeds to detail the methodology employed in this work, including lists and descriptions of the measurements and data collection protocols. Finally, in Section 3.3, the dataset is presented in the form of descriptive statistics and histograms of the tooth measurements and a map of the geographical distribution of the sample. Furthermore, assumptions of linearity and homogeneity of the sample are tested, and intraobserver measurement error is reported. Lastly, a proxy for body size is determined for use in the subsequent analyses carried out as part of this work.

3.1 Materials

3.1.1 Species

The choice of which macaque species to measure was based on careful consideration of a number of factors. Firstly, the goal was to obtain a sample that was representative of the biological populations of macaques. In terms of systematics this meant that the different species groups (or sublineages, reviewed in Chapter 2, Section 2.2.1) needed to be roughly equally represented so that not only a phylogenetic bias was reduced to a minimum, but the sample would allow for adequate testing of phylogenetic hypotheses. Moreover, one of the primary reasons for using the genus *Macaca* as the model taxon is the rich ecological and geographical diversity macaques represent. An effort was therefore made to capture the diversity in body size, the geographical variation in latitude/longitude, range size, and island

versus continental occurrence, as well as the ecological diversity with respect to climate, habitat, and diet. An additional, practical consideration concerned sample size and therefore the representation of macaque species in museum collections. Moreover, sexual dimorphism is a pervasive phenomenon in catarrhine primate skeletal morphology (Plavcan, 2001) and therefore the aim was to collect approximately equal numbers of male and female specimens per species.

Following a systematic evaluation of the above, in combination with a consideration of the time and resources available to carry out the data collection, I decided to take measurements of the following nine species: *M. sylvanus*, *M. silenus*, *M. nemestrina*, *M. nigra*, *M. maura*, *M. sinica*, *M. radiata*, *M. fascicularis*, and *M. mulatta*. Fortuitously, during the period of fieldwork the data collection became more efficient and occasionally longer access hours to the collections were granted than previously anticipated. As a result, more data were collected than expected. This meant that sample sizes for particular species were increased where possible, but also that the existing total sample was augmented with additional species. The decision of which species should be added was again made on the basis of potential diversity in the sample to be gained, as well as which species were available in the collections of museums where extra time was unexpectedly enjoyed. *M. assamensis*, *M. fuscata*, *M. cyclopis*, and *M. ochreata* were added to the sample, albeit with smaller sample sizes. *M. arctoides*, whose phylogenetic position within the genus is contested, would have been a valuable addition, but circumstances of time and place of data collection were not favourable to the inclusion of this species.

Table 3.1 lists the macaque species for which data were collected and their respective sample sizes. A comprehensive list of all specimens by museum, including accession numbers, taxonomy, and sex can be found in the specimen catalogue (Table A.2) in Appendix A. Abbreviations of museum names are explained in Appendix A.

Table 3.1 Macaque species used in this study, by species group (see Section 2.2.1), and specimen sample sizes.

Species group	Species	Total *N*	Age			Sex		
			Juvenile	Subadult	Adult	Male	Female	Unknown
sylvanus	*M. sylvanus*	74	17	11	46	37	37	-
silenus	*M. silenus*	46	15	12	19	24	21	1
	M. nemestrina	62	3	8	51	39	23	-
	M. nigra	74	8	22	44	37	37	-
	M. maura	54	10	13	31	34	20	-
	M. ochreata	9	1	2	6	6	3	-
sinica	*M. sinica*	91	21	18	52	51	39	1
	M. radiata	84	16	30	38	46	33	5
	M. assamensis	19	1	2	16	13	6	-
fascicularis	*M. fascicularis*	92	3	14	75	51	41	-
	M. mulatta	76	13	13	50	33	43	-
	M. cyclopis	18	-	4	14	7	11	-
	M. fuscata	45	2	5	38	25	20	-

Table 3.2 Classification of age categories.

Age class	Definition
Juvenile	From the time adult first molars start erupting until adult second molars are fully erupted.
Sub-adult	From the time adult second molars are fully erupted with minimal wear until adult third molars are fully erupted.
Adult	From the time adult third molars are fully erupted with minimal wear (entire adult dentition in occlusion).

Following Sirianni and Swindler (1985) and Schillaci and Stallmann (2005).

3.1.2 Demography

Age

To control for ontogenetic variation in the dental sample only data of permanent teeth were collected. To this end adult and subadult specimens were preferred, although juveniles were included when the sample size required it. However, in that case only measurements of the permanent teeth were taken. Standard linear measurements of the cranium and mandible (discussed in Section 3.1.3 below) were only recorded on specimens with fully erupted third molars as a means to control for ontogenetic cranial and orofacial variation. Age categories are defined in Table 3.2 following Sirianni and Swindler (1985) and Schillaci and Stallmann (2005). Table 3.1 gives a breakdown of the number of specimens by age for each species.

Sex

An approximately equal number of male and female specimens was measured per species to avoid a sex bias and to enable an analysis of sexual dimorphism by species. Sex determination in museum records (e.g. specimen labels) was always verified visually and manually. This was done especially by inspecting the canines, as these are sexually dimorphic in size and shape in macaques. Occasionally, sex was unknown because the canines were not visible and cranial morphology could not be interpreted adequately to assign sex. In this case the specimen was recorded as 'sex unknown'. The numbers of specimens by sex for each species are listed in Table 3.1.

Wild or captive origin

To control for the environmental effects associated with captivity, including possible microevolutionary changes that may have started to play a role in multi-generational captive

Table 3.3 Sample sizes for wild and captive specimens by species.

Species	Unknown	Wild	Captive (wild-born)	Captive
M. sylvanus	19	24	14	17
M. silenus	6	14	9	17
M. nemestrina	5	47	5	5
M. nigra	4	59	2	9
M. maura	13	22	14	5
M. ochreata	-	8	-	1
M. sinica	13	61	6	11
M. radiata	13	33	-	38
M. assamensis	-	19	-	-
M. fascicularis	-	89	2	1
M. mulatta	1	68	7	-
M. cyclopis	-	18	-	-
M. fuscata	4	31	1	9

colonies, neither of which are representative of the natural state and evolutionary past of species, wild-collected specimens were prioritised for the collection of data. Concessions have had to be made for certain species, e.g. *M. sylvanus*, *M. silenus*, and *M. fuscata*, in order to maximise sample size. It should be noted, however, that captive living does not necessarily introduce a bias. Firstly, teeth are highly canalised, and they do not remodel during an animal's lifetime in response to environmental influences (save for wear) (Fincham et al., 2000). Secondly, captivity is an environmental factor that pertains to relatively few generations and thus is not likely to strongly confound analyses of evolutionary patterns in the present work. Thirdly, Hlusko and Mahaney (2007) compared dental samples from wild and captive baboon populations and found no statistically significant difference in tooth size measurements. Table 3.3 shows, by species, the number of wild-collected and captive specimens, as well as those of unknown origin.

3.1.3 Measurements

Standard odontometric measurements of tooth length, width (i.e. breadth) and height were taken of all teeth using dental callipers. A select number of linear distances on the cranium and mandible were also measured for reference to overall size and integration within the skull.

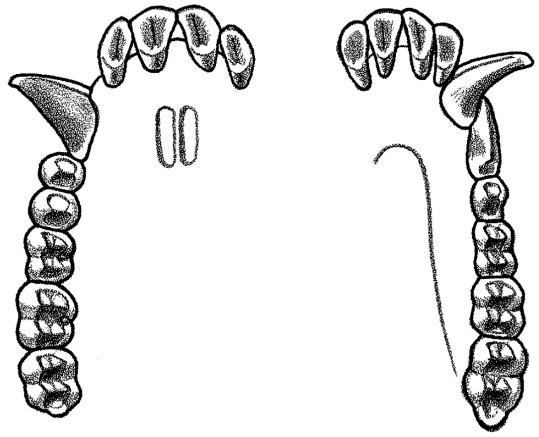


Fig. 3.1 Schematic drawing of macaque dentition (Swindler, 2002). Left: upper jaw, right: lower jaw.

Dental metrics

Linear distances of length, width, and height were measured on every adult tooth type. Figure 3.1 presents a schematic drawing of the macaque dentition (Swindler, 2002). Teeth in the upper as well as the lower dental arcade were measured, because isomeres (the same teeth in opposing jaws) are morphologically, functionally, and/or biomechanically not strictly symmetrical (Lucas, 2004). However, since the focus of this research is not to address developmental canalisation or fluctuating asymmetry between left and right antimeres (teeth on opposing sides in the same jaw), only the right side of the dentition was measured.

Macaques have bilophodont molars, with an anterior (mesial) 'loph' and a posterior (distal) 'loph' (Swindler 2002; see Figure 3.1). Molar width was measured at each loph separately. Furthermore, during the pilot studies a large degree of variation was observed in the length of the honing facet of the lower first premolar, and not only due to sexual dimorphism but seemingly also as a result of species differences. The honing facets of males are more extensive due to the proportionately bigger upper canines in males, which together form the C/P_3 honing complex (Zingeser, 1968). Therefore, P_3 length was measured in two ways: once for the entire tooth that included the honing facet, and once for the occlusal crown surface without the honing facet.

To sum up, three measurements (length, breadth, and height) were taken on every incisor, canine, and premolar (except P_3), and four measurements (length, two breadths, height) on every molar as well as P_3. A maximum total of 55 individual tooth measurements were taken on each specimen. Because not every specimen had a complete adult dentition, however, measurements were sometimes fewer. Measurement techniques are described in Section 3.2.3.

Cranial and mandibular metrics

In addition to the dental metrics a small set of measurements was taken of the skull, including the cranium, mandible, and face. These metrics serve to provide a cranial and orofacial morphometric context of tooth size variation. They were also tested for their utility in serving as a body size proxy (discussed in Section 3.3.5 below). Craniofacial measurements are meant to capture broad patterns of size variation in the cranium; mandibular and facial morphology are not the main focus here. For this purpose standard measurements commonly used in osteoarchaeology and described in Buikstra and Ubelaker (1994) formed the basis for a selection of craniometrics employed in this study. A further selection was then made following Pan and Oxnard (2002, 2004). These authors conducted an investigation of craniometric and craniodental variation in macaques and their results identified a number of measurements that were successful in separating macaques between and within species. The selected cranial and mandibular variables were subsequently tested and refined during two pilot studies (discussed below in Section 3.2.1). A number of measurements had to be discarded due to constraints associated with equipment and/or time (e.g. mandibular length). The final series of craniofacial measurements is listed in Table 3.4. Measurement techniques are described in Section 3.2.3 below.

3.1.4 Contextual Data

In addition to the odontometric and morphological data, species data were culled about habitat and dietary ecology, climate, and geography of macaques, and are presented here in a tabulated format. These data are meant to provide contextual information about the species biology and biogeography of macaques, which are relevant when associating dental variation with a suite of environmental variables or phylogeny and subsequently when interpreting the results.

The main data sources are Fooden's systematic reviews of all the macaque species (Fooden, 1969, 1975, 1979, 1981, 1982b, 1996, 2000, 2007; Fooden and Aimi, 2005; Fooden and Wu, 2001), the All the World's Primates (AWP) project (Rowe and Myers, 2011), and the PanTHERIA database (Jones et al., 2009). Fooden has published systematic review papers on all extant macaque species, which give thorough accounts of body size, reproductive behaviour, natural history, and population structure, often for many (or all) of the known wild populations of a particular species. The AWP is a collective effort and database comprising information on skeletal morphology, life history, biogeography, and (socio)ecology collected by over three hundred scientists of every primate species known. Lastly, PanTHERIA is a species-level database of the life history, ecology and geography of all extant mammals.

Table 3.4 Cranial and mandibular linear measurements.

Measurement	Description
Calvarium length	Length of the cranium minus the face.
Basion-prosthion distance	Distance (inferior) from the foramen magnum to the front of the maxilla.
Muzzle length	Length of the projecting part of the face.
Maxillo-alveolar width	Maximum width of the upper dental arcade.
Maxillo-alveolar length	Length of the palate.
Palatal width	Width of the palate.
Lower arcade width	Maximum width of the lower dental arcade.
Mandible height	Height of the lower jaw.
Mandible thickness	Thickness of the lower jaw bone.
Mandible width	Width of the entire lower jaw.
Incisal tooth row length (2x)	Distance spanning all four incisors (upper and lower).
Bicanine width (2x)	Distance from left to right canine (upper and lower).
Postcanine tooth row length (2x)	Distance from first premolar to last molar (upper and lower).
Condyle to first molar	Distance from the condylar process of the mandible to the mesial border of the lower first molar.

Adapted from Pan and Oxnard (2002, 2004).

As a rule, preference was given to data presented in Fooden, followed by the AWP. Often additional, individual publications were consulted in order to verify the nature of the data or to fill in gaps. The PanTHERIA data were generally used as a last resort only.

Body size

Body size is a major predictor of an animal's metabolism and therefore resource exploitation (Brown et al., 2004; Huxley, 1932). Mediated by the relationship to metabolic rate, organismal size also links to an array of other aspects of species biology, including life history parameters (e.g. age at first reproduction, gestation length, longevity) and population ecology (e.g. group size, population density, predation), among others (Brown et al., 2004; Peters, 1983; White et al., 2007).

Overall body size is also a predictor for other size variables, that is, sub-anatomical structures and regions within an animal (Huxley, 1932; Jungers et al., 1995; Martin, 1980); bigger individuals have bigger 'everythings'. The scaling relationship between organismal size and the size of sub parts may be characterised by isometry (e.g., lung and heart size or skeleton weight in primates) or by allometry (e.g., eye-to-body size or the well-known relationship between body and brain size in primates) (Martin, 1992; Schmidt-Nielsen, 1984). Therefore, it is important to be able to standardise tooth size across varying body sizes in comparative analyses, for instance to be able isolate the morphological variation that is due to factors other than size. In addition, body size is itself an adaption (Martin, 1980), evidenced by the many patterns of biological diversity that exist for size (Peters, 1983; West et al., 1997), and an understanding of the relationship of the dentition to overall size will therefore contribute significantly to our understanding of the evolutionary and developmental mechanisms underlying the dental phenotype.

For all thirteen macaque species used in this study, data for two body size traits were collected: body mass and head-body length. These data are presented in Table B.1 in Appendix B for each species. All data are based on wild populations.

Diet and habitat

Dietary ecology is a major driving force in evolution, on both a macroevolutionary and a microevolutionary scale. Temporal and spatial patterns of food distribution, abundance and quality are key and direct ecological factors affecting the survival, growth and evolution of animal populations (Krebs, 2009; Pianka, 1978). Ecological specialisation (stenotopy) refers primarily to an animal's dietary flexibility and secondarily to its habitat use, as animals can only live where their preferred foods exist. Ecological generalists (eurytopes) lack the

behavioural and morphological specialisations associated with a particular, typically narrow diet, but this is offset by the adaptation to environmental change and variability awarded by their ecological flexibility (Vrba, 1980). There is a trade-off between ecological stenotopy and eurytopy, and the advantage of one strategy over the other in relation to the fitness outcome will depend on a number of interrelated factors pertaining to an animal's body size, life history, and environment (Harcourt et al., 2002). An animal's dietary adaptations are under constant selection because of the critically important relationship between an individual's survival and fitness on the one hand and its energy demands associated with growth and reproduction on the other (Futuyma, 1998; Pianka, 1978). Given that natural selection acts to maximise fitness and that energy supplies from food present a principal proximate cause of survival and reproduction, many of the selective processes that operate on populations are mediated by dietary ecology.

The principal function of teeth are food ingestion (incisors) and mastication (premolars and molars). Therefore, dental morphology shows first and foremost a dietary signal (Kay, 1975, 1978; Lucas, 2004; Ungar, 2010). The aim of this work, however, is not to elucidate patterns of functional morphology in relation to particular food types in the macaque dentition. Rather, I mean to use the dentition as a representation of an important phenotypic trait under selection, and to understand evolutionary patterns of variation between species in how they relate to evolutionarily relevant parameters of diet and habitat, ecological flexibility, and niche partitioning.

The variables included in this category are proportion of frugivorous feeding, proportion of folivorous feeding, the intra-annual range of percentage of fruits in the diet, dietary breadth, habitat breadth, and ecological group. As different food types have differential spatial and temporal distributions across habitats, dietary strategies affect various other aspects of a species' ecology, including abundance and ranging patterns (Milton and May, 1976; Pulliam and Caraco, 1984), gregariousness (Sterck et al., 1997; van Schaik, 1983), and resource competition (Pulliam and Caraco, 1984; van Schaik, 1989; Wrangham, 1980) among others. Therefore, the degree of frugivory (as inversely related to the degree of folivory) as a feeding strategy is informative for questions relevant to evolutionary ecology. Degree of frugivory and folivory are measured here as the relative time spent feeding (%) on fruits and leaves, respectively. Data including sources are presented in Table B.2 in Appendix B.

Dietary breadth was determined on the basis of the variety of foods consumed by a species. Categories of food types were adapted from alltheworldsprimates.org (AWP) (Rowe and Myers, 2011) and the PanTHERIA database (Jones et al., 2009). Table B.3 lists the classification of diet categories used here. Diet breadth, then, reflects the total range of foods macaques have been observed to consume. Observational accounts differ by researcher and

species as not all macaques have been part of a long-term study or live in a habitat that is conducive to close monitoring. However, multiple data sources were consulted for each species to obtain as complete an account of their diet as possible.

Habitat breadth is measured as the number of habitat strata, or biomes, that are of major importance to a species. Data on occupied habitats were culled from the literature (mainly from Fooden's systematic reviews) and the AWP project, and cross-referenced with data published by the International Union for the Conservation of Nature (IUCN) Red List. Habitat strata were defined following the IUCN's habitat classification scheme. Artificial, that is human-made, habitats were together counted only once because they do not represent ancestral environments; they are included here to reflect habitat flexibility of macaques.

Lastly, Fooden (1982a) noticed that where species of macaques were sympatric in heartland Southeast Asia, they were separated ecogeographically such that there was no direct ecological competition between populations of different species. Macaques can broadly be divided into two ecological groups: species that prefer and predominantly occur in broadleaf evergreen (BE) forest (e.g., *M. silenus*, *M. assamensis*), and those that have no such preference and exist in a wide range of forest and non-forest (non-BE) habitats (e.g., *M. radiata*, *M. mulatta*) (Fooden, 1982a). This classification has been implemented by others (Ross, 1992) to test whether BE and non-BE macaques differ in their relative level of *r*- versus *K*-selection, which is associated with a lower or higher density-dependent mortality respectively. Results have demonstrated a significantly different rate of population increase between macaques of different ecological groups (Ross, 1992). This disparity reflects a difference in life history and socioecology between BE and non-BE macaques. Fooden's classification for the continental Southeast Asian macaques is followed here, while the remaining island species and the African Barbary macaque are assigned to either of the two ecological groups based on the habitat data available for them.

Geography and climate

Lastly, data on the abiotic environment were amassed. Together with the biotic environment, the physical environment of populations determines the ecological context in which microevolution – and macroevolution on a larger scale – occurs. Moreover, biotic factors such as food distribution, feeding competition, and predation, among others, are – directly or indirectly – associated with geography and climate (Brown and Lomolino, 1998). Therefore, species data for latitude, longitude, geographical range size, island/continental occurrence (Table B.4), altitude (Table B.5, and temperature and precipitation data were collected (Table B.6) and can be accessed in Appendix B.

Spatial coordinates, altitude, and range sizes Latitude is an important biogeographical predictor of a number of ecological variables, such as temperature and climatic variability, as well as food distribution in space and time (Brown and Lomolino, 1998; Harcourt, 2012). Moreover, latitudinal gradients exist for body size (the Bergmann effect; Blackburn et al. (1999)), biodiversity (the latitudinal diversity gradient; Hillebrand (2004)), and geographical range size (Rapoport effect; Gaston et al. (1998)). To enable an analysis of dental phenotypic variation in a spatial context, latitudinal and longitudinal data were collected on species level (Table B.4), as well as on specimen level to maximise data resolution and enable within-species analyses. On species level, latitude and longitude are represented by the coordinates of the central point in each species' geographical range (e.g., *M. fascicularis* is known from field observations to occur between 18°N and 10°S, so its mid-range latitudinal coordinate is therefore 4°N). Mid-range coordinates are taken from Jones et al. (2009). Specimen-specific geographic coordinates were gathered from the gazetteers published in Fooden's systematic reviews (preferred) or, alternatively and when the location was known, using Google Earth. Location precision was coded so as to distinguish between exact, approximate, or average (species) coordinates. Specimen-specific coordinates were not retrieved for captive specimens.

Geographical range size (km^2), latitudinal and longitudinal ranges (the ranges between the minimima and maxima), and altitudinal range were also included because they are indicative of environmental diversity. Populations and species are often exposed to a wider range of habitats and climates when they are geographically and altitudinally more widely distributed, and thus range sizes may reflect ecological flexibility of populations. To capture average altitude by species, the median was collated from the literature for each species (details are in Table B.5).

Island biogeography The ecology on islands is different from that on continents (MacArthur and Wilson, 1967). There is a well-known island effect on vertebrate body size ("the island rule"), with small species (<3 kg) becoming bigger and bigger species (>3 kg) becoming smaller than their mainland ancestors and conspecifics (e.g. Foster, 1964; Lomolino, 2005). Selection for large individuals during immigration and ecological release due to the absence of larger competitors and predators allows small-bodied vertebrates to increase in body size (e.g. Lomolino, 1985), while large-bodied vertebrates are characterised by dwarfism as a result of resource limitation on islands and ecological release from smaller species (e.g. Lomolino et al., 2010).

In addition to a change in selection pressures, the relative importance of microevolutionary processes may also operate differently on islands (MacArthur and Wilson, 1967).

Genetic drift may be stronger in insular environments when populations are small and/or isolated (Futuyma, 2013; Mayr, 1942; Wright, 1931), whereas gene flow with the mainland population(s) declines or ceases altogether as a result of geographical barriers (e.g., water straits). Here, species are categorised according to whether they are island or continental species, or whether they have a mixed distribution (Table B.4).

Climate Climatic conditions, notably temperature and precipitation, determine vegetation growth and therefore the temporal and spatial distribution of food resources. They of course also have a direct effect on animal homeostasis. Standard parameters of temperature and precipitation were extracted from among the bioclimatic variables in the WorldClim database (Hijmans et al., 2005) and imported using the *raster* package (Hijmans, 2016) in RStudio (RStudio Team, 2015), at a resolution of 2.5 arc-minutes. Data were extracted on specimen level for wild specimens for which the geographical coordinates of the locality were exactly or approximately (within 12 decimal degrees) known. To obtain species-level values, climate data were aggregated among specimen-level data by first retaining unique localities only, to avoid pseudo-replication, and second, by averaging the climate data across these unique localities to arrive at species means (Table B.4).

3.2 Methods

This section first briefly describes the two pilot studies of macaque dental variation. Next, the techniques used for the collection of the dentocranial data are explained in detail, and lists and definitions of the individual measurements and equipment used are presented.

3.2.1 Pilot Studies

Two pilot studies were conducted before the actual data collection. The first one was carried out at the British Museum of Natural History in London, and the second study was carried out during an academic visit at the University of California, Berkeley, at the Museum of Vertebrate Zoology. The purpose of these pilot studies was three-fold. The studies were necessary to first become familiar with the overall skull and dental morphology of macaques and the level of observable variation. Secondly, they served as the basis for the selection of metric and non-metric measurements and subsequently to refine established, standard measurements so that they may be appropriately applied to *Macaca*. This step included the design of macaque-specific protocols for scoring dental wear and a few additional non-

metrics. Thirdly, measurements for the intra-observer error study were taken during the pilot research.

Between the two museums the following species were studied: *M. silenus*, *M. nemestrina*, *M. nigra*, *M. maura*, *M. radiata*, *M. fascicularis*, *M. mulatta*, and *Macaca sp.* (undefined). Although *M. sylvanus*, the sole representative of the *sylvanus* group, was not sampled during the pilot studies, all other species groups were represented by one or (usually) more species. Thus, a good overview of macaque dental variation was obtained and therefore measurement techniques were specified such that they may appropriately be applied to all members of the genus.

Standard linear measurements of the teeth were taken using dental callipers according to various measurement protocols. The techniques typically used for human material (e.g., Kieser, 1990; Moorrees, 1957) were compared to those for primates (Swindler, 2002). As expected, human odontometric techniques are often not appropriate for the measurement of non-human primate teeth, and this was also the case here. Swindler's (2002) technique proved more suitable and was refined to suit the macaque dentition.

The same procedure was applied to a set of general measurements of the skull. Buikstra and Ubelaker's 1994 guide for measurements of the cranium, mandible and face of human remains were used as the basis. While macaque skull morphology is obviously different from that of modern humans, the landmarks are homologous and therefore the human protocol provided an adequate starting point. These measurements were complemented by skull (i.e. craniofacial) measurements used in a study of macaque morphometrics (Pan and Oxnard, 2002, 2004) and all were tested for applicability. Two measurements, mandibular length and mandibular angle, require measurement with a mandibulometer. It was found that due to the angular shape of the macaque mandible the lower anterior dentition interfered with the mandibular length measurement, and the asymmetry in the mandibular rami introduced substantial measurement error. Therefore, these measurements were discarded in the present work for practical reasons.

3.2.2 Recording Inventory and Tooth Wear

Inventory

Before calliper measurements were made each specimen's dentition was inventoried. Teeth were recorded for their state of eruption or damage. This was useful for later reference (e.g., during the data cleaning process). The inventory scoring protocol can be found in Table B.7 in Appendix B and was adapted from (Connell, 2004). When a particular measurement or set of measurements could not be taken on a tooth due to damage for instance, then this tooth

was replaced - where possible - by the tooth in the same tooth position on the left side of the dental arcade (i.e. its antimere). In that case however, all measurements for that tooth position were taken on the replacement tooth. When the tooth crown had not fully erupted measurements were still made provided the measurement protocol could be adhered to. For example, tooth length was still recorded even though incomplete eruption prevented tooth width(s) and height to be measured.

Tooth wear

In addition to recording inventory, tooth wear was also rated for each tooth. This was important because data were collected from specimens that varied in their age-at-death and diet, and as a result they exhibited different stages of dental wear. Wear may interfere with tooth size measurements: as the tooth crown wears down the shape and linear dimensions may change.

Ideally, only unworn teeth would have been measured so as to control for size variation due to abrasion (tooth wear associated with food particles and grit) and attrition (tooth-on-tooth wear). However, this was not feasible for several reasons. Firstly, adult specimens were preferred and they will always exhibit some level of tooth wear for most teeth. Secondly, due to non-simultaneous eruption of the various teeth variability exists in the degree of wear of one tooth relative to the adjacent tooth. Some parts of the dentition are therefore necessarily worn (e.g., the first molar) when others are still unworn (e.g., the third molar). Time and resources did not allow to limit data collection to unworn teeth without seriously compromising minimally viable sample sizes (i.e. ideally 30 specimens per sex per species). Moreover, this approach would have prevented the study of how teeth and tooth modules behave in relation to each other within individuals. However, in order to be able to account for tooth wear in some fashion, tooth wear scores were devised and each specimen was scored for level of wear on each tooth.

Tooth height is most obviously affected by the process of wear. The mesiodistal lengths, in the present work, are also sensitive to wear because these measurements were taken at the occlusal surface. Measuring teeth mesiodistally at the alveolar margin is impractical (even with fine-point dental callipers) because there is insufficient space for insertion of the callipers and therefore mesiodistal length cannot be adequately measured in this manner. Measurement of tooth breadths, i.e. widths, were not subject to this problem. Therefore, breadth of the tooth crown was measured at the point of maximum breadth (buccolabially for incisors, buccolingually for all other teeth).

Scoring systems for gross tooth wear have been devised by other authors for humans, non-human primates, and artiodactyls (Gantt, 1979; Grant, 1982; Scott, 1979; Smith, 1984).

Human scores, for example those by Smith (1984), are ill-advised to be applied to macaques (and indeed most non-human primates) because the dental morphology of the two taxa are substantially different; the molar cusp pattern canine height differs and consequently the dental wear pattern does too. Gantt (1979) delineated eight different stages of tooth wear based on pattern and degree of dentine exposure for cercopithecines, including two macaque species and one baboon species. However, during exploratory research of macaque dental morphology in the original nine macaque species in the present work, quite some variation in the pattern of dentine exposure was observed, notably in the molars. Dentine exposure and degree of enamel remaining are the main cues for visually scoring wear stages, and the variation in these two traits between different species of macaques was substantial enough to render Gantt's classification inapplicable due to the increased potential for observer error. Therefore, I devised macaque-specific dental wear scoring keys taking into account the observed variation between individual specimens and species. The scores are presented and explained in Tables B.8 and B.9 in Appendix B.

3.2.3 Measurement Techniques

Dental and craniofacial metrics

Linear measurements of the individual teeth constitute the primary data used in the present work. For this purpose a classic morphometrical approach (Kieser, 1990; Moorrees, 1957; Swindler, 1976). Measurement techniques were adapted from Kieser (1990, humans) and Swindler (2002, primates) and modified where necessary for application to macaque dental morphology. Tooth measurements are defined in Table B.10 (mesiodistal length), Table B.11 (buccolingual/buccolabial width), and Table B.12 (crown height) in Appendix B.

Secondary linear measurements of the skull are described in Table B.13. All cranial and orofacial measurements were taken on bony landmarks, except for tooth row measurements.

For the measurement of metric traits a pair of Mitutoyo digital dental fine-point sliding callipers was used (573 series, part number 573-721). These callipers have a range of 150 millimeters and an accuracy of 0.01 millimeters. All measurements were recorded in millimeters (mm). Measurements were input directly in a Microsoft Excel data spreadsheet using a Mitutoyo 264-012-10 input tool and food pedal. Data entry was monitored visually for errors during the measurement and input process.

3.3 Data

3.3.1 Data Provenance

Locality data for each specimen can be found in the specimen catalogue (Table A.2) in Appendix A. Figure 3.2 depicts the geographical distribution of the study sample. Specimens with the same geographical coordinates are represented by a single bubble, with bubble size indicating specimen density.

3.3.2 Intraobserver Error

Measurement error contributes to the variance of morphometric measurements. Since the presence of any signal, effect, or relationship is detected by studying trait variation, it is important to quantify how much of this variation is due to measurement error. There are two types of error: reliability or precision, and accuracy or bias. The first type refers to how consistent measurements of the same trait or subject are between observations or observers, and the second type refers to how much measurements deviate from the 'true' value (Ulijaszek and Kerr, 1999). In the present work, there was one observer, and so only the intraobserver error is relevant. Accuracy can only be determined when the true value is somehow known, which is not possible to determine for the skulls and teeth measured here. The only measurement error that can be assessed, therefore, is the precision with which measurements were taken.

Various statistics exist to quantify the reliability of measurements. A common statistic is the technical error of measurement (TEM):

$$TEM = \sqrt{\sum D^2/2N} \tag{3.1}$$

where D^2 are the squared deviations between measurements and N is the number of specimens (Ulijaszek and Kerr, 1999). TEM is therefore measured per trait, with N specimens measured multiple times (e.g., when measured twice, D = measurement 1 - measurement 2). Measurements that vary in scale, such as skull length and tooth length, will yield TEM values that are not directly comparable. Therefore, relative TEM expresses the error as the proportion of the trait mean:

$$rTEM(\%) = (TEM/mean) * 100 \tag{3.2}$$

TEM and rTEM are computed here for each individual morphometric measurement (i.e., 71). Furthermore, intraclass correlations can be computed to give an overall measure of

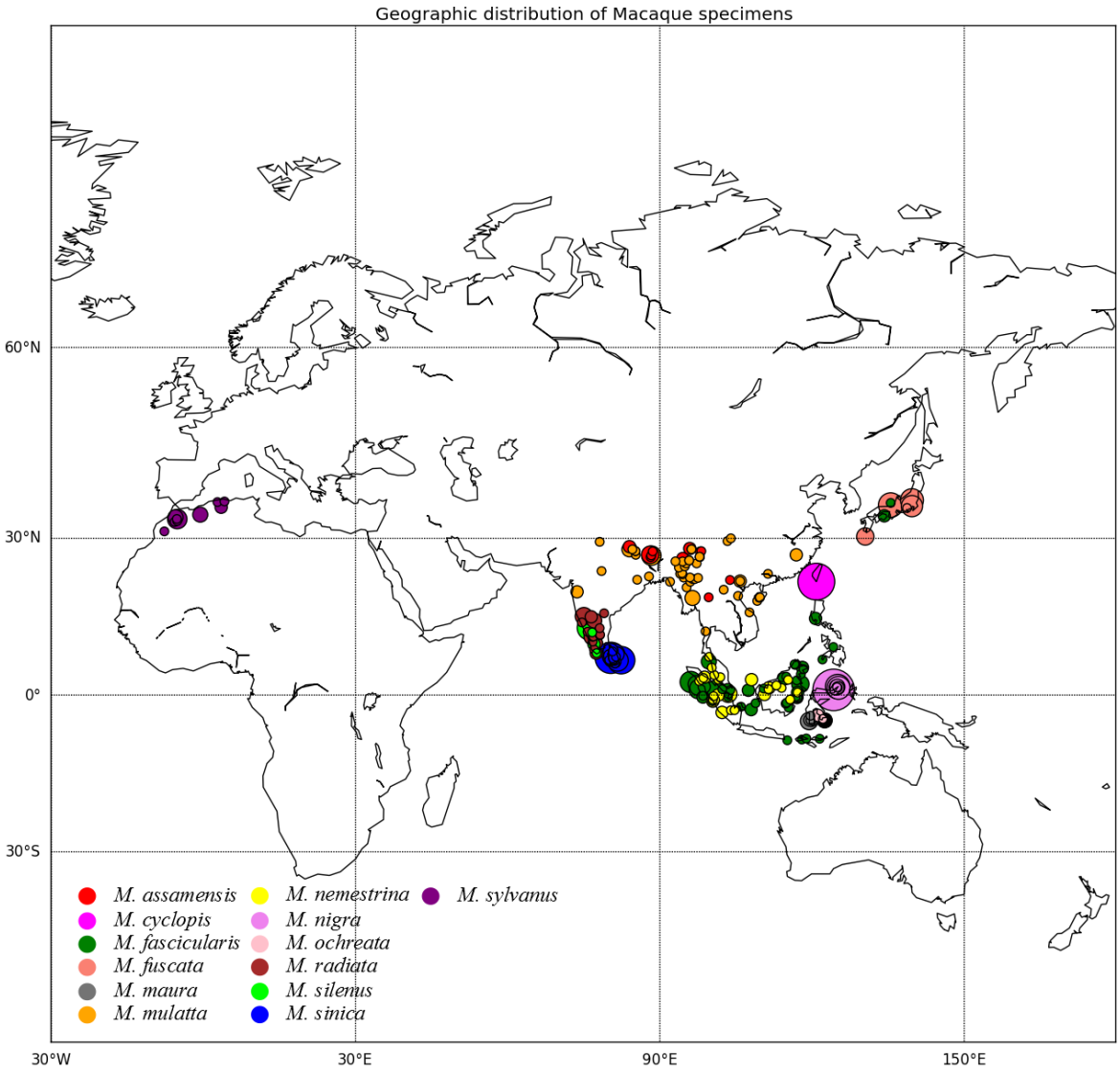


Fig. 3.2 Geographical distribution of the specimens measured in this study. Variation in bubble size reflects the number of specimens collected for a given location.

Table 3.5 Intraobserver measurement error values (TEM and relative TEM) computed from two sets of repeated measurements on 50 macaque specimens.

	TEM			rTEM (%)			% error of the mean
	mean	min	max	mean	min	max	
Dental	0.05	0.01[a]	0.19[b]	0.90	0.12[c]	4.54[b]	2.92
Cranial & mandibular	0.09	<0.01[d]	0.49[e]	0.31	0.02[d]	1.81[e]	0.73

[a] UM3PW, [b] LI2MD, [c] UCMD, [d] UIAW, [e] UBCB.

reliability across multiple variables between measurement sets (Shrout and Fleiss, 1979). As a measure of the intra-observer error across all my measurements, the concordance correlation coefficient is used here (Lin, 1989, 2000).

The intraobserver error study was conducted using a set of 50 macaque specimens from the Museum of Vertebrate Zoology (MVZ) at the University of California, Berkeley. These data served the purpose of finalising measurement protocols and to compute the intraobserver error, and are not included in the final dataset.

The mean, minimum, and maximum values of TEM and rTEM are reported for the primary tooth dimensions and supporting cranial and mandibular measurements separately in Table 3.5.

The concordance correlation coefficient (ρ_c) for all 17 supporting cranial and mandibular measurements is 1 (0.9998–0.9999 95% confidence intervals). For all 54 dental dimensions, ρ_c = 0.97 (0.96–0.98 95 % CI).

The mean deviation between repeated measurements, averaged across all 71 craniodental variables is 0.18 millimeters. Swindler reported a mean error of 0.2 mm for his own study of the dentition of multiple primate species by means of dental callipers (Swindler, 2002). The mean deviation by tooth dimension, i.e., mesiodistal length, labiolingual/buccolingual width, and height, was highly similar at 0.16 mm, 0.17 mm, and 0.17 mm, respectively. Error expressed as the proportion of the trait mean yields an average percentage (%) error of 2.92% for tooth dimensions (lengths, breadths, heights), and 0.73% for the cranial and mandibular measurements (Table 3.5).

3.3.3 Descriptive Statistics

Dental metrics

Tables 3.6 to 3.8 describe the primary data of tooth length, width and height, respectively. The mean, range, standard deviation, and variance are reported. In generating these statistics for tooth length and width, extreme scores (i.e.outliers) were omitted. The identification and criterion for outliers is discussed in Section 3.3.4 below. Tooth height is highly sensitive to dental wear and therefore only teeth of minimal to moderate wear (a tooth wear score less than 5) were used to generate the statistics reported here. These statistics are not used in any analysis, but serve to present an overview of the typical variation in size between tooth dimensions.

In addition, the coefficient of variation (CV) is presented, which is intended to account for the so-called mouse-elephant effect: the fact that variance of a morphological trait increases with trait size (Polly, 1998a; Sokal and Rohlf, 1995). Therefore, relative variance is often a more appropriate and informative measure, especially when comparing the variability between teeth and tooth dimensions that is independent of size, but which may reflect other genetic, developmental, or selective factors instead. The CV was calculated by dividing each measurement's mean by its standard deviation.

The distributions of the most important dental measurements, i.e., tooth lengths and widths, are also summarised in histograms. Tooth height measurements are omitted here, because the observed variation in dental height is suspected to be largely due to the variation in degree of wear and as such is likely predominantly a measure of age (the relationship between tooth height and macrowear is further addressed in Chapter 4). Data are separated by sex in each histogram to elucidate any present sex differences in tooth size or the distribution. Histograms by tooth measurement pertaining to the sample of all macaques (ignoring species classification) are presented in Figure 3.3. Further histograms detailing the distribution of tooth lengths and breadths by species can be found in Figures C.1 to C.39 in Appendix C. The key to variable abbreviations can be found in Table B.14 in Appendix B.

Table 3.6 Descriptive statistics of mesiodistal tooth lengths.[a]

Measurement	*N*	Mean	Range	Std. Dev.	Variance	CV
Maxilla						
central incisor, I^1	631	6.24	4.81	0.88	0.78	0.15
lateral incisor, I^2	648	3.97	3.49	0.61	0.37	0.16
canine, C	489	7.43	9.28	2.07	4.27	0.28
third premolar, P^3	634	4.95	3.23	0.58	0.34	0.12
fourth premolar, P^4	645	5.01	2.61	0.54	0.29	0.11
first molar, M^1	720	6.96	3.69	0.70	0.49	0.11
second molar, M^2	687	8.00	4.45	0.90	0.80	0.11
third molar, M^3	556	7.81	4.91	1.03	1.07	0.13
Mandible						
central incisor, I_1	653	4.34	3.36	0.56	0.32	0.14
lateral incisor, I_2	646	4.25	4.03	0.67	0.45	0.16
canine, C	575	4.36	4.90	0.98	0.97	0.23
third premolar, P_3 (occlusal)	615	6.41	8.73	1.51	2.28	0.24
third premolar, P_3 (total)	574	10.66	14.40	2.88	8.30	0.27
fourth premolar, P_4	630	5.58	3.98	0.70	0.49	0.13
first molar, M_1	713	6.84	3.49	0.66	0.44	0.10
second molar, M_2	686	7.91	5.16	0.86	0.74	0.11
third molar, M_3	530	9.63	6.20	1.34	1.80	0.14

[a]Excluding outliers => 3.

Table 3.7 Descriptive statistics of labiolingual or buccolingual tooth widths.[a]

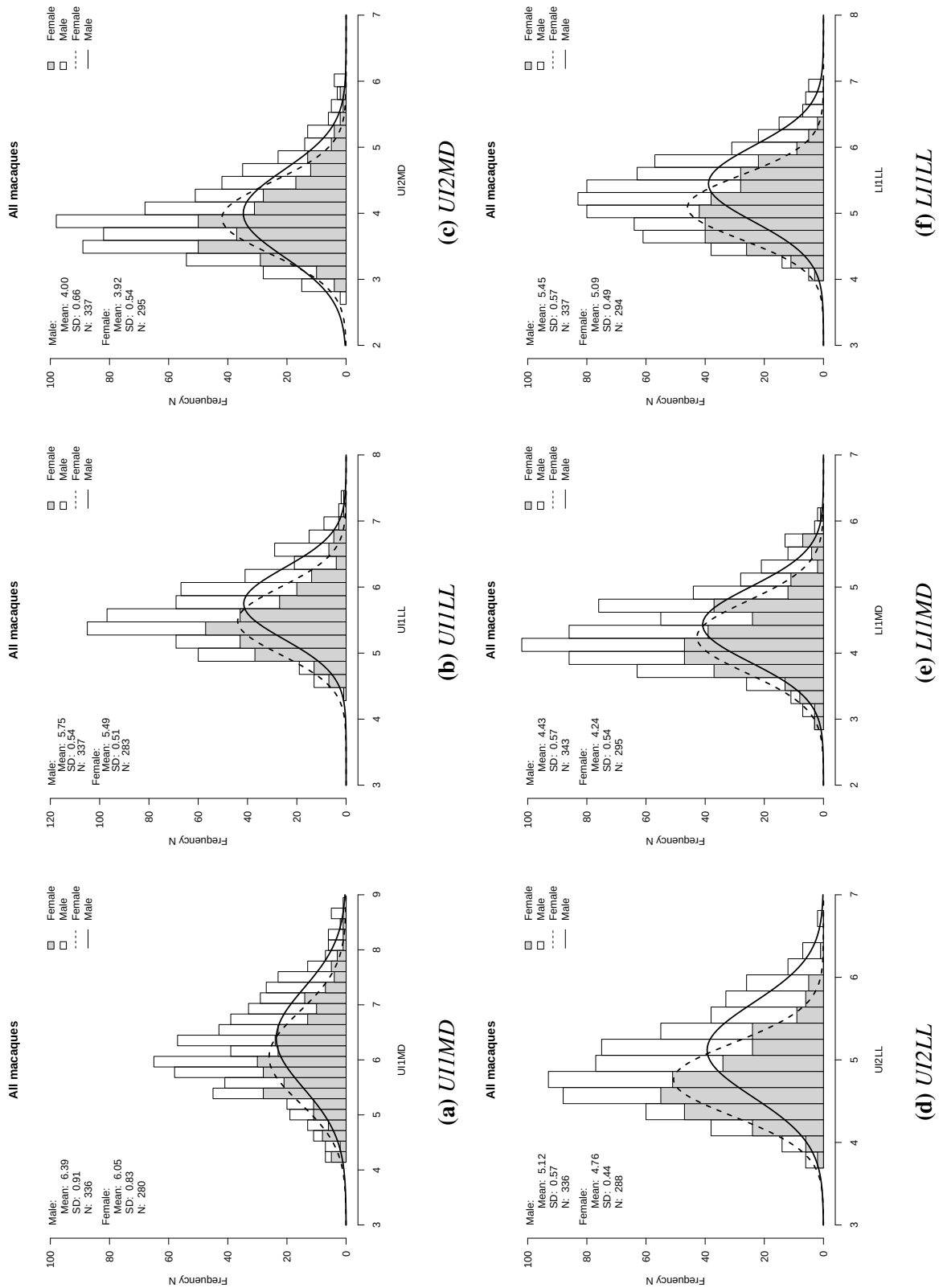
Measurement	N	Mean	Range	Std. Dev.	Variance	CV
Maxilla						
central incisor, I^1	633	5.63	3.18	0.54	0.29	0.10
lateral incisor, I^2	637	4.96	3.12	0.54	0.3	0.11
canine, C	477	6.04	5.69	1.13	1.28	0.20
third premolar, P^3	646	5.79	3.21	0.61	0.38	0.11
fourth premolar, P^4	644	6.23	3.35	0.61	0.37	0.10
first molar, M^1 (anterior)	722	6.7	3.63	0.63	0.4	0.10
first molar, M^1 (posterior)	716	6.21	3.28	0.56	0.32	0.09
second molar, M^2 (anterior)	674	7.74	4.23	0.84	0.7	0.11
second molar, M^2 (posterior)	664	7.07	4.03	0.74	0.54	0.11
third molar, M^3 (anterior)	529	7.63	4.56	0.97	0.94	0.13
third molar, M^3 (posterior)	529	6.53	4.59	0.88	0.78	0.14
Mandible						
central incisor, I_1	644	5.28	3.05	0.56	0.32	0.11
lateral incisor, I_2	641	4.9	3.3	0.61	0.38	0.13
canine, C	567	7.4	8.56	1.78	3.17	0.24
third premolar, P_3	628	4.25	3.66	0.72	0.52	0.17
fourth premolar, P_4	630	4.77	2.78	0.51	0.26	0.11
first molar, M_1 (anterior)	713	5.48	2.86	0.55	0.3	0.10
first molar, M_1 (posterior)	704	5.39	2.84	0.54	0.3	0.11
second molar, M_2 (anterior)	682	6.71	3.96	0.77	0.59	0.12
second molar, M_2 (posterior)	668	6.27	3.45	0.69	0.48	0.11
third molar, M_3 (anterior)	527	6.88	4.58	0.94	0.89	0.14
third molar, M_3 (posterior)	523	6.12	3.9	0.82	0.68	0.14

[a]Excluding outliers => 3.

Table 3.8 Descriptive statistics of tooth heights.[a]

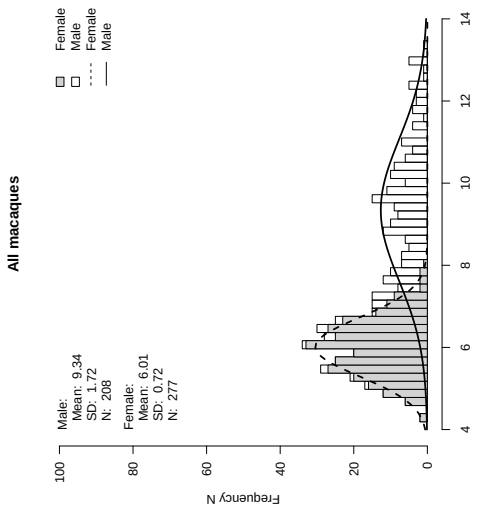
Measurement	N	Mean	Range	Std. Dev.	Variance	CV
Maxilla						
central incisor, I^1	326	10.7	12.27	1.67	2.78	0.28
lateral incisor, I^2	418	8.68	8.78	1.37	1.88	0.25
canine, C	202	15.84	26.99	7.41	54.97	0.50
third premolar, P^3	472	6.14	6.83	1.12	1.25	0.20
fourth premolar, P^4	493	5.26	4.63	0.76	0.57	0.17
first molar, M^1	525	4.23	3.69	0.57	0.33	0.16
second molar, M^2	579	5.09	4.18	0.7	0.5	0.15
third molar, M^3	476	5.05	4.39	0.83	0.68	0.17
Mandible						
central incisor, I_1	399	9.24	14.68	1.57	2.47	0.25
lateral incisor, I_2	449	7.78	8.37	1.3	1.69	0.22
canine, C	365	12.57	19.24	4.17	17.38	0.36
third premolar, P_3	466	10.6	16.29	3.1	9.58	0.30
fourth premolar, P_4	481	5.74	6.08	0.89	0.79	0.19
first molar, M_1	445	4.62	4.18	0.68	0.46	0.22
second molar, M_2	544	5.75	6.21	1.02	1.04	0.22
third molar, M_3	471	5.83	7.3	1.2	1.43	0.23

[a]For tooth wear <= 3.

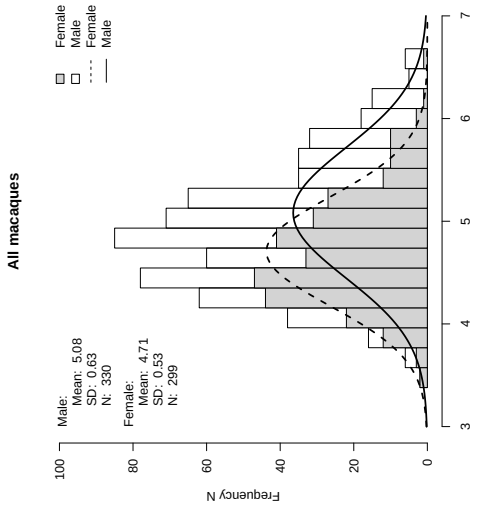


(a) *UI1MD* **(b)** *UI1LL* **(c)** *UI2MD*

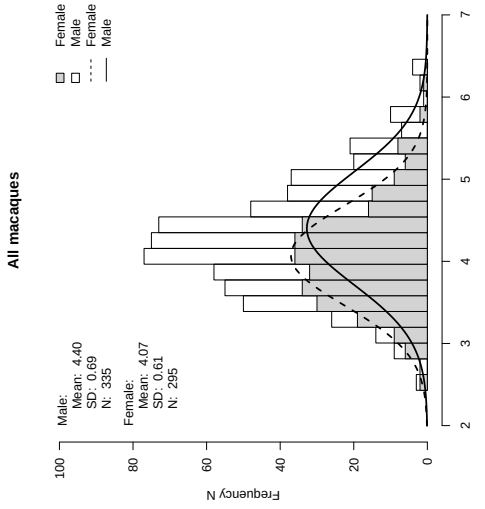
(d) *UI2LL* **(e)** *LI1MD* **(f)** *LI1LL*



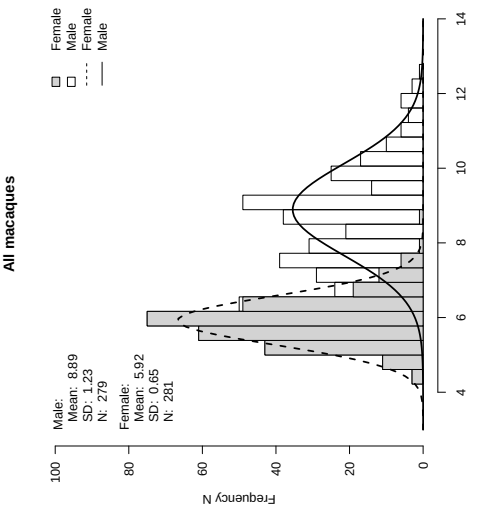
(i) *UCMD*



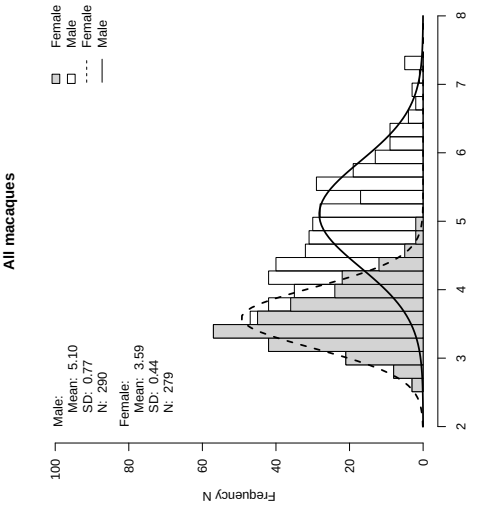
(h) *LI2LL*



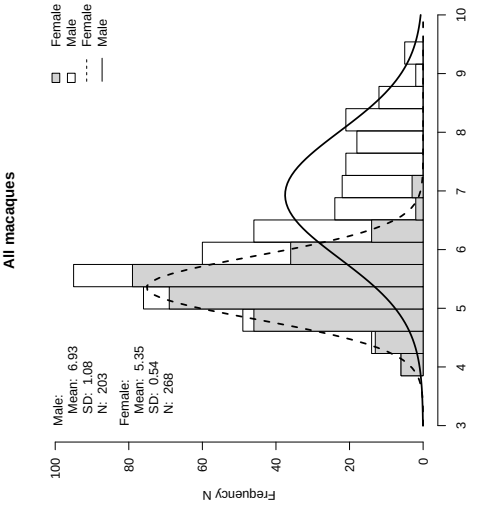
(g) *LI2MD*



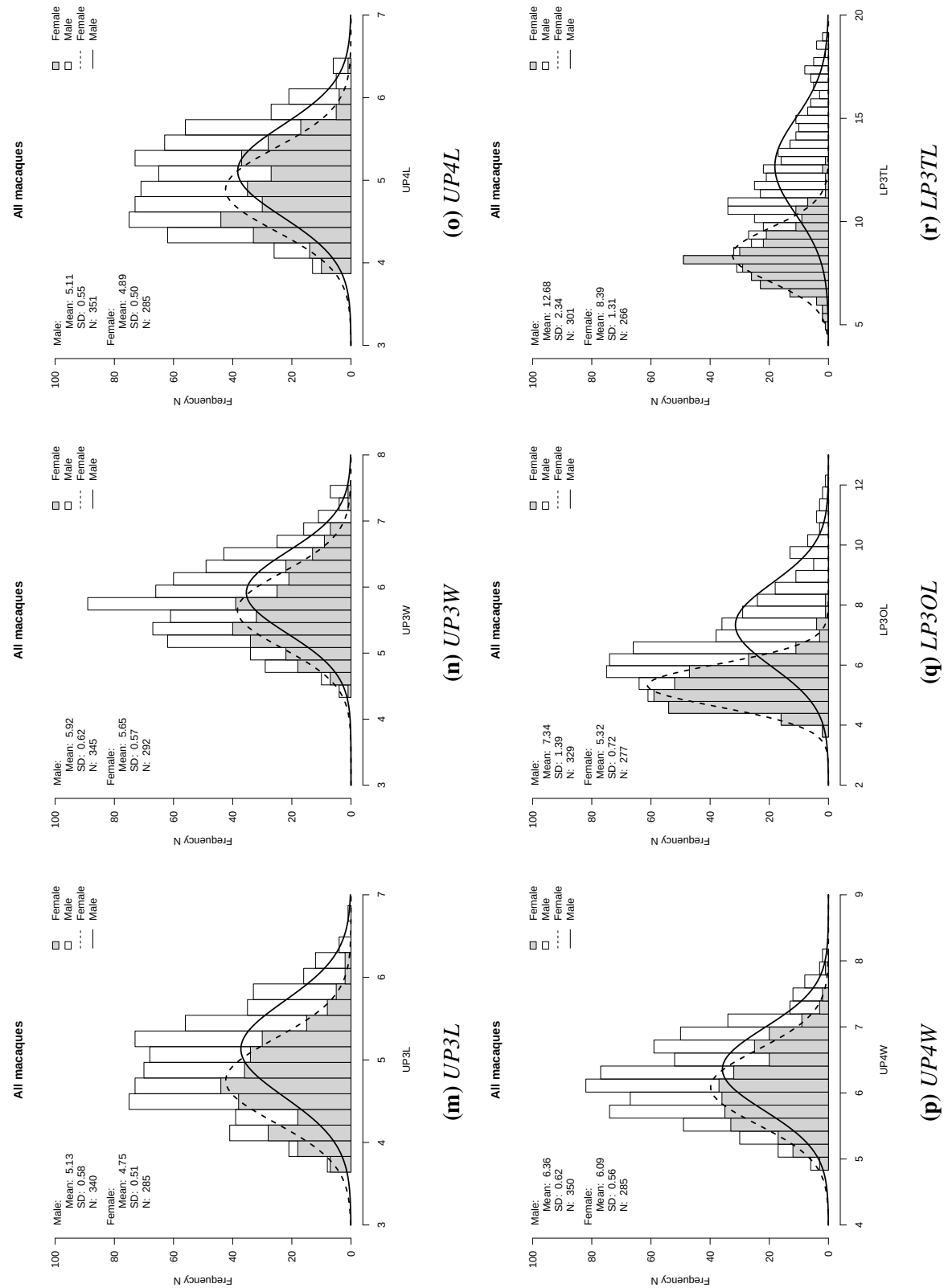
(l) *LCBL*



(k) *LCMD*

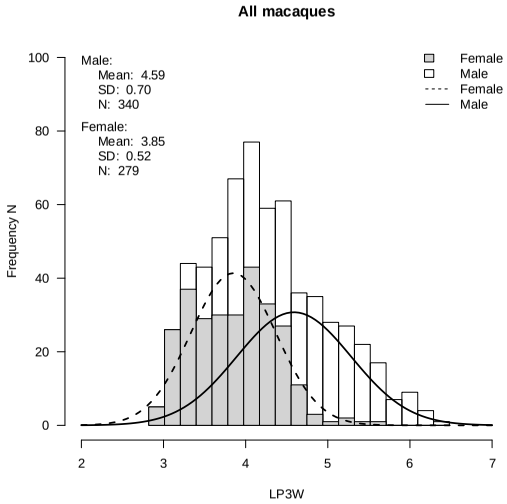


(j) *UCBL*

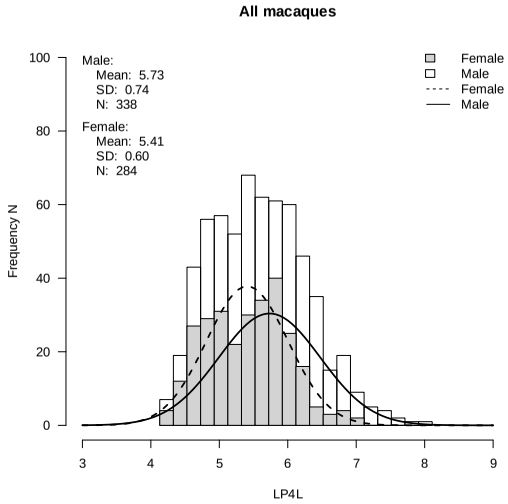


(m) *UP3L* **(n)** *UP3W* **(o)** *UP4L*

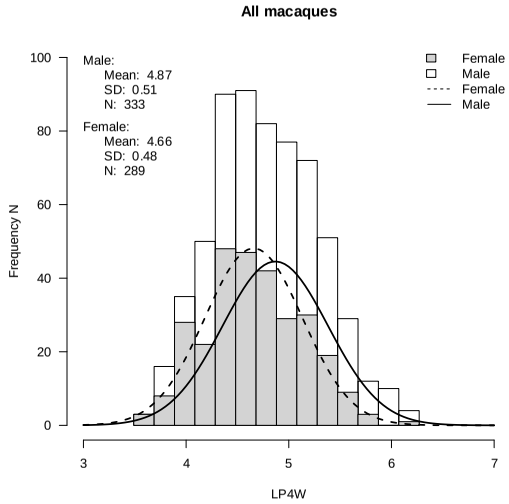
(p) *UP4W* **(q)** *LP3OL* **(r)** *LP3TL*



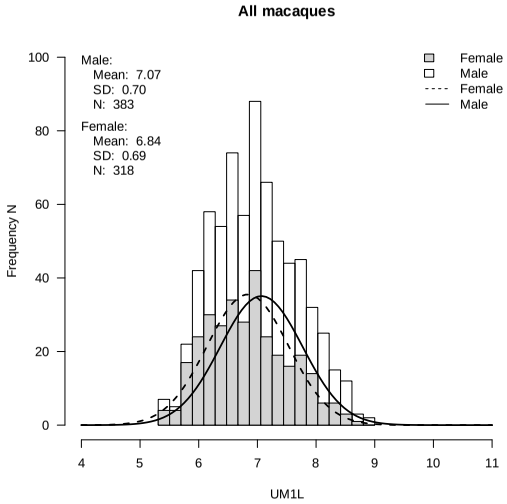
(s) *LP3W*



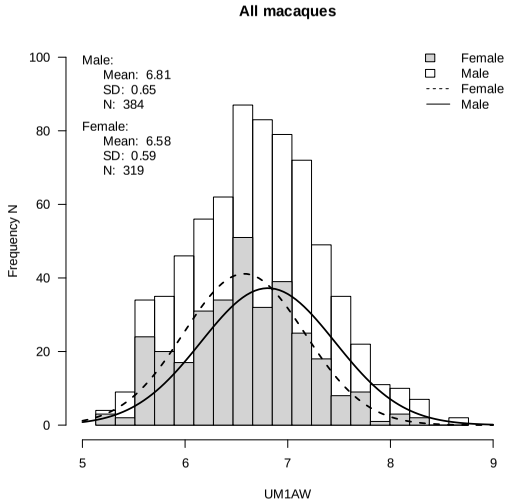
(t) *LP4L*



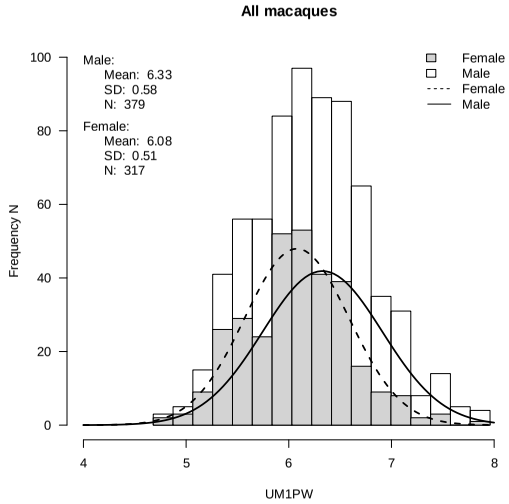
(u) *LP4W*



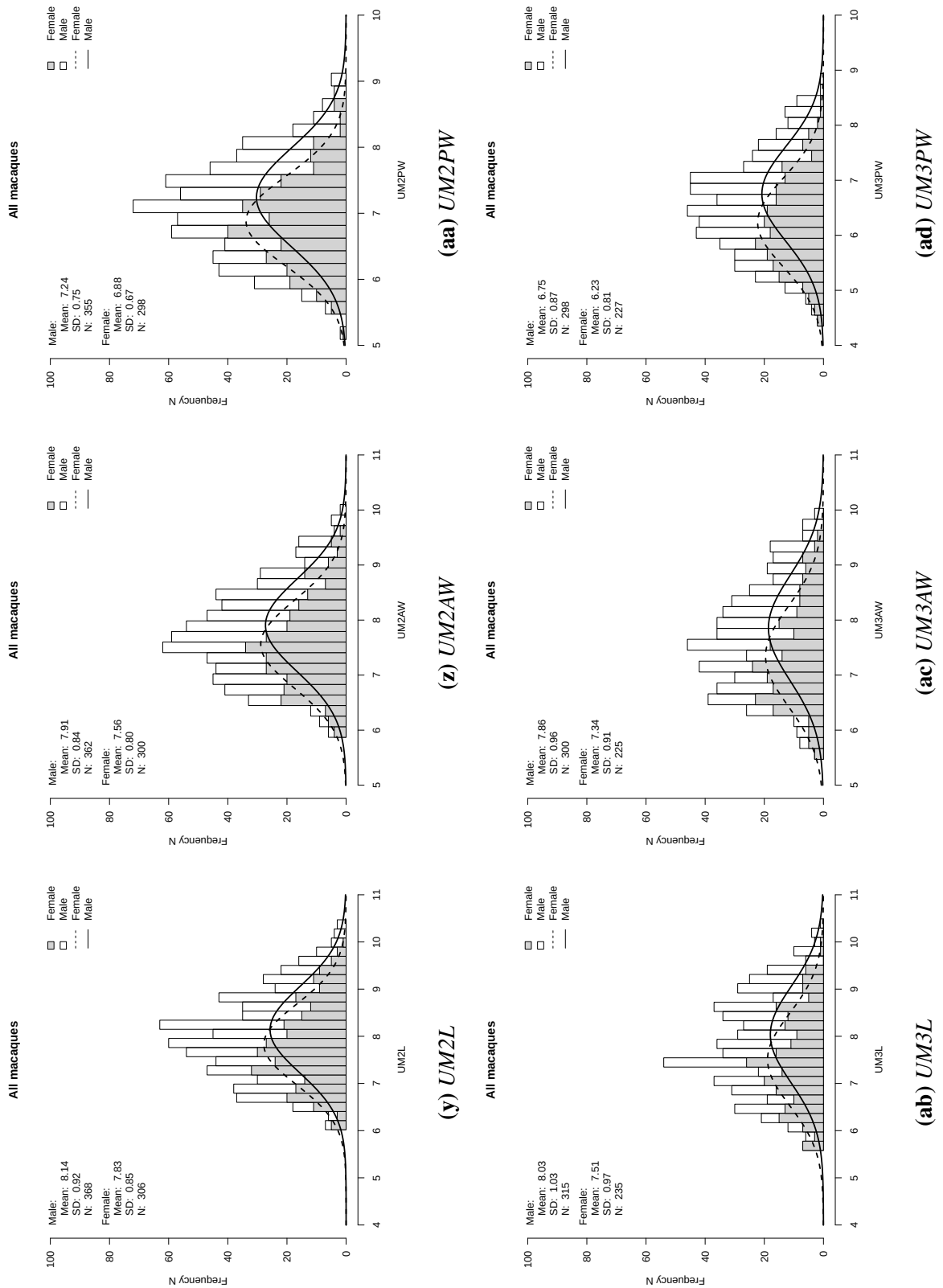
(v) *UM1L*



(w) *UM1AW*



(x) *UM1PW*



(y) *UM2L*

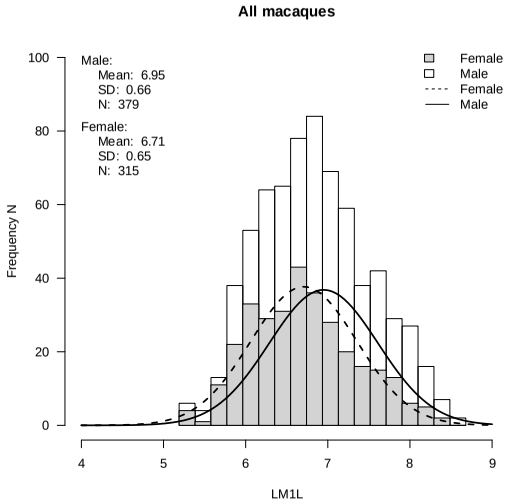
(z) *UM2AW*

(aa) *UM2PW*

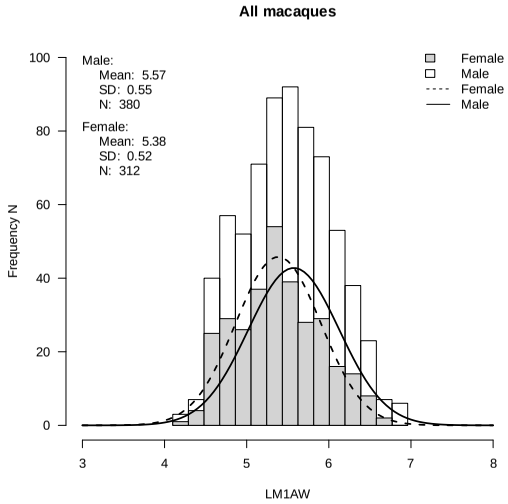
(ab) *UM3L*

(ac) *UM3AW*

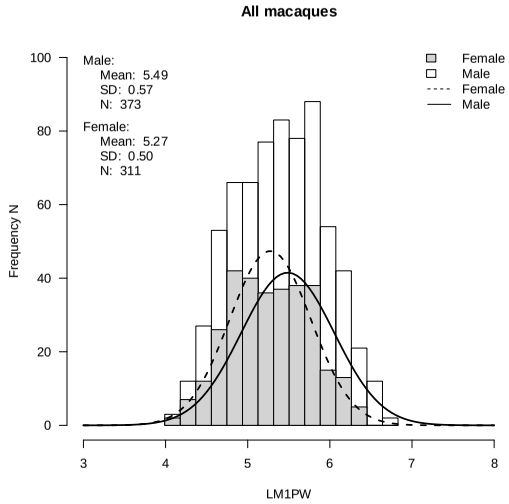
(ad) *UM3PW*



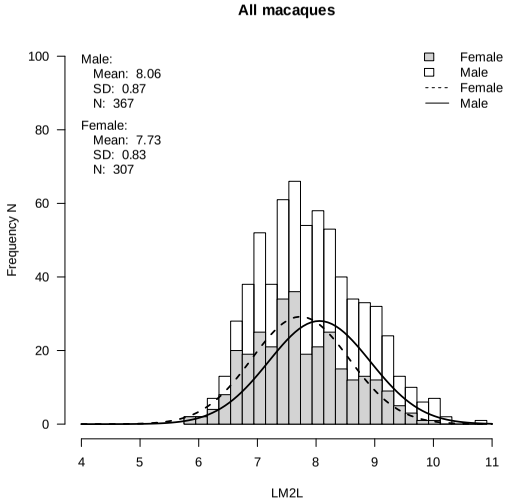
(ae) *LM1L*



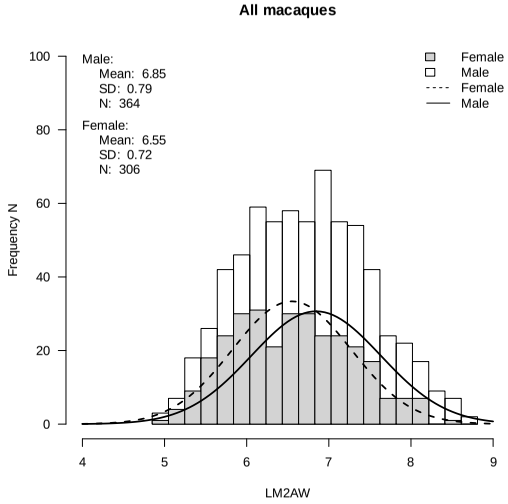
(af) *LM1AW*



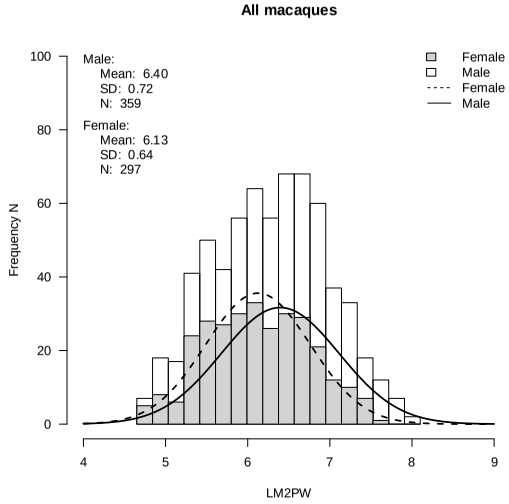
(ag) *LM1PW*



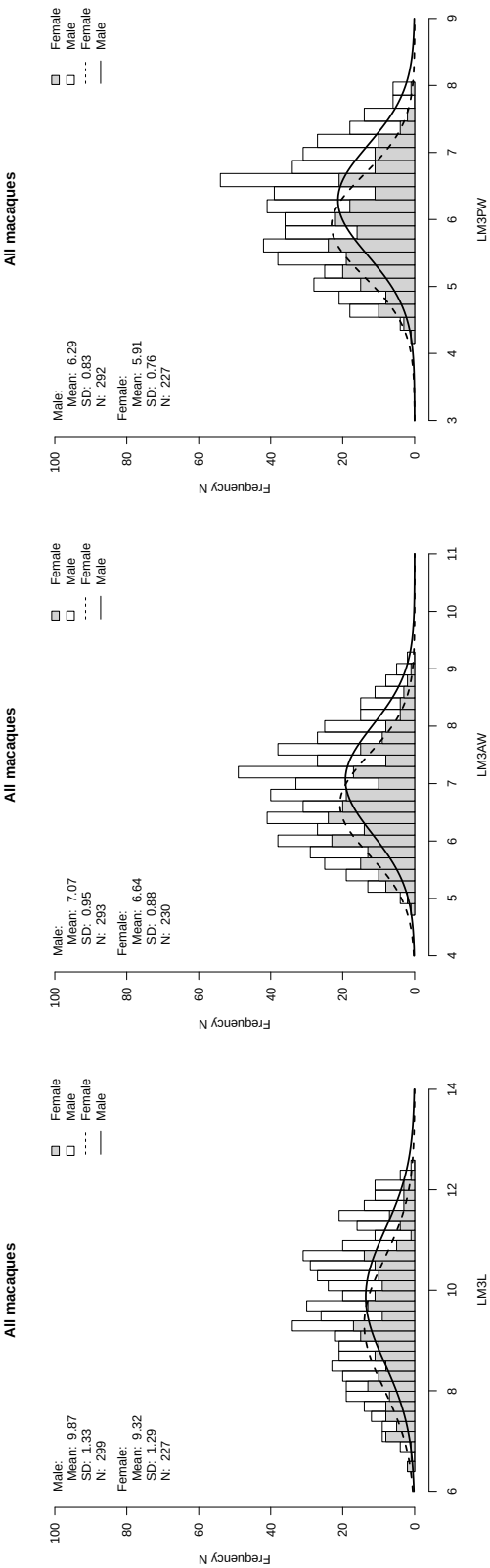
(ah) *LM2L*



(ai) *LM2AW*



(aj) *LM2PW*



(ak) *LM3L* **(al)** *LM3AW* **(am)** *LM3PW*

Fig. 3.3 Histograms summarising dental mesiodistal lengths and breadths across all macaques, disregarding species classification.

Cranial and metrics metrics

A summary of the remaining linear skull measurements is presented in Table 3.9.

Table 3.9 Descriptive statistics of cranial and mandibular measurements.[a] The top half pertains to neuro-/viscerocranial measurements, the bottom half to mandibular measurements.

Measurement	*N*	Mean	Range	Std. Dev.	Variance
Calvarium length	507	84.46	47.70	7.99	63.79
Basion to prosthion	503	85.57	73.18	13.80	190.32
Muzzle length	469	42.65	47.63	10.15	103.08
Upper incisal tooth row length	411	20.35	18.63	3.00	9.00
Upper bicanine width	463	30.82	29.88	5.76	33.20
Upper postcanine tooth row length	521	32.25	24.79	3.75	14.03
Maxillo-alveolar width	509	39.40	22.49	4.58	21.00
Maxillo-alveolar length	486	52.43	50.55	9.64	92.89
Palate width	524	22.24	17.49	3.35	11.22
Lower incisal tooth row length	458	13.55	9.88	1.96	3.82
Lower bicanine width	520	19.70	19.96	3.31	10.96
Lower postcanine tooth row length	514	39.54	28.36	5.42	29.40
Lower arcade width	512	33.35	18.05	3.84	14.76
Mandible height	470	19.13	19.26	3.49	12.18
Mandible thickness	528	12.51	14.72	2.47	6.11
Mandible width	490	37.21	35.37	6.67	44.44
Condyle to first molar	462	60.94	46.29	9.27	85.88

[a]Excluding outliers ≥ 3.

3.3.4 Exploring Statistical Assumptions

Outliers

First off, all linear data were screened for outliers, because outliers may bias the mean and inflate the standard deviation, affect the normality of the data distribution and consequently render the data unsuitable for parametric testing (Field, 2009). The datafile was split by species and subsequently histograms and boxplots were used to explore the data and check for outliers. As such, data were marked as outliers when they were extreme scores for a particular species of macaque.

Among the 744 specimens, 55 linear dental variables, and 17 skull measurements there were some outliers. All outliers marked with a * in the boxplots – identified by SPSS as data points that are three or more standard deviations removed from the mean – were checked in

the raw data and, where they represented genuine errors these were corrected (e.g., extreme values that were obviously unrealistic and which were usually changed to a missing datum). The majority of remaining outliers were less extreme scores and a randomised sample was checked for errors. It was found that they represent normal biological variation.

In order to be able to omit extreme outlier scores from analyses, all linear data were assigned an outlier code, on the basis of which the data may be filtered. To achieve this, a recoding procedure described in Field (2009) was employed. First, all data were transformed to absolute *z*-scores. In a standardised normal distribution with a mean of 0 and a standard deviation of 1, we expect 95% of cases to fall within -1.96 and 1.96 (or 0 and 1.96 when using absolute values), or two standard deviations. Three standard deviations on both sides of the mean are expected to contain 99.7% of all cases. Thus, scores between 1.96 and 2.58 are between one and two standard deviations away from the mean, values between 2.58 and 3.29 between two and three standard deviations, and values beyond 3.29 as four or more standard deviations away from the mean (following Field, 2009). Next, then, the *z*-scores derived from the dental and craniofacial data were assigned a score of 1, 2, 3, or 4, respectively, corresponding to which standard deviation interval they were in. Thus, each original linear measurement now has an 'outlier' code by which it may be identified as an outlier or not and subsequently filtered out in analyses. The approach followed in any subsequent analysis is that outlier scores of 4 represent true outliers.

Normality

Normality is an important assumption for parametric statistics. It can refer to either of two types of normally distributed data: 1) a sampling distribution that approximates a normal (bell-shaped) distribution, or 2) normally distributed errors in a general linear model. The latter will have to be tested in each respective regression analysis carried out further on, but the first assumption will be tested here so as to know how skewed the raw data are prior to the analytical stage.

The histograms in Appendix C demonstrate that, save for occasional positive skew, tooth length and width data are generally normally distributed, both on genus and on species level. Notable exceptions are measurements of the upper and lower canines and the lower third premolar; their bimodal distribution is due to the sexual dimorphism in the CP_3 complex.

The Kolmogorov-Smirnov and Shapiro-Wilk tests were run for all measurements of length and width and were found to be significant in nearly all cases. It is well known, however, that this is common in large samples because the *p*-value is dependent on sample size. Therefore, Q-Q plots were inspected and the data were found to meet the assumption of normality.

3.3.5 Body Size Proxy

Body size is one of the most salient aspects of an animal. Overall size is an adaptive trait under selection as well as an important predictor of ontogenetic processes, anatomy, reproductive behaviour, dietary ecology, among many other factors, and it therefore likely mediates the evolution of various organismal traits. In the study of skeletal and dental evolution, in particular, we take account of overall size in order to understand variations in relative size and shape, to separate the allometric component of morphological variation from other components, and/or to study phenotypic variation in a comparative context (Jungers et al., 1995). These objectives also pertain to the research presented in this thesis.

Body size data, such as body mass, however, were not available for the specimens measured in this study. Moreover, the use of average, literature-derived species body masses is not always advisable due to a weak relationship to the sample, which can inflate statistical confidence limits (Corruccini and Henderson, 1978). Also, literature-derived body size measures tend to be species means and are therefore not suitable when studying within-species variation. Alternatively, postcranial measurements (femur length or head-body length) are widely used estimators of body mass, but not all museum specimens measured for this study had associated postcrania. A reliable size proxy must therefore be derived from skull measurements.

The geometric mean of all metric measurements (here, of the skull) is a common method to retrieve and represent overall size (Darroch and Mosimann, 1985; Jungers et al., 1995). Unfortunately, due to the frequency of missing data on damaged skulls, the geometric mean could only be calculated for a too-small number of individuals per species ($N < 30$) for which all 17 cranial and orofacial variables could be measured. This method is thus unsuitable for use on the present dataset. Instead, a single variable will have to be employed as the body size proxy so that the impact of missing data is limited and the size-adjusted metric data remain available on specimen level and can be used in analyses that require standardisation against overall size (e.g., in Chapter 4).

A frequently used proxy for body mass in primates and other mammals is skull length (e.g., Delson et al., 2000; Gould, 1975; Pan and Oxnard, 2004; Ungar, 2014). Calvarium length, one measure of skull length (defined in Table B.13 in Appendix B), has previously been employed as a successful body mass proxy in macaques (Pan and Oxnard, 2004). The verification of calvarium length as a suitable proxy for body mass in the macaque sample is detailed below.

Analysis

The performance of calvarium length as a body mass proxy was determined through ordinary least squares (OLS) regression, a common method for determining the predictive power of biometric estimators (Delson et al., 2000; Sokal and Rohlf, 1995). Since body mass information for the present sample exists of species means derived from the literature, species means of the cranial and mandibular metrics are also used for the analysis. Average body mass for each macaque species (by sex) are in Table B.1 in Appendix B

An isometric relationship must exist between the target variable and its proxy, for an allometric relationship would entail that the proxy changes by a different proportion depending on the magnitude of the target variable (i.e. body size), something that might act as a confounding factor in further analyses. In order to asses isometry, all data were transformed using the common logarithm ($\log_{10}$). Following logarithmic transformation the relationship between the estimator (Y) and body mass (X) is a linear one that takes the form:

$$log(Y) = log(b) + a \cdot log(X) \tag{3.3}$$

where b is a constant and a is the scaling coefficient of the relationship (Huxley, 1924; Jungers et al., 1995). The latter is represented by the regression slope in logarithmic space. Isometry is demonstrated by a slope not significantly different from 1.0, whereas allometry exists when the slope is significantly different from 1.0 (Jungers et al., 1995; Strauss, 1993).

A linear regression of logged species means for calvarium length and the cube root of body mass yields a slope of 1.35, with a 95% confidence interval ranging from 0.89 – 1.80 and a standard error of 0.21. With such a wide confidence interval, likely the result of a limited sample size of 13 (i.e. the number of macaque species in the dataset), we cannot reject allometry. Performing bootstrapping did not improve on these results.

However, previous studies have shown that the size of the postcanine tooth row tends to scale isometrically with body mass, either in whole or in parts (in which case typically the size of the second molar), in mammals in general (Gould, 1975), and in primates (Kay, 1975, 1978), including the Cercopithecidae (Delson et al., 2000; Scott, 2011), separately. I therefore used total size of the upper molar row and lower second molar size to verify the isometric relationship between skull length and body mass, as individual data is available for these variables. Results are presented in Table 3.10. The regression slopes are not significantly different from 1.0 (with narrow confidence intervals) and thus isometry is verified. These results confirm that calvarium length can be assumed to scale isometrically with body mass in macaques. By inference then, second molar size and total molar size can also be used as body mass proxies, but nevertheless it is useful to employ a proxy for overall size that is not

Table 3.10 Results of the linear regression of the predictor calvarium length onto total upper molar row size and lower second molar size. All data were log-transformed.

Response variable	N	R^2	slope B	SE	99% CI
Upper total molar area[a]	450	0.695	0.98	0.031	0.90 – 1.06
M_2 size[b]	478	0.667	0.99	0.032	0.91 – 1.07

[a]Defined as the summed geometric means of the length and anterior and posterior widths of each molar.
[b]Defined as the geometric mean of M_2 length and anterior and posterior width.

functionally, anatomically or morphologically too closely linked to the dentition (Coleman, 2008).

Lastly, log-log plots of calvarium length against M_2 size were inspected for the presence of any signficant sexual dimorphism or species deviations, which would indicate that calvarium length is not equally suitable as a size proxy across males and females and/or macaques of different species. No such differences were found (not shown).

3.3.6 Statistical Analysis

All further analytical procedures that test specific hypotheses and aim to answer particular research questions are discussed as part of those analyses in their respective chapters in this thesis.

Chapter 4

Phenotypic Variability: Patterns of Variation and Covariation

4.1 Introduction

The ability of a population to respond to selection or undergo nonadaptive change through genetic drift, is termed evolvability (Houle, 1992; Klingenberg, 2005). Evolvability is described both by the magnitude as well as the direction of the evolutionary response (Hansen and Houle, 2008). In a univariate context, the amount of available genetic variance and the degree to which this accounts for the expressed phenotypic variance – the heritability of a trait – will determine the rate of evolution; natural selection determines the direction of change (Hansen and Houle, 2008). In complex organisms such as metazoans, however, genetic and morphological integration exists at all hierarchical levels of the organismic structure (Cheverud, 1982a; Wagner and Altenberg, 1996). This means that, e.g., due to genetic pleiotropy, many morphological traits covary and will therefore evolve together (Cheverud, 1996). Integration can either facilitate or constrain the evolutionary response of a trait (Rolian, 2014; Villmoare, 2012). Phenotypic plasticity refers to the ability of the genotype to produce a range of phenotypes in response to environmental variation (Pigliucci, 2001; Schmalhausen, 1949; Via et al., 1995).

In this chapter I examine the patterns of variation and covariation in macaque tooth size in order to determine how and where the macaque dental phenotype varies. Specifically, variances within and between species will be explored by linear dental measurements, so that we may appreciate which teeth and tooth dimensions exhibit the most and least variation. Inferences about the variational properties of teeth based on (relative) differences in variance are discussed. Furthermore, patterns of covariation in the macaque dentition will

be investigated by means of correlation matrices and correlational magnitudes, in order to gain an understanding of what parts of the dentition are more and less interdependent, or integrated, with each other, and how constrained or free individual macaque teeth are to vary through evolutionary time.

4.1.1 Variability and Variation of the Phenotype

'Variation' is often confused with 'variability' (Wagner et al., 1997; Willmore et al., 2007). *Variability* is defined as the ability to vary and is thus a propensity or a dispositional property of a phenotype (Wagner and Altenberg, 1996; Wagner et al., 1997). It refers to the full range of *potential* variation and cannot be directly measured (Willmore et al., 2007). Variation, on the other hand, is the *realised* range of observable phenotypic variants that have resulted from particular gene-environment interactions. Variation thus constitutes the measurable patterns that can serve only as a proxy for variability (Wagner et al., 1997; Willmore et al., 2007). This distinction is important for the conceptual framework in which we study evolution, because without it a conflation of pattern and underlying process(es) is likely to ensue.

Phenotypic variability is structured by several components, which mostly limit or direct it. Among these are genetic variability, canalisation, developmental stability, phenotypic plasticity, and morphological integration and modularity (Debat and David, 2001; Hallgrímsson et al., 2002; Houle, 1998). There is no complete definitional consensus for many of these components (Debat and David, 2001; Dworkin, 2005; Hallgrímsson et al., 2009) and mostly the definitions vary according to whether one takes a developmental or evolutionary genetic approach, as they are described as properties of the developmental or the genetic system, respectively (Gibson and Wagner, 2000).

Genetic variability will not be discussed here as the present data do not allow this property to be investigated and it is thus beyond the scope of this research. Similarly, developmental stability, which refers to the process of buffering against antimeric (left-right) differences within an individual and is typically measured by fluctuating asymmetry (Van Valen, 1962; Willmore et al., 2007), is also outside of the research focus.

Canalisation

Canalisation refers to the disposition of a biological system to follow the same trajectory toward producing the phenotype under varying conditions, by buffering against genetic (e.g., mutations) and environmental perturbations (e.g., extreme temperatures) (Hallgrímsson et al., 2002; Waddington, 1942). Genetic mutations are known to increase the phenotypic variance (Hallgrímsson et al., 2006; Waddington, 1942; Wagner, 2003). Similarly, pheno-

typic plasticity, the ability of a genotype to produce different phenotypes across a range of environments (Debat and David, 2001)), increases phenotypic variance due to environmental influences. Canalisation acts to maintain phenotypic stability and to constrain variability (Gibson and Wagner, 2000; Wagner et al., 1997). Sometimes two types of canalisation are distinguished: genetic canalisation, which suppresses genetic mutations (Wagner et al., 1997), and environmental canalisation, which controls the sensitivity to influences arising from the macroenvironment (i.e., the environment extraneous to the individual) (Debat and David, 2001). However, such a distinction cannot (and therefore will not) be made in the present work. Finally, a related concept to canalisation is developmental stability. This is the tendency of the developmental system to produce a stable phenotype under the same genotypic and external environmental conditions, buffering against developmental noise or other random noise within the individual (Waddington, 1942; Wagner et al., 1997). Whereas developmental stability is often assessed through the measurement of fluctuating asymmetry (FA) (Van Dongen, 2006; Van Valen, 1962), canalisation is commonly measured by the range of among-individual phenotypic variation present in a population. The smaller the variance for a trait, the higher the inferred level of canalisation for that trait (Gibson and Wagner, 2000; Van Dongen, 2006; Willmore et al., 2007).

Phenotypic plasticity

Phenotypic plasticity is the tendency of a genotype to express a phenotype as a function of the environment (Pigliucci, 2001; Scheiner, 1993). Also called 'macroenvironmental sensitivity' (Wagner et al., 1997), phenotypic plasticity has an effect on phenotypic variation that is inverse to that of (environmental) canalisation (Debat and David, 2001; Dworkin, 2005; Stearns, 1989). Plasticity is sometimes used interchangeably with the *norm of reaction*, which is the phenotypic range expressible by a particular genotype across a range of environments (Scheiner, 1993; Via et al., 1995). Others take a less general stance and in fact define phenotypic plasticity as an attribute of the reaction norm (Pigliucci, 2001). Within the latter framework, every genotype has a reaction norm - a function that describes the relationship between the environment and the phenotype - but not every genotype is plastic. For example, a genotype whose phenotype is not influenced by the environment has a reaction norm with a slope of 0, with the latter denoting its (lack of) plasticity (Pigliucci, 2001).

Another use of the term 'plasticity' is to describe a statistical attribute of a population rather than a single genotype. In this case it describes the phenotypic change in response to the environment across genotypes (Pigliucci, 2005). This definition of phenotypic plasticity will be used in this thesis henceforth, as the data herein capture across-genotype, among-individual variation. Plasticity in this sense is measured by the range of variation comprised

of a set of static observations across a range of environments (e.g. temperature or latitude) (e.g., Pigliucci, 2005).

Morphological integration and modularity

Morphological integration refers to the interdependence of traits (Willmore et al., 2007), and exists between traits that develop or function together, are affected by the same genetic processes, or evolve together (Cheverud, 1982a; Rolian and Willmore, 2009). Definitions of integration vary depending on whether it is meant to describe statistical associations or underlying biological processes (Mitteroecker et al., 2012). But in terms of dispositional properties, integration is the ability to covary (Hallgrímsson et al., 2009): the propensity of a biological system to produce coordinated variation in size and shape, on a developmental, genetic, functional, or evolutionary level, among others (Cheverud, 1996; Klingenberg, 2013). Modularity is a related concept and can best be understood as 'nested integration' (Willmore et al., 2007). It is described as the tendency of trait units ('modules') to be internally highly integrated while being relatively independent from other such units (Klingenberg, 2013; Wagner and Altenberg, 1996; Wagner et al., 2007). Morphological integration and modularity are ubiquitous phenomena that exist at various hierarchical levels within an organism (Müller, 2007). It is thought that on the level of the individual, traits become integrated when they develop and function together, which leads them to be inherited together and become genetically integrated on a population level. Finally, they evolve together through a coordinated response to selection (Cheverud, 1996; Klingenberg, 2013).

On the whole, integration constrains the variability of morphological structures and is understood to promote stability of the organism (Willmore et al., 2007). The coinciding modular organisation of phenotypic variation, however, promotes the evolvability of traits. Modularity permits the evolutionary flexibility of a trait or set of related traits necessary to respond to selection (or undergo nonadaptive evolution through genetic drift), by removing the constraint on variation from traits with different functional demands (Klingenberg, 2013; Wagner et al., 2007). The pattern of covariation highlights an important evolvability component because it is informative of how selection on one trait produces correlated evolution in other traits (Darwin, 1859; Hallgrímsson et al., 2009; Hansen and Houle, 2008; Lande and Arnold, 1983).

The underlying, proximate mechanisms of integration and modularity may be developmental, genetic, or functional in nature. Traits may be developmentally integrated as the result of global, or common growth factors; sets of traits can be modular within an overarching (integrated) structure when the control by local developmental processes (e.g., local growth factors) exceeds that of general growth factors (Mitteroecker and Bookstein,

2007; Mitteroecker et al., 2012). Genetic integration arises when multiple traits are controlled by the same genes, *genetic pleiotropy*, or due to *linkage disequilibrium*, the co-inheritance of genes that are physically close on a chromosome (Mitteroecker et al., 2012). Genetic integration can also arise from traits that share a common function and are therefore inherited together (Cheverud, 1996).

Integration and modularity are manifest in the covariance structure between traits in phenotypic space, and this covariance structure in turn determines the direction and degree of evolutionary change that is possible (Hansen and Houle, 2008; Wagner and Altenberg, 1996). The nature and level of integration and modularity, like other components of variability, are not directly measurable, but are assessed through patterns of covariation (e.g., Hallgrímsson et al., 2009; Klingenberg, 2013; Mitteroecker et al., 2012). Not surprisingly, there are many different ways to measure integration and modularity, and many of them differ according to the nature of the process they are aimed at measuring (genetic, developmental, etc.). The following methodologies are relevant here and are examples of phenotypic variation-based approaches. Principal components analysis is useful for investigating the dimensionality of variance in multivariate space (Klingenberg, 2013). The eigenvalues of the principal components give an indication of the amount of variation present in the respective dimensions, and is therefore a fruitful tool for identifying the axes along which change can occur (Klingenberg, 2005). The patterns of covariation visible in the phenotypic covariance matrix and its variance-standardised counterpart, the correlation matrix, are commonly examined and interpreted to reflect patterns of integration and modularity (e.g., Grieco et al., 2013; Marroig and Cheverud, 2001; Willmore et al., 2007). The strength of covariation, or correlation magnitude, can be assessed by the average of the squared correlation coefficients (Marroig and Cheverud, 2001). This may aid in elucidating differences in the strength of integration.

4.1.2 Research Questions

In this chapter I ask a few straightforward questions. Firstly, what is the dimensionality of macaque craniodental variation in multivariate space? How many latent variables, each linear combinations of the original variables, underlie the total variation? In order to explore this, latent variables in macaque craniodental variation will be explored both within and between species to compare the microevolutionary and macroevolutionary multivariate patterns of variation, respectively. Allometric size is expected to be an important underlying component structuring craniodental size variation.

Next, I inspect the levels of intra- and interspecific variation of tooth size measurements in macaques. Although it is impossible to measure variability directly (for theoretical reasons, see review above), a comparison between tooth variances will be made and cautiously inter-

preted with respect to relative differences in variability between macaque teeth. Particularly, to evaluate how canalised or plastic different elements of dental size are in relation to each other (e.g., first molars compared to third molars). Although properties such as canalisation (i.e., environmental canalisation) and phenotypic plasticity are often measured across different environments to detect the phenotype's sensitivity to environmental variation (Debat and David, 2001; Dworkin, 2005), here I compare levels of variation between measurements without examining their phenotypic change against an environmental variable, because the assumption is that all tooth measurements share a common range of experienced ecological and geographical environments because per specimen all teeth were measured. (The slight inaccuracy of this statement refers to the inclusion of juvenile and subadult specimens in the sample on which not every tooth dimension could be measured, but there is no ecological or geographical bias in the age distribution.)

Next, I investigate the pattern of covariation in macaque tooth size. Covariation structures variation, and the dentition constitutes a meristic phenotype: a structure of repeated homologous elements performing a joint function (Butler, 1995). They are thus expected to evolve in unison rather than have individual evolutionary trajectories (Gomez-Robles and Polly, 2012). Covariation structure will be investigated by jaw. Comparing the presence of dental modules in macaques to modular patterns found in other taxa will elucidate whether patterns of dental covariation are stable across taxa (as has been found for cranial morphology; Marroig and Cheverud 2001). Furthermore, it will show whether (and which) different parts of the dentition may have been subject to different evolutionary pressures or processes.

4.2 Materials and Methods

4.2.1 Patterns of Variation

The multivariate pattern of macaque craniodental variation is investigated by means of principal components analysis (PCA). PCA decomposes the variation into underlying (latent) structures, called principal components (PCs). For all 13 species, all 72 variables are considered in the analysis: tooth lengths, breadths, and heights, as well as the craniofacial and mandibular measurements. PCA is carried out within as well as between species using the open-source software PAST (Hammer et al., 2001). A within-group PCA standardises the values within each group (i.e., species) by the respective group mean. This removes between-species differences so that the pooled within-species variation structure is considered. A between-species PCA, conversely, is conducted using the group means, thereby ignoring

intraspecific variation. The option for within- or between-species principal components analysis is implemented in the function *PCA* in PAST.

Due to the relatively large differences in average size between some of the variables, especially between cranial (e.g., calvarium length) and tooth size measurements, all variables were log-transformed prior to the PCA to standardise against size-related variance. PCA was subsequently carried out on the variance-covariance (V-CV) matrix (rather than the correlation matrix) of the data.

Moreover, missing data are handled by the process of iterative imputation as a built-in option of a PCA in PAST. The iterative imputation procedure computes the estimated parameters based on the observed data, replaces the missing data with the conditionally estimated data, then runs through the data again to refine the estimated parameters until convergence (Orchard and Woodbury, 1972). To minimise the amount of missing data, especially within specimens as a result of unfinished growth, juveniles were omitted from the analysis and only subadults and adults were used.

The univariate analysis is limited to measurements of teeth only. Lengths and widths pertaining to every tooth of every tooth class (incisors, canines, premolars, and molars) in the maxilla and mandible are considered. The total number of dental variables is 39. Patterns of variation (and covariation; see below) will not be examined within each individual species, as this is beyond the scope of this chapter. Interspecific differences in tooth size and ranges of variation can be inspected in the histograms in Section 3.3.3 in Chapter 3.

Pooled within-species variances are computed. These represent the average within-species variance for each measurement. If we assume that evolutionary processes predominantly operate on population level within a species, and a species is defined as those individuals that interbreed but have been reproductively isolated from members of other species, then the level of within-species variation is the most appropriate measure of variation that is available for microevolutionary processes to operate on (notably selection). Pooled within-species variances are derived from the residual sum of squares (SS_R) divided by their degrees of freedom (df) (Hunt, 2007). This procedure weights the average (i.e. pooled) within-species variance by the sample size of each species, which is appropriate given the disparate species sample sizes. The resultant pooled within-species variances are thus represented by the residual mean squares (MS_R) obtained in an analysis of variance (ANOVA), and are a measure of population-level variance (Field, 2009). The pooled mean ($\overline{x}$) for each tooth measurement can be directly obtained from the ANOVA, and the pooled standard deviation (s) is calculated as the square root of MS_R. Because variance may be dependent on the mean and teeth differ in size, the coefficient of variation (CV) is also computed as a measure of the

pooled (i.e. intraspecific) variance adjusted for size and is used to compare levels of variation between tooth dimensions. The coefficient of variation is computed as $s / \bar{x}$.

The between-species variance (MS_M) and F-ratio are also retrieved per dental measurement as part of the ANOVAs. The between-species variance is represented by the model mean squares (MS_M), which is the model sum of squares (SS_M) averaged across species. The F-ratio measures the mean between-species variance relative to the mean within-species variance (MS_M/MS_R) (Field, 2009). This is a measure of the morphological differentiation between species, or 'phenotypic divergence' (not phylogenetic divergence; phylogeny may structure phenotypic differences between taxa, but this will be explored in Chapter 7). One-way ANOVAs were carried out for each dental measurement. Outliers were filtered out (i.e. those cases with an outlier code of 3 or 4; see Section 3.3.4 in Chapter 3), because they can strongly bias the variance. In order to obtain maximum sample sizes, ANOVAs were run separately for each dental variable by only omitting outliers pertaining to one variable at a time. There are normally good reasons to use multivariate statistics to analyse multivariate data (e.g., MANOVA) rather than repeated univariate analyses (e.g., ANOVA) (Sokal and Rohlf, 1995). However, the ANOVAs are not used here for hypothesis-testing; concerns with respect to multiple comparisons and inflated Type I error rates therefore do not apply.

4.2.2 Patterns of Covariation

Correlation matrices are constructed by jaw to elucidate how dental variation is structured by covariation, and to give insight into the integration and modularity in the macaque dentition. Once again, only tooth lengths and breadths are used. Dental correlations are retrieved across and within species, as well as by sex. This work is exploratory and does not involve hypothesis-testing, and therefore p-values are irrelevant and will not be displayed. The pattern of covariation will be found in the effect sizes (i.e., correlation coefficients). Matrices of correlations, i.e., relationships standardised by the variables' variance, are preferred over variance-covariance matrices in this case, because they illustrate more clearly the differences in strengths of the relationships between dental measurements. I will compare between the macroevolutionary (between-species) and the microevolutionary (within-species) patterns, as well as see if there are systematic differences between males and females in dental covariation. The within-species pattern of dental integration will suggest how different elements of the dental phenotype may be developmentally, functionally, and genetically integrated (Cheverud, 1996). Mechanistic explanations must be based on within-species patterns. It is also on this level that patterns of covariation are informative about the directions of, and possible constraints on, microevolutionary responses. The between-species correlation matrices

represent the macroevolutionary pattern of evolutionary integration within the macaque dentition (Cheverud, 1996).

Matrices of Pearson's product-moment correlation coefficients, r, between species (using species means) and by sex (ignoring species classification) are generated using bivariate correlational analysis. Pooled correlation matrices are obtained as part of a multivariate analysis (MANOVA) (Field, 2009) in SPSS. Phenotypic covariance patterns have been found to be highly stable across evolutionary time and between species for primate skull morphology (Marroig and Cheverud, 2001), and so covariance patterns will not be analysed separately for each species here.

Next, tooth dimensions are considered for their total degree of integration within the dentition by comparing their overall correlation magnitudes. These are calculated by taking the average of squared correlation coefficients (r^2) as per Marroig and Cheverud (2001). Overall correlation magnitudes, r^2, are then also computed by tooth (i.e., the average r^2 for tooth length and width) and by tooth class (i.e., the average of r^2 for all the teeth of a particular tooth type, such as the molars).

4.3 Results

4.3.1 Multivariate Patterns of Variation

Within species

A PCA on the within-species variation extracted a total of 72 (unrotated) components, of which the first two PCs account for 76% of the total variance. The eigenvalues and the percentage explained variance of the first ten PCs are presented in Table 4.1. A scatterplot of PC 2 onto PC 1 is presented in Figure 4.1. Loading plots of the variable loadings on the principal components for the first three principal components are in Figures 4.2 to 4.4. Females (represented by triangles) have consistently lower scores on PC 1 than males (represented by circles). All variable loadings on PC 1 are positive and so this first principal component represents the relationship of the individual variables to overall size (Marroig and Cheverud, 2005). There is hardly any overlap between males and females of any species along PC 1 (see Figure 4.1), which indicates that this first dimension includes overall size-related sexual dimorphism.

PC 2 represents an allometry-free component that accounts for the next biggest portion of within-species variance. Along this dimension there is considerable overlap between the sexes (Figure 4.1). Inspection of the variable loadings onto PC 2 (Figure 4.3) reveals a

Table 4.1 PCA results of all 72 craniodental variables within and between species.

All variables				
	Within-species		Between-species	
PC	Eigenvalue	% variance	Eigenvalue	% variance
1	0.172	54.69	0.095	73.12
2	0.064	20.33	0.019	14.30
3	0.014	4.32	0.007	5.37
4	0.008	2.51	0.004	2.92
5	0.005	1.68	0.001	1.07
6	0.005	1.55	0.001	0.91
7	0.004	1.25	0.001	0.68
8	0.003	0.94	0.001	0.56
9	0.003	0.87	0.001	0.41
10	0.002	0.77	0.000	0.29
...	...	...	...	...
Total	0.314	100	0.130	100

'...' indicates that additional PCs were extracted, but because they explain negligible amounts of variance they are not displayed.

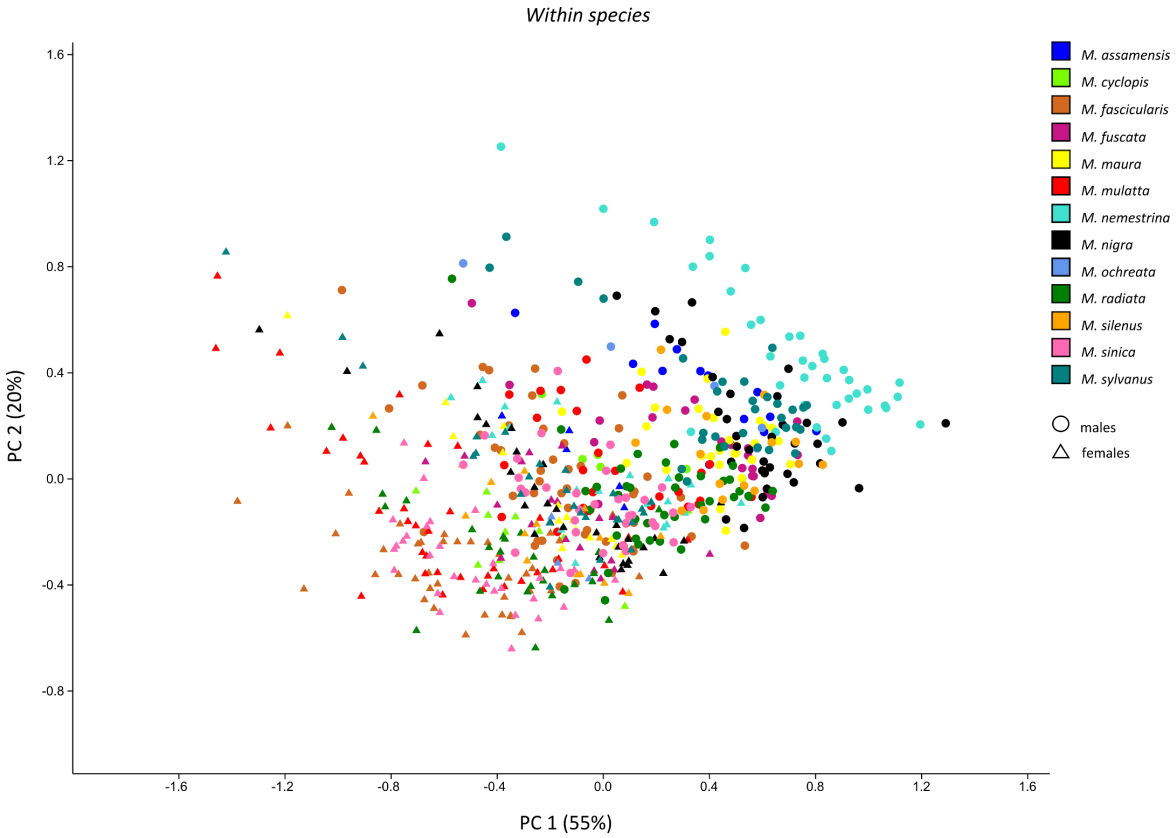


Fig. 4.1 Scatterplot of the within-species PCA scores for PC 1 and PC 2. These results pertain to the full dataset of 72 craniodental variables (key to variables can be found in Table B.13 and Table B.14 in Appendix B). No convex hulls were drawn here so as not to crowd the figure.

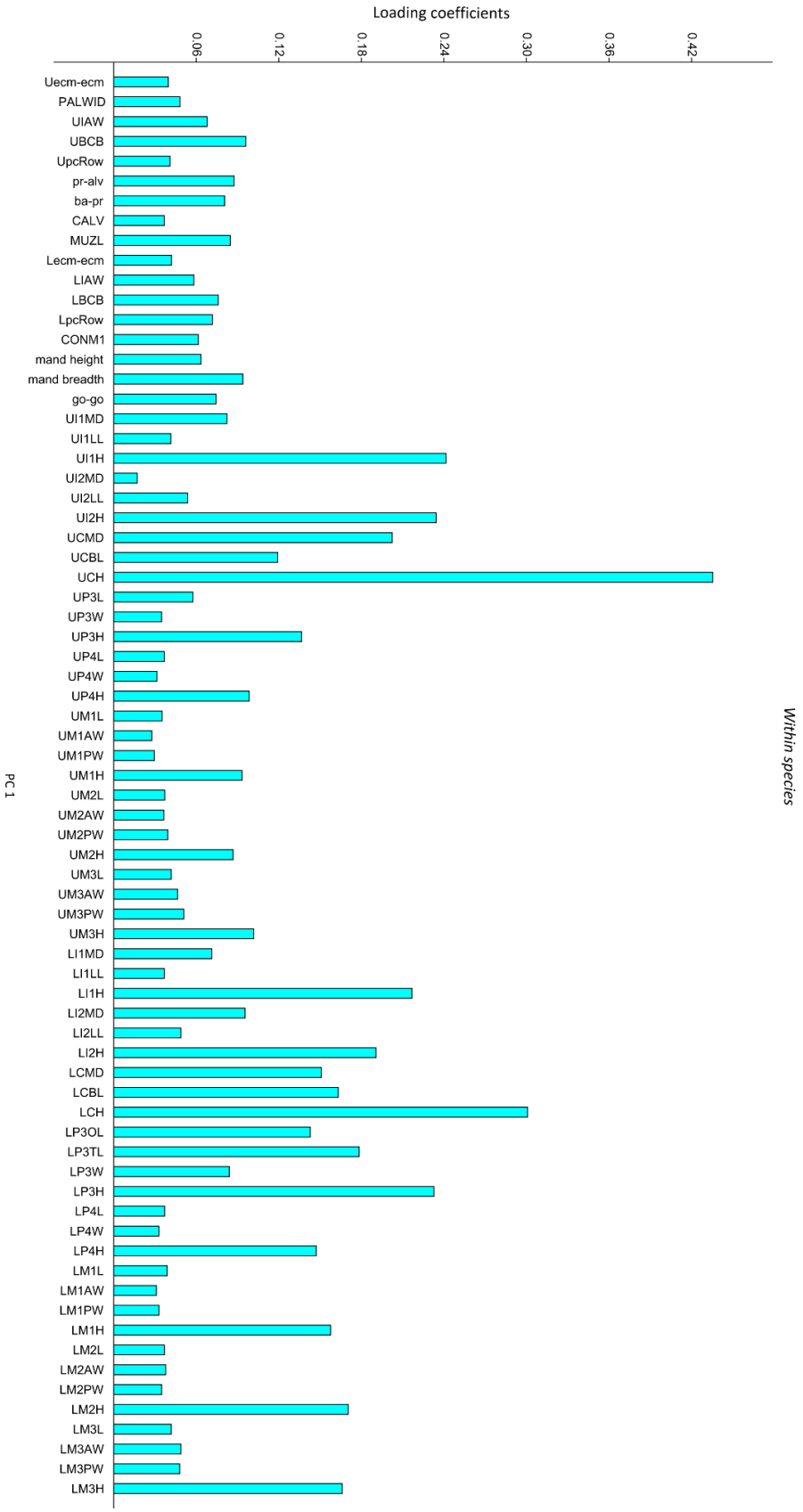


Fig. 4.2 Loading plot of the variable loadings onto PC 1, of the within-species PCA.

Fig. 4.3 Loading plot of the variable loadings onto PC 2, of the within-species PCA.

Fig. 4.4 Loading plot of the variable loadings onto PC 3, of the within-species PCA.

contrast between tooth height and the rest of the dentition. PC 2 therefore likely represents the effect of tooth wear on individual variation within species.

For PC 3, the factor loadings (Figure 4.4) are negative for the CP_3 complex and positive for the rest of the dentition. Due to the involvement of the $CP-3$ complex, this contrast is indicative of sexual dimorphism. However, PC 3 indicates a contrast in the *relative* size of teeth, as variance related to *absolute* or *overall* size is concentrated in PC 1. Along the third dimension, females tend to have larger non-CP_3 teeth; males tend to have larger canines and lower third premolars.

Between species

A PCA on the between-species variation extracted a total of 12 components, of which the first two PCs account for 87% of the total variance (Table 4.1). The scatterplot in Figure 4.5 reveals poor separation of macaque species on PC 1 and PC 2. PC 1 scores appear to reflect variation in size, as indicated by the overlap of species of similar body size (e.g., small *M. sinica* and *M. fascicularis*, and large *M. sylvanus* and *M. nemestrina*). The loading plot in Figure 4.6 confirms that PC 1 represents allometric size, as all variable loadings are positive. (The one exception is the height of the lower first incisor, which has a negative loading on PC 1. Inspection of the raw data suggests that this is likely due to large-bodied *M. assamensis* on the one hand, which is represented by relatively few but worn specimens, and smaller species, such as *M. fascicularis* that are represented by a larger number of specimens, including many with relatively unworn and thus tall incisors.) Species separate equally poorly along consecutive PCs (not shown).

PC 2 accounts for most of the remaining, non-allometric variance between species. However once again, separation between species is poor (Figure 4.5). Figure 4.7 shows a dental contrast underlying PC 2. Measurements pertaining to the incisors and canines – the anterior dentition – tend to be negatively associated with PC 2 while premolars and molars – the posterior dentition – are positively associated with PC 2. However, P_3 is more similar to the canines, and therefore the anterior dentition, than it is to the other postcanine teeth. PC 2 shows that, once allometric size variance is accounted for (along PC 1), species differ in the relative size of their anterior compared to their posterior dentition.

Tooth wear

Variation in tooth height in the present dataset is very likely predominantly the result of tooth wear. The fact that specimens at various tooth wear stages were included in the study, and the observation that tooth height explains within-species but not between-species differences,

supports this notion. The focus in this chapter (and further on in the thesis) is to elucidate variation between individuals and species that are due to genetic, developmental, or past evolutionary processes, not macrowear processes related to age, attrition, and abrasion. Therefore, tooth height measurements were omitted and the analysis repeated to see if this changed the PCA results. Tooth height measurements related to the CP_3 complex were retained, however, because these measurements are expected to carry information regarding sexual dimorphism (within species), and sexual selection or socioecology (between species) that are unlikely to be overridden by tooth wear.

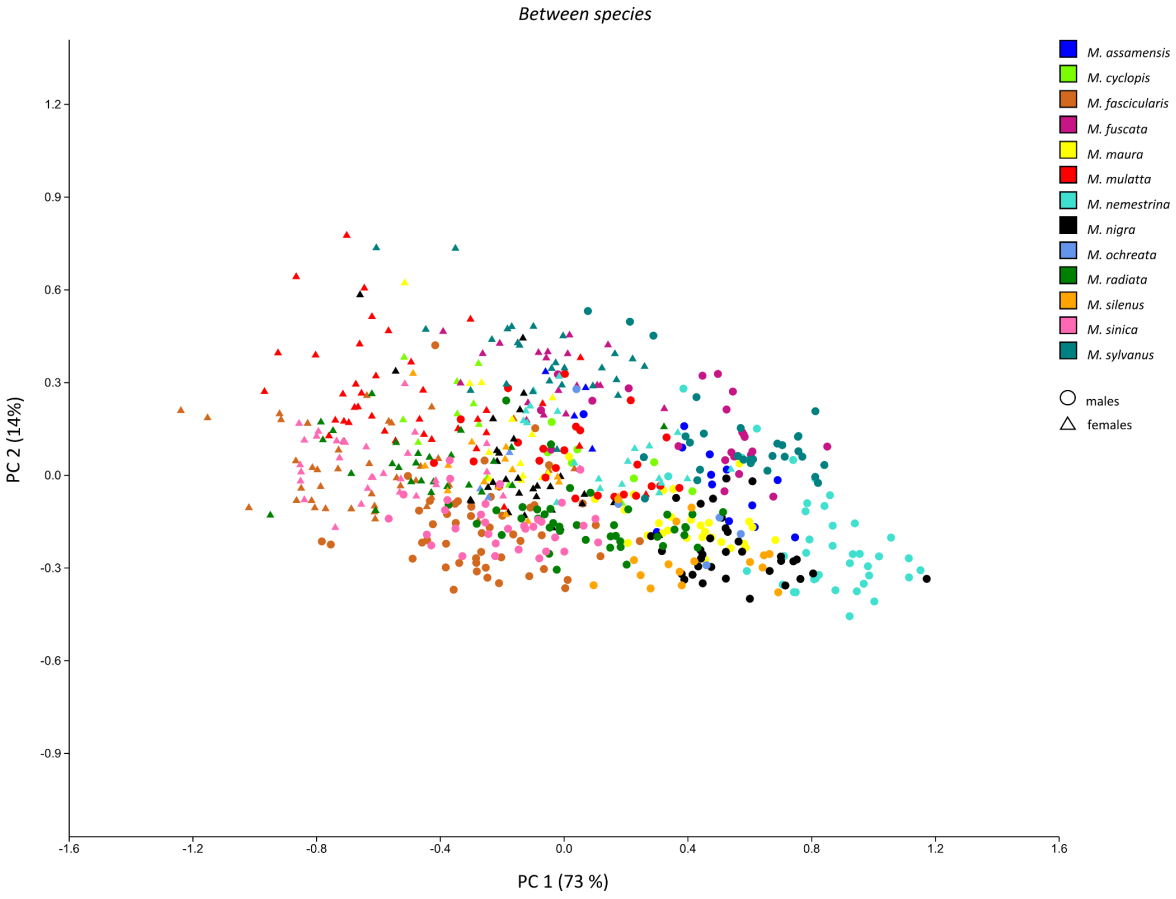


Fig. 4.5 Scatterplot of the between-species PCA scores for PC 1 and PC 2. These results pertain to the full dataset of 72 craniodental variables. No convex hulls were drawn here so as not to crowd the figure.

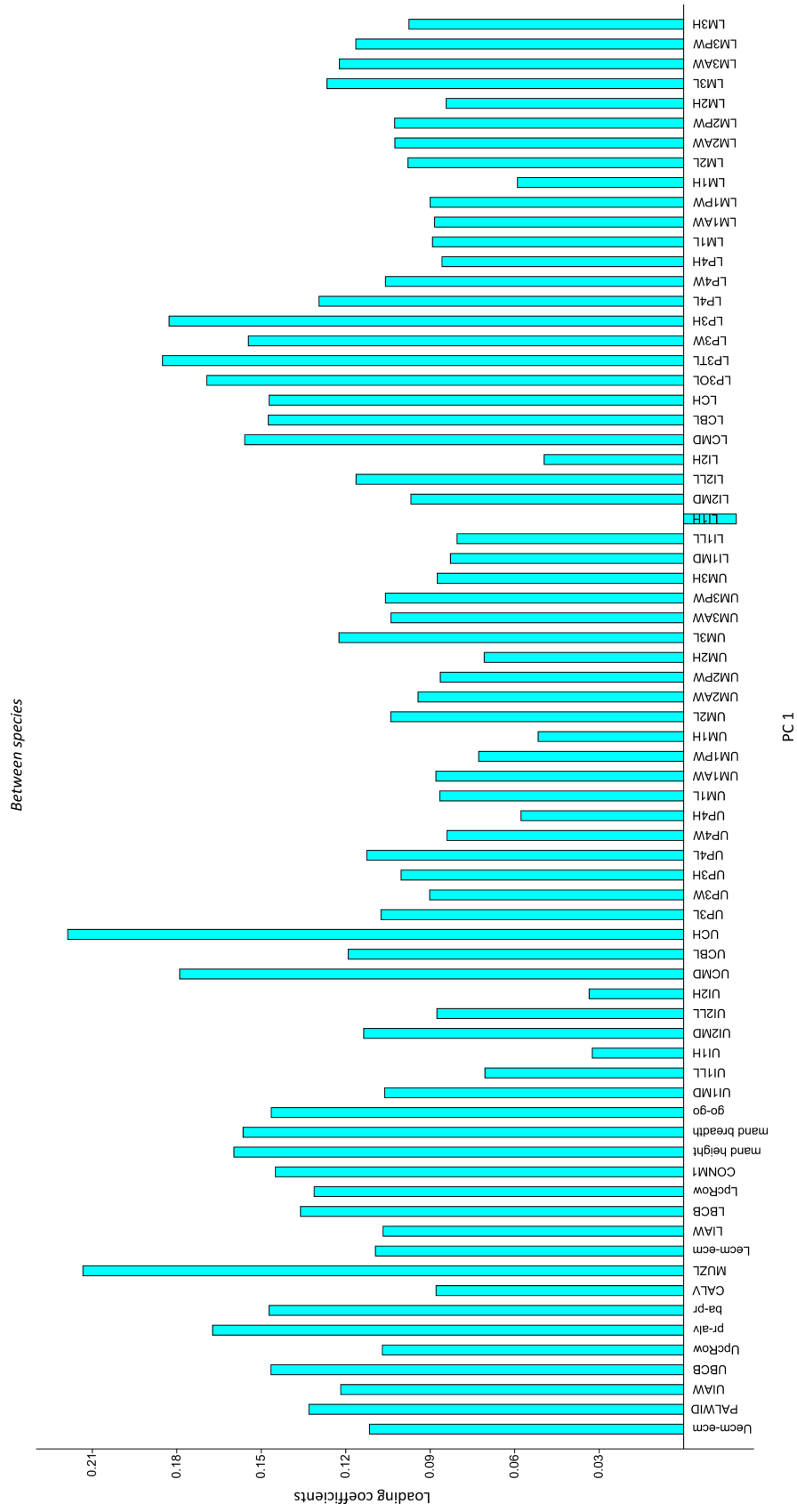


Fig. 4.6 Loading plot of the variable loadings onto PC 1, of the between-species PCA.

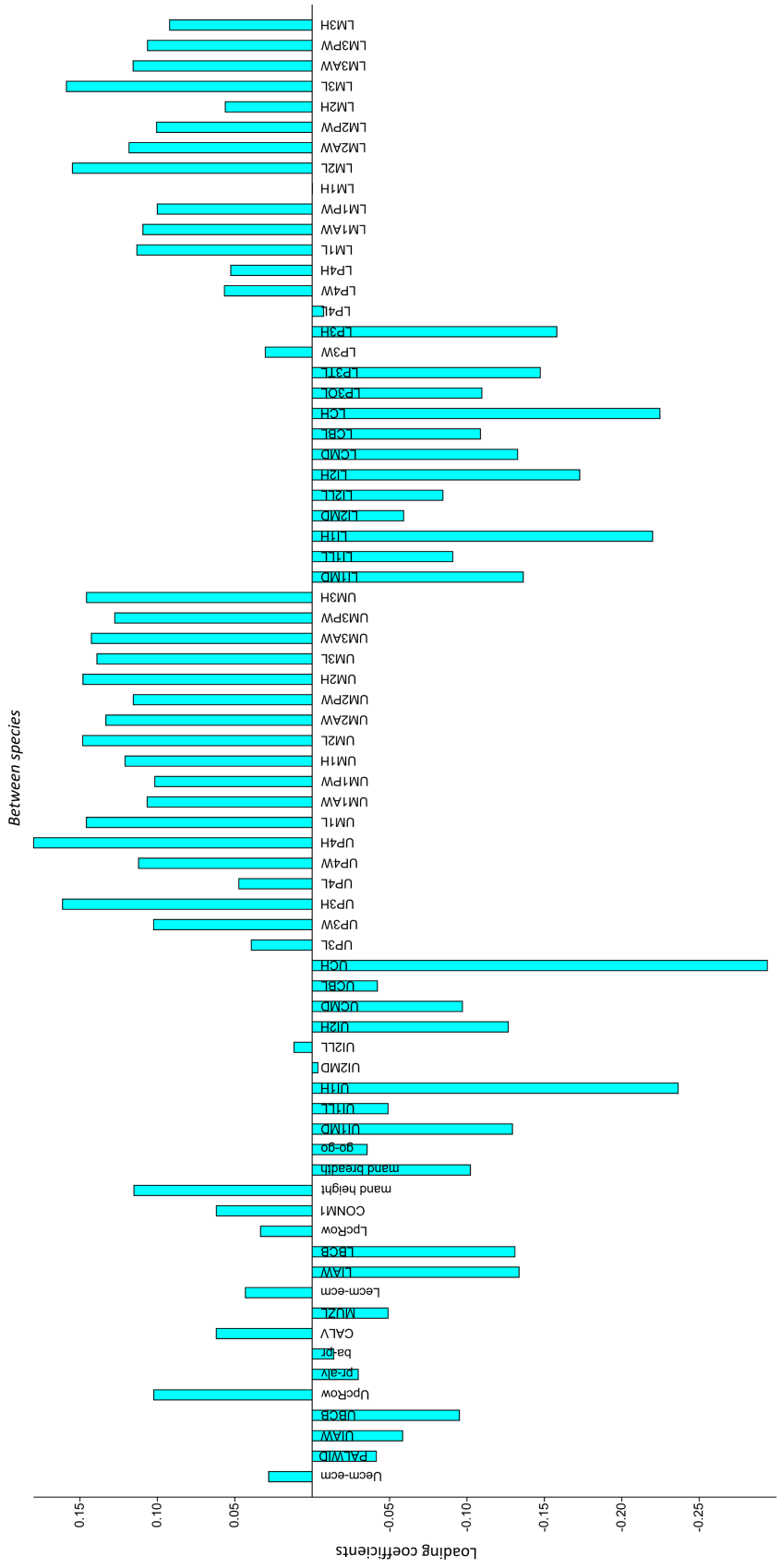


Fig. 4.7 Loading plot of the variable loadings onto PC 2, of the between-species PCA.

A comparison of the results before and after omitting tooth height reveals that the patterns of between-species craniodental variation do not change; the first two PCs now account for 94% of the variance (see Table D.1 in Appendix D) and PC 2 scores plotted on PC 1 scores depict the same pattern as in Figure 4.5, including substantial overlap between the species (not shown). Thus, omitting tooth height appears to only reduce noise in the interspecific data. Moreover, the total eigenvariance of the between-species PCA after omitting tooth heights has changed minimally (from 0.130 to 0.121), further illustrating the small impact tooth heights have on explaining between-species patterns of craniodental variance.

Within species, by contrast, variance is apportioned differently among the components following omission of tooth height. PC 1 and 2 now account for 71% and 9%, respectively (Table D.1 in Appendix D). PC 1 still accounts for overal size differences between individuals, and especially between males and females. PC 2, despite accounting for a smaller portion of the variance than before, still seems to represent some effect of tooth wear as there is now a contrast between tooth height (but not lengths and breadths) of the canines and P_3, and the rest of the dentition. The sexual dimorphism in relative tooth size that involves the entire CP_3 complex (i.e., also the lengths and breadths of these teeth) remains concentrated in PC 3 (3% of within-species variance accounted for). After excluding tooth heights, the total eigenvariance was reduced from 0.314 to 0.195, highlighting that height measurements (as a proxy for macrowear) make up a substantial portion of within-species variation.

Sexual dimorphism

Due to the influence of sexual dimorphism on the within-species PCs, a PCA of the sex-corrected data was conducted. This yields a more representative picture of intraspecific multivariate patterns of craniodental variation and how they might give rise to interspecific patterns.

Sexual dimorphism was removed from the data by subtracting the male mean from each individual male value and the female mean from each individual female value, by species. The species mean was then added back to the individual values (male and females alike) to maintain size differences *between* the species. The 'sex-corrected' PCA was carried out on the V-CV matrix of 56 log-transformed craniodental variables (excluding tooth height).

Figure 4.8 shows that following correction of sexual dimorphism in the data males and females overlap. The majority of the variance exists along PC 1, both within and between species. PC 1 (still) represents allometric size both within and between species, as demonstrated by roughly equal and positive loadings for all variables (Figures 4.9 and 4.10). PC 2 now also shows a similar pattern between the two levels of analysis: the posterior teeth load positively onto PC 2, whereas the anterior teeth tend to be negatively associated with

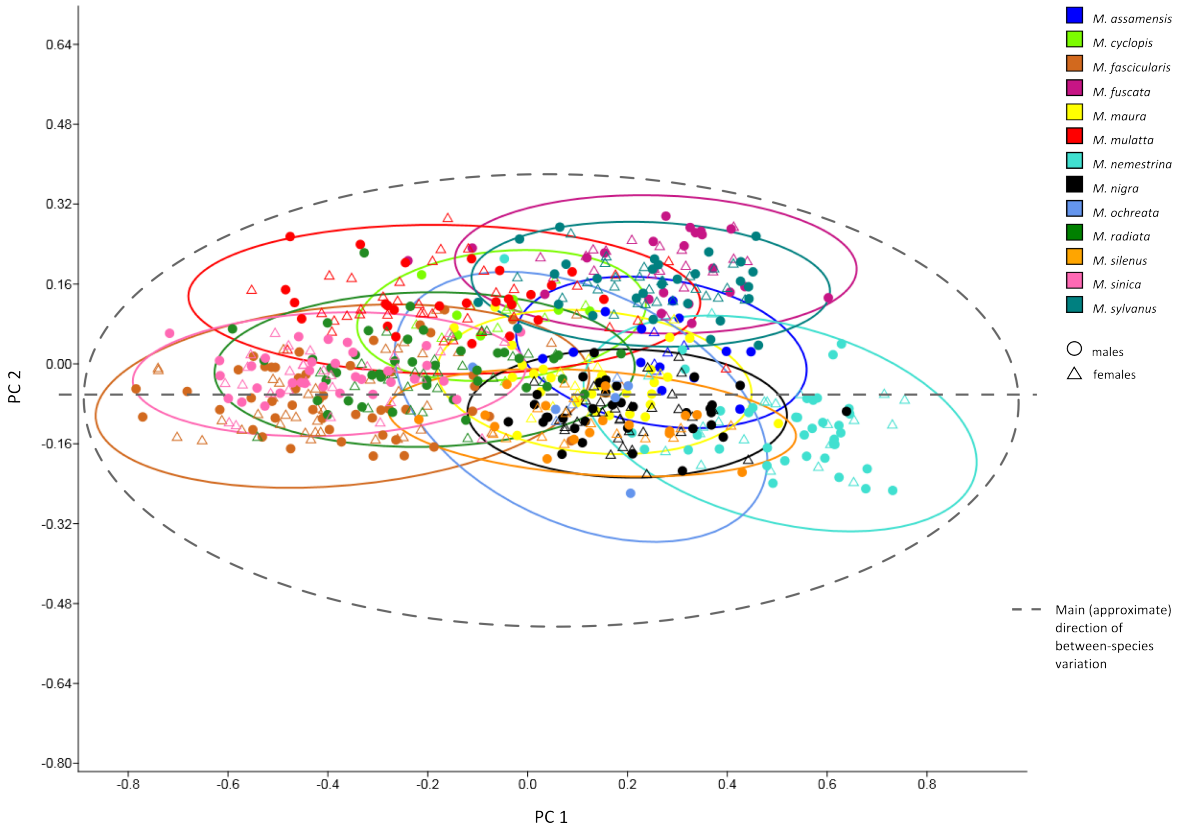


Fig. 4.8 Scatterplot of the PCA scores for PC 1 and PC 2 after correction for sexual size dimorphism, with equal axes. Groups are disregarded in the PCA (results are therefore neither standardised for within- or between-species differences). 95 % Ellipses are displayed to illustrate the intraspecific multivariate pattern for each species. These results pertain to a dataset of 56 craniodental variables (excludes all tooth heights).

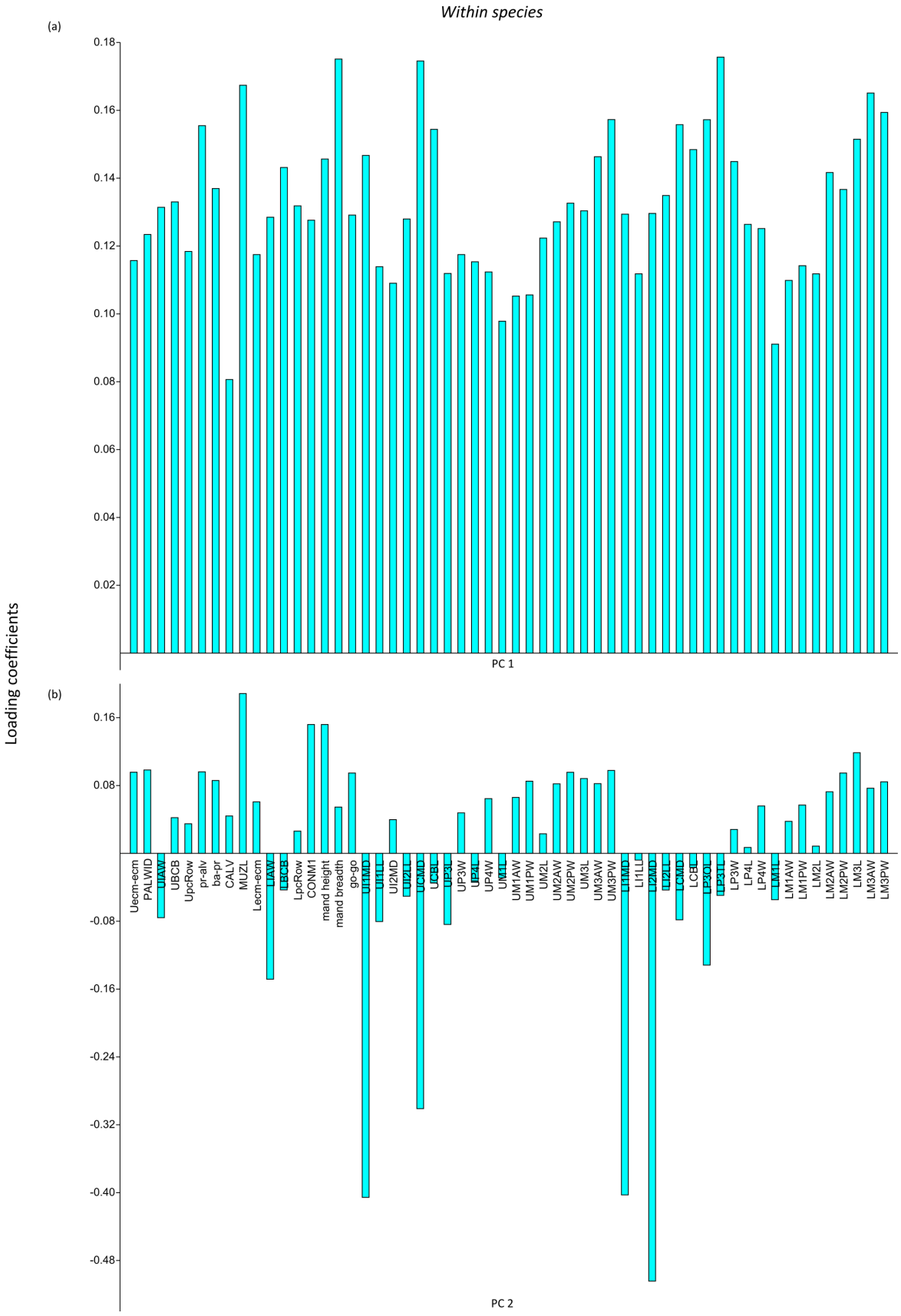


Fig. 4.9 Within-species PC loading plot for (a) PC 1 and (b) PC 2 after correcting for sexual size dimorphism. PC 1 represents allometric size and the anterior and posterior teeth show opposing relationships with PC 2.

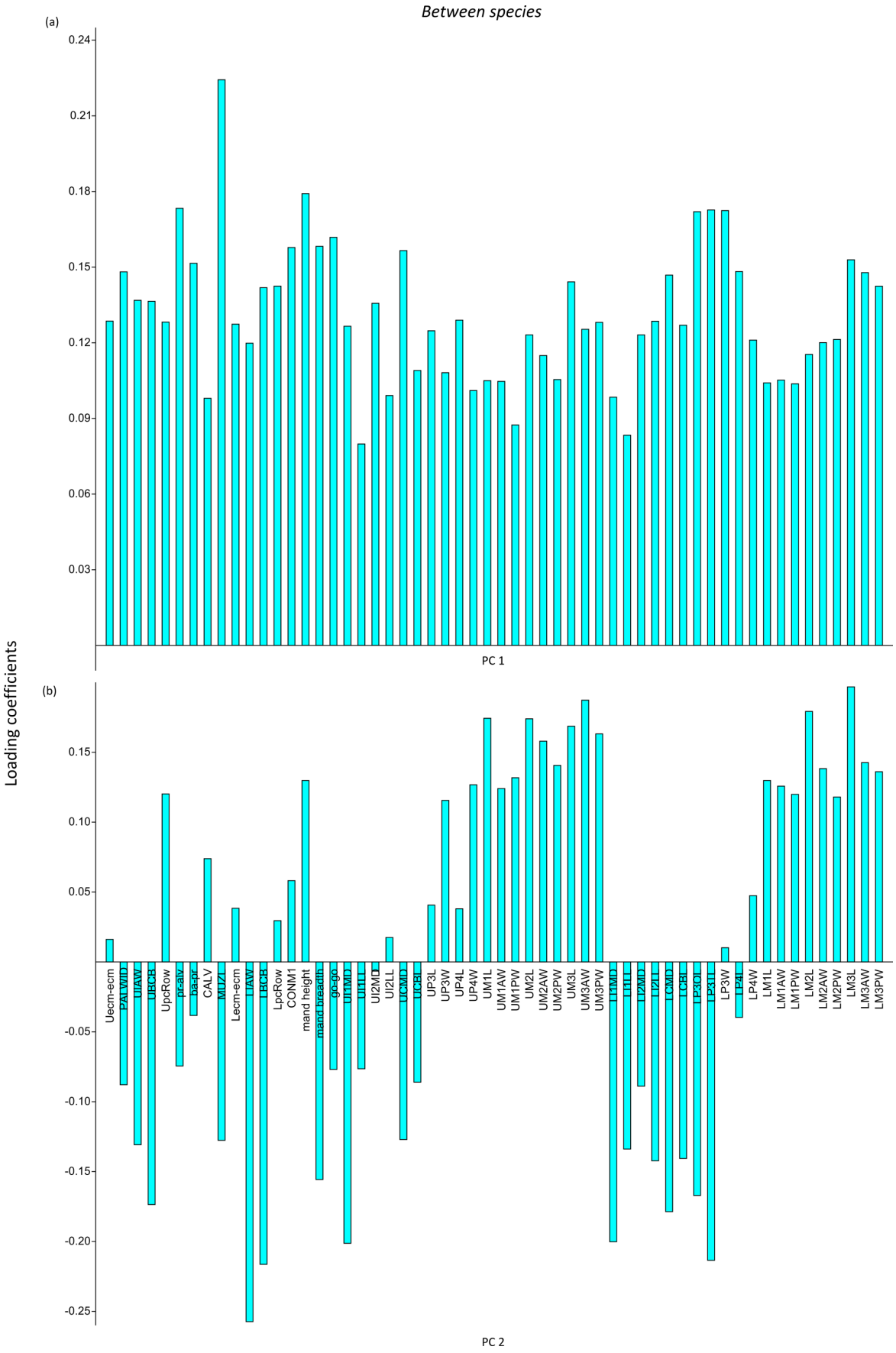


Fig. 4.10 Between-species PC loading plot for (a) PC 1 and (b) PC 2 after correcting for sexual size dimorphism. PC 1 represents allometric size and the anterior and posterior teeth show opposing relationships with PC 2.

Table 4.2 PCA results of 56 craniodental variables corrected for sexual dimorphism within and between species. Tooth height measurements are excluded.

All variables				
	Within-species		Between-species	
PC	Eigenvalue	% variance	Eigenvalue	% variance
1	0.025	43.46	0.073	80.65
2	0.004	17.56	0.012	13.30
3	0.004	6.58	0.002	2.52
4	0.002	3.92	0.001	1.01
5	0.002	3.44	0.001	0.71
6	0.002	2.94	0.000	0.47
7	0.001	2.36	0.000	0.36
8	0.001	2.15	0.000	0.34
9	0.001	2.00	0.000	0.29
10	0.001	1.84	0.000	0.15
...	...	...	...	...
Total	0.059	100	0.091	100

'...' indicates that additional PCs were extracted; because they explain negligible amounts of variance they are not displayed.

PC 2 (compare Figure 4.7). Together, the first and second principal components account for 61% and 94% of craniodental variance within and between macaque species, respectively (Table 4.2). When variance as a result of sexual size dimorphism is factored out, the amount of craniodental variance is slightly less within than between species (see 'eigenvariance' in Table 4.2). Previously, the disparity in eigenvariance was greater between the intraspecific and interspecific level (Table 4.1 and Table D.1 in Appendix D).

4.3.2 Univariate Patterns of Variation

Variance levels per tooth measurement are listed in Table 4.3. Differences in variance exist between teeth as well as between tooth dimensions. Although the degree of phenotypic variation is a property of the measured sample and therefore does not necessarily reflect the full range of phenotypic variability that a biological system is able to produce, a comparison between dental measurements taken from one and the same sample can elucidate the pattern of *relative* variability of teeth.

Table 4.3 Variances, within and between macaque species, for tooth lengths and breadths, and the ratio between them (F-ratio). The pooled (i.e., within-species) standard deviation (s) and mean ($\bar{x}$) are also presented for each tooth dimension, as well as the coefficient of variation (CV) to represent the variance adjusted for the mean. Data are ranked by within-species variation as expressed by the CV (from large to small). See text for the definition of statistical denotations.

Measurement[a]	N	MS_M	MS_R	F-ratio	s	$\bar{x}$	CV
UCMD	485	38.65	3.42	11.32	1.85	7.44	0.248
LP3TL	567	128.37	5.71	22.50	2.39	10.67	0.224
LCBL	560	35.08	2.47	14.19	1.57	7.40	0.212
LCMD	569	13.63	0.70	19.48	0.84	4.36	0.192
LP3OL	606	46.22	1.41	32.85	1.19	6.42	0.185
UCBL	471	11.93	1.00	11.94	1.00	6.03	0.166
LI2MD	635	8.82	0.29	30.27	0.54	4.24	0.127
LP3W	619	13.41	0.27	50.15	0.52	4.26	0.121
UI2MD	637	9.62	0.19	50.51	0.44	3.97	0.110
UI1MD	621	20.46	0.40	51.74	0.63	6.23	0.101

Continued on next page

– continued

Measurement[a]	N	MS_M	MS_R	F-ratio	s	$\bar{x}$	CV
LI1MD	644	8.24	0.17	49.03	0.41	4.34	0.094
UM3PW	525	19.66	0.34	58.61	0.58	6.53	0.089
LI2LL	633	11.29	0.17	67.38	0.41	4.90	0.084
LM3PW	519	18.84	0.24	77.19	0.49	6.12	0.081
UI2LL	626	7.16	0.16	44.42	0.40	4.95	0.081
LM3L	526	53.74	0.59	91.49	0.77	9.63	0.080
LI1LL	635	7.88	0.17	45.87	0.41	5.28	0.079
LM3AW	523	26.28	0.29	90.35	0.54	6.88	0.078
UP3L	625	10.23	0.14	71.16	0.38	4.96	0.077
UM3L	550	34.31	0.33	103.83	0.57	7.81	0.074
UM3AW	525	27.97	0.31	91.08	0.55	7.63	0.073
LM2AW	672	20.59	0.23	88.66	0.48	6.71	0.072
UI1LL	623	6.87	0.16	42.14	0.40	5.63	0.072
LP4L	622	17.29	0.16	110.89	0.39	5.59	0.071
LM2PW	658	16.37	0.19	87.80	0.43	6.27	0.069
UP3W	637	11.64	0.16	72.66	0.40	5.79	0.069
UM2PW	655	17.50	0.23	76.44	0.48	7.08	0.068
LP4W	622	8.22	0.10	81.77	0.32	4.77	0.066
UM2AW	664	26.02	0.24	109.54	0.49	7.75	0.063
LM1PW	691	10.52	0.12	91.44	0.34	5.39	0.063
UM2L	676	32.04	0.25	130.98	0.49	8.00	0.062
UP4L	636	10.51	0.10	109.80	0.31	5.01	0.062
UM1PW	703	10.42	0.14	73.51	0.38	6.21	0.061
LM1AW	699	10.96	0.11	99.09	0.33	5.49	0.061
LM2L	676	29.60	0.23	130.35	0.48	7.91	0.060

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Measurement[a]	N	MS_M	MS_R	F-ratio	s	$\bar{x}$	CV
UP4W	635	12.55	0.14	89.68	0.37	6.24	0.060
UM1L	708	20.13	0.16	127.54	0.40	6.96	0.057
LM1L	701	16.93	0.15	111.61	0.39	6.84	0.057
UM1AW	710	15.62	0.14	111.07	0.38	6.70	0.056

[a]Key to variable names are in Table B.14.

Intraspecific variation

Linear traits pertaining to the CP_3 complex stand out as being the most variable part of the dentition (Table 4.3. The magnitude of the CV demonstrates that this remains true after size (i.e., the mean) is taken into account (Table 4.3). Ostensibly, this high level of intraspecific variation is due to sexual dimorphism, with male primates typically having distinctly larger canines and lower third premolars than females (Plavcan, 2001).

Third molars (especially M_3 length) followed by second molars appear to be the next most 'variable' teeth, as they show large variances (MS_R; Table 4.3). However, when using the mean-adjusted CV as a measure of variation, incisors are the most variant tooth class (after the the CP_3 complex). More specifically, incisal mesiodistal lengths vary more greatly than measurements of other teeth, followed by incisal labiolingual breadths and third molar widths and lengths, respectively. The premolars and the widths of the second molars are moderately invariant, with the first molars and second molar lengths being the most invariant elements in the dentition. When adjusted for tooth size, the molars as a tooth class are relatively invariant.

Interspecific variation

The between-species variances (MS_M) are largest for lengths of the upper canine, the lower third premolar, and the third molars (Table 4.3). These are followed by mesiodistal lengths and buccolingual widths of the second and third molars, while the fourth premolars, first molars, and incisors tend to vary the least between species.

The F-ratios in Table 4.3 reflect the degree of species differentiation in the data. The highly variable elements of the CP_3 complex are associated with a seemingly weak species divergence relative to other dental elements (F ranges between 11.32 and 32.85 for CP_3). This can be explained by their elevated within-species variation due to sexual dimorphism.

Molars, and their mesiodistal lengths especially, stand out in showing relatively high species divergence as judged by both the F-ratios and MS_M. This pattern is slightly stronger for upper than for lower molars. The length of the fourth premolar is also relatively divergent between species, which appears due to a low within-species variance (in absolute terms) rather than to a high between-species variation (again in absolute terms). Lastly, like MS_M, the F-ratios of incisors are relatively low, with the exception of the upper central incisor (I^1).

Sexual dimorphism

The presence of sexual dimorphism in dental variability was explored to see if there is a variational basis for selective and evolutionary differences between male and female macaques. One-way ANOVAs split by sex (with species as a factor, as per above) revealed no large differences between males and females. Grand variances (ignoring species) and pooled within-species variances were highly similar between the sexes, with the exception of the CP_3 complex. In this case, the pattern of differences between male and female within-species variances was consistent with expectations, with males having larger variances (e.g. UCMD: MS_R = 1.50, LP3TL: MS_R = 1.42) than females (UCMD: MS_R = 0.25, LP3TL: MS_R = 0.73). Species differences reflected by MS_M and the F-ratio were more pronounced for males than females on all tooth measurements except for upper canine mesiodistal length. This sexual dimorphism in between-species variation was quite pronounced in the majority of the cases. Sex differences in between-species differences were lowest for the lateral incisors. For the sake of brevity and space the results of these ANOVAs are not displayed in full here.

The level of variance is related to the scale and size of measurement. This means that, all else being equal, larger bodies tend to exhibit larger size-related phenotypic variance. Thus, between-species tooth size variation is in part an effect of species variation in body size. Moreover, degree of sexual dimorphism often increases with primate body size (Leutenegger and Cheverud, 1982). This may explain why males vary more between species in tooth size than females.

4.3.3 Patterns of Covariation

To inspect the pattern and degree of covariation in the dentition as a measure of morphological integration and modularity, several correlation matrices were generated. These are displayed in Figures 4.11 and 4.12 (between species) and Figures 4.13 and 4.14 (within species), showing the patterns of covariation between the various tooth dimensions by jaw.

Intra- and interspecific integration

Firstly, teeth tend to covary most strongly within their own tooth class, both between and within species (Figures 4.11 to 4.14). This pattern of integration and modularity is most evident for the molars, followed by the premolars. The incisors appear to be less tightly integrated among themselves, especially within species (Figures 4.13 to 4.14). This may at least in part be an artefact of dental wear, independent of underlying 'integrative processes'. Upper central incisors in particular experience a high degree of wear from the moment they come into occlusion, and their mesiodistal length at the occlusal surface changes as a result. It is likely that this introduces a source of variation not shared with other incisal measurements, thus yielding lower pairwise correlations. Indeed, correlations between incisal lengths and labiolingual widths are higher in the mandible than in the maxilla, probably because the dimensions of mandibular incisors change less with wear due to their relatively uniform mesiodistal shape from occlusal edge down to the CEJ. Variation due to tooth wear affect correlations between measurements on the within-species level; between-species correlations based on species means are much less affected.

Secondly, between tooth classes, the strongest association exists between premolars and molars, especially through the fourth premolars, in both the upper and the lower jaw. This pattern is visible both between and within species (Figures 4.11 to 4.14). Moreover, the canines are more weakly correlated to the other teeth, except in the mandible where they correlate strongly with P_3. Ostensibly, this is due to P_3 being part of the canine/premolar complex (Zingeser, 1968). Within species (Figures 4.13 to 4.14), P_3 is more strongly correlated to the canines than it is to other teeth, including adjacent P_4. Between species, the incisors are increasingly more weakly correlated to teeth that are increasingly posterior (Figures 4.11 to 4.12). Within species, the incisors appear equally weakly correlated with all non-incisor teeth.

	I1MD	I1LL	I2MD	I2LL	CMD	CBL	P3L	P3W	P4L	P4W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW
I1MD	1	0.722	0.694	0.626	0.778	0.692	0.705	0.502	0.687	0.499	0.322	0.516	0.413	0.395	0.484	0.479	0.460	0.433	0.493
I1LL		1	0.815	0.877	0.670	0.513	0.721	0.690	0.724	0.619	0.432	0.570	0.500	0.505	0.524	0.546	0.539	0.505	0.577
I2MD			1	0.939	0.569	0.418	0.777	0.783	0.741	0.758	0.595	0.791	0.764	0.640	0.744	0.761	0.690	0.718	0.751
I2LL				1	0.662	0.530	0.859	0.892	0.834	0.834	0.712	0.825	0.806	0.746	0.787	0.810	0.775	0.783	0.810
CMD					1	0.944	0.823	0.610	0.877	0.579	0.607	0.631	0.567	0.633	0.564	0.563	0.679	0.558	0.556
CBL						1	0.697	0.530	0.800	0.528	0.608	0.572	0.513	0.637	0.521	0.492	0.683	0.541	0.521
P3L							1	0.907	0.943	0.869	0.818	0.878	0.849	0.811	0.850	0.874	0.823	0.830	0.828
P3W								1	0.885	0.977	0.896	0.925	0.920	0.911	0.943	0.957	0.898	0.944	0.950
P4L									1	0.884	0.861	0.897	0.846	0.892	0.869	0.864	0.906	0.862	0.855
P4W										1	0.915	0.946	0.931	0.936	0.972	0.963	0.923	0.978	0.973
M1L											1	0.939	0.951	0.977	0.932	0.917	0.963	0.946	0.882
M1AW												1	0.986	0.951	0.981	0.973	0.960	0.965	0.930
M1PW													1	0.943	0.968	0.968	0.947	0.963	0.918
M2L														1	0.955	0.937	0.992	0.965	0.930
M2AW															1	0.990	0.948	0.984	0.963
M2PW																1	0.929	0.972	0.963
M3L																	1	0.959	0.926
M3AW																		1	0.981
M3PW																			1

species $N = 13$

- 0.8 ≤ Pearson's r ≤ 1 (very strong)
- 0.6 ≤ Pearson's r < 0.8 (strong)
- 0.4 ≤ Pearson's r < 0.6 (moderate)
- 0.2 ≤ Pearson's r < 0.4 (moderate to weak)
- 0 < Pearson's r < 0.2 (weak to negligible)

Fig. 4.11 Between-species correlation matrix of tooth lengths and widths in the maxilla. Correlations are Pearson's *r*.

	I1MD	I1LL	I2MD	I2LL	CMD	CBL	P3OL	P3TL	P3W	P4L	P4W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW
I1MD	1	0.801	0.875	0.776	0.797	0.569	0.827	0.735	0.707	0.769	0.615	0.269	0.370	0.355	0.215	0.386	0.435	0.295	0.440	0.418
I1LL		1	0.620	0.916	0.800	0.799	0.819	0.836	0.706	0.744	0.686	0.443	0.465	0.423	0.371	0.476	0.503	0.389	0.482	0.472
I2MD			1	0.750	0.779	0.561	0.839	0.674	0.847	0.883	0.775	0.512	0.615	0.626	0.477	0.618	0.705	0.561	0.685	0.696
I2LL				1	0.925	0.917	0.922	0.923	0.842	0.883	0.815	0.590	0.613	0.596	0.506	0.609	0.668	0.541	0.628	0.633
CMD					1	0.908	0.945	0.946	0.841	0.918	0.802	0.575	0.600	0.616	0.485	0.576	0.606	0.555	0.618	0.585
CBL						1	0.864	0.908	0.743	0.813	0.740	0.612	0.570	0.578	0.524	0.542	0.567	0.547	0.578	0.566
P3OL							1	0.940	0.858	0.936	0.811	0.575	0.616	0.637	0.504	0.615	0.654	0.576	0.679	0.655
P3TL								1	0.787	0.858	0.729	0.537	0.551	0.560	0.439	0.541	0.546	0.510	0.562	0.509
P3W									1	0.974	0.959	0.831	0.888	0.872	0.784	0.871	0.890	0.846	0.862	0.823
P4L										1	0.945	0.774	0.823	0.832	0.718	0.806	0.838	0.788	0.836	0.808
P4W											1	0.901	0.937	0.934	0.864	0.922	0.948	0.895	0.923	0.909
M1L												1	0.978	0.971	0.987	0.958	0.922	0.984	0.921	0.866
M1AW													1	0.986	0.971	0.988	0.965	0.985	0.955	0.908
M1PW														1	0.956	0.965	0.958	0.983	0.949	0.913
M2L															1	0.962	0.915	0.982	0.937	0.882
M2AW																1	0.965	0.961	0.973	0.919
M2PW																	1	0.925	0.956	0.963
M3L																		1	0.935	0.876
M3AW																			1	0.967
M3PW																				1

species $N = 13$

- 0.8 ≤ Pearson's r ≤ 1 (very strong)
- 0.6 ≤ Pearson's r < 0.8 (strong)
- 0.4 ≤ Pearson's r < 0.6 (moderate)
- 0.2 ≤ Pearson's r < 0.4 (moderate to weak)
- 0 < Pearson's r < 0.2 (weak to negligible)

Fig. 4.12 Between-species correlation matrix of tooth lengths and widths in the mandible. Correlations are Pearson's *r*.

	I1MD	I1LL	I2MD	I2LL	CMD	CBL	P3L	P3W	P4L	P4W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW
I1MD	1	0.536	0.137	0.530	0.459	0.415	0.505	0.328	0.466	0.368	0.449	0.328	0.273	0.462	0.379	0.375	0.377	0.418	0.394
I1LL		1	0.270	0.733	0.440	0.503	0.519	0.541	0.516	0.582	0.475	0.553	0.504	0.542	0.607	0.592	0.462	0.563	0.546
I2MD			1	0.360	0.117	0.229	0.268	0.248	0.278	0.281	0.304	0.308	0.265	0.268	0.305	0.238	0.202	0.276	0.189
I2LL				1	0.534	0.608	0.568	0.594	0.520	0.612	0.504	0.568	0.504	0.551	0.646	0.595	0.487	0.627	0.530
CMD					1	0.798	0.652	0.475	0.464	0.464	0.468	0.433	0.376	0.454	0.487	0.497	0.494	0.548	0.518
CBL						1	0.559	0.496	0.462	0.533	0.453	0.464	0.436	0.476	0.548	0.545	0.538	0.598	0.560
P3L							1	0.635	0.734	0.626	0.626	0.535	0.447	0.688	0.604	0.583	0.567	0.615	0.555
P3W								1	0.565	0.812	0.511	0.662	0.579	0.604	0.715	0.702	0.547	0.693	0.628
P4L									1	0.664	0.644	0.554	0.466	0.748	0.658	0.618	0.572	0.621	0.538
P4W										1	0.547	0.715	0.607	0.665	0.817	0.780	0.579	0.759	0.658
M1L											1	0.659	0.578	0.772	0.620	0.609	0.586	0.605	0.506
M1AW												1	0.765	0.648	0.837	0.742	0.552	0.773	0.628
M1PW													1	0.571	0.696	0.729	0.470	0.649	0.624
M2L														1	0.770	0.757	0.692	0.712	0.626
M2AW															1	0.871	0.641	0.891	0.745
M2PW																1	0.624	0.825	0.820
M3L																	1	0.772	0.739
M3AW																		1	0.851
M3PW																			1

species N = 6 - 61

- 0.8 ≤ Pearson's r ≤ 1 (very strong)
- 0.6 ≤ Pearson's r < 0.8 (strong)
- 0.4 ≤ Pearson's r < 0.6 (moderate)
- 0.2 ≤ Pearson's r < 0.4 (moderate to weak)
- 0 < Pearson's r < 0.2 (weak to negligible)

Fig. 4.13 Pooled within-species correlation matrix of tooth lengths and widths in the maxilla. Correlations are Pearson's *r*.

	I1MD	I1LL	I2MD	I2LL	CMD	CBL	P3OL	P3TL	P3W	P4L	P4W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW
I1MD	1	0.438	0.601	0.476	0.335	0.260	0.304	0.234	0.272	0.346	0.351	0.495	0.392	0.354	0.390	0.383	0.352	0.277	0.399	0.340
I1LL		1	0.321	0.745	0.489	0.501	0.491	0.463	0.502	0.520	0.461	0.453	0.522	0.543	0.512	0.579	0.565	0.520	0.561	0.499
I2MD			1	0.386	0.383	0.334	0.387	0.349	0.346	0.385	0.365	0.505	0.364	0.367	0.435	0.353	0.372	0.301	0.424	0.395
I2LL				1	0.568	0.572	0.565	0.552	0.551	0.549	0.482	0.521	0.534	0.569	0.534	0.558	0.566	0.544	0.574	0.527
CMD					1	0.928	0.873	0.882	0.787	0.519	0.482	0.477	0.454	0.500	0.490	0.498	0.493	0.468	0.530	0.494
CBL						1	0.866	0.927	0.790	0.508	0.439	0.468	0.443	0.497	0.476	0.478	0.482	0.477	0.496	0.478
P3OL							1	0.896	0.784	0.640	0.479	0.552	0.473	0.519	0.546	0.496	0.485	0.503	0.505	0.440
P3TL								1	0.809	0.551	0.462	0.486	0.452	0.504	0.501	0.484	0.469	0.476	0.490	0.458
P3W									1	0.614	0.680	0.513	0.591	0.607	0.563	0.610	0.590	0.510	0.602	0.527
P4L										1	0.670	0.564	0.570	0.554	0.741	0.668	0.652	0.629	0.628	0.539
P4W											1	0.502	0.709	0.643	0.665	0.790	0.751	0.570	0.726	0.640
M1L												1	0.662	0.677	0.707	0.587	0.593	0.553	0.575	0.560
M1AW													1	0.863	0.638	0.792	0.749	0.602	0.739	0.654
M1PW														1	0.609	0.694	0.786	0.607	0.652	0.676
M2L															1	0.776	0.737	0.682	0.691	0.626
M2AW																1	0.871	0.669	0.859	0.719
M2PW																	1	0.713	0.818	0.835
M3L																		1	0.748	0.740
M3AW																			1	0.855
M3PW																				1

species N = 5 - 52

- 0.8 ≤ Pearson's r ≤ 1 (very strong)
- 0.6 ≤ Pearson's r < 0.8 (strong)
- 0.4 ≤ Pearson's r < 0.6 (moderate)
- 0.2 ≤ Pearson's r < 0.4 (moderate to weak)
- 0 < Pearson's r < 0.2 (weak to negligible)

Fig. 4.14 Pooled within-species correlation matrix of tooth lengths and widths in the mandible. Correlations are Pearson's *r*.

Sexual dimorphism

Patterns of dental covariation were inspected separately for males and females to see if these vary between the sexes. The correlation matrices of the maxilla and mandible separated by sex can be found in Figures D.1 and D.2 in Appendix D. The patterns of dental correlations are highly similar between males and females. The only exception is in the lower premolars (see Figure D.2). P_3 correlates more strongly with the lower canine in male than in female macaques, most likely because it is part of the CP_3 complex, which plays a more prominent role in catarrhine males.

Overall strength of correlations for individual teeth and tooth classes are also highly similar between the sexes, as evinced by r^2 (see Tables D.2 and D.3 in Appendix D). Most of the (slight) differences in correlation magnitudes between males and females are likely insignificant. However, the lower canine and P_3 exhibit a bigger difference in the average correlation between males and females (Table D.3).

Allometry as an integrating factor

An important caveat of interpreting covariance patterns to demonstrate integration is that covariances may arise from a variety of factors, not all of which (or potentially none of which) reflect genetic and/or developmental processes that cause morphological integration (Mitteroecker and Bookstein, 2007; Mitteroecker et al., 2012). An example is allometry, the relationship between size and shape (Klingenberg, 2013; Mitteroecker et al., 2013). Due to allometric effects two traits may covary if they have the same relationship to the duration of growth, even though genetically and developmentally they may be completely independent (Mitteroecker et al., 2012). In this case, they would be uncorrelated after controlling for organismal size. Allometry often dominates the first dimension of morphological variation (Klingenberg, 2013; Mitteroecker et al., 2012), as it does here, and it may therefore also structure trait covariation.

The fact that patterns of integration may arise from allometry alone, rather than from developmental (e.g., local growth factors) or genetic (e.g., pleiotropy) processes, also has ramifications for the detection and interpretation of modularity. If modularity is conceptualised as the dissociation of developmental, functional, or evolutionary processes, then 'true' modules are those that remain associated through local factors when common factors (i.e., those affecting all traits) are accounted for (Mitteroecker and Bookstein, 2007). Statistically speaking, modules are sets of variables that have non-zero covariances within, but near-zero covariances between them; the effect of overall size (e.g., through common growth factors)

Table 4.4 A comparison of the magnitude of dental correlations in the maxilla between and within species, by tooth measurement, tooth, and tooth class.

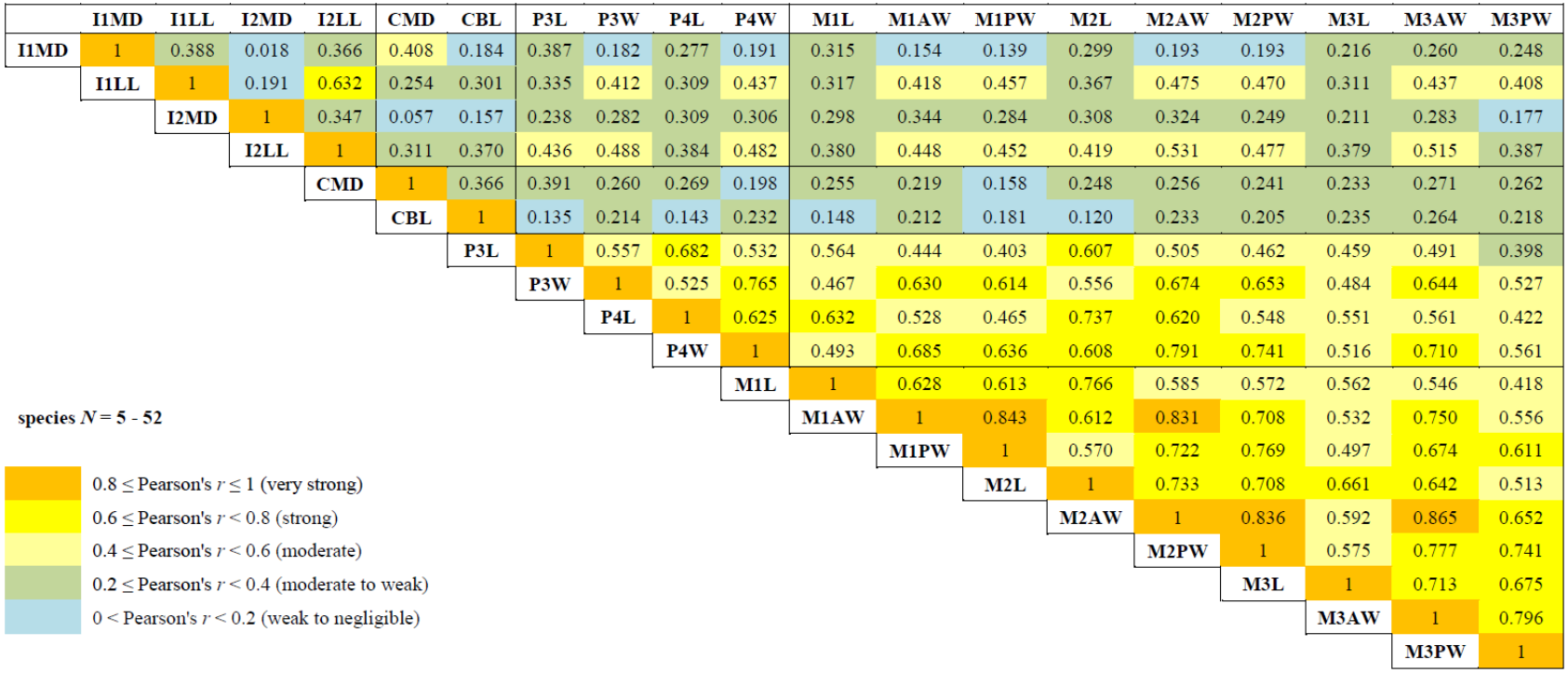
	Between-species			Within-species		
	Measurement	Tooth	Class	Measurement	Tooth	Class
I1MD	0.320	0.355	0.466	0.169	0.227	0.210
I1LL	0.391			0.285		
I2MD	0.529	0.576		0.067	0.193	
I2LL	0.624			0.319		
CMD	0.448	0.410	0.410	0.249	0.261	0.261
CBL	0.371			0.274		
P3L	0.686	0.706	**0.715**	0.336	0.342	0.352
P3W	0.727			0.347		
P4L	0.720	**0.724**		0.326	0.362	
P4W	**0.728**			0.398		
M1L	0.666	0.704	0.711	0.314	0.330	**0.379**
M1AW	0.741			0.376		
M1PW	0.705			0.300		
M2L	0.703			0.391		
M2AW	0.724	0.716		**0.457**	**0.427**	
M2PW	0.722			0.433		
M3L	0.719			0.319		
M3AW	0.718	0.714		0.452	0.381	
M3PW	0.704			0.372		

Values are averages of r squared (r^2) representing correlational magnitudes (Marroig and Cheverud, 2001). Derived from correlation coefficients in Figures 4.11 and 4.13. Values in bold represent the strongest correlations.

Table 4.5 A comparison of the magnitude of dental correlations in the mandible between and within species, by tooth measurement, tooth, and tooth class.

	Between-species			Within-species		
	Measurement	Tooth	Class	Measurement	Tooth	Class
I1MD	0.360	0.390	0.459	0.143	0.209	0.219
I1LL	0.420			0.275		
I2MD	0.489	0.529		0.155	0.229	
I2LL	0.568			0.302		
CMD	0.557	0.519	0.519	0.342	0.338	0.338
CBL	0.482			0.334		
P3OL	0.584	0.598	**0.659**	0.350	0.352	0.346
P3TL	0.503			0.336		
P3W	0.708			0.370		
P4L	0.709	**0.719**		0.335	0.339	
P4W	**0.729**			0.344		
M1L	0.606	0.632	0.622	0.307	0.346	**0.369**
M1AW	0.648			0.367		
M1PW	0.642			0.364		
M2L	0.564	0.617		0.367	**0.398**	
M2AW	0.636			0.412		
M2PW	0.650			**0.414**		
M3L	0.604	0.618		0.327	0.363	
M3AW	0.647			0.409		
M3PW	0.603			0.354		

Values are averages of *r* squared representing correlational magnitudes (Marroig and Cheverud, 2001). Derived from correlation coefficients in Figures 4.12 and 4.14. Values in bold represent the strongest correlations.



	I1MD	I1LL	I2MD	I2LL	CMD	CBL	P3L	P3W	P4L	P4W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW
I1MD	1	0.388	0.018	0.366	0.408	0.184	0.387	0.182	0.277	0.191	0.315	0.154	0.139	0.299	0.193	0.193	0.216	0.260	0.248
I1LL		1	0.191	0.632	0.254	0.301	0.335	0.412	0.309	0.437	0.317	0.418	0.457	0.367	0.475	0.470	0.311	0.437	0.408
I2MD			1	0.347	0.057	0.157	0.238	0.282	0.309	0.306	0.298	0.344	0.284	0.308	0.324	0.249	0.211	0.283	0.177
I2LL				1	0.311	0.370	0.436	0.488	0.384	0.482	0.380	0.448	0.452	0.419	0.531	0.477	0.379	0.515	0.387
CMD					1	0.366	0.391	0.260	0.269	0.198	0.255	0.219	0.158	0.248	0.256	0.241	0.233	0.271	0.262
CBL						1	0.135	0.214	0.143	0.232	0.148	0.212	0.181	0.120	0.233	0.205	0.235	0.264	0.218
P3L							1	0.557	0.682	0.532	0.564	0.444	0.403	0.607	0.505	0.462	0.459	0.491	0.398
P3W								1	0.525	0.765	0.467	0.630	0.614	0.556	0.674	0.653	0.484	0.644	0.527
P4L									1	0.625	0.632	0.528	0.465	0.737	0.620	0.548	0.551	0.561	0.422
P4W										1	0.493	0.685	0.636	0.608	0.791	0.741	0.516	0.710	0.561
M1L											1	0.628	0.613	0.766	0.585	0.572	0.562	0.546	0.418
M1AW												1	0.843	0.612	0.831	0.708	0.532	0.750	0.556
M1PW													1	0.570	0.722	0.769	0.497	0.674	0.611
M2L														1	0.733	0.708	0.661	0.642	0.513
M2AW															1	0.836	0.592	0.865	0.652
M2PW																1	0.575	0.777	0.741
M3L																	1	0.713	0.675
M3AW																		1	0.796
M3PW																			1

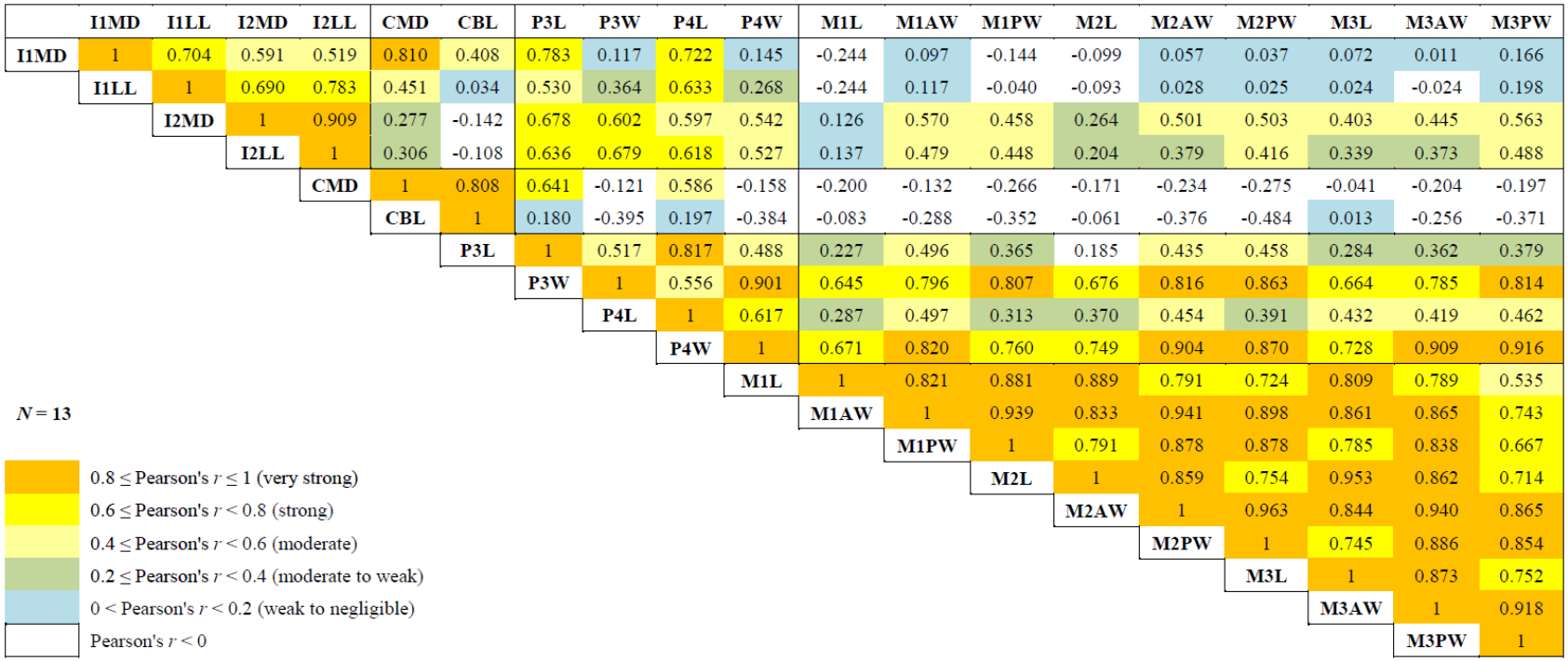
Fig. 4.15 Pooled within-species correlation matrix of size-adjusted tooth lengths and widths in the maxilla. Correlations are Pearson's *r*.

	I1MD	I1LL	I2MD	I2LL	CMD	CBL	P3OL	P3TL	P3W	P4L	P4W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW
I1MD	1	0.267	0.528	0.361	0.365	0.220	0.132	0.198	0.181	0.153	0.228	0.347	0.282	0.188	0.237	0.250	0.185	0.096	0.240	0.179
I1LL		1	0.141	0.626	0.286	0.377	0.211	0.248	0.298	0.307	0.260	0.197	0.317	0.344	0.285	0.388	0.365	0.279	0.339	0.284
I2MD			1	0.253	0.283	0.235	0.263	0.299	0.223	0.295	0.269	0.415	0.294	0.240	0.376	0.290	0.283	0.191	0.324	0.293
I2LL				1	0.394	0.484	0.396	0.370	0.393	0.426	0.396	0.404	0.445	0.467	0.432	0.464	0.472	0.430	0.451	0.410
CMD					1	0.548	0.384	0.500	0.395	0.347	0.399	0.318	0.369	0.347	0.372	0.459	0.420	0.286	0.442	0.369
CBL						1	0.541	0.463	0.503	0.420	0.381	0.334	0.390	0.404	0.387	0.471	0.481	0.351	0.475	0.404
P3OL							1	0.559	0.556	0.481	0.444	0.391	0.413	0.425	0.460	0.493	0.467	0.364	0.458	0.389
P3TL								1	0.486	0.562	0.437	0.503	0.424	0.427	0.497	0.448	0.435	0.395	0.405	0.300
P3W									1	0.556	0.648	0.470	0.586	0.583	0.505	0.583	0.562	0.421	0.531	0.421
P4L										1	0.644	0.522	0.514	0.496	0.713	0.608	0.597	0.557	0.542	0.424
P4W											1	0.495	0.683	0.609	0.631	0.767	0.717	0.481	0.663	0.526
M1L												1	0.646	0.633	0.688	0.555	0.551	0.507	0.544	0.505
M1AW													1	0.844	0.592	0.764	0.718	0.508	0.716	0.574
M1PW														1	0.555	0.668	0.760	0.515	0.628	0.611
M2L															1	0.734	0.687	0.638	0.640	0.532
M2AW																1	0.855	0.584	0.829	0.635
M2PW																	1	0.637	0.790	0.765
M3L																		1	0.682	0.664
M3AW																			1	0.809
M3PW																				1

species N = 4 - 45

- 0.8 ≤ Pearson's r ≤ 1 (very strong)
- 0.6 ≤ Pearson's r < 0.8 (strong)
- 0.4 ≤ Pearson's r < 0.6 (moderate)
- 0.2 ≤ Pearson's r < 0.4 (moderate to weak)
- 0 < Pearson's r < 0.2 (weak to negligible)

Fig. 4.16 Pooled within-species correlation matrix of size-adjusted tooth lengths and widths in the mandible. Correlations are Pearson's *r*.



	I1MD	I1LL	I2MD	I2LL	CMD	CBL	P3L	P3W	P4L	P4W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW
I1MD	1	0.704	0.591	0.519	0.810	0.408	0.783	0.117	0.722	0.145	-0.244	0.097	-0.144	-0.099	0.057	0.037	0.072	0.011	0.166
I1LL		1	0.690	0.783	0.451	0.034	0.530	0.364	0.633	0.268	-0.244	0.117	-0.040	-0.093	0.028	0.025	0.024	-0.024	0.198
I2MD			1	0.909	0.277	-0.142	0.678	0.602	0.597	0.542	0.126	0.570	0.458	0.264	0.501	0.503	0.403	0.445	0.563
I2LL				1	0.306	-0.108	0.636	0.679	0.618	0.527	0.137	0.479	0.448	0.204	0.379	0.416	0.339	0.373	0.488
CMD					1	0.808	0.641	-0.121	0.586	-0.158	-0.200	-0.132	-0.266	-0.171	-0.234	-0.275	-0.041	-0.204	-0.197
CBL						1	0.180	-0.395	0.197	-0.384	-0.083	-0.288	-0.352	-0.061	-0.376	-0.484	0.013	-0.256	-0.371
P3L							1	0.517	0.817	0.488	0.227	0.496	0.365	0.185	0.435	0.458	0.284	0.362	0.379
P3W								1	0.556	0.901	0.645	0.796	0.807	0.676	0.816	0.863	0.664	0.785	0.814
P4L									1	0.617	0.287	0.497	0.313	0.370	0.454	0.391	0.432	0.419	0.462
P4W										1	0.671	0.820	0.760	0.749	0.904	0.870	0.728	0.909	0.916
M1L											1	0.821	0.881	0.889	0.791	0.724	0.809	0.789	0.535
M1AW												1	0.939	0.833	0.941	0.898	0.861	0.865	0.743
M1PW													1	0.791	0.878	0.878	0.785	0.838	0.667
M2L														1	0.859	0.754	0.953	0.862	0.714
M2AW															1	0.963	0.844	0.940	0.865
M2PW																1	0.745	0.886	0.854
M3L																	1	0.873	0.752
M3AW																		1	0.918
M3PW																			1

Fig. 4.17 Between-species correlation matrix of size-adjusted tooth lengths and widths in the maxilla. Correlations are Pearson's *r*.

	I1MD	I1LL	I2MD	I2LL	CMD	CBL	P3OL	P3TL	P3W	P4L	P4W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW
I1MD	1	0.792	0.909	0.787	0.846	0.448	0.666	0.835	0.777	0.887	0.594	-0.095	0.065	0.010	-0.239	0.097	0.260	-0.107	0.267	0.230
	I1LL	1	0.512	0.882	0.723	0.657	0.722	0.680	0.627	0.664	0.618	-0.027	0.001	-0.121	-0.186	0.077	0.142	-0.145	0.058	0.069
		I2MD	1	0.583	0.698	0.223	0.479	0.776	0.739	0.862	0.548	-0.052	0.153	0.158	-0.166	0.185	0.418	-0.006	0.411	0.407
			I2LL	1	0.857	0.778	0.820	0.787	0.631	0.705	0.526	-0.162	-0.105	-0.132	-0.381	-0.038	0.159	-0.318	-0.040	0.004
				CMD	1	0.741	0.898	0.886	0.631	0.819	0.418	-0.214	-0.138	-0.075	-0.455	-0.130	-0.011	-0.293	-0.001	-0.056
					CBL	1	0.812	0.696	0.282	0.476	0.235	-0.183	-0.356	-0.257	-0.396	-0.309	-0.276	-0.365	-0.257	-0.224
						P3OL	1	0.847	0.640	0.758	0.424	-0.008	-0.002	0.023	-0.286	0.013	0.009	-0.088	0.011	-0.097
							P3TL	1	0.772	0.929	0.605	-0.017	0.082	0.125	-0.198	0.121	0.211	-0.011	0.294	0.253
								P3W	1	0.901	0.728	0.342	0.534	0.411	0.156	0.512	0.546	0.359	0.463	0.298
									P4L	1	0.736	0.202	0.345	0.344	0.003	0.335	0.423	0.210	0.454	0.361
										P4W	1	0.505	0.643	0.602	0.407	0.689	0.753	0.463	0.667	0.668
											M1L	1	0.878	0.825	0.913	0.813	0.592	0.910	0.602	0.349
N = 13												**M1AW**	1	0.902	0.834	0.927	0.806	0.921	0.749	0.542
													M1PW	1	0.710	0.764	0.723	0.830	0.626	0.478
														M2L	1	0.829	0.571	0.918	0.717	0.509
															M2AW	1	0.857	0.847	0.862	0.681
																M2PW	1	0.604	0.764	0.771
																	M3L	1	0.730	0.495
																		M3AW	1	0.877
																			M3PW	1

0.8 ≤ Pearson's r ≤ 1 (very strong)
0.6 ≤ Pearson's r < 0.8 (strong)
0.4 ≤ Pearson's r < 0.6 (moderate)
0.2 ≤ Pearson's r < 0.4 (moderate to weak)
0 < Pearson's r < 0.2 (weak to negligible)
Pearson's r < 0

Fig. 4.18 Between-species correlation matrix of size-adjusted tooth lengths and widths in the mandible. Correlations are Pearson's *r*.

can obscure the effect of local developmental factors that underpin modularity (Mitteroecker and Bookstein, 2007).

In order to assess the effect of allometry on the patterns of integration and modularity in the macaque dentition, I constructed and examined correlation matrices of the dental variables using size-free residuals. Size-free residuals are derived by log-transforming the raw data, regressing each variable onto the body size proxy, calvarium length, and saving the residuals. The residuals were then transformed back to the original data space (i.e., antilog-transformed). Both the pooled within-species and the between-species correlation matrices are displayed Figures 4.15 to 4.18. Mechanistic explanations about developmental integration and modularity can be made based on the former; interpretations about evolutionary integration follow from the latter.

The patterns of dental covariation after allometric-size correction are very similar to those prior to size correction. Correlation coefficients are a bit lower than they were before, but fairly evenly across the dentition, such that the pattern of relative strength of covariation between teeth and tooth types is the same. In fact, the pattern has become even more clearly defined, with a clear separation between the anterior and the posterior dentition on the within-species (Figures 4.15 and 4.16) as well as the between-species level (Figures 4.17 and 4.18). On the individual level (i.e., within species), the incisors and canines are not strongly correlated within their own tooth type, nor with the rest of the dentition. The premolars and molars remain strongly correlated, within and between tooth types (i.e., premolars and molars).

On the macroevolutionary level, the pattern is largely the same except for two differences. There is a strong relationship between the premolars and the anterior teeth, especially in the mandible (Figures 4.17 and 4.18), which did not exist in the intraspecific patterns. This may be due to the role of P_3 in the CP_3 complex, or as a result of adaptation (discussed in Section 4.4). Furthermore, the canines now have negative correlations with the molars, as do some incisal measurements. The negative correlations visible in both the maxilla and mandible are (at least in part) a statistical artefact. To correct for size means to hold size constant. That means that as one part of the dentition (e.g., the molars) get bigger, another part of the dentition (e.g., the canines or the incisors) must become smaller, as a mathematical necessity. For if both parts still become larger, yielding a positive correlation, then this would only be possible if overall size was becoming larger too, which would in fact mean that size was not (successfully) being held constant. In morphometrics, where allometric size often dominates trait variance, negative correlations are expected (and found) between substructures (e.g., parts of the tooth row) that are part of one and the same overarching structure (e.g., the jaw).

Correlational magnitudes, or mean inter-tooth correlations, r^2, were computed from the size-free tooth correlations. Overall, r^2 was lower for each tooth measurement, tooth, and tooth class than before allometric-size correction, as expected. However, the *pattern* of differences in r^2 is very similar, on the intraspecific and interspecific level. The maxilla always has higher values of r^2. Within species, the highest correlational magnitudes are found in the molars in both the maxilla (M^2 anterior width: $r^2 = 0.378$, M^2: $r^2 = 0.345$, molars: $r^2 = 0.307$), and the mandible (M^2 anterior width: $r^2 = 0.354$, M^2: $r^2 = 0.339$, molars: $r^2 = 0.295$). Between species, like before, the highest correlational magnitudes in the mandible are found for P_4 length ($r^2 = 0.374$), P_4 ($r^2 = 0.358$), and premolars ($r^2 = 0.338$). In the maxilla, the upper fourth premolar previously had the strongest correlations with the other maxillary teeth; after size correction, the second molar has the highest correlational magnitudes (M^2 anterior width: $r^2 = 0.487$, M^2: $r^2 = 0.444$, molars: $r^2 = 0.425$). In all cases, the incisors and canines once again have low mean inter-tooth correlations.

4.4 Discussion

In this chapter I investigated a few simple questions related to the ranges of variation of individual teeth, and how the dentition varies as a multi-trait structure. I also asked how teeth covary with one another. In both cases, a comparison of the within-species and between-species patterns yields insight about the extent to which within-species processes, such as development or genetics, can explain the evolutionary patterns visible between species. Here, these questions are discussed in the context of evolvability: how evolvable is the macaque dentition and to what extent can this evolvability explain the observed macroevolutionary differences between macaques?

How Canalised or Plastic Are Teeth?

In the univariate analyses of variance, the canine-premolar (CP_3) complex stood out as having the largest variance within species. The molars are the least variable, although the third molars had decidedly higher variances than the first and second molars. Based on the coefficient of variation (variance standardised by tooth size) the order from high to low variation was approximately CP_3 > incisors > third molars > premolars $\approx$ second molars > first molars. The large variance for the CP_3 complex predominantly reflects sexual dimorphism rather than degree of canalisation or phenotypic plasticity. As for the rest of the dentition, first molars appear the most canalised, or the least plastic, teeth, closely followed

by fourth premolars and second molars. Third molars are the most plastic, followed by the incisors.

There were no substantial differences in dental variances between the sexes, except with regard to the CP_3 complex, indicating that in general teeth are similarly canalised or plastic in both sexes. Part of the increased phenotypic variance of canines in males compared to females may be due to size (i.e., variance may be dependent on the mean). It could also reflect processes related to sexual selection that increase phenotypic differences among males, but that do not affect phenotypic variability in females. The larger between-species variances (MS_M) and F-ratios of dental measurements in males indicate that males of different species are more different in tooth size than females of different species. This is most likely a result of differences in body size rather than different processes operating on males and females.

These differences in level of variation between teeth observed in the sample correspond to known differences in 'variability'. Third molars have often been reported to be (among) the most variable teeth in the dentition in humans (Dahlberg, 1945; Hillson, 2005; Keene, 1965), primates (Gingerich and Schoeninger, 1979; Swindler, 2002), and some other mammals (Gingerich, 1974). First molars are often found to be the most 'stable' (Gingerich, 1974; Keene, 1965). Macaques follow this pattern of relative variability among the molars. The canines are found to be variable in both male and female primates (Gingerich and Schoeninger, 1979), which also matches the macaque findings. Fourth premolars of macaques, especially the mandibular ones, vary less compared to fourth premolars of some other primate species, including humans (Gingerich, 1974; Swindler, 2002). Many studies have reported levels of variation based on the coefficient of variation, but its use as a measure of variability has been criticised (Polly, 1998b). Its utility is based on a presumed positive relationship between the standard deviation (or variance) and the mean of a variable, but when such a relationship does not exist, larger measurements may appear less variable when judged by their CV (Polly, 1998b). However, a reassessment of the relative variability of teeth in macaques using the variance (MS_R), yields the same pattern. Third molars are the most variable (when disregarding the CP_3 complex; mean $MS_R = 0.35$), and first molars and fourth premolars are the least variable ($MS_R = 0.14$ for both).

Canalisation refers to the process by which phenotypic variance due to the environment is minimalised (Hallgrímsson et al., 2002). If we take the intraspecific level of variation to be a proxy for degree of canalisation, then we may conclude that first molars are *comparatively* canalised and less plastic. Third molars, by comparison, are more plastic. Differences in phenotypic variation may also arise from differences in genetic variation. However, evidence about gene regulatory networks that are responsible for tooth morphogenesis and tooth family differentiation (Salazar-Ciudad and Jernvall, 2002; Sharpe, 2000) suggests that there are no

differences between molars in terms of genetic variability that could explain differences in phenotypic variation between them.

How Integrated and Modular Is The Dentition?

The dentition of macaques proved to be a highly integrated structure, within as well as between species. The posterior dentition, i.e., the molars and the premolars, seems to be more integrated within itself than it is with the anterior dentition (i.e., the incisors and the canines), suggesting a degree of modularity. By comparison, the anterior teeth are less strongly integrated among themselves. The lower third premolar shows a different pattern of correlation with the surrounding teeth than the upper third premolar. This suggests that despite its position in the tooth jaw and premolar morphology, it has overridden genetic and developmental constraints that characterise the development of the other premolars, to become more strongly phenotypically correlated to the anterior dentition, specifically the canines. The lower third premolar performs a honing function to the upper canine, so it is likely that its covariation pattern reflects functional integration with the canines.

Thus, the macaque dentition consists of 'variational modules' (Wagner et al., 2007), which mostly reflect the different tooth types. Allometry proved to be an integrating factor for all teeth in the jaw, as evinced by the PCAs and the size-corrected correlation matrices. The first principal component, which explained the most variance in the data, showed a positive relationship with all craniodental metrics, thus representing an overall size effect. Once cranial size-related variance was removed from the bivariate dental correlations, the modular pattern in the dentition became even clearer. This suggests that although teeth are linked through general growth factors associated with body size, they are also the result of dissociated developmental factors (Mitteroecker and Bookstein, 2007, 2008). Caution is warranted, however, with respect to interpretations about development purely on the basis of statistical patterns. Observed statistical patterns do not necessarily reflect an underlying pattern of developmental integration and modularity, because low correlations – which may be interpreted as evidence for modularity – can arise from developmental factors that are linked (developmental pleiotropy) but have opposing effects (Mitteroecker et al., 2012).

That said, the pattern of phenotypic correlations in macaques match the genetic correlations between teeth found in baboons and mice well (Hlusko and Mahaney, 2009; Hlusko et al., 2011). Hlusko and colleagues also used linear measurements of tooth lengths and breadths and retrieved the genetic correlation patterns in known pedigrees of baboons (*Papio hamadryas*) and various species of mice (*Mus sp.*). The baboon and mice patterns were remarkably similar to each other and offer good support for genetic independence of the incisors from the rest of the dentition (canines were omitted in both, and premolars are

absent in mice Hlusko et al. 2011). Baboon data lends further support for genetic pleiotropy for the molars, but 'incomplete' pleiotropy between the premolars and molars, leading the authors to characterise these two tooth types as different submodules. The morphological correlation matrices obtained here closely resemble the genotypic pattern in the same baboon pedigree (Hlusko and Mahaney, 2009) and various other Old World Monkeys (Grieco et al., 2013). These observations of a tight *genotype-phenotype map*, supported by the present results in macaques, support the existence of underlying genotypic modularity and that developmental processes act to realise the phenotype as close to the genotype as possible. Developmental genetic studies have shown that certain homeobox genes that are implicated in the development of molars (e.g., *Dlx-1/2* and *Barx-2*) do not affect incisor development in transgenic mice (Sharpe, 2000).

There is a caveat about the use of correlation coefficients in inferring integration. Correlation coefficients are standardised against trait variances, but differences in variance become relevant when comparing correlation coefficients in order to evaluate which variables are more integrated. Namely, when the variances of two traits become larger such that they increase the covariance but not the residual variance (the width of the scatter around the regression line), then the correlation coefficient will be higher. If the variances of a second set of traits are comparably smaller, such that the absolute covariance between them is also smaller while the residual variance is exactly the same as for the previous set of variables, the correlation coefficient second set of variables will nonetheless be lower. Conceptually, however, it is not possible to determine in that case which of the two variable sets constitutes a more integrated unit (P. Mitteroecker pers. comm.). It is therefore important to compare the variance levels between incisors and molars before drawing conclusions about any differences in level of integration. Calculating mean variance levels from MS_R in Table 4.3 reveals that, within species, the variance is slightly smaller for incisors (0.21) than for molars (0.24). However, this difference is small. Moreover, when developmental integration is strong, increased variation in one trait will result in stronger phenotypic integration of that trait with other traits through shared developmental effects. If, on the other hand, a character is weakly integrated with others, an increase of its variance will reduce the morphological integration because the proportion of shared variance will be reduced, yielding an associated decrease in phenotypic covariation (Hallgrímsson et al., 2005). From this, one can predict that teeth with high variances should show lower correlations with other teeth if they are in fact *not* strongly developmentally integrated, and conversely, high correlations if they are strongly integrated. The upper central incisor (I^1) and third molars (M3s) both have high variances, but whereas third molars have been shown to correlate strongly with all other molars and

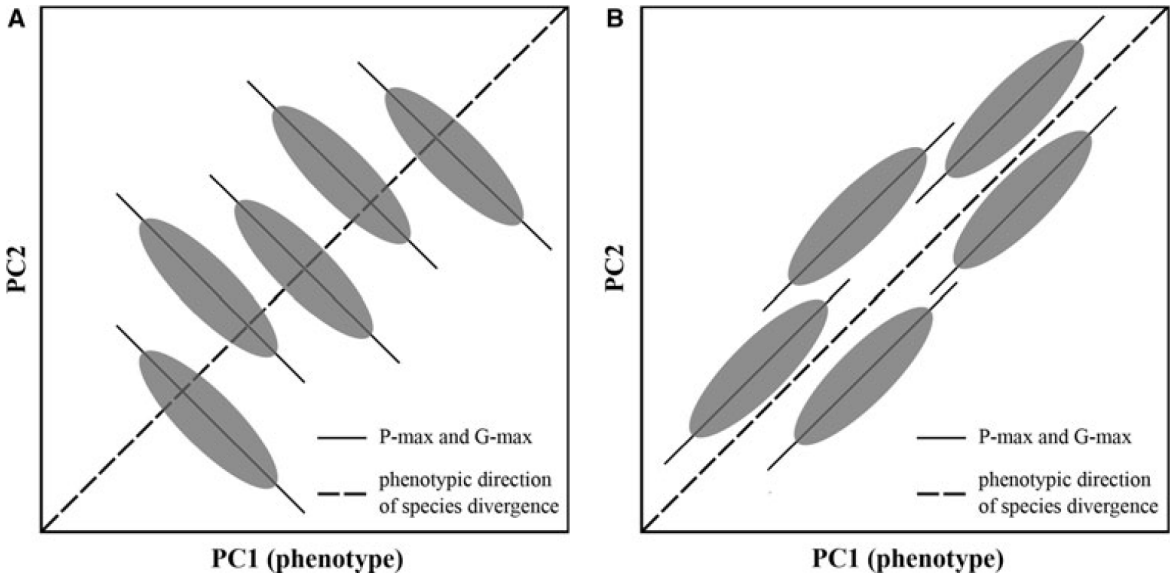


Fig. 4.19 Adapted from (Grieco et al., 2013). "Macroevolutionary divergence (A) under a modular framework and (B) under lines of least evolutionary resistance (LLER). Schematic of population variation and species phenotypic divergences in phenotypic space (PC 1 and PC 2 of the common morphospace). Ellipses represent individual species and their clouds of population variation, with the major axis defined by P-max. Under a genetic modular framework, species diversify along a distinct axis while P-max vectors (within-species variation) parallel each other (panel A). Under LLER, species diversify along P-max (panel B)." (Grieco et al., 2013, p. 255)

even the premolars, the upper first incisor always had comparatively weak correlations. It would thus appear that molars do represent a more tightly integrated module than incisors.

The strong integration as suggested by the correlation patterns in the posterior dentition, corresponds to what one might expect from a set of traits that perform the same function, namely the mastication of food. There is likely a strong selection pressure on the dentition as a whole, but the cheek teeth in particular, to be coordinated in their size and shape in order to maximise their mechanical efficiency in food processing by ensuring optimal occlusion. It is possible that incisors play a less vital role in food ingestion, or that their function is not compromised by a decrease in coordinated variation between them, and therefore selective pressures on incisor morphology may be comparatively weaker.

Micro vs. Macroevolution

Principal component analysis demonstrated an allometric size component that accounted for the majority of the variance between conspecifics as well as between species. The intraspecific multivariate direction of greatest *phenotypic* variation, $\mathbf{p}_{max}$, can be considered a proxy measure for the direction of greatest *genotypic* variation, $\mathbf{g}_{max}$, along which evolutionary

change is the least constrained (Hunt, 2007; Lande, 1979; Marroig and Cheverud, 2005). This has been called the line of least evolutionary resistance (LLER) by Schluter (1996a). PC 1 is, by definition, the multivariate direction of greatest phenotypic variation, and represents allometric size in the macaque data. But evolution does not always follow the LLER; selection for change in other directions can result in macroevolutionary patterns that differ from the microevolutionary ones (Marroig and Cheverud, 2005; Schluter, 1996a). This is illustrated in Figure 4.19. A comparison of the between-species to the within-species PCA results in macaques, however, shows that PC 1 is similarly oriented within and between macaque species, especially after correcting for sexual size dimorphism (Figure 4.8). And this primary axis of variation corresponds to allometric size on both the intraspecific and interspecific level (Figures 4.9 and 4.10). There are no differences between species in the orientation of the intraspecific data cloud (i.e., the orientation of the ellipses in Figure 4.8); only *M. nemestrina* and *M. ochreata* are rotated with respect to their congeners, but the difference is minimal and further analysis needs to elucidate whether these are significant. Thus, we can conclude that the evolutionary differentiation in macaque craniodental size occurred in a direction similar to the LLER. In other words, macroevolutionary divergence followed a microevolutionary trajectory in craniodental size. The extent of differentiation between species is minimal, however, because considerable overlap remains between macaques. This may be attributable to the young age of the *Macaca* lineage (<10 MY) or to evolutionary processes. This will be explored further on in this thesis.

The decoupling of the anterior from the posterior dentition explains most of the remaining between-species craniodental variation. There is a similar tooth size contrast visible on the population level, although it is less pronounced at this level (Figure 4.9a). Tying this in with the patterns of dental integration, it seems likely that a dissociation in local developmental mechanisms and reduced (or even absent) genetic pleiotropic effects between incisors and the molars (Grieco et al., 2013; Hlusko and Mahaney, 2009; Hlusko et al., 2011) has allowed macaques to differentiate evolutionarily with respect to the relative size of their anterior versus their posterior dentition.

The moderately strong phenotypic correlation between premolars and molars found in macaques was also observed in other Old World monkeys (OWM) (Grieco et al., 2013) and hominids, including humans (Gomez-Robles and Polly, 2012). In both those studies, premolar-molar integration was weaker than within-molar integration, matching the macaque results. In the Old World monkeys as a group (based on six species from five different genera), there was also a weak correlation between incisors and the postcanine dentition (Grieco et al., 2013).

Conclusion

Patterns of variation and covariation in the dentition of macaques align with known patterns in other taxa. Allometric effects structure both dental variances and integration of the dentition as a whole. Although there is some modularity in the dentition, it is generally a tightly integrated unit. Integration and modularity exist on different hierarchical levels (Wagner et al., 2007), so the dentition forms a developmental module largely independent from the skull it is housed in, but also shows a modular pattern within itself (Stock, 2001). Individual teeth will therefore not have independent evolutionary 'fates' and are best regarded as subparts of a trait. However, the results presented here indicate that a distinction between the anterior dentition of macaques (notably the incisors) and the posterior dentition (notably the molars) can be made. Phenotypic integration affects evolvability of a phenotype by shaping the direction of evolutionary change (Goswami et al., 2014; Hansen and Houle, 2008; Mitteroecker et al., 2012), and it appears that, in macaques at least, the incisors and molars may be subject to different evolutionary processes and diverge independently from each other. Within these modules, however, different teeth are so tightly integrated that selection on one of them (e.g., the first molar) will result in correlated evolution in another (e.g., the third molar).

Chapter 5

Size and Allometry

5.1 Introduction

Body size is one of the most important aspects of an animal's biology. It "dictates, constrains, underlies, and is highly correlated with" (Copes and Schwartz, 2010, p. 188) various parameters believed to be key adaptations of any organism, such as diet, locomotion, ecological competition (including predation), energetics, habitat ecology, life history, sociosexual behaviour, physiology, and of course morphology (references in Copes and Schwartz 2010). For this reason, body size has been extensively studied in relation to these factors, in neontological as well as palaeontological studies.

The relationship between teeth and body size has been studied in particular detail. Due to their high mineral content teeth fossilise well and make up a large part of the data record of most fossil taxa. Knowing how teeth scale with body size in extant species allows for the prediction of body size in extinct taxa, and thereby potentially a suite of other adaptations and ecological aspects (e.g., locomotion, diet, habitat, competition, or life history) (e.g., Creighton, 1980; Delson et al., 2000; Fleagle, 1985; Gingerich et al., 1982). Another reason tooth-to-body size scaling, that is dental allometry, has received a lot of scientific attention has been to provide a baseline of dental scaling against which outliers can be identified that require special adaptive explanations (Gingerich and Smith, 1985; Gould, 1975). In addition, dental allometry has been studied to understand how relative tooth size is mediated by an animal's energy requirements and diet (e.g., Corruccini and Henderson, 1978; Gingerich and Smith, 1985; Kay, 1975; Organ et al., 2011; Ungar, 2014).

The first half of the 20th century saw a number of important publications on the study of allometry. Of pivotal importance was Julian Huxley's (1932; 1924) seminal work on the growth of organs and other sub-anatomical structures relative to overall body size. Huxley showed that the shape and relative size of animals and plants is the outcome of differing

organic growth rates during ontogeny. He formalised the relationship between the size of two traits regulated by a common growth mechanism in the following power function, his simple allometry equation:

$$Y = b * X^a \tag{5.1}$$

in which Y and X are two traits, e.g., organ size and overall body size, b is a constant, and a the *scaling exponent* (Gayon, 2000; Huxley, 1924; Pélabon et al., 2013). The scaling exponent expresses the rate of growth relative to overall size (or any body part used for comparison). Although Huxley's model of allometric growth is an approximation of a more complex process of relative growth, it has been hugely influential and allometry-related terminology is widespread today (Strauss, 1993). *Isometry*, also known as geometric similarity, holds when something scales in proportion to body size (Ungar, 2014). It thus entails the independence of relative size or shape to overall size (Jungers et al., 1995). When traits have the same unit of measurement, isometry is characterised by a scaling exponent of 1 (M_b^1). When something is *negatively allometric* it increases *relatively less* than body size for every unit of body size increase, and thus the allometric scaling exponent is smaller than 1. *Positive allometry* describes the situation where something increases *relatively* more than expected on the basis of body size, and is described by a scaling exponent larger than 1 (Jungers et al., 1995; Klingenberg, 1998).

Another pivotal contribution was that of Kleiber (1947), who discovered that metabolic rate scales with body mass to the power of $\frac{3}{4}$ ($M_b^{0.75}$). Metabolic scaling is therefore negatively allometric with body size. Kleiber's 'law' entails that larger animals are more effective in their energy use for their body size. This discovery was influential for the study of dental allometry. Kleiber's rule led Pilbeam and Gould (1974) and Gould (1975) to hypothesise that the size of the postcanine occlusal surface should increase in proportion to the amount of food required to meet an animal's metabolic demands, and therefore it should scale allometrically with body size, namely to the power of 0.75. Because isometry between an area and volume, or mass, is characterised by a scaling exponent of 0.67, a scaling exponent of 0.75 reflects positive allometry. Gould (1975) found marginal support for his hypothesis in some groups of artiodactyls and rodents and he consquently suggested that such *metabolic scaling* should be the presumed standard pattern of dental allometry (the "criterion for subtraction" or null hypothesis; Gould, 1975, p. 351). Many researchers have tested Gould's scaling law in a wide variety of mammals and found limited support for it (reviewed in Copes and Schwartz, 2010). Depending on the taxon, the taxonomic level, the body size measure, and the analytical methods used, postcanine occlusal area (PCOA) has been found to scale with isometry, or positive or negative allometry relative to body size (reviewed in Copes and Schwartz, 2010, and in Ungar, 2014).

Positive allometry of primate postcanine tooth size has been explained by diet. Kay (1975) figured that positive allometry in the postcanine dentition arises from adaptive differences between primates of different body sizes in response to diet. Large-bodied primates tend to feed on low-quality foods, e.g., foliage, that is energy-poor relative to foods such as fruit and insects eaten by smaller-bodied primates. Thus, in order to meet their energy demands large primates need to eat larger amounts of the low-quality food, for which a large postcanine tooth area is adaptive. That folivores tend to have larger postcanine teeth for their body size or facial size is a well-known trend in primates (e.g. Kay, 1975; Lucas et al., 1986; Scott, 2011, 2012; Vinyard and Hanna, 2005). Indeed, when inspecting dental allometry patterns within dietary categories, PCOA often scales with isometry in primates and other mammals (e.g. Copes and Schwartz, 2010; Corruccini and Henderson, 1978; Gingerich et al., 1982; Kay, 1975, 1978; Scott, 2011).

If PCOA matches metabolic demands, then one might expect PCOA to scale negatively allometrically with body mass (rather than positive allometry if one hypothesises a scaling exponent of 0.75, as per Pilbeam and Gould, 1974). In this case isometric scaling of PCOA within dietary categories remains a deviation from the expectation of negative allometry (Copes and Schwartz, 2010; Ungar, 2014). This conundrum may be explained by differences in chewing rate. When tooth size scales isometrically with body size and metabolism scales with negative allometry, then larger-bodied animals would obtain more energy than they require. Fortelius (1988) discovered that this scaling discrepancy is resolved due to a slower chewing rate in larger animals. In his research on ungulates, he discovered that chewing rate scales with negative allometry, resulting in metabolic scaling of tooth size to body size when chewing rate is controlled. A negative allometric scaling relationship has been confirmed in a wide range of mammalian (including primate) taxa (Gerstner and Gerstein, 2008). Other, not mutually exclusive, explanations are that low-quality foliage requires relatively more energy to be digested, compensating to some extent for the surplus of energy acquired by large-bodied mammals, and differences in time spent feeding. Whether large-bodied mammals would actually consume more energy than they needed depends on the total time they feed per day.

Sexual dimorphism also contributes to variation in dental allometry. Sexual dimorphism is especially pronounced in the canine size of anthropoid primates, particularly in cercopithecoid monkeys (Harvey et al., 1978; Plavcan, 2001; Plavcan and van Schaik, 1992; Swindler, 2002). Sexual dimorphism in primate body mass and canine size has traditionally been explained in the framework of sexual selection (e.g., Clutton-Brock et al., 1977; Darwin, 1871; Leigh et al., 2008; Leutenegger and Kelly, 1977; Mitani et al., 1996; Plavcan, 2011; Plavcan and van Schaik, 1992; Thorén et al., 2006). The two main components of sexual selection

are mate competition and mate choice. These two mechanisms have traditionally been invoked to explain the pattern of sexual dimorphism in primates (reviewed in Plavcan, 2001, 2011). The study of mate competition centres around male-biased intrasexual competition for access to females. Male dominance rank is established through agonistic interactions and in many primate species a male's rank subsequently determines the level of access to sexually receptive females (Clarke et al., 2008; Cowlishaw and Dunbar, 1991). There is thus reproductive skew among males. Sperm competition is another form of male-male competition that occurs post-coitus. Any male trait that may be decisive in physical conflicts, display, or competition in the female reproductive tract and which enhances reproductive fitness should be heavily selected for (e.g., Darwin, 1871; Dixson, 1997; Harcourt et al., 1995; Kay et al., 1988; Leigh et al., 2008; Leutenegger and Kelly, 1977; Plavcan and van Schaik, 1992; Thorén et al., 2006). Although in principle mate choice can be exercised by both sexes, in primates the focus has primarily been on female choice (Darwin, 1871; Reynolds and Harvey, 1994). Female choosiness manifests when exaggerated male traits such as body or canine size are considered attractive by females, when female advertisement of sexual swellings incites male-male competition and the winner of the fight is subsequently allowed to mate with the receptive female(s), or when females choose to mate with newly immigrated males through sneaky copulation (Leigh et al., 2008; Plavcan, 2001, 2011; Thorén et al., 2006).

Mechanisms of natural selection other than sexual selection have also been put forward to explain canine size dimorphism throughout the years. These range from predation defence in terrestrial species (Clutton-Brock et al., 1977; DeVore and Washburn, 1963; Harvey et al., 1978; Plavcan and van Schaik, 1992), locomotory constraints (Clutton-Brock et al., 1977; Leutenegger and Kelly, 1977), early female maturation (Leigh and Shea, 1995), to agonistic interactions among females (Plavcan et al., 1995; Plavcan, 1998). Furthermore, the expression of sexual dimorphism has been argued to be a result of variation in body mass (Rensch' rule; Clutton-Brock et al., 1977; Leutenegger and Cheverud, 1982; Rensch, 1959), a sign of correlated evolution (Greenfield, 1992, 1996; Lande, 1980), or constrained by 'phylogenetic inertia' (Cheverud et al., 1985). Empirical support has been obtained for a variety of different mechanisms driving sexual dimorphism in primate body mass and canine size, leading most workers to accept sexual dimorphism as multifactorial in origin (reviewed in Plavcan, 2001, 2011).

The pattern of dental allometry may vary between species as a result of sexual dimorphism or dietary differences. Originally, however, the concept of allometry was coined by Huxley to describe variation within species, namely the changes in relative dimensions (and therefore shape) that are dependent on overall size with regard to ontogenetic growth ('narrow-sense'

allometry; Voje and Hansen, 2013). But the term 'allometry' has been expanded to include *static* and *evolutionary allometry* in the years following Huxley's seminal work (Strauss, 1993). Static allometry (sometimes called intraspecific allometry) refers to size-dependent variation in shape or relative size between individuals of a population within a specific age stage (typically adults) (Cheverud, 1982b; Klingenberg, 1998; Mitteroecker et al., 2013). Evolutionary allometry refers to the covariation of shape and size across species (Cheverud, 1982b; Klingenberg, 1998; Mitteroecker et al., 2013). Static allometry has often be interpreted as similarity in growth rates between individuals, i.e., to reflect ontogenetic allometry, but the two are conceptually different as static allometry "cuts across" ontogenetic trajectories (Strauss, 1993). Although static and ontogenetic patterns often closely resemble each other, they need not be expected to be similar and in fact may be uncorrelated (Cheverud, 1982b; Pélabon et al., 2013; Strauss, 1993). Similarly, evolutionary allometry is often assumed to follow static allometry. However, patterns of static allometry are most often based on observed phenotypic variances and covariances, whereas evolutionary allometry can only arise from genetic size-shape dependencies (Cheverud, 1982b; Lande, 1979). These two patterns therefore do not need to be strongly correlated (Cheverud, 1982b; Lande, 1985; Voje and Hansen, 2013). Moreover, differential selection may break up allometric associations between traits that alter the between-species pattern of evolutionary allometry (Klingenberg, 1998; Voje and Hansen, 2013).

5.1.1 Research Questions

Several topics related to body size and allometric scaling will be addressed in this chapter. First, the patterns of allometric scaling are investigated in the macaque dentition. In order to evaluate whether evolutionary allometry in macaques follows the static allometric pattern, dental allometry between and within species is compared. Previous studies have often used composite measures of tooth size, typically molar or postcanine occlusal area (e.g., Creighton, 1980; Gingerich et al., 1982; Gould, 1975; Scott, 2011; Vinyard and Hanna, 2005) or only a single tooth dimension (e.g., Hylander, 1975; Kay, 1975), but less often both lengths and breadths separately (Delson et al., 2000). However, teeth grow along several dimensions and may be subject to different genetic, developmental, or spatial constraints along these dimensions (Hlusko et al., 2006). These differences may be reflected in the scaling relationship of different tooth dimensions (e.g., lengths versus breadths) to overall size. Therefore, allometric scaling is investigated in tooth breadths and lengths separately.

The pattern of evolutionary allometry in macaque postcanine size is subsequently investigated for the presence of a dietary signal. Diet has been found to explain positive allometry of postcanine tooth size in anthropoid primates across higher clades (Corruccini

and Henderson, 1978; Kay, 1975; Scott, 2011, 2012). I test here whether variation in the degree of frugivory influences the scaling relationship between the postcanine teeth and overall size in macaques. Although macaques are all characterised as frugivorous monkeys, variation in their dietary composition does exist. For example, variation in the proportion of fruit in the diet relative to other food items exists between species, variation that may be important for dental morphology generally and allometric scaling in particular. In this chapter I will investigate if postcanine occlusal area (PCOA) has a distinct scaling relationship with overall size depending on the degree of frugivory.

Next, the importance of sexual selection is investigated in *Macaca* through a study of sexual size dimorphism in body size and craniodental, including canine, size. To this end, I address three questions. First, does sexual dimorphism in body mass increase with body mass on the level of macaques? Second, what is the pattern of craniodental, and specifically canine, size dimorphism in the present sample of macaques? To answer this, scaling in the size of the skull, the dentition, and the CP_3 complex will be investigated in females relative to males at the species level. This will demonstrate whether the degree of sexual dimorphism is constant across species and yield insight into whether sexual dimorphism may be a result of selection on males alone or also on females. Third, I investigate whether the degree of sexual size dimorphism (SSD) in the CP_3 complex is a function of body mass in order to ascertain whether the canine/premolar complex is the result of correlated evolution in body size or independent selection. The relationship of canine dimorphism to both absolute body mass and body mass dimorphism is tested. If canine dimorphism is proportional to the degree of sexual dimorphism in body mass then sexual dimorphism in the canine/premolar complex can be adequately explained by sexual dimorphism in body size. This would support the notion that selection acts mainly on body size and no independent selection on the canine/premolar complex needs to be invoked to explain canine dimorphism (Thorén et al., 2006). A number of presumed measures of the intensity of sexual selection are investigated to yield further insight into sexual selection in macaques.

Primate canine dimorphism biased towards larger male canines has mainly been interpreted as a sign of male-male competition for access to females. Data on actual competition (e.g., intensity or frequency; Plavcan and van Schaik, 1992) between males could not be retrieved for macaques. Instead, the operational sex ratio (OSR) and breeding seasonality (strong or moderate) are used as proxies for male intrasexual competition and tested for their relationship with canine/premolar dimorphism. OSR measures the balance in the number of sexually mature males to the number of sexually mature females in the group (Emlen and Oring, 1977; Mitani et al., 1996). If OSR is high (close to 1), the number of males approaches the number of females and consequently it is more difficult for single males to

successfully compete with all the other males and monopolise oestrous females. If OSR is low («1), there are only a few males competing over access to females and thus the potential pay-off of successfully monopolising receptive females outweigh the risks and investment of engaging in physical competition. Male-male competition is thus expected to be high in the latter case but low(er) in the former. When intrasexual competition is strong, sexual selection will act to enhance those traits that confer an adaptive advantage, in this case large canines as weaponry and for display.

Breeding seasonality relates to male-male competition in a slightly different way. In social primates, strongly seasonal breeders concentrate their matings in a relatively short period of the year, usually as a result of a temporally spaced distribution of resources. In this scenario, female primates synchronise their ovarian cycles and come into oestrous at the same time, making it difficult for males to engage in successful mate guarding and monopolise all receptive females (Alberts et al., 2006; Altmann, 1962). Under these conditions, male dominance rank has little to no impact on reproductive success and there is reduced reproductive skew among males (Plavcan, 2001). Therefore, the success of male-male competition for priority of access to females is reduced when breeding seasonality is strong. In a-seasonal or less strongly seasonal breeders, females within a group come into estrous at different times throughout the year and therefore only a single or a small number of females will be sexually receptive at a particular point in time. Monopolisation potential is high in this case and tactics of mate-guarding and male-male competition for dominance pay off. Intrasexual selection for exaggerated sexual traits is expected to be greater in the latter case compared to the former.

Male reproductive success is not only influenced by the reproductive strategies of males; females may have their own mating tactics, which do not always align with the reproductive interests of males. Patterns of sexual dimorphism and processes of sexual selection are therefore not solely contingent on male behaviour. There is mounting evidence for the impact of female mate choice, including female resistance to mating attempts by males, as well as the impact of sperm competition on male reproductive success (Engelhardt et al., 2006; Soltis, 2004). Moreover, male mating success does not equal paternity success. Nevertheless, if there is competition among males for access to females, then males are subject to selection for traits that enhance their competitive potential irrespective of other mechanisms that may be operating alongside it, such as independent selection on females. The relationships between OSR, breeding seasonality, and sexual dimorphism can be tested here. However, it is not suggested that they are the only relevant factors affecting the phenotypic outcome of sexual selection in macaques.

5.2 Materials and Methods

5.2.1 Dental Allometry

Molars have been the primary focus in dental allometry studies (e.g., Copes and Schwartz, 2010; Corruccini and Henderson, 1978; Gould, 1975; Kay, 1975; Scott, 2011; Vinyard and Hanna, 2005). This study will therefore begin with a comparison of static and evolutionary patterns in macaque molars. Bivariate allometric scaling coefficients are derived for molar dimensions using calvarium (skull) length as the body size proxy. The use of a cranial body size proxy, rather than body mass, allows scaling patterns to also be verified within species, at which level no body mass data is known for the specimens studied. To turn the allometric scaling relationship, which is a power relationship, into a linear relationship that can be investigated by means of linear regression, the allometric equation will be log-transformed. Equation (5.1) then becomes

$$logY = logb + a * logX \tag{5.2}$$

where Y is still tooth size and X the body size measure, while the former exponent a is now the regression slope. Species means are used in the interspecific analysis of evolutionary allometry, with pooled male and female means. On the intraspecific level a subset of four macaque species are used, namely *M. sylvanus*, *M. nemestrina*, *M. radiata*, and *M. fascicularis*. These species capture a range of different body sizes as well as phylogenetic positions within the genus. All data are transformed using the common logarithm (log_{10}).

Macaques are phylogenetically related in a hierarchical fashion (Figure 5.1), and thus some species share a more recent common ancestor than others. In the between-species analysis, data points represented by species means are not independent and therefore violate the assumption of independence of residuals in a regression (Felsenstein, 1985). To correct for this problem, a phylogenetic generalised least squares (PGLS; Grafen 1989; Martins and Hansen 1997) analysis is conducted to obtain the bivariate scaling coefficients. Such a 'phylogenetic regression' takes the evolutionary relatedness between species into account (Symonds and Blomberg, 2014a).[1] This method adjusts for phylogeny by correcting the covariance or correlation between residuals in a bivariate (or multivariate) regression for the covariance structure as expected on the basis of the phylogenetic variance-covariance (V-CV) matrix (Grafen, 1989; Hansen and Martins, 1996). A phylogenetic tree with branch lengths that carry information about time or evolutionary rate can be transformed into a

[1] The biological and statistical theory behind phylogenetic correction and phylogenetic signal is discussed in detail in Chapter 7.

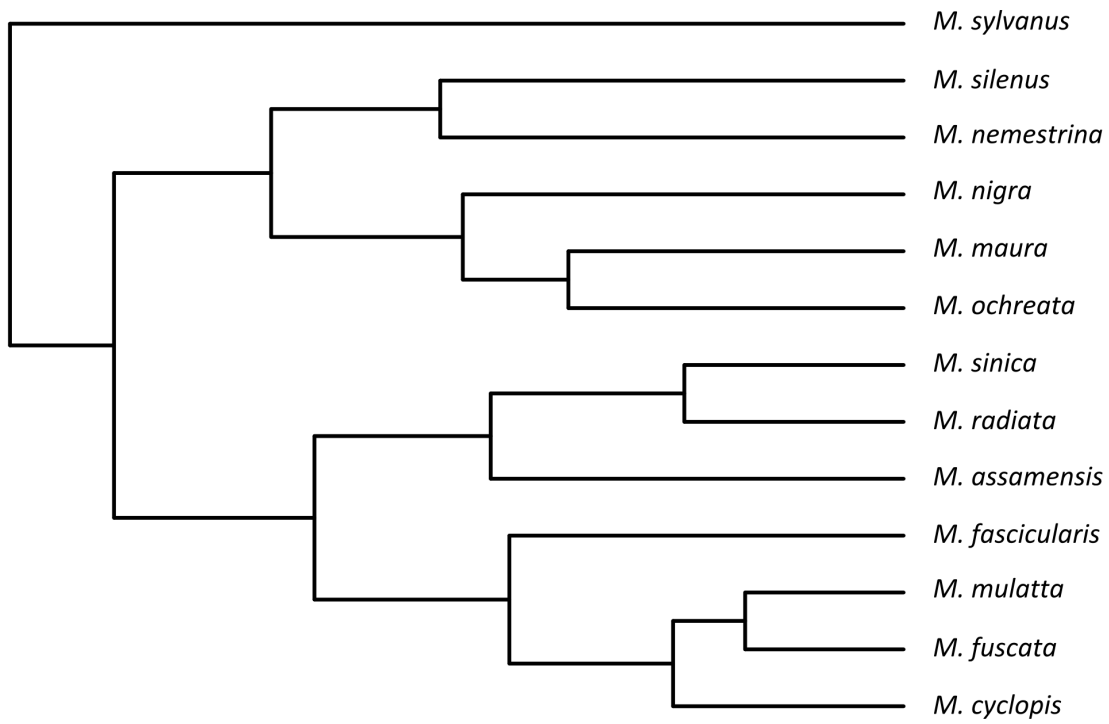


Fig. 5.1 Ultrametric tree describing the phylogenetic relationships between the macaque species in the sample.

matrix containing pairwise evolutionary covariances (Hansen and Martins, 1996). In this case, the matrix diagonal represents the variances, which are the distances from the root of the tree to each tip (Rohlf, 2001). In an ultrametric tree where branch lengths are scaled to time, the variances are the same for all extant species. The covariance, on the other hand, between any two species is their shared evolutionary history, namely the branch length from the root of the tree (i.e., the ancestor to all macaques) to the most recent common ancestor of both species (Felsenstein, 1985). An illustration of this conversion process can be found in Figure E.1 in Appendix E.

Next, there are several assumptions one can make with regard to the amount of expected phylogenetic signal. A commonly used model of evolution is that of Brownian motion (BM). BM assumes a constant evolutionary rate over time and thus shared branch lengths are in direct proportion to expected phenotypic similarity (Hansen and Martins, 1996; Rohlf, 2001). In a BM model, the phylogenetic V-CV matrix is assumed to accurately reflect the pattern and the magnitude of the expected phenotypic similarity due to phylogenetic history. As part of PGLS, the distribution of species in data space will subsequently be corrected (down-

weighted) for the 'phylogenetic dependence' between data points, consequently rendering them independent (Revell, 2010; Symonds and Blomberg, 2014a).

Alternatively, one may correct the data only for the amount of detected similarity that corresponds to the phylogeny, that is, the strength of phylogenetic signal. This is a good alternative when there is reason to believe that using BM could over-correct the data (Diaz-Uriarte and Garland, 1996; Revell, 2010). The same consideration applies to using independent contrasts, which also assumes BM. Several scaling parameters and indices of phylogenetic signal have been developed (discussed in more detail in Chapter 7). One example is Pagel's lambda, λ (Pagel, 1999), which uses a Maximum-Likelihood (ML) approach to estimate the *amount* of phylogenetic signal and which subsequently acts as a scaling parameter of the branch lengths of the phylogeny. Pagel's lambda corrects only for the detected amount of phylogenetic signal in the data by rescaling the length of the internal branches (the branches that represent shared evolutionary history between taxa) relative to the terminal branches of the phylogeny. This procedure is implemented as part of a PGLS regression (Symonds and Blomberg, 2014a). The rescaling procedure is further illustrated in Figure E.2 in Appendix E.

In brief, phylogenetic signal metrics vary between 0 and 1 (or beyond), where 0 and other low values indicate weak phylogenetic signal, 1 and other high values indicate strong phylogenetic signal, and intermediate values reflect intermediate signal (Blomberg et al., 2003; Kamilar and Cooper, 2013; Revell et al., 2008). Brownian motion assumes a phylogenetic signal of 1, whereas PGLS using Pagel's λ assesses the amount of phylogenetic signal present in the residuals and thereby protects against over-correction of the data (Revell, 2010; Symonds and Blomberg, 2014a). The disadvantage of using Pagel's λ, however, is that ideally this approach requires sample sizes of >30 in order to arrive at estimates with good confidence limits (Münkemüller et al., 2012). Either option, BM or Pagel's λ, can be used as part of PGLS. Here, I employ a phylogenetic correction by means of Pagel's λ as the preferred method so as to adjust only for the amount of phylogenetic bias in the residuals. Phylogenetic adjustment by means of Pagel's λ is implemented in the function 'pgls' in the 'caper' package for R (Orme et al., 2013). Alternatively, if the confidence limits of λ are too wide and the λ parameter cannot be confidently estimated, I also correct for phylogeny assuming BM using the function 'gls' of the 'nlme' package, implemented in R (RStudio Team, 2015), and compare the results.

Debate has existed about which regression model is the most appropriate to study allometry, although no consensus appears to have been reached to date (e.g., Hansen, 2014; Legendre and Legendre, 1998; Riska, 1991; Seim and Sæther, 1983; Ungar, 2014). A detailed account of the arguments in favour and against different regression models is beyond the scope of this chapter. In brief, most often the choice is between either using ordinary least

squares (OLS), a Type I regression, or (reduced) major axis ((R)MA), a Type II regression. An important difference exists in the method of line-fitting through the residuals (Legendre and Legendre, 1998). The decision about which regression model to use seems to ultimately hinge on a combination of mathematical properties of the data (e.g., does the random error lie in Y or do X and Y both exhibit error that is roughly equal in mangitude?) and underlying biological questions (e.g., is the goal to predict Y from X or to retrieve a functional, symmetrical relationship? Which of the two variables can reasonably be assumed to be the dependent variable and which the independent one?). The use of RMA regression can lead to serious misinterpretations of the results when analysing evolutionary allometry across species because, in that case, residual error is not random, but reflects phylogenetic history (Hansen, 2014; Riska, 1991). Evolutionary allometry is investigated here using PGLS. Static (within-species) allometry, on the other hand, is analysed by means of reduced major axis (RMA) regression, because error exists both in the X (calvarium length) and Y variable (tooth dimension), and because the goal is not to predict tooth size based on overall size (as is typical of OLS), but rather to inspect the scaling pattern (Copes and Schwartz, 2010). Each regression of molar dimension on calvarium length is inspected for outliers in the residual plots. When present, outliers are removed and the regression slope is calculated again.

In order to compare static and evolutionary allometry in the complete macaque dentition, a PCA is conducted. Rather than regressing all remaining individual tooth measurements on the body size measure separately, I use Jolicoeur's 1963 multivariate method of deriving scaling coefficients from a PCA. When the first PC makes up a substantial portion of the overall variance and represents allometric size, the PC loadings of the log-transformed variables onto PC 1 represent their scaling coefficients with overall size (Cheverud, 1982b; Jolicoeur, 1963). To scale the loading coefficients so that isometry has a scaling coefficient of 1, loadings are divided by $\sqrt{1/k}$ where k is the number of variables (Cheverud, 1982b). The total number of craniodental variables in the dataset is 56 (i.e., omitting tooth height), and thus $\sqrt{1/56}$ is 0.134. Variables with an unscaled loading coefficient larger than 0.134 are positively allometric, and those smaller than 0.134 are negatively allometric.

Within- and between-species PCAs carried out in Chapter 4 showed that size dominated the first PC, which means that the loadings of the different tooth measurements on PC 1 can be interpreted as the allometric scaling coefficients of these measurements on overall craniodental size. Tooth height is not included in the present analysis because these measurements reflect differences in tooth wear and age (see Chapter 4) and therefore the signal of size is expected to be obscured in height variation. Molars are included again to verify the scaling pattern derived in the bivariate regressions. The total number of craniodental variables is therefore 56, 39 of which constitute tooth breadths and lengths. To avoid further 'noise',

I control for the effect of sexual dimorphism by using sex-corrected data (see Chapter 4). The loading coefficients from the within-species and between-species PCA are extracted to compare between taxonomic levels. PCA is carried out in PAST (Hammer et al., 2001).

It should be noted that the exact values of the scaling coefficients will almost certainly differ between methods. This is not surprising given the fact that the methods (PCA, PGLS, and RMA) are computationally different and are based on different combinations of variables. Different regression techniques are known to yield different slopes and therefore different interpretations with respect to the nature of allometric scaling (e.g., RMA tends to yield higher slopes than ordinary least squares (OLS) regression) (Copes and Schwartz, 2010). The same applies to differences between taxonomic levels,whether data are aggregated or not, and what body size measure is used (Copes and Schwartz, 2010; Gingerich and Smith, 1985; Smith, 1981). Some of these differences, e.g., between intraspecific and higher-order patterns, may require biological explanations, but, in part, these discrepancies have been demonstrated to be artefactual. There is therefore no point in comparing the exact scaling coefficients – and absolute differences between them – between levels and methods. Rather, the pattern of allometric scaling of different teeth (or tooth dimensions) relative *to each other* may be evaluated. Interpretation of the results therefore also does not hinge on whether RMA or OLS was used to obtain the within-species bivariate allometric coefficients.

5.2.2 Diet

Macaque species in the sample are divided into a frugivorous group and a more omnivorous group. The omnivorous group is characterised by a lower proportion of fruit in the diet and a higher proportion of leaves. Assignment of species to one of these two dietary groups is based on the amount of fruit relative to leaves in the diet, namely when the percentage time spent feeding on fruits is three (or more) times as high as the percentage time spent feeding on leaves (% fruits / % leaves), a species is defined as frugivorous, and as omnivorous when this ratio is smaller than three. Table 5.1 presents the % fruit and % leaves for each species, the ratio between them, and the resulting dietary classification. The classification designed here corresponds well to Kay's (1975) criterion for a dietary specialist: when a particular food type (e.g., fruit, insects, or leaves) makes up 45% or more of the total food consumption, a species can be considered a specialist in that category. No macaque species in the present sample has approximately 45% of both fruits and leaves in its average diet (Table 5.1) and thus all can be classified as either mainly frugivorous or more omnivorous. The dietary labels assigned to each species match field observations of their dietary behaviour (Thierry, 2007a).

Next, PGLS regression is carried out for total postcanine occlusal area (PCOA) on body size for all macaques considered together (N = 13), and for the two dietary groups separately

(frugivores: $N = 8$, omnivores: $N = 5$). For the sub-group analyses, the phylogenetic tree of macaques ($N = 13$) is pruned, twice, to create the phylogenetic trees for the frugivorous and omnivorous taxa. These trees are then used in the respective PGLS analyses.

For body size, the cube root of species mean body mass is used, as well as calvarium length (separately). The cube root of body mass yields a one-dimensional measure that is directly comparable with calvarium length. Two different measures of body size are tested so as to increase the robustness of the results; sample sizes are low and therefore the results from a single test may not be meaningful. If the two different body size measures yield the same result, it supports the notion that there is an effect of size. Total PCOA is computed as the geometric mean of the mesiodistal lengths and buccolingual widths of the postcanine teeth. The geometric mean is used to create a one-dimensional variable, and is computed as $\sqrt[n]{x_1, x_2, ..., x_n}$. Upper and lower premolars and molars are used in the representation of PCOA except for P_3, because of its honing function for the upper canine and the strong integration with the canines relative to the rest of the postcanine dentition (see Chapter 4). All regressions are conducted on log-transformed variables to derive the scaling coefficient in the form of the regression slope.

Due to the small sample sizes and associated low statistical power, the phylogenetic signal in the residuals will be difficult to assess reliably by means of Pagel's λ (Münkemüller et al., 2012). Therefore, each regression is carried out with λ estimated by means of maximum likelihood (ML) as well as with λ fixed to 1. The latter conforms to a Brownian motion (BM) model of evolution. The results are then compared for the coefficient of determination, R^2 and Akaike's Information Criterion (aic). These statistics assess the goodness of fit and will therefore elucidate which model – phylogenetic correction by Pagel's λ or by BM – better describes the data. A total of 3 (groups) x 2 (body size measures) x 2 (Pagel's λ through ML and BM) = 12 PGLS regressions are carried out.

5.2.3 Allometric Scaling of Sexual Dimorphism

To test for allometric scaling of sexual size dimorphism (SSD), the log of female body mass is regressed on the log of male body mass. If the slope is significantly higher or lower than 1, it means that SSD in body mass gets stronger or weaker with increasing species' mean body size, respectively. This is equivalent to an expected regression slope of significantly higher or lower than 0 of the ratio of mean male-to-female mass (a measure of SSD) on species mean body mass. PGLS regression is used to test and control for phylogenetic signal in the relationship of female to male body mass.

In addition, scaling of SSD in the craniodental variables is investigated. To this end, male and female means are computed for each variable, by species, from the raw data (i.e.,

Table 5.1 Dietary composition in terms of proportion of fruits and leaves in the diet for 13 macaque species. Species with a ratio of % fruits to % leaves (F:L) ≥ 3 are classified as a frugivore (F), and those with a ratio <3 are classified as more omnivorous (O). Data from the literature (for sources, see Table B.2 in Appendix B).

species	% fruit	% leaves	ratio (F:L)	Dietary category
M. assamensis	40	38.85	1.0	O
M. cyclopis	50.5	26.95	1.9	O
M. fascicularis	74.35	9.4	7.9	F
M. fuscata	22.95	25.3	0.4	O
M. maura	71	8.4	8.5	F
M. mulatta	28.65	50	0.6	O
M. nemestrina	74.6	8.25	9.0	F
M. nigra	66	5	13.2	F
M. ochreata	66	12	5.5	F
M. radiata	53.5	13.6	3.9	F
M. silenus	70	0	n/a	F
M. sinica	70	11	6.4	F
M. sylvanus	2.55	13.45	0.2	O

not corrected for sexual dimorphism). Subsequently, the average craniodental size by sex is computed across all variables. Rather than use the arithmetic mean for this, which is biased towards larger values from larger measurements (e.g., calvarium or muzzle length), the geometric mean is taken as the average. The geometric mean is useful when averaging variables that have different numeric ranges. Female craniodental size is then regressed on male craniodental size, in logarithmic space. SSD is computed as the ratio of male and female geometric means, resulting in a single variable (craniodental SSD). This ratio is subsequently regressed onto craniodental size, without log-transformation, to check if the degree of SSD is dependent on craniodental size.

This procedure is repeated for sexual dimorphism in teeth (i.e., excluding cranial and mandibular dimensions) and in the CP_3 complex, respectively. Teeth are less plastic than bone and may show a different signal than bony structures of the skull. Among the teeth, sexual dimorphism is especially pronounced in the canines of most primate species, which has been explained through sexual selection on body mass or on the canines specifically as a result of mating competition or predation defence, among other things (reviewed in Plavcan, 2001). Canine dimorphism is investigated here by using the CP_3 complex as a whole, because dimorphism exists not only in macaque canines, but also in the lower third premolar (P_3). Moreover, the upper and lower canines and the lower third premolar (P_3) are morphologically strongly integrated (as judged by their high phenotypic correlations; see Chapter 4) and likely form a genetic and developmental sub-module (discussed in Chapter 4). Although dimorphism is especially pronounced in the height of the upper canine, crown height is also subject to wear. In the present sample, there is a considerable effect of macrowear in male canine height, the extent of which differs between species (personal observations). The use of canine height would likely introduce substantial error. Therefore, the geometric mean of mesiodistal lengths and buccolingual widths, but not heights, of the whole CP_3 complex is used here to study canine/premolar dimorphism because this measure likely reflects a strong enough signal that is minimally affected by tooth wear.

Finally, I investigate whether CP_3 dimorphism can be explained by the OSR or breeding seasonality in macaques. Data for these predictors are presented in Table 5.2. For all analyses of sexual dimorphism, PGLS regression is used with Pagel's λ, estimated through a maximum-likelihood (ML) approach.

Table 5.2 Operational sex ratio (OSR) and breeding seasonality (BS) data for 12 species. *M. ochreata* is omitted due to a lack of data. Data from the literature (for sources, see Table B.1 in Appendix B).

species	OSR (M:F)	breeding seasonality[a]
M. assamensis	0.44	2
M. cyclopis	0.49	2
M. fascicularis	0.59	1
M. fuscata	0.65	2
M. maura	0.67	1
M. mulatta	0.33	2
M. nemestrina	0.20	1
M. nigra	0.30	1
M. radiata	0.59	2
M. silenus	0.38	2
M. sinica	0.40	1
M. sylvanus	0.84	2

[a] 1 = moderate (33-67 % of births fall in a 3-month period), 2 = strong (>67% of births fall in a 3-month period).

5.3 Results

5.3.1 Dental Allometry

Bivariate allometric scaling

The bivariate allometric scaling pattern was first tested in the linear dimensions of molars. The results of the interspecific and intraspecific bivariate regressions are presented in Tables 5.3 and 5.4, respectively. For the between-species analysis, Pagel's λ was estimated by a maximum-likelihood (ML) approach to be 0 for all molar dimensions based on a comparison of the covariances between residuals and the phylogenetic covariances (a procedure implemented in the PGLS regression; see Section 5.2). A λ value of 0 reflects the lack of phylogenetic signal in the phenotypic data. However, ML confidence limits were estimated to range from 0-1, which means that a higher value than 0 for λ cannot be excluded. Therefore, PGLS was run again with λ fixed at 1. The latter is consistent with a BM model of evolution.

Table 5.3 Interspecific bivariate scaling coefficients for molar dimensions on calvarium length. PGLS with Pagel's λ assessed through maximum likelihood (ML) yielded $\lambda = 0$ (with confidence limits between 0 and 1) for all molar dimensions. The allometric scaling coefficients for λ fixed at 1 (Brownian motion) are presented for comparison.

	Pagel's $\lambda = 0$		Brownian motion ($\lambda = 1$)	
	PGLS slope a	95% CI	PGLS slope a	95% CI
		Maxilla		
M1 length	1.09	0.34	1.14	0.32
M1 anterior width	0.95	0.31	1.02	0.35
M1 posterior width	0.83	0.31	0.91	0.32
M2 length	1.22	0.34	1.26	0.32
M2 anterior width	1.06	0.39	1.10	0.40
M2 posterior width	0.99	0.34	1.03	0.32
M3 length	1.36	0.38	1.43	0.41
M3 anterior width	1.18	0.43	1.23	0.41
M3 posterior width	1.17	0.45	1.20	0.41
		Mandible		
M1 length	1.05	0.25	1.10	0.25
M1 anterior width	1.02	0.25	1.01	0.25
M1 posterior width	1.00	0.25	1.01	0.24
M2 length	1.19	0.28	1.21	0.28
M2 anterior width	1.12	0.34	1.09	0.34
M2 posterior width	1.13	0.29	1.15	0.31
M3 length	1.48	0.34	1.49	0.34
M3 anterior width	1.26	0.36	1.26	0.35
M3 posterior width	1.29	0.39	1.30	0.35
	mean slope		mean slope	
Length	1.23		1.27	
Width	1.08		1.11	
Ratio (length:width)	1.14		1.15	

95% Confidence intervals (CI) were calculated by relating to the t-distribution, using the formula $t(\alpha, df) * SE_a$, where $t(\alpha, df)$ is the critical value of the t-statistic for probability level α and number of degrees of freedom (df), and SE_a is the standard error of the regression slope (Sokal and Rohlf, 1995). For 95% CI, α is 0.05, and df is $N - 2 = 11$.

The allometric patterns visible in the phylogeny-corrected ($\lambda = 1$) and the phylogeny-uncorrected ($\lambda = 0$) scaling coefficients are strongly congruent (Figure 5.2). Namely, M1 dimensions scale with lower coefficients than M2 dimensions, while M3 dimensions have the highest scaling coefficients. Moreover, the ratio of the average scaling coefficients of molar lengths to widths is larger than 1. Thus, molar mesiodistal lengths consistently have higher scaling coefficients than the buccolingual widths of the same molar (Table 5.3). This means that as molars increase in size with body size between species, molar lengths tend to increase more relative to molar widths. On the whole, the molars exhibit a scaling gradient along an antero-posterior direction: third molars are relatively larger in relation to overall size than second molars, which in turn are relatively larger for a given body size than first molars (M1 < M2 < M3).

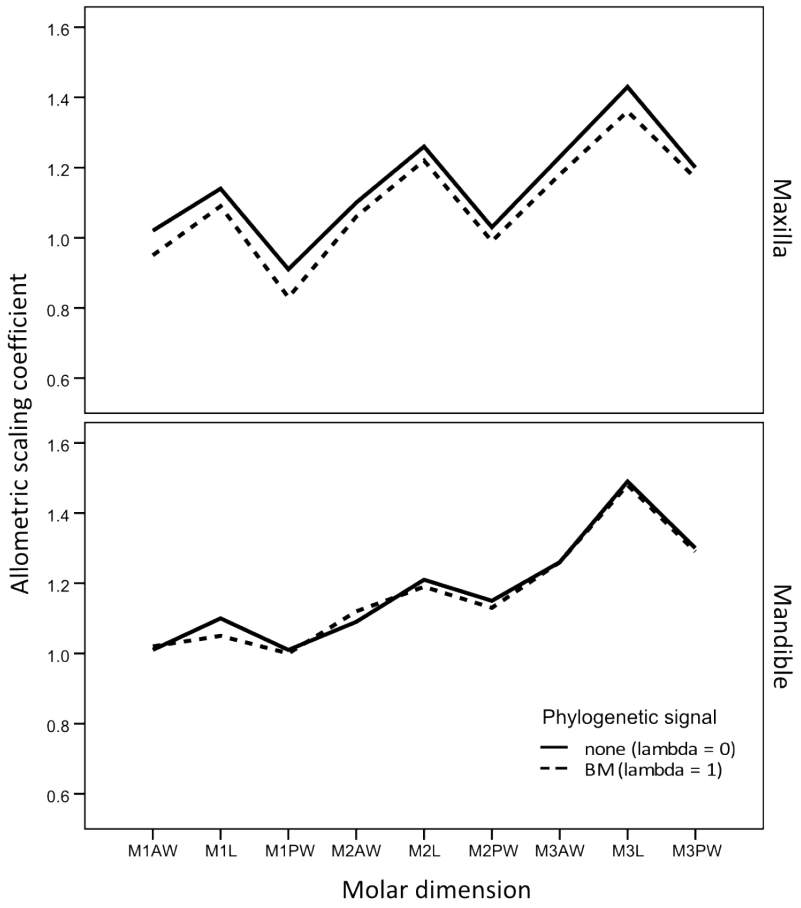


Fig. 5.2 Line plot of bivariate allometric scaling coefficients of molar lengths and widths on calvarium length between macaque species. Scaling coefficients were derived as PGLS regression slopes, with (Pagel's $\lambda = 1$, Brownian motion) and without phylogenetic correction (Pagel's $\lambda = 0$). Sexual dimorphism in size was removed prior to regression.

Table 5.4 Intraspecific bivariate scaling coefficients obtained through RMA regressions of molar dimensions on calvarium length for *M. sylvanus*, *M. nemestrina*, *M. radiata*, and *M. fascicularis*.

	M. sylvanus (*N* = 52-57)	*M. nemestrina* (*N* = 55-59)	*M. radiata* (*N* = 64-67)	*M. fascicularis* (*N* = 86-89)
		RMA slope *a*, Maxilla		
M1 length	1.14	-1.33	0.98	1.33
M1 anterior width	0.65	-1.56	1.29	1.34
M1 posterior width	0.84	-1.57	1.24	1.50
M2 length	1.15	-1.36	1.26	1.50
M2 anterior width	1.05	1.60	1.29	1.49
M2 posterior width	1.36	1.53	1.18	1.72
M3 length	1.29	1.98	1.45	1.50
M3 anterior width	1.19	2.00	1.43	1.60
M3 posterior width	1.58	2.23	1.75	1.92
		RMA slope *a*, Mandible		
M1 length	1.27	-1.39	0.93	1.29
M1 anterior width	0.81	1.70	1.20	1.31
M1 posterior width	0.83	1.71	1.30	1.46
M2 length	1.13	-1.28	1.12	1.37
M2 anterior width	1.35	1.86	1.25	1.68
M2 posterior width	1.15	2.07	1.31	1.63
M3 length	1.09	1.91	1.84	2.02
M3 anterior width	1.38	2.42	1.60	1.69
M3 posterior width	1.27	2.06	1.74	1.89
		Mean RMA slope *a*		
Length	1.01	-0.24	1.26	1.50
Width	1.12	1.34	1.38	1.60
Ratio (length:width)	0.90	-0.18	0.91	0.94

This gradient (M1 < M2 < M3) is consistent between taxonomic levels, as the same scaling differences exist on the within-species level (Table 5.4 and Figure 5.3). Although the absolute scaling coefficients differ between the four species – as is to be expected – the same pattern of M1 < M2 < M3 of relative size increase is visible within species. Among the four sample species, however, *M. nemestrina* stands out with a more exaggerated pattern (Figure 5.3). Some dimensions of first and second molars in this species scale negatively with calvarium length, which implies that these tooth dimensions actually get smaller with increasing body size. Sexual dimorphism cannot explain these results, because size dimorphism was removed. Confidence intervals for all dimensions with a negative slope were extremely wide ($> \pm 3.0$) and scatterplots revealed a seemingly random pattern. Thus, it is most plausible that the regression coefficients could not be estimated confidently for these dimensions. The negative slopes may be an artefact of how RMA regression slopes are computed in that case (Hansen, 2014).

On the intraspecific level, molar widths, on average, scale with positive allometry with higher coefficients than molar lengths, as evidenced by a ratio smaller than 1 (Table 5.4). In other words, if we calibrate molar lengths to isometric scaling, then molar widths scale with positive allometry in this case. This is true for all four species and is in contrast to what is observed between species.

Multivariate allometric scaling

The loading coefficients on PC 1, scaled to the number of variables used in the PCA (see Section 5.2), are presented in Tables 5.5 and 5.6 pertaining to the intraspecific and interspecific analysis, respectively. Figure 5.4 summarises the multivariate allometric scaling relationship of individual teeth. Supporting measurements of the cranium and mandible were entered into the PCA to verify that PC 1 represented allometric size, but as they are not the primary focus their loading coefficients are not presented here. In addition, the phylogenetic regressions elucidated lack of phylogenetic signal in molar allometry (see above), and the scaling patterns (M1 < M2 < M3 and lengths > widths) did not change with phylogenetic correction. Therefore, the results of a phylogenetically uncorrected PCA are presented here. To aid interpretation, individual scaling coefficients are designated isometric or (positively/negatively) allometric relative to each other in Tables 5.5 and 5.6.

The results elucidate a pattern of dental allometry that is consistent between jaws and between taxonomic level. The congruency between the intraspecific and interspecific dental scaling is once again shown to be high for the molars (see also above). The incisors and premolars show a more mixed pattern. Within species, the upper central incisor, the most prominent incisor in terms of size, seems to increase in proportion to overall size whereas

Table 5.5 Between-species allometric scaling coefficients by tooth measurement. Coefficients were derived from a PCA as the scaled loading coefficients on PC 1 (see text for explanation). Sexual size dimorphism was removed prior to the PCA. Key to symbols: 'I' isometry, '-' negative allometry, '+' positive allometry.

	Maxilla			Mandible	
	a	Allometry		*a*	Allometry
I1 length	0.95	-		0.74	-
I1 breadth	0.60	-		0.62	-
I2 length	1.02	I		0.92	-
I2 breadth	0.74	-		0.96	I
Canine length	1.17	+		1.10	+
Canine breadth	0.82	-		0.95	+
P3 length	0.93	-	occlusal	1.29	+
			total	1.29	+
P3 width	0.81	-		1.29	+
P4 length	0.97	I		1.11	+
P4 width	0.76	-		0.91	-
M1 length	0.79	-		0.78	-
M1 anterior width	0.78	-		0.79	-
M1 posterior width	0.65	-		0.78	-
M2 length	0.92	-		0.86	-
M2 anterior width	0.86	-		0.90	-
M2 posterior width	0.79	-		0.91	-
M3 length	1.08	+		1.14	+
M3 anterior width	0.94	-		1.11	+
M3 posterior width	0.96	I		1.07	+

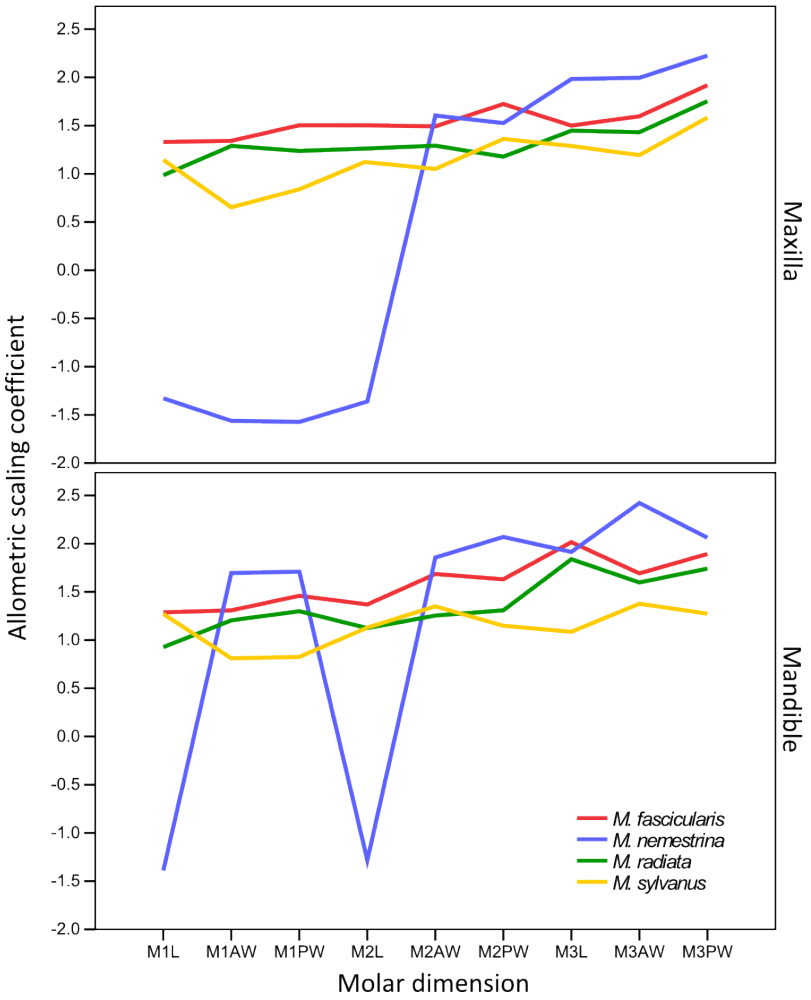


Fig. 5.3 Line plot of bivariate allometric scaling coefficients of molar lengths and widths on calvarium length within four macaque species. Scaling coefficients were derived as RMA regression slopes. Sexual dimorphism in size was removed prior to regression.

the upper lateral incisor is negatively allometric (Figure 5.4, solid blue line). Between species, however, the upper central incisor scales rather strongly negatively with overall size (Figure 5.4, solid red line). The lower third premolar has a scaling relationship that is clearly similar to the canines but not the lower fourth premolar. The CP_3 complex scales strongly positively with size, even after correcting for sexual size dimorphism. Interestingly, the intraspecific scaling coefficient of the upper canine is much higher than the interspecific one (1.24 times higher when averaged across length and breadth). The molars exhibit a scaling gradient along an antero-posterior direction: third molars are relatively larger in relation to overall size than second molars, which in turn are relatively larger for a given body size than first molars.

One can also express scaling coefficients as ratios between two traits, rather than of a single trait and overall size (the 'traditional' scaling coefficient). A ratio of two scaling coefficients expresses how much one trait changes in relation to the other per unit increase in size (Cheverud, 1982b). The ratio in scaling coefficients of lengths to breadths is 1:1 on the within-species level, but 1.16:1 on the between-species level. Thus, taken on average, tooth lengths and breadths tend to increase in proportion to overall size on a microevolutionary level, but the macroevolutionary pattern shows that tooth lengths tend to increase more with overall size relative to tooth breadths.

Table 5.6 Within-species allometric scaling coefficients by tooth measurement. Coefficients were derived from a PCA as the scaled loading coefficients on PC 1 (see text for explanation). Sexual size dimorphism was removed prior to the PCA. Key to symbols: 'I' isometry, '-' negative allometry, '+' positive allometry.

	Maxilla		Mandible		
	a	Allometry		*a*	Allometry
I1 length	1.10	+		0.97	I
I1 breadth	0.85	-		0.84	-
I2 length	0.82	-		0.97	I
I2 breadth	0.96	I		1.01	I
Canine length	1.31	+		1.17	+
Canine breadth	1.16	+		1.11	+
P3 length	0.84	-	occlusal	1.18	+
			total	1.31	+
P3 width	0.88	-		1.08	+
P4 length	0.86	-		0.95	-
P4 width	0.84	-		0.94	-
M1 length	0.73	-		0.68	-
M1 anterior width	0.79	-		0.82	-
M1 posterior width	0.79	-		0.85	-
M2 length	0.92	-		0.84	-
M2 anterior width	0.95	+		1.06	+
M2 posterior width	0.99	I		1.02	I
M3 length	0.98	I		1.13	+
M3 anterior width	1.09	+		1.24	+
M3 posterior width	1.18	+		1.19	+

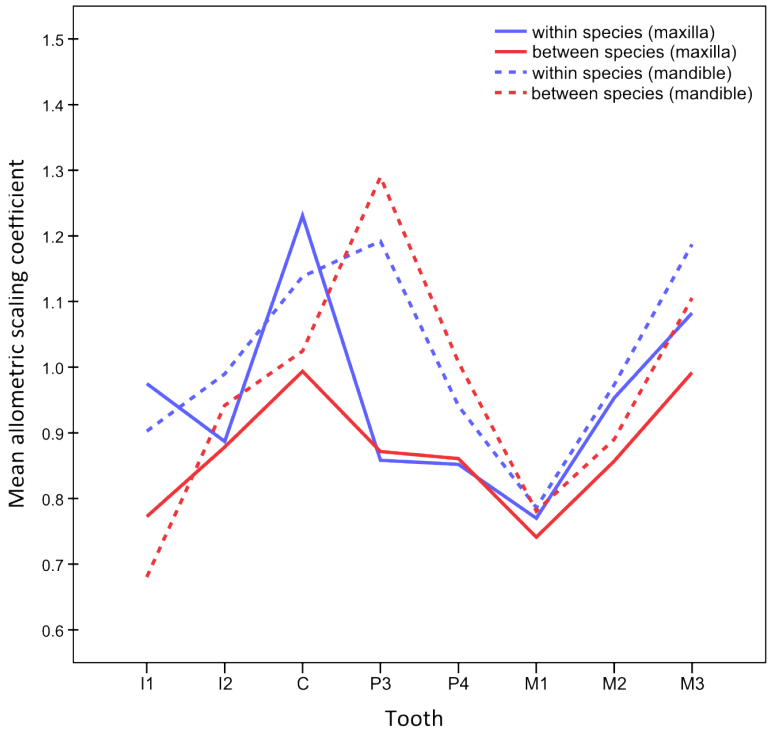


Fig. 5.4 Line plot of mean allometric scaling coefficients by tooth, by jaw, between and within species. Scaling coefficients were derived from a PCA as the scaled loading coefficients on PC 1 (see text for explanation), and averaged here to present the mean values by tooth (i.e., of length(s) and width(s)). Sexual dimorphism in size was removed prior to the PCA.

5.3.2 Diet

The pattern of evolutionary allometry in postcanine occlusal size (PCOA) was investigated for all macaques combined and in frugivorous and omnivorous macaques separately. The results of the PGLS regressions of the three groups are presented in Table 5.7. Pagel's λ was estimated to be 0 by ML in all regressions with confidence limits ranging from 0-1 (not significant). As expected, the confidence limits of λ could not be estimated more precisely due to the low statistical power arising small sample sizes. Nonetheless, phylogenetic correction yields minimally different regression coefficients. Moreover, the coefficient of determination (R^2) and Akaike's Information Criterion demonstrate that the uncorrected PGLS models outperform the phylogeny-corrected PGLS models. Therefore, the results uncorrected for phylogeny are interpreted here.

These results show that there are no significant differences between frugivorous and more omnivorous macaques in how their postcanine occlusal size scales with body size. The slopes of all three groups (all macaques, frugivores, and omnivores) fall within each other's 95% confidence intervals (see Table 5.7). The two different dietary groups do not represent grade

shifts. This is clear from the intercepts, which do not differ significantly between the groups (although they were difficult to estimate within narrow confidence intervals). Figure 5.5 illustrates the relationship between PCOA and body mass, which is negatively allometric in macaques. Furthermore, there is no separation visible between frugivorous and omnivorous macaques.

Although body mass and calvarium length both show no difference between dietary groups in allometric scaling, there is a difference in how PCOA scales with these two measures of body size. Namely, PCOA shows metabolic scaling ($a \approx 0.75$) when scaled to body mass, but scales with isometry ($a \approx 1$) when calvarium length is used as the body size measure.

5.3.3 Allometric Scaling of Sexual Dimorphism

PGLS regression of mean male onto mean female body mass reveals an isometric relationship ($a = 1.06$, ± 0.19 95% CI, $p < 0.001$; Figure 5.6). Figure 5.6 furthermore shows that male are larger than females of the same species. Pagel's λ was estimated at 1 (based on ML, confidence limits 0 - 1), indicating a phylogenetic signal consistent with Brownian motion. When λ was fixed at 0, for comparison, the result was the same ($a = 1.06$, ± 0.22 95% CI, $p < 0.001$). As expected, SSD in body mass, expressed as the ratio of male-to-female body mass, does not change with species mean body mass ($a \approx 0$, $p = 0.33$). A plot of SSD in body mass on mean body mass reveals a seemingly random scatter (not shown). Thus, male and female body masses increase in proportion among species.

Next, a PGLS regression of female craniodental size on male craniodental size (represented by the geometric mean, and both variables log-transformed) yields a slope that includes the value 1 in the 95% confidence intervals ($a = 0.85$, $\pm$ 0.16 95 % CI, $p < 0.001$, $\lambda = 0$). Because isometry is only just within the confidence limits, the male-to-female ratio in craniodental size was regressed on mean craniodental size to test for size-dependency in SSD. SSD in craniodental size increases very weakly with mean craniodental size, but this is not significant (PGLS: $a = 0.01$, $\pm$ 0.02 95% CI, $p = 0.296$, $\lambda = 0.279$). Thus, while there is sexual dimorphism in overall craniodental size, the degree of SSD is not dependent on size.

The same is found for sexual dimorphism in the average size of teeth only: isometry of female-on-male dental size cannot be ruled out (PGLS: $a = 0.85$, $\pm$ 0.18 95% CI, $p < 0.001$, $\lambda = 0$), and SSD in dental size does not vary significantly with dental size (PGLS: $a = 0.02$, $\pm$ 0.04 95% CI, $p = 0.276$, $\lambda = 0.014$). Figure E.3 in Appendix E shows the lack of a relationship between SSD and size in the craniodental variables and the dentition, respectively.

Table 5.7 Allometric scaling pattern of postcanine occlusal area (PCOA) in frugivorous macaques compared to omnivorous macaques. Scaling coefficients are derived on log-transformed variables in PGLS, with ($\lambda = 1$) and without phylogenetic correction ($\lambda = 0$).

	slope a	slope 95% CI	intercept b	intercept 95% CI	R^2	aic
			species mean body mass (cube root)			
$\lambda = 0$						
all	0.77***	± 0.17	0.28	± 0.52	0.89	-54.30
frugivores	0.88***	± 0.27	-0.04	± 0.80	0.91	-33.60
omnivores	0.70*	± 0.67	0.48	± 1.99	0.79	-18.80
$\lambda = 1$						
all	0.82***	± 0.22	0.13	± 0.64	0.86	-47.40
frugivores	0.80**	± 0.39	0.13	± 1.14	0.81	-30.60
omnivores	0.92*	± 0.83	-0.21	± 2.57	0.80	-14.30
			species mean calvarium length			
$\lambda = 0$						
all	1.13***	± 0.26	-2.45***	± 1.19	0.88	-53.20
frugivores	1.16***	± 0.34	-2.59**	± 1.54	0.92	-34.10
omnivores	0.96	± 1.27	-1.72	± 5.67	0.66	-16.30
$\lambda = 1$						
all	1.13***	± 0.26	-2.46***	± 1.19	0.89	-49.60
frugivores	1.05**	± 0.44	-2.12*	± 1.93	0.85	-32.70
omnivores	1.36*	± 1.15	-3.50	± 5.19	0.82	-14.80

Significantly different from 0 at *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

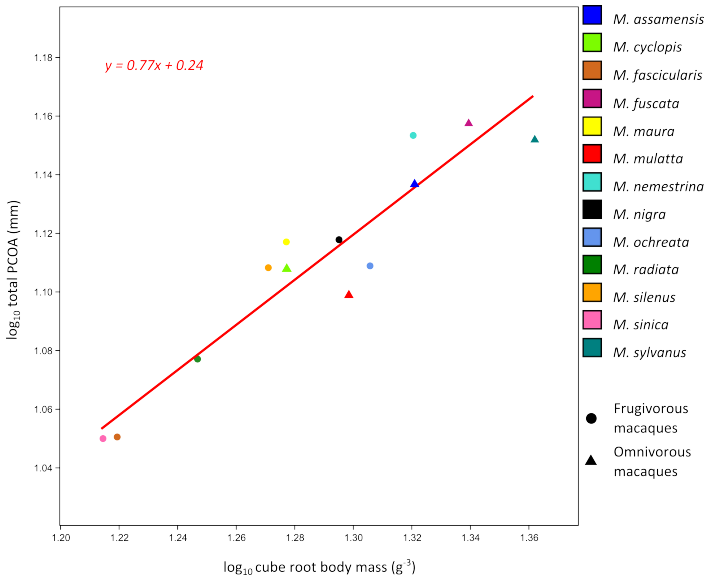


Fig. 5.5 Log-log plot of species mean total postcanine occlusal area (geometric mean) on species mean body mass (cube root), including the PGLS regression line for all macaques without phylogenetic correction ($\lambda = 0$, assessed in a maximum-likelihood approach). There is no significant difference in allometric scaling of PCOA between frugivorous (circles) and omnivorous macaques (triangles) (see also Table 5.7).

Conversely, the degree of sexual dimorphism in the CP_3 complex does change with CP_3 size. Figure 5.7a shows that the size of the CP_3 complex increases relatively less in female macaques than in male macaques ($a = 0.64$, $\pm$ 0.19 95% CI, $p < 0.001$, $\lambda = 0$). In logarithmic space, female CP_3 size (Y) is predicted by male CP_3 size (X) by the function $Y = 0.64X + 0.41$. In raw space, female CP_3 size is therefore negatively allometric with male CP_3 size. Moreover, the M:F ratio of CP_3 size is significantly correlated with mean CP_3 size: Spearman's rank correlation, r_s, is 0.60 ($p = 0.031$), and the regression slope of the CP_3 size ratio (M:F) on CP_3 size is significantly larger than 0 ($a = 0.08$, $\pm$ 0.05 95% CI, $p < 0.01$, $\lambda = 0$; see Figure 5.7b).

Of the traits investigated here, the canine/premolar complex is the only trait for which the divergence between males and females is dependent on its size. In other words, CP_3 SSD is allometric with CP_3 size. In order to see if the degree of canine dimorphism is also a function of overall body size and may thus be linked to selection on body size, the pattern of covariation between these two variables is inspected. Figure 5.8a shows a non-linear relationship between CP_3 SSD and body mass and Spearman's rank correlation is not significant ($r_s = 0.20$, $p = 0.505$). Figure 5.8b gives more insight into how this non-linearity arises. In the following species both males and females have smaller canines than expected on the basis of their body mass: the rhesus macaque (*M. mulatta*), the Japanese macaque (*M.*

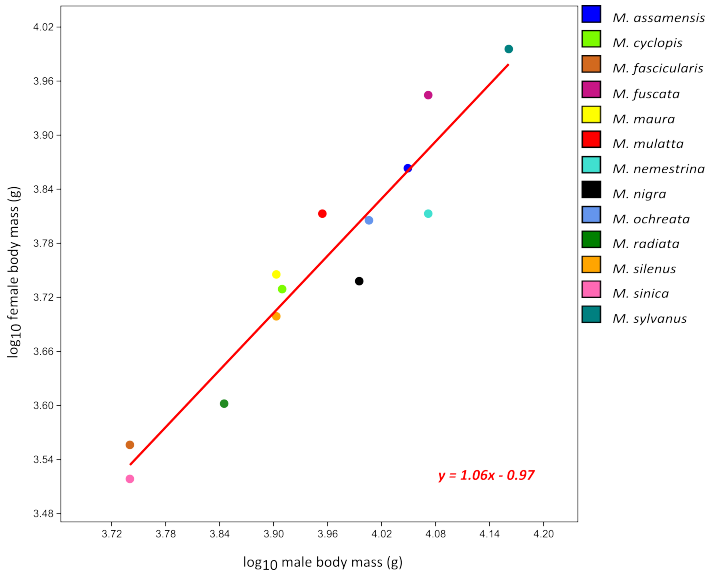
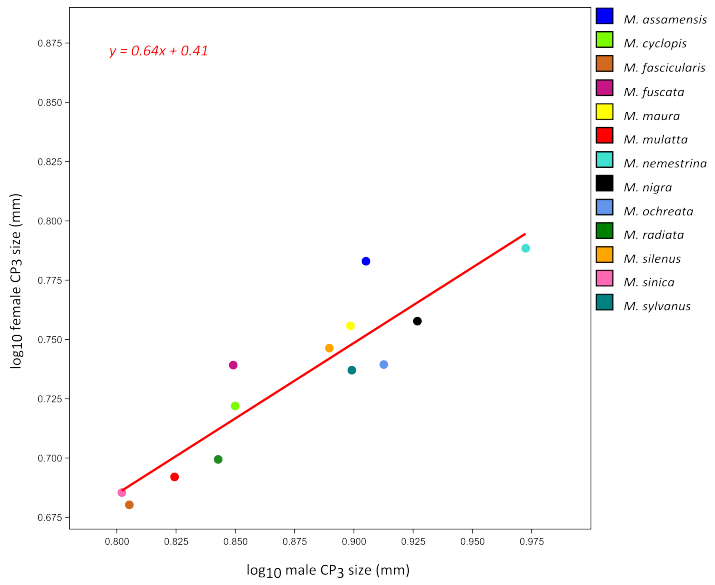


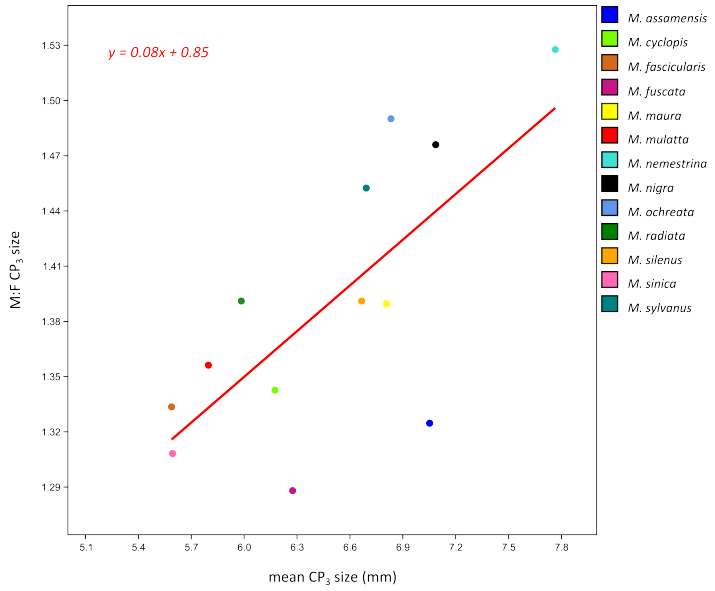
Fig. 5.6 PGLS regression of mean female on mean male body mass (log-transformed). Data points represent raw body mass (g), but the PGLS regression line reflects the intercept and slope after phylogenetic correction ($\lambda = 1$ based on a maximum-likelihood approach). The regression slope of 1.06 ($p < 0.001$, 0.87 - 1.25 95% CI) indicates that female and male body mass vary in proportion to each other in the macaque species studied. Sexual dimorphism therefore does not change with species mean body size. The phylogeny-uncorrected slope is also 1.06 (see main text).

fuscata), and the Barbary macaque (*M. sylvanus*). In the Assamese macaque (*M. assamensis*), females have the largest CP_3 complex second only to the southern pigtailed macaque (*M. nemestrina*), whereas Assamese males have 'only' the fourth-largest CP_3 complex. In other words, several mid-to-large species of macaque have smaller canine/premolar complexes and associated sexual dimorphism as a result of reduced CP_3 size in both sexes or one sex.

There may be an effect of diet in the degree of CP_3 dimorphism and the distribution of residuals (i.e.,species) in Figure 5.8. *M. sylvanus*, *M. fuscata*, *M. assamensis*, and *M. mulatta* all feed on either a relatively high proportion of leaves or a low proportion of fruit (or both), as does *M. cyclopis* (Table 5.1). The other macaques are more clearly frugivorous. Previous studies have found that sexual dimorphism can be stronger in folivores (e.g., gorillas, proboscis monkeys) than in frugivores (Leigh and Shea, 1995; Plavcan, 2001). Work on colobine sexual dimorphism has demonstrated low body mass dimorphism but strong canine dimorphism (Plavcan and van Schaik, 1997). To test the hypothesis that the relationship between canine/premolar dimorphism and body mass is mediated by a dietary effect, multiple PGLS regression was carried out. SSD in CP_3 (i.e., the M:F ratio) was the response variable; species mean body mass (g) and % leaves in the diet were the predictor variables. Proportion of leaves is chosen as the dietary variable here because in principal all

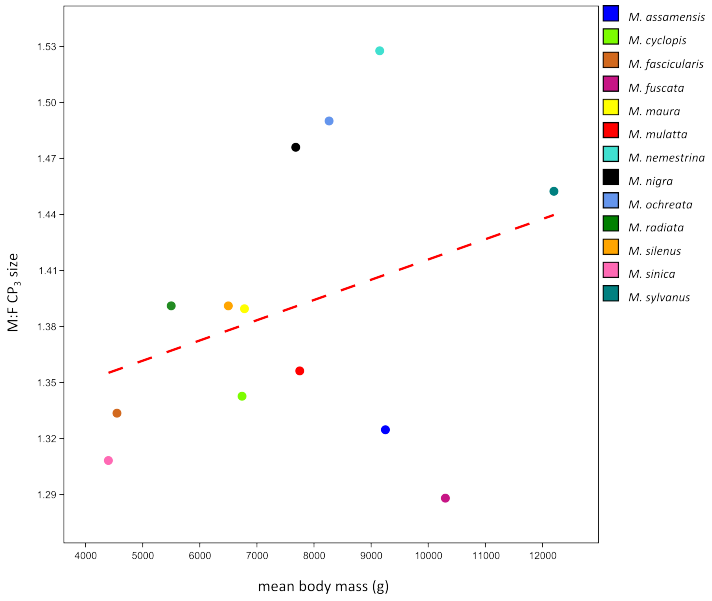


(a)

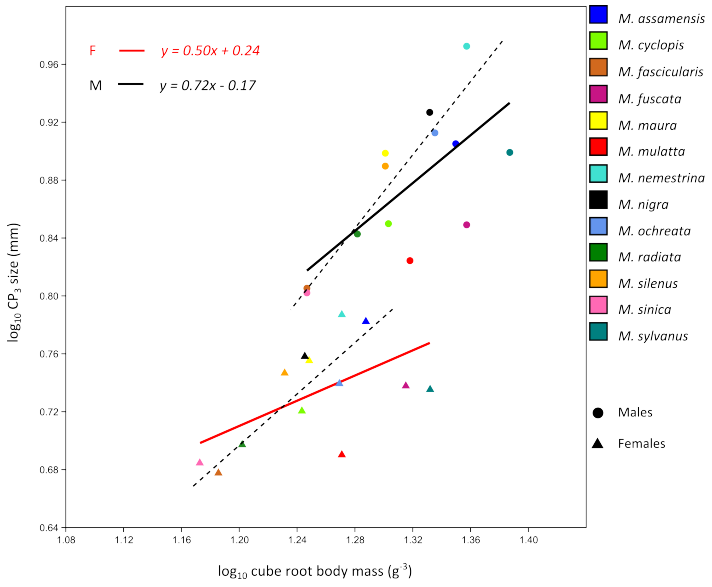


(b)

Fig. 5.7 Sexual dimorphism in the size of the canine/premolar (CP_3) complex increases with CP_3 size and is therefore not equal among macaques. CP_3 size is represented by the geometric mean of mesiodistal lengths and breadths of the canines and P_3. **(a)** PGLS regression of mean female on mean male size of the CP_3 complex (log-transformed). The regression slope of 0.64 ($p < 0.001$, 0.45 - 0.82 95% CI) indicates that CP_3 size in female macaques increases relatively less than male CP_3 size. **(b)** PGLS regression of the male-to-female (M:F) ratio in CP_3 size on CP_3 size (un-transformed). The regression slope of 0.08 is statistically significantly larger than 0 ($p < 0.01$, 0.03 - 0.13 95% CI), confirming that canine/premolar size dimorphism increases with CP_3 size. No phylogenetic signal was detected in CP_3 dimorphism ($\lambda = 0$ based on a maximum-likelihood approach implemented in PGLS) in either **(a)** or **(b)**.



(a)



(b)

Fig. 5.8 The relationship between sexual dimorphism in the canine/premolar (CP_3) complex and mean body mass. **(a)** Scatterplot of sexual dimorphism in CP_3 size (M:F ratio) and species mean body mass. The dashed line represents the PGLS regression slope ($a = 0.039$, $\pm$ 0.10 95% CI, $\lambda = 0.662$), but it is not significant ($p = 0.395$), which can be explained by the non-linearity of the relationship between the two variables. **(b)** PGLS regressions of male and female CP_3 size on the cube root of male and female body mass, respectively. CP_3 size visibly increases more with body mass in males than in females. However, several species show small CP_3 complexes for their body size, notably *M. sylvanus*, *M. fuscata*, and *M. mulatta*. Solid lines represent the PGLS models of the relationship between CP_3 size and body mass in the two sexes. Phylogenetic signal was estimated to be strong in both males and females ($\lambda = 1.0$ and $\lambda = 0.884$, respectively). Dashed lines are approximate regression slopes when the aforementioned three species are ignored (assuming they are subject to a different selection regime) and are for visual illustration only.

Table 5.8 Multiple PGLS results of sexual dimorphism in the CP_3 complex (M:F ratio) on species mean body mass (g) and % leaves in the diet (all variables were log-transformed). Pagel's λ was estimated at 0 through a maximum-likelihood approach. $F_{(3,9)} = 19.69$ ($p < 0.001$), $R^2 = 0.87$.

	coefficient	95% CI	p
Intercept	-6.46	3.39	0.002
$\log_{10}$ body mass	0.77	0.38	0.001
$\log_{10}$ % leaves	2.37	1.34	0.003
$\log_{10}$ body mass $*$ % leaves	-0.27	0.15	0.003

macaques are frugivorous; the proportion of non-frugivorous food items, particularly foliage, distinguishes macaques from each other.

Multiple PGLS regression yields a significant relationship of CP_3 dimorphism to body mass and % leaves (Table 5.8). Furthermore, there is a significant interaction between body mass and % leaves. This result means that SSD in the CP_3 complex increases with body mass, as well as with an increasing proportion of foliage in the diet, except in large-bodied folivorous macaques where the CP_3 dimorphism is reduced. The latter pattern is illustrated by the position of *M. mulatta*, *M. assamensis*, and *M. fuscata* in Figure 5.8a. Multiple PGLS with % fruits as the dietary variable was run for comparison, but yielded no significant results.

Finally, CP_3 dimorphism is only moderately correlated to body mass dimorphism ($\rho = 0.57$, $p = 0.043$). The PGLS slope of CP_3 SSD (M:F ratio) on body mass SSD is 0.27 ($p = 0.027$, $\pm$ 0.24 95% CI). The phylogenetic signal estimated through ML was strong for this relationship ($\lambda = 0.886$). A slope of 0.27 indicates that canine/premolar dimorphism does not increase in proportion to body mass dimorphism (expected slope, $a \approx 1$). Figure 5.9 shows that there is considerable variation among macaques in the relationship between body mass dimorphism and canine/premolar dimorphism ($R^2 = 0.37$).

The effect of male-male competition was tested in 12 species (omitting *M. ochreata*) by relating variation in sexual dimorphism to the operational sex ratio (OSR) and breeding seasonality. Body mass dimorphism is moderately negatively correlated with OSR (Pearson's $r = -0.55$, $p = 0.065$ for $\lambda = 0.412$), meaning that as the number of females for every male declines, yielding a higher OSR, the sexual dimorphism in body mass decreases. Canine/premolar dimorphism shows a similar but weaker signal (Pearson's $r = -0.35$, $p = 0.271$ for $\lambda = 0.823$).

Breeding seasonality has a small effect on the degree of body mass dimorphism (Pearson's $r = -0.45$, $p = 0.147$ for $\lambda = 0$), although it is not statistically significant. When macaques

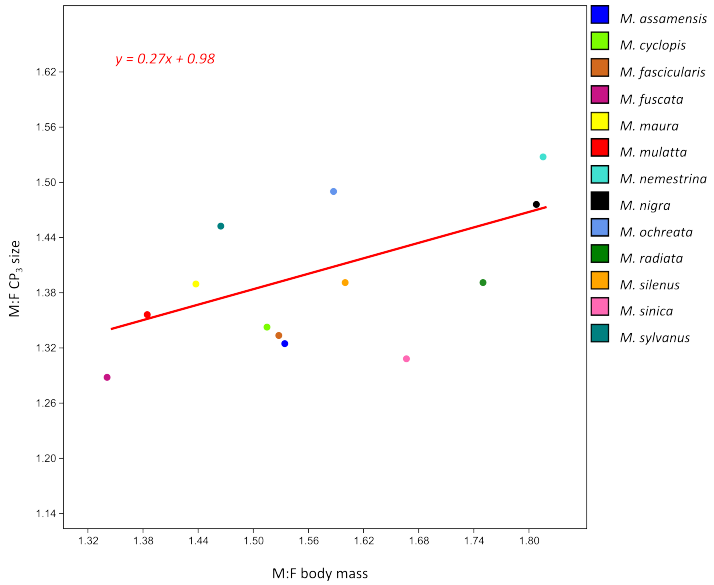


Fig. 5.9 PGLS regression of sexual dimorphism in CP_3 size (M:F ratio) on sexual dimorphism (M:F ratio) in species mean body mass (not transformed). Strong phylogenetic signal was detected in the residuals (λ = 0.886 through ML). The data points are ratios of the raw data, but the PGLS regression slope is adjusted for the amount of phylogenetic signal ($y = 0.27x + 0.97$). The slope indicates that sexual dimorphism in the canine/premolar (CP_3) complex increases less than body mass dimorphism (a = 0.27, p = 0.027, $\pm$ 0.24 95% CI).

are categorised as either strong or moderate seasonal breeders, then macaques that are strong seasonal breeders tend to have lower sexual dimorphism in body size. There is no difference in the size of the canine/premolar complex between strong seasonal breeders or moderately strong seasonal breeders (Pearson's r = -0.14, p = 0.672 for λ = 0.667). This test was repeated using only the upper canine, represented by length, width, and height, in case the signal was only present in the size (and particularly height) of the most dimorphic tooth in the CP_3 complex, but no relationship was detected.

5.4 Discussion

Static and Evolutionary Dental Allometry

Dental allometry in the macaque dentition shows a mixed pattern across teeth, but one that is largely consistent with dental allometry patterns across primates as a group (Gingerich and Smith, 1985; Gingerich et al., 1982). Incisors and central cheek teeth (P4s and M1s) have the lowest scaling coefficients, and third molars and teeth of the canine/premolar complex have some of the highest scaling coefficients. The postcanine dentition, with the exception of P_3,

shows a scaling pattern that is consistent between jaws and across taxonomic levels (within and between macaques). First molars have lower scaling coefficients than second molars, which in turn have lower scaling coefficients than third molars: M1 < M2 < M3 with respect to dental allometry. Fourth premolars have scaling coefficients similar to second molars. The molar scaling gradient corresponds to what has been observed between anthropoid primates, where first molars were found to scale with negative allometry (or close to isometry), second molars with positive allometry (just above isometry), and third molars with strong positive allometry (Gingerich et al., 1982).

The anterior teeth, namely the incisors, canines, and P_3, show a mixed scaling pattern between jaws. The upper central incisor (I^1) has a higher scaling coefficient than the lower central incisor (I_1). The opposite is true for the lateral incisors (I^2 and I_2). This suggests that differences in allometric scaling between isomeres (the same teeth in opposing jaws) may be compensated for by the scaling in adjacent teeth. To ensure that the anterior dental arcade in the maxilla occludes well with the same region in the lower jaw and size disparity between the jaws is at a minimum, the scaling of the lower central and lateral incisors may be coordinated to match the scaling pattern of the upper incisal row. Indeed, when averaging the scaling coefficients of the dimensions of the incisors and the canines (Tables 5.5 and 5.6), the anterior dentition has a mean scaling coefficient of 1 in both the maxilla and the mandible within species, and a mean scaling coefficient of 0.88 in both jaws between species. This is evidence of integration among teeth in the two jaws.

The CP_3 complex, relative to most other teeth in the dentition, is positively allometric. Sexual dimorphism was removed on the intraspecific as well as on the interspecific level. This makes the static positive allometry of the CP_3 complex a notable result, because it cannot be explained by size differences between typically larger males and typically smaller females. Rather, the observed pattern suggests that, irrespective of sex, larger macaques have relatively larger canines compared to smaller conspecifics. It is possible that the multivariate scaling coefficient of >1 is a result of how it was obtained; allometric scaling coefficients obtained in a PCA (where PC 1 represents allometric size) are scaling magnitudes relative to the rest of the variables entered into the analysis (Cheverud, 1982b; Jolicoeur, 1963; Lande, 1985). Thus, caution is warranted here and the result is best interpreted as a disproportionately large contribution of the CP_3 complex to the allometric size variation present in the craniodental variable set.

Overall, the patterns of dental allometry are highly congruent between the intraspecific and the interspecific level, especially in the postcanine dentition. Evolutionary allometry in the dentition can thus be said to follow static dental allometry in macaques. This finding supports the notion that the pattern of static (within-species adult) allometry observed in

macaques reflects genotypic allometry, because the evolution of allometric scaling relationships between species can only follow a genetically controlled trajectory (Cheverud, 1982b; Hlusko et al., 2006; Lande, 1979, 1985). There are, however, a few discrepancies. Firstly, the evolutionary allometry of central incisors and the canines is negative compared to the positive static allometry. Secondly, tooth lengths and breadth scale with overall size to the same proportion (1:1) within species, whereas tooth lengths scale with positive allometry compared to tooth breadths between species (1.2:1). Both are examples of ways in which evolutionary allometry deviates from the static allometric pattern.

Within species, the upper central incisor (I^1) has a multivariate scaling coefficient (i.e., derived from a PCA) approaching 1, whereas between species I^1 has a scaling coefficient below 0.8. This discrepancy reflects a species effect. Namely, that larger macaque species apparently have relatively smaller upper incisors compared to their smaller-bodied congeners.[2] In other words, intraspecifically, the upper central incisor increases approximately in proportion to overall size between individuals. Between species however, the evolution of I^1 size has become decoupled from overall size and shows a negative allometric trend across macaques. Similarly, there is a trend for larger macaque species to have relatively smaller canines. These discrepancies can be the result either of low genetic correlations between anterior teeth and body size (Hlusko et al., 2006; Lande, 1979, 1985), the action of selection on these teeth independent of body size (Cheverud, 1982b; Lande, 1985), or both. In the case of the former, central incisors and canines do not increase in proportion to body size across species to the extent that they do within species, possibly due to reduced genetic covariance between these teeth and body size. In the case of the latter, there is selection independent of body size acting to reduce the size of the anterior dentition, for example for dietary and/or sociosexual reasons.

Similarly, the discrepancy of length-to-breadth allometric scaling ratios between the intraspecific and the interspecific level highlights the fact that phenotypic patterns do not strictly reflect the genotypic variances and covariances. In adult macaques within the same species, tooth lengths and breadths scale, on average, to the same proportion with overall size (the ratio of the scaling coefficients is 1:1). Between species, however, tooth lengths increase more with overall size than tooth breadths do on average (the ratio is 1.2:1). Regardless of whether evolutionary patterns of dental allometry reflect correlated evolution to changes in body size or independent adaptations of tooth size, they can only arise from the heritable part of phenotypic variation and covariation. Lande (1979) showed that genetic correlations can exist between traits that lack phenotypic correlations, highlighting the influence of the

[2]This matches my own observations with regard to the size of the anterior dentition in large-bodied species compared to smaller-bodied macaques while taking the calliper measurements.

environment during development in translating the genotype into the phenotype. Genetic correlations of tooth size to body size (e.g., through genetic pleiotropy), need not be the same for different dimensions of the same tooth (e.g., length and breadth), as has been found for molars in a pedigreed baboon colony (Hlusko et al., 2006).

A comparison of dental correlations to overall size within and between species may yield insight into how differences between static and evolutionary allometry patterns can arise. Genetic correlations could not be retrieved for the macaque specimens used in this work. However, phenotypic correlations between individual tooth measurements and craniodental size (as a proxy for body size) were obtained in a PCA. These correlations, within and between species, can be found in Appendix E. A comparison between the intraspecific and interspecific correlations reveals that 1) phenotypic correlations are always higher across taxa than they are within, as is commonly the case (Hlusko et al., 2006; Lande, 1979) and 2) that more often than not, mesiodistal lengths have lower correlations with size than the breadths of the same tooth *within* species, but that *between* species tooth lengths tend to have higher correlations than breadths of the same tooth. The same is true for dental correlations with calvarium length, retrieved in the bivariate regressions, within and between species (not shown).

If the within-species phenotypic correlations are proportional to the genetic correlations, then we would also expect higher between-species phenotypic correlations for tooth breadths compared to mesiodistal lengths. The opposite is in fact observed. A possible explanation is that *genetic* correlations between macaque tooth lengths and body size are higher compared to tooth breadths despite what the within-species *phenotypic* correlations suggest, and thus that this stronger genetic relationship between tooth lengths and body size results in higher evolutionary allometric coefficients for tooth lengths. That tooth lengths have lower correlations within species could be due to the random noise in the data arising from the effect of tooth wear – which particularly affects the mesiodistal length measurements – or due to individual differences in development. This could then also explain why the allometric scaling pattern (of tooth lengths in relation to breadths) differs between taxonomic levels: between individuals and populations differences in development and environment help shape the phenotypic variance and covariance with size, compounded by tooth wear impacting dental covariances of mesiodistal tooth lengths especially, whereas these factors likely have a negligible impact on the between-species variation, because developmental 'noise' is cancelled out and the effect of tooth wear is reduced due to the use of species means.

Diet

I tested whether postcanine occlusal size scaled differently with body size in frugivorous and omnivorous macaques, as a result of differences in energy requirements connected to different diets. The results were negative, with differences in regression slopes of postcanine occlusal size on body mass not being significantly different between the two groups. Carrying out such an analysis in a comparatively small group necessarily suffers from low statistical power. Indeed, 95% confidence intervals were too wide to refute the null hypothesis of no difference in allometric scaling between groups. That said, the scaling patterns (the PGLS regression slopes) did not appear different enough to suggest a clear difference in allometry. Moreover, depending on whether phylogeny was corrected for or not ($\lambda = 0$ or $\lambda = 1$) either frugivores or omnivores had higher scaling coefficients, highlighting that the pattern is not robust (Table 5.7). It was not possible to determine definitively whether phylogenetic correction or no correction was the most appropriate course of action, because λ could not be confidently estimated due to the small sample sizes. There is therefore no evidence that an effect of diet on allometric scaling of total postcanine occlusal size exists in macaques based on these data. If there had been a clear difference in PCOA scaling between dietary groups, the pattern likely would have been visible despite low statistical power. It is therefore reasonable to assume that the present findings reflect a true lack of a dietary signal. This is in contrast to what has been found in primates at higher phylogenetic levels (Kay, 1975; Lucas et al., 1986; Scott, 2011). There are a few possible explanations. The relative size of the postcanine dentition may be evolutionarily constrained and allometric relationships of teeth to body size are not easily changed or not enough time has passed for natural selection to cause a divergence in postcanine tooth scaling in response to dietary differences (or both). In additionally, the current dietary composition of macaques may be unrepresentative of past diets but rather be plastic to locally varying conditions. Also, the diets of macaque species possibly do not differ enough to lead to differential selection gradients. The aforementioned factors probably all contribute in explaining the lack of a dietary effect in allometric scaling.

The above result also entails that macaques can be considered to belong to the same dietary category and that no diet-related shift in dental scaling has occurred for the macaque postcanine dentition to maintain "functional equivalency" (Pilbeam and Gould, 1974). Kay (1975) and Corruccini and Henderson (1978) found that measures of postcanine tooth size scaled with positive allometry in primates when differences in energy content of different food items were ignored. When testing within frugivorous and folivorous categories, postcanine teeth scaled isometrically with overall size measures (Corruccini and Henderson, 1978; Kay, 1975). The allometric scaling coefficients obtained here are slightly different depending on whether body mass or calvarium length is used as the body size measure. Relative to body

mass, the postcanine dentition in macaques scales with negative allometry (although in some cases isometry cannot be ruled out). Relative to calvarium length, the macaque results are similar to what was found in other primates, namely isometric dental scaling. It must be pointed out, however, that Kay (1975) and Corruccini and Henderson (1978) used different measures of postcanine tooth size (one-dimensional measurements of M_2, among others, by Kay (1975) and the square root of occlusal area of P^4, M^2, M_1 and M_3 by Corruccini and Henderson (1978)) than the one employed here (one geometric mean of MD lengths and BL widths of all postcanine teeth, excluding P_3), as well as different statistical techniques, and so this may help explain the differences in results. On the other hand, it is possible that isometry is found at higher taxonomic (or phylogenetic) levels, such as when several genera or families are combined into single groups. At this level, differences in chewing rate (or other factors) may exist between animals of different body sizes (Fortelius, 1988), and the isometric relationships in fact reflect metabolic scaling (i.e., negative allometry) once those differences are accounted for. On the level of macaques, all species are likely similar enough in body size and other physiological aspects (e.g., chewing rate) that this does not play a role. The postcanine tooth scaling pattern is consistent with metabolic scaling ($\alpha \approx 0.75$). By 'metabolic scaling' is meant here a negatively allometric relationship that mirrors the negative allometry between basal metabolic rate and body mass (*sensu* Kleiber, 1947). The aforementioned scaling coefficient of ≈ 0.75 (where isometry would be represented by a coefficient of 1) is therefore not the same as the one describing positive allometry of tooth *area* to *volumetric* body mass (*sensu* Pilbeam and Gould, 1974). Calvarium length yielded positive allometry (although isometry could not be ruled out), but body mass has been argued to be a more appropriate measure in metabolic scaling studies, as body mass determines metabolism.

Sexual Dimorphism

The degree of sexual dimorphism in macaque body mass was found to be constant, that is isometric, across macaques, and therefore does not match the pattern of positive allometry found in primates at higher phylogenetic levels (Leutenegger and Cheverud, 1982). Similarly, the degree of sexual dimorphism in craniodental and dental size did not change with the size of the skull or the dentition, respectively. Only the degree of CP_3 dimorphism has a positively allometric relationship with CP_3 size: the size of the female canine/premolar complex increases relatively less than the male canine/premolar complex across species, and thus CP_3 dimorphism increases with CP_3 size. To some degree this corresponds to the variation in macaque body size, namely that some of the bigger overall macaques (e.g., *M. nemestrina*) also tend to have the more pronounced canine/premolar dimorphism. Some

macaques, on the other hand, stand out as having disproportionately low sexual dimorphism in the CP_3 complex for their body mass compared to the other macaques. These species are *M. fuscata*, *M. assamensis*, *M. sylvanus*, and to some extent *M. mulatta* (see Figures 5.7b and 5.8a). The pattern of sexual dimorphism is not identical for these species. In all species except for *M. assamensis*, both males and females fall well below the regression line of CP_3 size on body mass; in Assamese macaques it appears that the relatively low sexual dimorphism is primarily a result of comparatively large female canine/premolar size. The sample of *M. assamensis* was small and included a relatively large number of highly worn male specimens. It is therefore possible that mesiodistal and buccolingual measurements of the canines and P_3 were affected by tooth wear, yielding a misleadingly small canine/premolar complex for Assamese males.

The sexual dimorphism in the CP_3 complex is not isometric with CP_3 size, unlike size dimorphism in body mass. Body mass nor body mass dimorphism could explain canine/premolar dimorphism. Taken together, these findings offer strong support for the notion that selection is likely acting on macaque canines independently of body size. I investigated whether the operational sex ratio (OSR) or breeding seasonality, as measures of the monopolisation potential of females and therefore male-male competition, could explain the variation in CP_3 dimorphism. There was a slight (but non-significant) trend for a higher OSR (more reproducing females per reproducing male) to be associated with a reduction in body mass dimorphism, and an even weaker trend for this to be associated with a reduction in canine dimorphism. Similarly, strongly seasonally breeding macaques tended to be less sexually dimorphic in body size (but this association was non-significant). Breeding seasonality did not correlate with canine dimorphism in macaques. Although the observed associations were not very strong, particularly in the canine/premolar complex, they do suggest that sexual dimorphism decreases as breeding seasonality becomes stronger and the number of females per male in the group increases, rendering mate guarding tactics and male-male agonistic competition either not effective or too costly, as expected on the basis of sexual selection theory (Altmann, 1962; Harvey et al., 1978; Leutenegger and Kelly, 1977; Mitani et al., 1996).

Patterns of sexual dimorphism likely have a multifactorial origin (Oxnard et al., 1985). Unfortunately multifactorial models could not be tested here due to the small sample size and attendant low statistical power that would have meant statistical overfitting of regression models with multiple predictors. Possible relevant explanations are discussed here instead. For instance, there was an indication that diet may mediate the relationship between overall size and canine size dimorphism in macaques. The results showed that, typically, larger macaques have more pronounced canine/premolar dimorphism, unless they subsist on

relatively more low-quality foods, in which case these species exhibit reduced canine size dimorphism. *M. sylvanus*, *M. fuscata*, and *M. mulatta* conform to this pattern. There are several possible explanations to consider that might explain the reduced canine dimorphism in these species.

In general, sexual dimorphism in a trait is a function of the male as well as the female trait expression (Plavcan, 2011). Therefore, reduced canine dimorphism can result from relaxed selection on large canine size in males or increased selection on large canine size in females. There may be less intense sexual selection for canine size in male primates when the monopolisation potential of females is low, such as when breeding seasonality is strong and females synchronise their ovarian cycles, or when males have the option of using reproductive strategies other than engaging in direct male-male competition, such as sneaky copulations (Brauch et al., 2008; Paul, 1997; Plavcan, 2001). Female mate choice, either through resisting mating attempts from dominant males or engaging in sneaky copulations with subordinate males, undermine the effect of male-male agonistic interactions. Breeding seasonality is strong in *M. sylvanus*, *M. fuscata*, and *M. mulatta* (as well as in *M. assamensis*; Table 5.2). Breeding seasonality may also help explain why diet was found to contribute to the relationship between body mass and CP_3 dimorphism: macaque species that subsist relatively more on leaves and other non-fruit items are those that live in seasonal or colder environments, where fruit is not an abundant food resource and breeding seasonality likely optimises the survival rate of offspring (Ross, 1992). Furthermore, sneaky copulations have been demonstrated to yield reproductive success to low-ranking males in *M. mulatta* (Berard et al., 1994), in *M. sylvanus* (Brauch et al., 2008), *M. fuscata* (Soltis et al., 2001), and possibly also in *M. assamensis* (Fürtbauer et al., 2011). Female mate choice has also been recorded to influence paternity success in these species (Brauch et al., 2008; Soltis, 2004). Mate guarding and male dominance rank, by contrast, have been found to be better predictors of male reproductive success in longtailed macaques *M. fascicularis*; Engelhardt et al., 2006, and may also be important in other macaques living in a-seasonal environments (e.g., the liontailed macaque (*M. silenus*)). In recent years, it has become increasingly widely accepted (and corroborated) that sexual dimorphism is as much a function of selection on male as well as on female traits (Plavcan et al., 1995; and reviewed in Plavcan, 2011). It is therefore plausible that canine/premolar dimorphism reflects separate evolutionary processes pertaining to males and females, and that this is why there is no consistent relationship between macaque CP_3 dimorphism and body size, diet, OSR, and breeding seasonality. Future research using detailed information on the social group dynamics among female macaques, e.g., the formation and use of coalitions in agonistic interactions (Plavcan et al.,

1995), may yield more insight into the contribution of selection on female canine size to macaque canine size dimorphism.

Another potential explanation for the variation in macaque canine/premolar dimorphism relates to gape. In most haplorhine primates, male canines serve as weaponry in actual combat, a means of display to prevent costly physical aggression, or display for other social reasons (e.g., mate attraction). In order to display or use the canines, the jaws must be able to part far enough for the canines to depart the occlusal plane of the opposing jaws. On the other end of the extreme, it seems logical that it is unnecessary for a jaw gape to be disproportionately large relative to canine size and that it is actually counter-productive because a large gape would make the canines appear relatively small, which would be disadvantageous to the purpose of display. In catarrhine primates there is a strong association between maximum jaw gape size (the distance from the upper incisal edge to the lower incisal edge when the jaws are maximally opened), jaw length, canine overlap (measured as the distance between the upper canine cusp tip and the lower canine cusp tip when the jaws are in occlusion), and canine height (Hylander, 2013, 2017; Lucas, 1982, 1981; Terhune et al., 2015). This association exists within species, with males consistently having relatively larger gapes and larger canines than female conspecifics (with the exception of humans and hylobatids; Hylander, 2013; Terhune et al., 2015), as well as between catarrhine species (Hylander, 2013; Lucas, 1982). Japanese male and female macaques (*M. fuscata*) stand out among catarrhines as having the smallest relative jaw gapes (adjusted for jaw length) and canine overlap (Hylander, 2013).

Absolute gape size can be increased by lengthening the mandible. Further extension of the jaw gape, to increase also relative gape size, requires a repositioning of the jaw muscle adductors on the mandible, a lengthening of the muscle fibers, or both (Hylander, 2013; Terhune et al., 2015). Male longtailed macaques (*M. fascicularis*) have longer anterior muscle fibers of the masseter (but not different positions of the masseter and temporalis muscles) than females that contribute to their wider gapes (Terhune et al., 2015). There exists a trade-off between the lengthening of muscle fibers and repositioning of muscle attachment sites to increase gape size and bite force (Hylander, 2013, 2017). Variation in feeding behaviour and dietary composition is one of the proposed explanations for catarrhine diversity in gape size and canine overlap (Hylander, 2013, 2017; Terhune et al., 2015). Although there is likely strong selection on males to engage in effective gape display during their social interactions, the biomechanical properties of diet may also exert some influence. Namely, tough foods, such as mature leaves, and other resistant foods that require more forceful chewing may have led to the evolution of shorter jaw muscles and muscle fibers in order to increase the biomechanical efficiency of the muscle tissue (Hylander, 2013; Terhune et al., 2015). An

alternative strategy to maintaining the same bite force is to increase the muscle mass, but this is energetically more costly to develop and maintain throughout the animal's life (Hylander, 2013, 2017). Although it remains speculative without further testing, the four species with low sexual dimorphism in the canine/premolar complex (*M. assamensis*, *M. mulatta*, but especially *M. fuscata* and *M. sylvanus*), have among the highest proportion of non-fruit food items in their diet (mostly leaves, except in the case of *M. sylvanus*, which subsists on a higher proportion of seeds than leaves; for dietary data and sources, see Table B.2). Given the amount of unexplained variation in canine/premolar size and dimorphism between male and female macaques, this is an interesting and promising avenue for future research, testing hypotheses of sexual selection related to canine display in combination with natural selection related to feeding behaviour.

Lastly, the phylogenetic signal detected in the relationships between the various variables of size, dimorphism and (socio)ecology differed in strength. Particularly the associations between male and female body mass, the size of the canine/premolar complex and body mass in males and females, canine/premolar dimorphism and body mass, and canine/premolar dimorphism and body mass dimorphism had moderate to strong values of Pagel's λ. Macaques thus tend to resemble other, closely related macaques more so than distantly related macaques, in how their body mass relates to other aspects of size, particularly dimorphism in body mass and the canine/premolar complex. The phylogenetic structuring in these associations could have arisen as a result of neutral evolution, notably due to the effect of genetic drift (Blomberg and Garland, 2002; Revell et al., 2008). However, body mass itself is one of the most important organismal traits and it is likely to be under strong selection. Similarly, canine size in males and females and the attendant sexual dimorphism is probably also under strong selection, possibly in both sexes, given the observed variation in macaques and primates on the whole (Hylander, 2013; Plavcan, 2001), and their role in social conflict, display, and possibly many other behaviours (Plavcan, 2001, 2011 for review).

Conclusion

By and large, evolutionary allometry patterns followed static allometry patterns, which means that ontogenetic growth trajectories (inferred from the static allometry patterns) can explain much of the between-species pattern of dental allometry. There appears to have been some decoupling of body size and tooth size evolution, however, in the anterior dentition. Incisors and canines have lower allometric scaling coefficients between rather than within species, due to several large-bodied macaque species have a relatively small anterior dentition. This suggests that there has been selection on a reduction of relative size in the anterior teeth of these species. Furthermore, no evidence was found for allometric shifts in the size of the

macaque postcanine dentition in relation to diet. Sexual dimorphism in body mass scales isometrically with body mass. Conversely, canine/premolar (CP_3) dimorphism scales with positive allometry to CP_3 size. Variation in canine dimorphism cannot be explained by body mass dimorphism, supporting the view that sex differences in the canine/premolar complex do not constitute a correlated response to selection on body mass but rather that there is selection (or other evolutionary processes) operating independently on macaque canines. Among the investigated variables, canine dimorphism cannot be explained by a single factor. Rather, body mass, body mass dimorphism, diet, and sexual selection on males for access to females are all associated to a small degree to canine size dimorphism. Future research efforts should be directed at testing hypotheses regarding selection on female canine size in addition to male canine size. Sexual size dimorphism in macaque body mass appears more clearly influenced by sexual selection on males arising from male-male competition for access to females.

Chapter 6

Signals of Ecogeography in the Macaque Dentition[1]

6.1 Introduction

A major goal of evolutionary morphology is to reveal how the phenotype has evolved in and adapted to the ecological and geographical environment. Many studies have shown that phenotypic variation in primates carries both geographical and environmental signals (Cardini and Elton, 2009; Cardini et al., 2007; Dunn et al., 2013; Frost et al., 2003; Ito et al., 2014; Kamilar et al., 2012; Lehman et al., 2005; Meloro et al., 2014; Viguier, 2004). However, the exact patterns often differ between taxa living in different environments and exposed to different selective forces. But similar ecogeographical patterns can nonetheless result from different evolutionary processes (Meiri, 2011). For example, Bergmann's rule describes a general tendency for endotherms to have larger body sizes at higher latitudes, within (Ashton et al., 2000; Mayr, 1956; Rensch, 1938) as well as between species (Bergmann, 1847; Millien et al., 2006). Explanations of this pattern typically invoke a thermoregulatory effect of cold temperatures on animal body size at higher latitudes (Mayr, 1956; Meiri and Dayan, 2003), but in some taxa rainfall may better explain the relationship between size and latitude (Ashton et al., 2000; Millien et al., 2006), including some non-human primates (Cardini et al., 2007; Frost et al., 2003). Such contrasting ecological correlates of Bergmann's rule indicate that different selective forces may give rise to the same pattern (Meiri and Dayan, 2003).

[1] At the time of printing, the work presented in this chapter was under revision with the American Journal of Physical Anthropology at the time of thesis submission, with the following authors and title: Grunstra, N.D.S., Mitteroecker, P., and Foley, R.A. A Multivariate Ecogeographic Analysis of Macaque Craniodental Variation. *American Journal of Physical Anthropology* (under revision).

In a taxon-wide study of Bergmann's rule in primates, a positive relationship between latitude and body mass was found among non-Malagasy primates (Harcourt and Schreier, 2009). However, at a lower taxonomic level, and after controlling for phylogeny, the pattern only persisted in macaque species living on the Asian continental shelf (Harcourt and Schreier, 2009). Furthermore, size gradients that correlate not with latitude but with longitude have been retrieved for cranial size within several African cercopithecid primates (vervet monkeys: Cardini et al., 2007; red colobus monkeys: Cardini and Elton, 2009; greater spot-nosed and blue monkey: (Cardini et al., 2010); and baboons: Dunn et al., 2013). By contrast, cranial shape varies more strongly along a latitudinal than a longitudinal gradient between several Neotropical species of howler and capuchin monkeys (Cáceres et al., 2014; Meloro et al., 2014), and between some (but not all) macaques (Ito et al., 2014).

To date, only a limited number of primate studies have included multiple climate and ecological variables (e.g., Cardini et al., 2007; Harvati and Weaver, 2006; Kamilar et al., 2012; Meloro et al., 2014; Viguier, 2004). From these studies, a mixed pattern of the environmental correlates of morphological size and shape variation in primates emerges. Rainfall and other humidity measures, as indicators of habitat productivity, are relevant in explaining cranial variation in vervet monkeys (Cardini et al., 2007), some Malagasy sifakas (Lehman et al., 2005), and lemurs (Viguier, 2004). In New World capuchin monkeys, however, both rainfall and temperature are important climatic predictors of skull shape (Cáceres et al., 2014). A recent environmental analysis of Malagasy strepsirrhine body mass revealed that diet and climate were weak predictors of body size, but that there was a strong phylogenetic effect (Kamilar et al., 2012). In modern humans, signals of population history in cranial variation have been found to be stronger than, or even drive, climatic signatures, highlighting the role of population structure and genetic drift (Betti et al., 2010; Harvati and Weaver, 2006; Roseman and Auerbach, 2015). It is becoming increasingly apparent that primate evolution, within and between species, has been characterised by a complex interplay of different selective forces and neutral processes.

6.1.1 Aim and Questions

Here, I carry out, to my knowledge, the first detailed multivariate analysis of craniodental dimensions and their relation to geographical distribution, climate and species' ecology, and the effect of phylogeny in the radiation of macaques (Cercopithecidae: *Macaca*). Macaques are an interesting taxon because they diversified widely and rapidly during times of considerable environmental change in the Pliocene and Pleistocene (Abegg and Thierry, 2002; Brandon-Jones, 1996), and because they continue to occupy a range of different habitats across southern, central, eastern and insular Asia and North Africa today (Fooden, 1982a).

The main focus of this chapter is to elucidate the role of the environment in phenotypic and taxonomic diversification at the macroevolutionary level by studying between-species variation. The multivariate phenotype is, once again, the dentition and associated cranial structures, as teeth are minimally plastic and are therefore likely to carry evolutionary signals. I compare the interspecific patterns to the intraspecific patterns in order to infer evolutionary processes. Using a large dataset comprising a broad spectrum of variables pertaining to spatial geography, climate, and ecology, I explore how different environmental variables interact in their association to macaque craniodental variation. Specifically, I test if the Bergmann effect is reflected in dental patterns, as expected on the basis of a Bergmannian trend in macaque body mass (Harcourt and Schreier, 2009). I also look for the presence of both longitudinal and latitudinal gradients in macaque dental variation given both the wide longitudinal and latitudinal extent of the geographical range of macaques, and the presence of such gradients in other cercopithecids (e.g., Cardini et al., 2010; Cardini and Elton, 2009; Cardini et al., 2007; Dunn et al., 2013). Finally, the effect of species' phylogenetic relatedness on observed relationships is often either not modelled or simply removed as part of the analysis. Here, I examine in detail how the patterns and magnitude of covariation between phenotype and ecogeography in macaques are influenced by phylogeny. To this end, I carry out the between-species analyses both with and without phylogenetic correction.

6.2 Materials and Methods

6.2.1 Morphometric and Contextual Data

A total of twelve macaque species were used in this study (Table 6.1. Only *M. ochreata* was omitted due to its small sample size and multiple unknown environmental parameters. None of the 12 species in this study have a contested phylogenetic position within the genus (Morales and Melnick, 1998; Tosi et al., 2003), which is relevant for the phylogenetic component of the analyses. All species groups are represented in the analysis.

Tooth lengths and breadths were included for all teeth, complemented by tooth height for the anterior dentition (incisors and canines), amounting to a total of 46 tooth dimensions used. Linear tooth dimensions were supplemented by the craniodental and mandibular measurements (skeletal measurements; see Chapter 3). Note that these supporting cranial and mandibular measurements were only recorded on adult specimens – from among the 711 specimens – showing full eruption of their third molars (M^3/M_3) to minimise ontogenetic variation. Since the skeletal and dental measurements showed the same results separately as they did combined, I only present the results for the combined phenotypic dataset.

Table 6.1 Macaque species included in the present set of analyses, including their geographical distribution, as well as the number of specimens used in the analysis (includes only specimens of known sex, subadult and adult individuals).

Binomial name	Distribution	Males (*N*)	Females (*N*)	Total (*N*)
M. assamensis	Continental Southeast Asia	13	6	19
M. cyclopis	Taiwan	7	11	18
M. fascicularis	Indochinese peninsula, Indonesia, Philippines	51	41	92
M. fuscata	Japan	24	20	44
M. maura	Southwest Sulawesi	34	20	54
M. mulatta	Continental South and East Asia	33	43	76
M. nemestrina	Malay peninsula, Sumatra, Borneo	39	23	62
M. nigra	North Sulawesi	37	37	74
M. radiata	South and West India	46	33	79
M. silenus	Southwest India	24	21	45
M. sinica	Sri Lanka	40	35	75
M. sylvanus	Algeria, Morocco	36	37	73
Total		**384**	**327**	**711**

Between species

For the interspecific analysis species means were computed for the morphometric variables to correct for differences in sample size. Means were derived from the morphological data by taking the arithmetic mean of the female and male means of each species. To this end only specimens of known sex were used. Furthermore, outliers were inspected (by species, by variable) in the raw data. Those that were more than three standard deviations away from the mean turned out to be either obvious mistakes or they were individuals whose taxonomy was uncertain (this had been noted during the data collection). These outliers were removed from the sample prior to mean computation. Ultimately, data from a total of 711 specimens were used for this macroevolutionary ecogeographical study. The sample sizes for each species, by sex, are presented in Table 6.1. This table also reiterates the species' geographical occurrence.

Contextual data pertaining to macaque ecogeography were collected from published sources (see Tables B.1 to B.6 in Appendix B. Henceforth, I use 'ecogeography' to refer to geographical, environmental, and ecological parameters relating to macaque spatial distribution, climate, and habitat and dietary ecology. Among the ecogeographical parameters, spatial geography (latitude and longitude) and the environment (climate, habitat, and dietary ecology) are analysed separately. Here, spatial geography is represented by geographical coordinates and reflects the central point in the geographical distribution of each macaque species. Thus defined, spatial geography therefore describes spatial distances between species and need not be an indicator of (dis)similar environments (although it may, which is the reason latitude is often used as an environmental proxy), but rather may simply reflect patterns of dispersal. Conversely, climate, range variables, and ecological parameters are taken to describe species' environments irrespective of where species occur geographically (i.e., similar annual temperatures describe a real similarity in environment, even if the localities are spatially far apart). The analytical techniques used to investigate both of these components – spatial geography and environment – is described further down below.

Latitude and longitude are taken to reflect spatial geography, and are represented by the coordinates of the central point in each species' geographical range (e.g., *M. fascicularis* is known from field observations to occur between 18°N and 10°S, so its mid-range latitudinal coordinate is 4°N; Jones et al., 2009). These coordinates, as well as geographical, latitudinal, and longitudinal ranges, and actual evapotranspiration rate (AET; a measure of habitat productivity) were obtained from the PanTHERIA database (Jones et al., 2009). Geographical coordinates and ranges were presented in Table B.4 in Appendix B. Several macaque species have successfully dispersed to insular Southeast and East Asia. Species were assigned to one of the following categories: 1) island(s) only, 2) mixed, 3) continental mainland only. Species'

elevational distributions were derived from field observations reported in the literature. Data on both the median altitude and the range in altitude were collated (Table B.5 in Appendix B). I have chosen to use species-level data as they are known from the literature, rather than values derived from the sample, because the goal of this work is to analyse the association between environment and phenotype in evolved species differences, which all members of the same species are assumed to share among each other. The same applies to the use of latitudinal and longitudinal coordinates and ranges as they pertain to entire species rather than the present samples (see above).

Table 6.2 Climate variables used in this study (extracted from the WorldClim database (Hijmans et al., 2005).

Variable	WorldClim	Definition
T mean	BIO 1	Annual mean temperature
T max	BIO 5	Maximum temperature of warmest month
T min	BIO 6	Minimum temperature of coldest month
T seasonal	BIO 4	Temperature seasonality (standard deviation)
P annual	BIO 12	Annual precipitation
P max	BIO 13	Precipitation of wettest month
P min	BIO 14	Precipitation of driest month
P seasonal	BIO 15	Precipitation seasonality (coefficient of variation)

Climate variables were derived from among the bioclimatic variables in the WorldClim database (Hijmans et al., 2005) and imported using the *raster* package (Hijmans, 2016) in RStudio (RStudio Team, 2015), at a resolution of 2.5 arc-minutes. The variables used in this study correspond to common measures of climatic variation and are listed in Table 6.2. Climate data were aggregated for each species on the basis of the geographical coordinates of the specimens in the sample. In order to minimise the bias towards sample-specific climate data rather than species-specific data (e.g., if the present sample of rhesus macaques were disproportionately represented by northern Indian rhesus macaques), data were aggregated on species level following extraction in the following way: first, each unique localit was counted and retained only once to avoid pseudo-replication. Next, the climate data were averaged across these unique localities to arrive at species means. Climate data by species (except for *M. ochreata*) can be found in Table B.6 (Appendix B).

Macaques can broadly be divided into two ecological groups: species that predominantly occur in broadleaf evergreen (BE) forest, and those that exist in a wide range of forest and non-forest (non-BE) habitats (Fooden, 1982a). In addition, habitat breadth was measured

as the number of biomes that are of major importance to a species (with all human-altered habitats counting as one). Dietary ecology is represented by dietary breadth (the number of food types that species commonly include in their diet), the degree of frugivory and folivory, and the range of the proportion of fruits in the diet. Finally, mean male and female adult body masses were used to represent overall body size. Data (including sources) on species body mass, habitat and diet are presented in Table B.1 and Table B.2 in Appendix B, respectively.

Within species

For the intraspecific analysis I use those species for which adequate spatial and climatic variation exists in the sample. These are *Macaca nemestrina* ($N = 43$), *M. fascicularis* ($N = 70$) and *M. mulatta* ($N = 44$). Of these three, specimens of *M. nemestrina* and *M. fascicularis* have been collected from insular Southeast Asia (primarily Borneo and Sumatra), occupying tropical habitats, and *M. mulatta* has been sampled from subtropical and temperate localities in India, through to Myanmar, Nepal, and Vietnam, up to China. Figure 6.1 depicts the geographical distribution of the sample for the three species. An interactive version of these maps showing the topography of the land surface and the sea bed can be accessed at *https://nicolegrunstra.github.io/GeoMaps_3_species/*.

Here, only morphological data pertaining to adult, wild specimens with known provenience were used. Adult, because then all dental and cranial and mandibular measurements can be included, and with known provenance because the focus is on wild-caught specimens. Due to damage to specimens there were missing data, which were substituted using Expectation-Maximisation (EM) imputation. EM imputation is an iterative imputation procedure that uses Maximum Likelihood (ML) methods to determine the relationship between variables (the variance-covariance matrix) (Graham, 2009). Based on the observed relationship between variables the EM technique finds 'expected' values for missing data and substitutes the latter with the former. Subsequently, it runs the model again to find updated ML estimates, re-imputes the data, and does this reiteratively until convergence ('maximisation'; Dempster et al., 1977; Graham, 2009; Gunz et al., 2009).

Due to the paucity of data on ecological (habitat and dietary) variation between populations, only elevation and climate were used in the intraspecific 2B-PLS analysis. Both types of data were gathered from the WorldClim database (Hijmans et al., 2005) and analysed on specimen level. The same eight climatic variables as in the macroevolutionary analysis were used (Table 6.2). The effect of spatial geography was investigated using the geographical coordinates of the specimens, as per the interspecific analysis (detailed below).

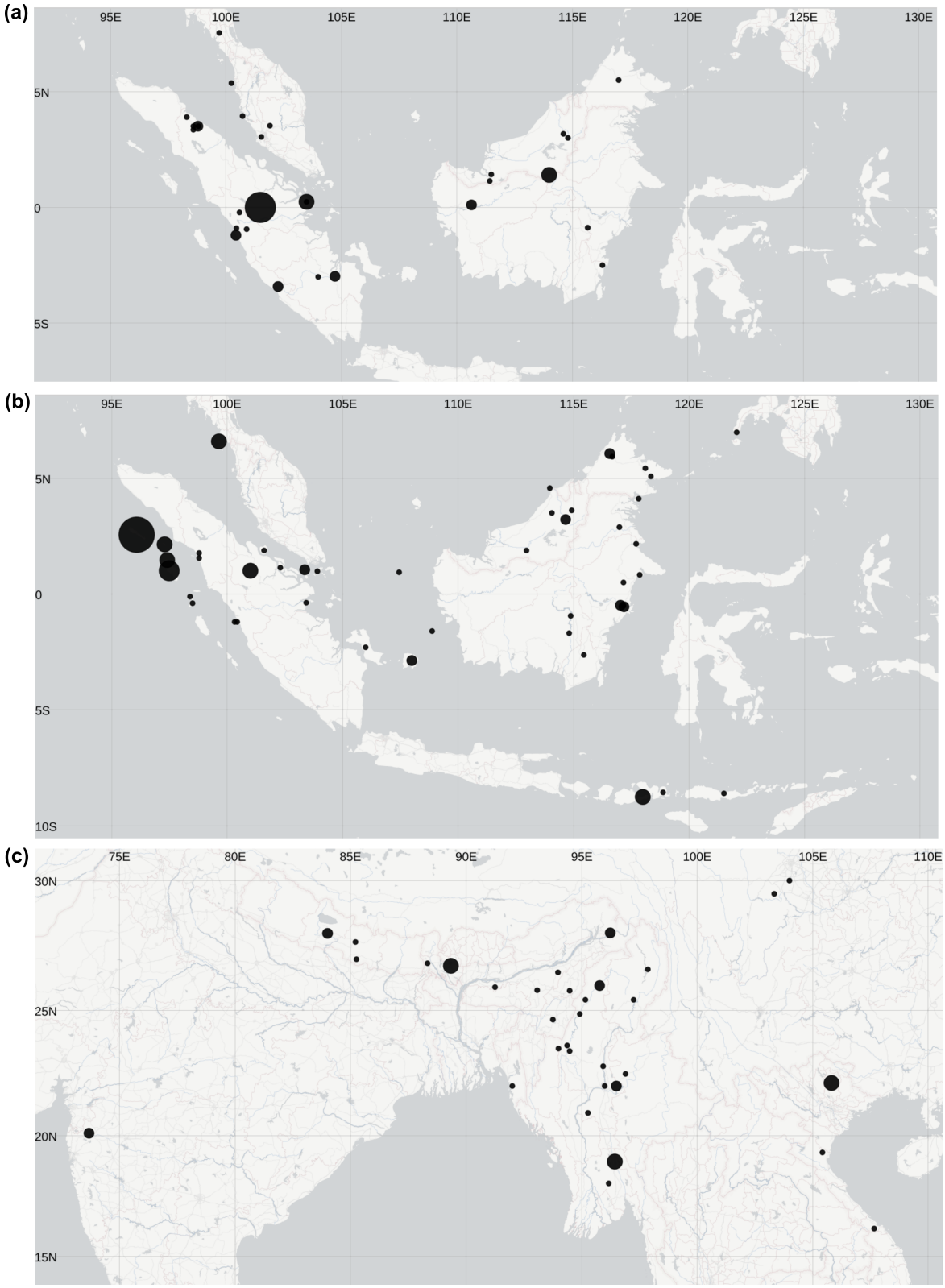


Fig. 6.1 Maps showing the distribution of sample of adult and wild-caught specimens for a) *M. nemestrina*, b) *M. fascicularis*, and c) *M. mulatta*. Bubble size is standardised across the subfigures and represents the number of specimens sampled from any one particular locality (*M. nemestrina*: *N* = 1-6; *M. fascicularis*: *N* = 1-7; *M. mulatta*: *N* = 1-3). *M. nemestrina* and *M. fascicularis* have been collected from insular Southeast Asia (Borneo and Sumatra and surrounding islands), occupying tropical habitats, and *M. mulatta* has been sampled from subtropical and temperate localities in India, through to Myanmar, Nepal, and Vietnam, up to China.

6.2.2 Statistical Analysis

In the between-species analysis males and females were pooled; the pattern of association between sexual dimorphism and ecogeography is outside of the scope of this paper. In the within-species analysis, sex differences were removed by subtracting the value of each male specimen from the male mean, and each individual female value from the female mean (by species).

Between species

Since species means are used the sample size equals twelve. Considering the much larger number of predictor and response variables to be modelled, the number of statistical parameters far exceeds the number of observations and, therefore, there are insufficient degrees of freedom that are required to produce reliable results (Babyak, 2004). This problem of statistical 'over-fitting' renders standard regression techniques (including multiple multivariate regression) invalid. The over-fitting of a regression model results in unreliable regression coefficients, p-values, and coefficients of determination (R^2), which means the model would perform poorly when applied to a different sample (Babyak, 2004). An alternative multivariate approach suitable for the present purpose is two-block partial least squares analysis (2B-PLS; Bookstein et al., 1996; Rohlf and Corti, 2000). 2B-PLS finds the axes of successively maximum covariance between blocks of variables. These axes of highest mutual covariance are represented by pairs of latent variables (henceforth LVs) in the data (Bookstein et al., 2003; Mitteroecker and Bookstein, 2007; Rohlf and Corti, 2000). LVs are linear combinations of the individual scores (e.g., species in an interspecific analysis) weighted by the contribution of the original variables in describing the covariance pattern. The weightings of the original variables are called loading coefficients and they are typically visualised by loading plots, one per block of variables per axis (dimension) of covariance. The different axes are orthogonal to each other and are therefore (geometrically) independent, similar to principal components ina PCA. 2B-PLS is a common approach in morphometrics to study morphological integration (e.g., Bookstein et al., 2003; Mitteroecker and Bookstein, 2007; Rohlf and Corti, 2000) or to investigate the relationship between phenotypical and environmental variation (e.g., Cáceres et al., 2014; Frost et al., 2003; Meloro et al., 2014; Monteiro et al., 2003; Piras et al., 2012). It is a useful technique when the number of variables exceeds sample size, and it makes no assumptions about which are the predictor and the response variables (Adams and Felice, 2014). 2B-PLS was employed to investigate the relationship between the environmental variables, in block 1, and the morphometric measurements, in block 2. Environmental variables were scaled to unit variance to eliminate

differences in measurement scale. Morphological measurements were transformed by the common logarithm to account for differences in size-related variance between the variables (e.g., calvarium length compared to tooth length).

Even though 2B-PLS has also been used to study the multivariate association of morphological and geographical variables (Frost et al., 2003), I use a different method here. In ecology, such an association is typically construed as a spatial cline or gradient, represented by the slope of the surface that results from mapping a particular biological variable on a geographical map. Locally, this slope can be estimated by regressing the variable on both latitude and longitude. The two resulting partial regression coefficients (one for latitude, one for longitude) determine the spatial direction with maximum regression slope, i.e., with the steepest local gradient on the surface. In the current multivariate context, this translates into finding a linear combination of morphological variables that has a maximum slope when regressed on a linear combination of geographical coordinates. This is achieved by a singular value decomposition of the p x 2 matrix of partial regression coefficients of all p morphological variables on latitude and longitude (for a mathematical proof see Mitteroecker et al., 2016). The singular values equal the maximal slopes, and the singular vectors contain the morphological and geographical loadings that determine the corresponding LVs. This approach is similar to reduced rank regression (Izenman, 1975), hence I use this name to refer to this multivariate strategy here. Similarly to 2B-PLS, reduced rank regression yields two pairs of latent variables in this application, but they maximize the regression slope (not the covariance) of the morphological LV on the geographical LV, and the LVs are uncorrelated, not orthogonal as in 2B-PLS. Furthermore, in contrast to reduced rank regression, 2B-PLS would be largely driven by the actual geographical variation. For instance, if the habitat range of a species was much wider in one direction than another, the first dimension of PLS would be aligned with this direction of maximal spatial variation, rather than the direction of the steepest cline.

Furthermore, as part of the phylogenetic comparative component of this study a phylogenetic 2B-PLS and reduced rank regression by means of a PGLS-based algorithm was performed (Adams and Felice, 2014; Mitteroecker et al., 2016). An independently derived molecular phylogeny of the macaque species in the sample (Arnold et al., 2010) was used for the phylogenetic correction. This phylogeny is presented in Figure 6.2 and corresponds to other published macaque phylogenies (Chatterjee et al., 2009; Springer et al., 2012; Tosi et al., 2003). To investigate precisely how the effect of phylogeny on macaque morphology manifests itself in the associative patterns, I carried out the between-species analyses first without and then with phylogenetic correction. Phylogenetic branch lengths were scaled proportional to time, assuming Brownian motion evolution.

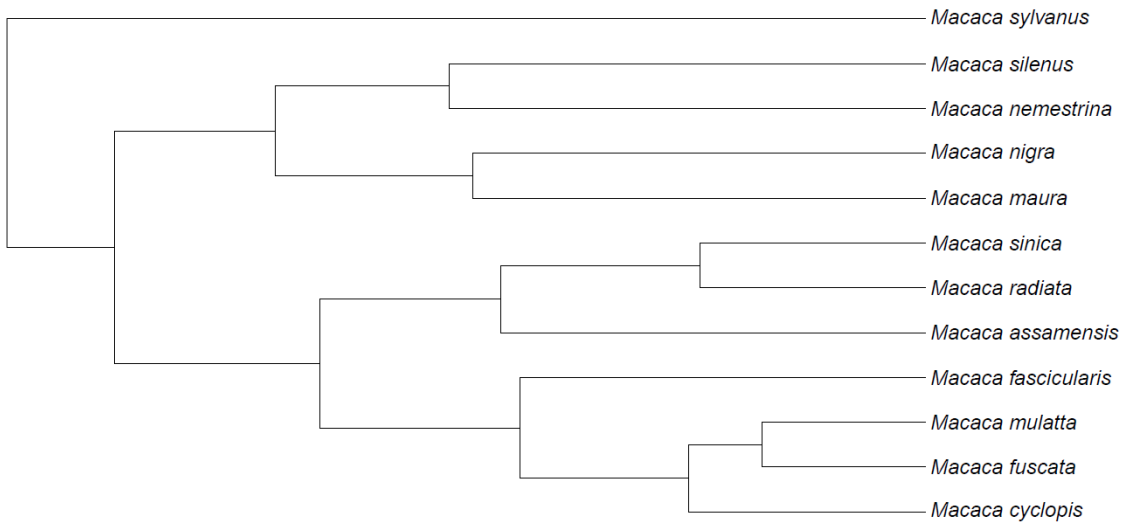


Fig. 6.2 Molecular macaque phylogeny from the *10kTrees Project* (version 2; Arnold et al., 2010). This tree only includes those species used in the present analysis (N = 12).

Within species

As in the between-species analysis, 2B-PLS and reduced rank regression were used to investigate intraspecific phenotype-environment associations and spatial signals, respectively.

Lastly, in the absence of strong selection and when gene flow decreases with geographic distance, patterns of isolation by distance (IBD) emerge between populations of the same species. To test for IBD, I carried out Mantel tests on the geographic and phenotypic distance matrices within *M. nemestrina*, *M. fascicularis*, and *M. mulatta* separately, with 10,000 random permutations. Geographic distances were represented by geodesic distances, and multivariate phenotypic distances were computed as Euclidean distances of both the original and log-transformed measurements.

The 2B-PLS analyses (between and within species) and Mantel tests (within species) were carried out in RStudio (RStudio Team, 2015) using the packages 'geomorph' (Adams and Otarola-Castillo, 2013) and 'vegan' (Oksanen et al., 2016), respectively. The reduced rank regressions (between and within species) were carried out in Mathematica [9.0] (Wolfram Research Inc., 2012) using code written by P. Mitteroecker. [2]

[2]The analyses were carried out by Philipp Mitteroecker in Mathematica, and repeated by me where possible in RStudio. Results were identical. The reduced rank regression technique, developed by P. Mitteroecker specifically for this purpose, is not available in R code and the results from this analysis are therefore the outcome of collaborative work with P. Mitteroecker.

6.3 Results

6.3.1 Between Species

Environment

The phylogeny-uncorrected 2B-PLS yielded two latent variables that cumulatively account for 97% of the squared covariance between the blocks of variables, and individually 63% and 34%, respectively (see scree plot in Figure F.1 in Appendix F). The correlation between blocks is strong along both dimensions (LV 1: $r = 0.81$, LV 2: $r = 0.81$)[3]. The phylogeny-adjusted 2B-PLS extracted only one significant latent variable (LV 1), which accounts for 94% of the squared covariance between blocks ($r = 0.67$), while the contribution of LV 2 has decreased to 4%, despite a strong correlation between blocks ($r = 0.85$) (see scree plot in Figure F.1 in Appendix F).

The PLS loadings of the environmental and morphological variables onto LV 1 showed a very similar pattern before and after phylogenetic adjustment (Figures 6.3 and 6.4). Body size and temperature seasonality had high positive loadings, whereas temperature (mean, maximum, and minimum), geographic range size, habitat breadth, and ecological group had high negative loadings onto LV 1. All morphological variables loaded positively on LV 1, a common allometric (i.e., overall size) effect (Mitteroecker et al., 2012). The PLS scores in Figure F.2 (Appendix F) further show that macaques vary along a size gradient from small-bodied species (e.g., *M. sinica* and *M. fascicularis*) to larger-bodied species (e.g., *M. sylvanus* and *M. fuscata*).

loading patterns of LV 2 also showed a highly similar pattern before and after accounting for phylogeny (Figures 6.5 and 6.6). Annual and minimum precipitation, minimum temperature, AET, and percentage of fruit in the diet had relatively high positive loadings for LV 2, whereas range variables, seasonality, measures of dietary variability, and percentage of leaves in the diet all loaded negatively onto LV 2. The associated craniodental pattern showed a tooth size contrast. Measurements pertaining to the anterior dentition loaded positively onto LV 2, i.e., in the same direction as precipitation levels and percentage of fruits. Conversely, measurements of the posterior dentition loaded negatively on LV 2, in the same direction as precipitation seasonality and percentage of leaves. A larger anterior dentition is thus associated with fruit-eating and high degree of rainfall, whereas a larger posterior dentition is associated with more leaf-eating and drier, more seasonal environments. As mentioned,

[3]I do not report p-values here as their meaning is limited in this small sample of selected species, and because the biological significance of the results depends on the covariance patterns and the effect sizes, not on the p-values.

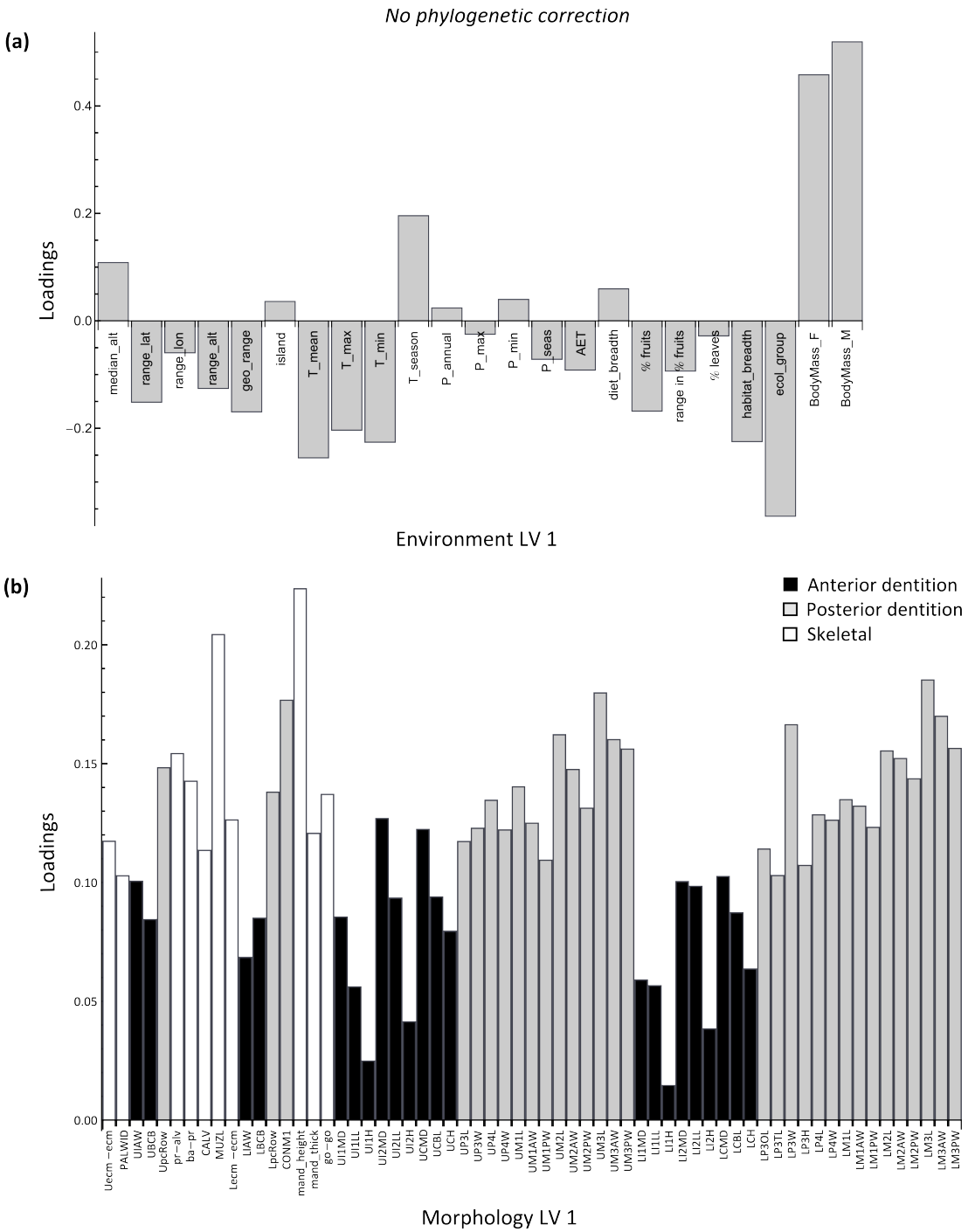


Fig. 6.3 Results of the two-block partial least squares (2B-PLS) analysis. Latent variable (LV) 1 describes the pattern of maximum covariance between environment and morphology prior to phylogenetic correction. a) Environment loadings, and b) morphology loadings onto LV 1. Variable definitions can be found in Tables B.13 and B.14 (morphology), and Tables B.1 to B.6 (environment) in Appendix B. This first, main factor represents the association between low temperature, high temperature seasonality, and large body mass with large absolute craniodental size (all morphological loadings are positive).

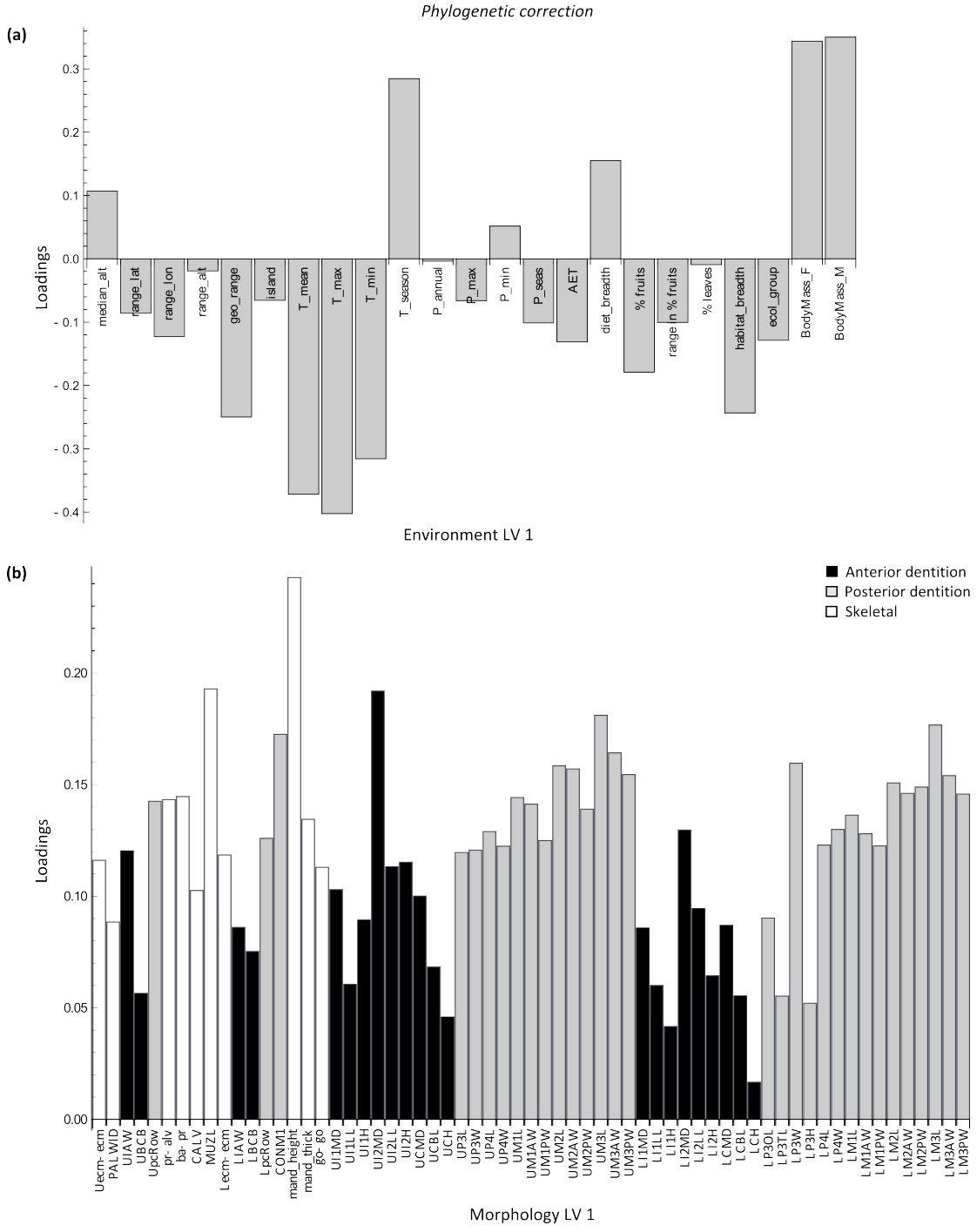


Fig. 6.4 Results of the phylogenetic two-block partial least squares (2B-PLS) analysis. Latent variable (LV) 1 describes the pattern of maximum covariance between environment and morphology after phylogenetic correction. a) Environment loadings, and b) morphology loadings onto LV 1. Variable definitions can be found in Tables B.13 and B.14 (morphology), and Tables B.1 to B.6 (environment) in Appendix B. Note the similarity in patterns with Figure 6.3.

however, the association between blocks along this dimension was greatly diminished once phylogeny is taken into account (see Figure F.1b).

Geography

The results of the reduced rank regression after phylogenetic correction are presented in Figures 6.7 and 6.8. The results without phylogenetic adjustment were highly similar and are therefore not presented this time. North African *M. sylvanus* was omitted due to its outlying geographical location. The spatial vectors representing LV 1 and LV 2 roughly correspond to south-to-north and west-to-east gradients, respectively. Prior to phylogenetic correction, LV 1 accounts for 75% of the association between spatial geography and morphology ($r = 0.91$) and LV 2 for the remaining 25% ($r = 0.41$) (see the scree plot in Figure F.3 in Appendix F). After phylogenetic correction, however, LV 1 accounts for nearly a 100% of the covariance ($r = 0.39$), whereas the association along LV 2 is now negligible ($r = 0.39$) (see Figure F.3). The effect of phylogeny is further exemplified by the drop in strength of the correlation coefficient along LV 1 (from 0.91 to 0.39).

Before as well as after phylogenetic adjustment, all craniodental measurements (with a few exceptions) are positively correlated with LV 1 (see Figure 6.8). Thus, macaque teeth and skulls tend to get larger along a south-to-north gradient. LV 2 is positively associated with measurements pertaining to the anterior teeth and muzzle, and negatively with posterior tooth measurements and calvarium length. LV 2 thus discriminates between a relatively larger posterior dentition in the west and a relatively larger anterior dentition in the east, although the effect size of this association is very weak when phylogeny is taken into account.

6.3.2 Within Species

Environment

2B-PLS returned no significant linear combinations between climate, altitude, and morphology for any of the three species (LV 1: *M. nemestrina*: $r = 0.27$, $p = 0.40$; *M. fascicularis*: $r = 0.40$, $p = 0.22$; and *M. mulatta*: $r = 0.35$, $p = 0.28$). Scatter plots of the PLS scores revealed no discernable relationship between environment and morphology (not shown).

Geography

Reduced rank regressions also did not find any significant associations between latitude, longitude and morphology for any of the three species (*M. nemestrina*: $r = 0.20$, $p = 0.76$; *M. fascicularis*: $r = 0.33$, $p = 0.11$; and *M. mulatta*: $r = 0.36$, $p = 0.14$). Furthermore, there

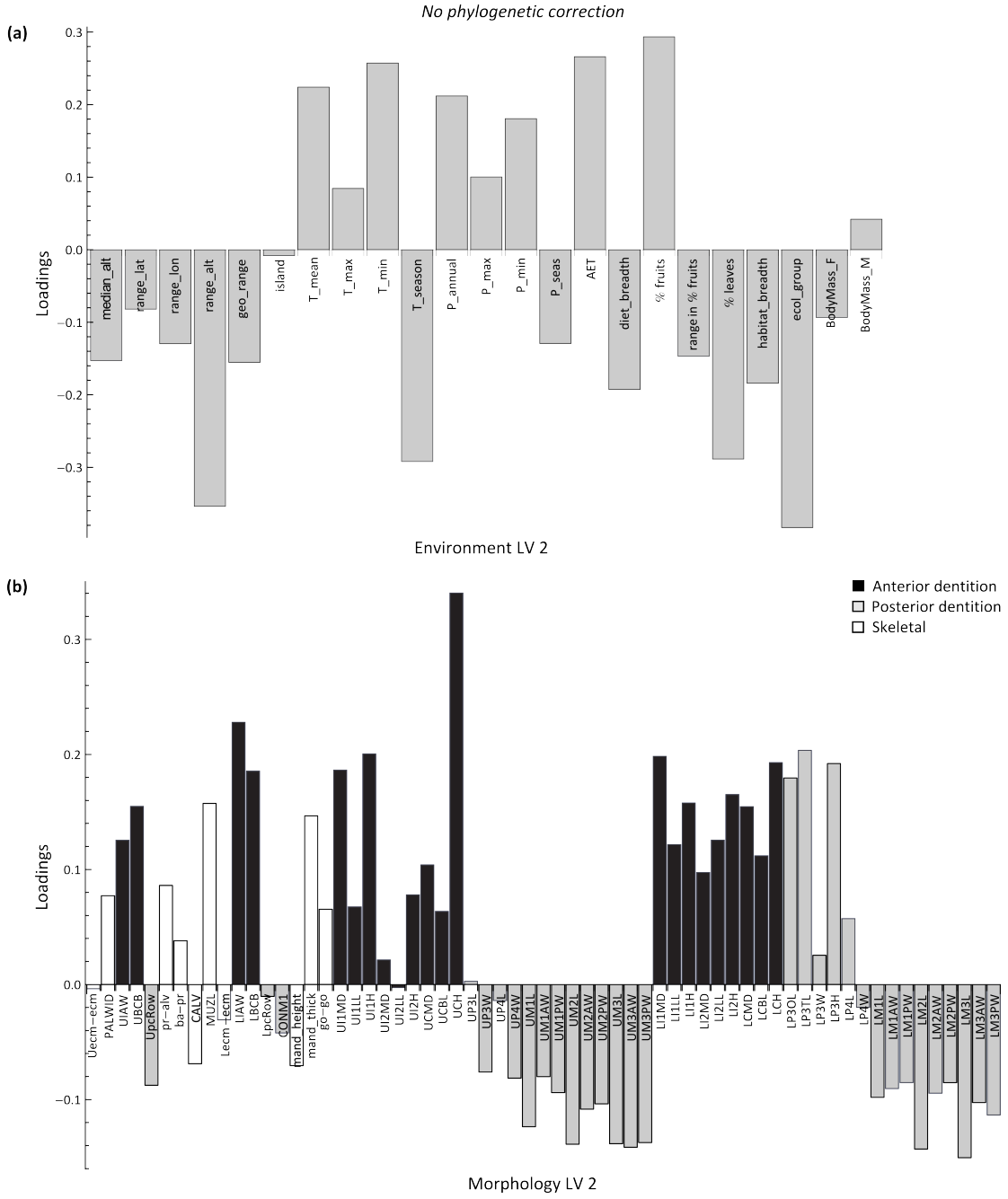


Fig. 6.5 Results of the two-block partial least squares (2B-PLS) analysis. Latent variable (LV) 2 describes the next largest covariance between environment and morphology prior to phylogenetic correction. a) Environment loadings, and b) morphology loadings onto LV 2. Variable definitions can be found in Tables B.13 and B.14 (morphology), and Tables B.1 to B.6 (environment) in Appendix B. This second, ecological factor represents the association of high rainfall and habitat productivity, low rainfall seasonality, a high percentage of fruits in the diet, low variation in the amount of fruits, and a low percentage of leaves in the diet with an antero-posterior dental contrast.

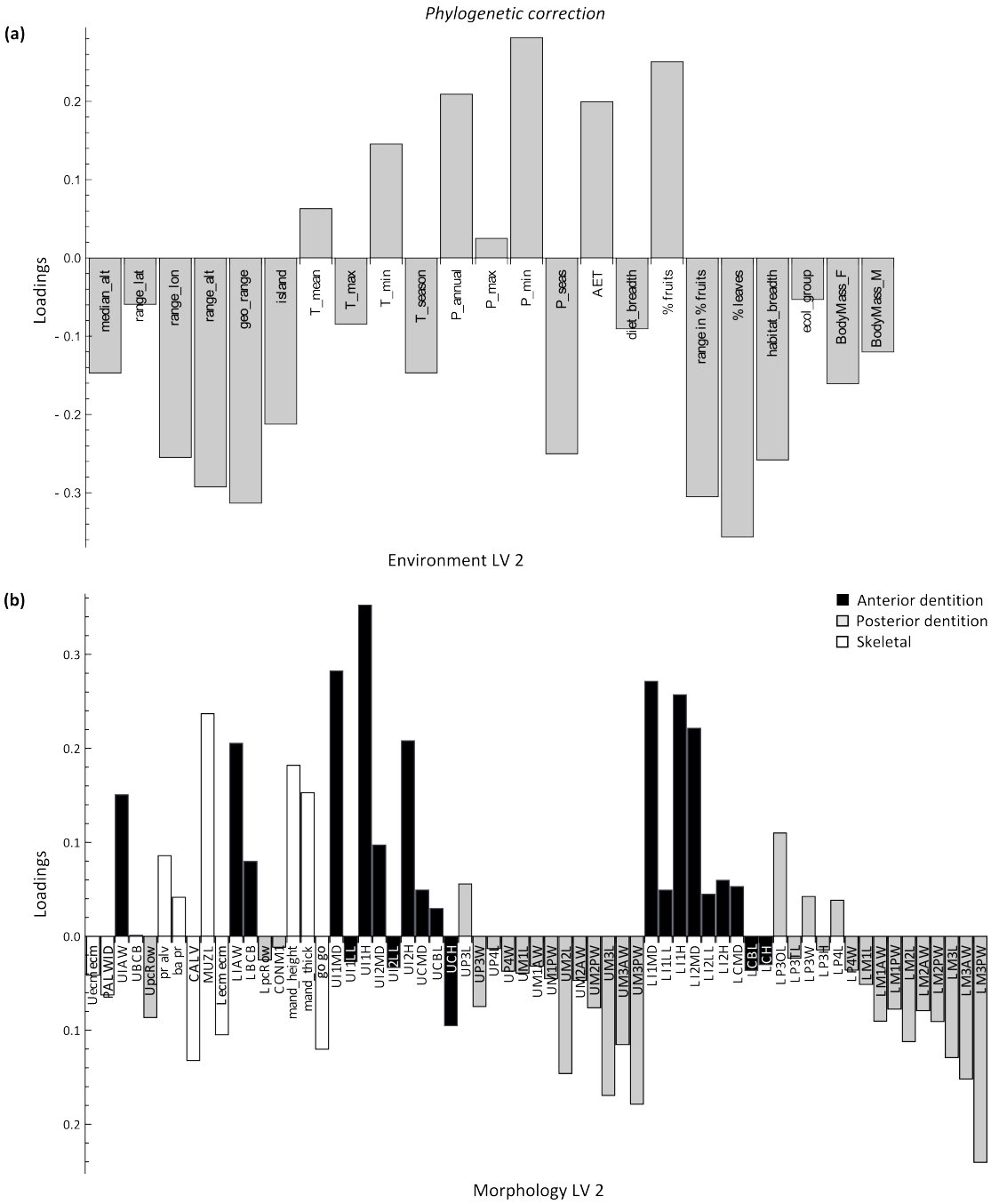


Fig. 6.6 Results of the phylogenetic two-block partial least squares (2B-PLS) analysis. Latent variable (LV) 2 describes the next maximum amount of covariance between environment and morphology after phylogenetic correction. a) Environment loadings, and b) morphology loadings onto LV 2. Variable definitions can be found in Tables B.13 and B.14 (morphology), and Tables B.1 to B.6 (environment) in Appendix B. Despite the similarity of the patterns to those in Figure 6.5, LV 2 is diminished in effect size after phylogenetic correction (see also the scree plot in Figure F.1 in Appendix F).

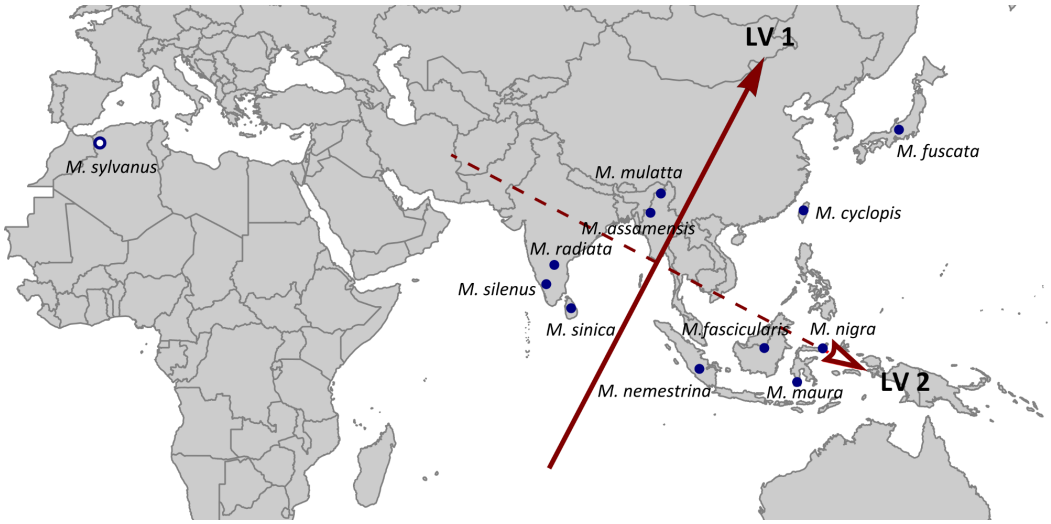


Fig. 6.7 Results of the reduced rank regression after phylogenetic correction. The orientation of the vectors prior to correction are highly similar and these results are therefore not displayed. *M. sylvanus* was omitted due to its outlying geographical position, and thus $N = 11$. Latent variable (LV) 1, the direction with the steepest morphological cline, corresponds to a south(west)-to-north(east) gradient, and LV 2 to a (north)west-to-(south)east gradient.

were no visible trends in the regression plots (not shown). Lastly, I found no correlations between geographical proximity and morphological (dis)similarity (*M. nemestrina*: $r = 0.07$, *M. fascicularis*: $r = 0.02$, and *M. mulatta*: $r = 0.01$). (Using the original, un-transformed phenotypic measurements yielded similar results.)

6.4 Discussion

Signals of geography, climate, and ecology were detected in the interspecific variation of macaque craniodental morphology, although these patterns are variably mediated by phylogeny. The between-species analyses demonstrated the presence of only two environmental and spatial gradients in the macaque craniodental phenotype, despite the diversity of variables in the ecogeographic and phenotypic datasets. The first factor is dominated by overall craniodental size and varies (weakly) along a latitudinal cline, with a tendency for macaques to be smaller near the equator (e.g., *M. sinica*, *M. fascicularis*, and *M. radiata*) and larger at higher latitudes (e.g., *M. assamensis* and *M. fuscata*). Concomitant with this latitudinal cline is the positive relationship of absolute craniodental size with body mass, colder temperatures, and increased temperature seasonality. Taken together, these results are in agreement with a classic Bergmann effect (Millien et al., 2006), and match the positive relationship that has been found between macaque body mass and latitude (Harcourt and Schreier, 2009; Ito et al.,

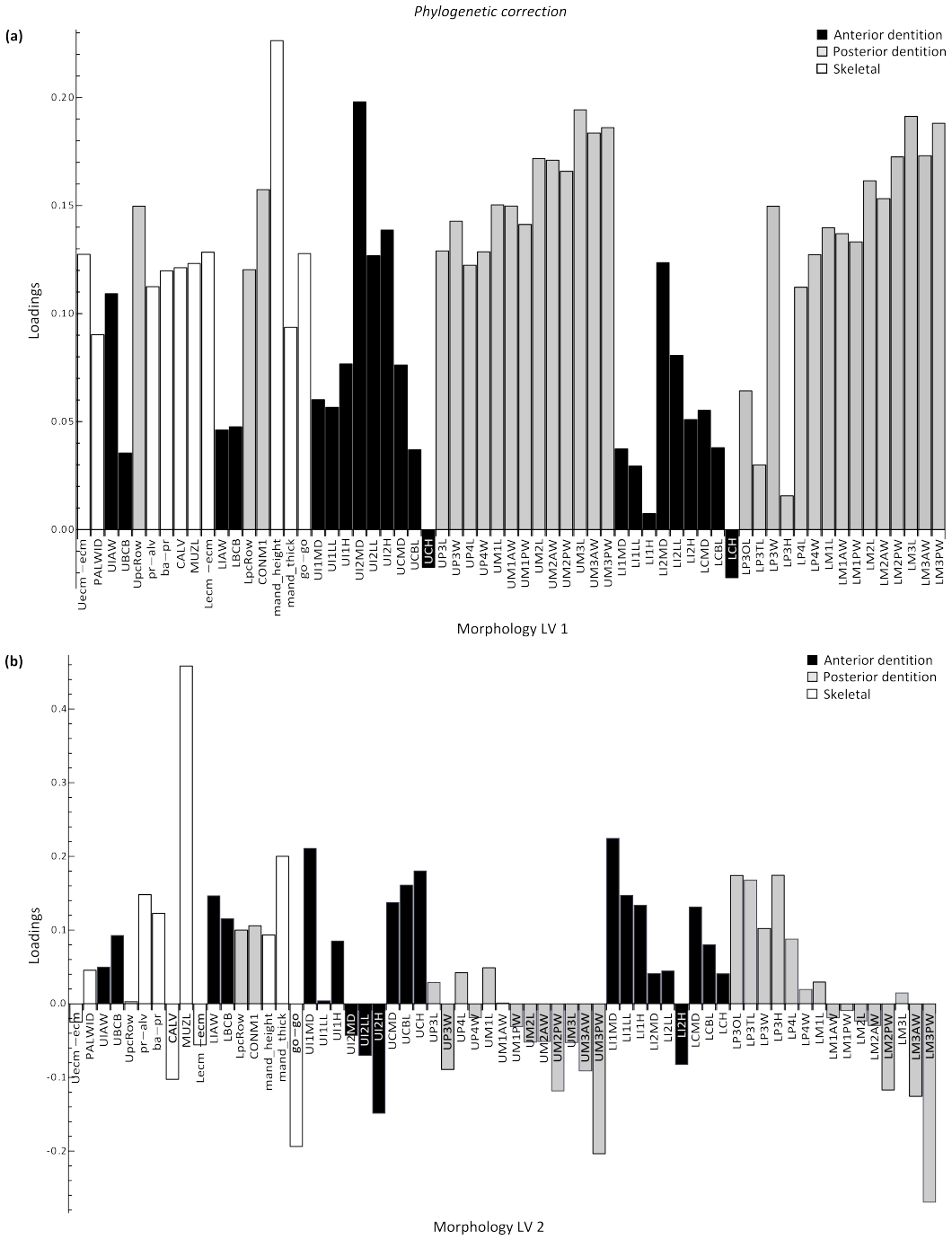


Fig. 6.8 Results from the reduced rank regression with phylogenetic correction. This figure shows the loadings of the morphological variables onto the spatial gradients, latent variable (LV) 1 (a) and LV 2 (b). Variable definitions can be found in Tables B.13 and B.14 (Appendix B). LV 2 is diminished in effect size after phylogenetic correction (see the scree plot in Figure F.3 in Appendix F), and therefore this pattern (b) warrants only limited interpretation. LV 1, on the other hand, describes the association between essentially latitude and overall craniodental size (all morphological loadings are positive, with the exception of canine height).

2014). The observed pattern along the first axis was minimally affected by phylogenetic correction: the PLS correlation was only slightly reduced from 0.81 to 0.67, the effect size along this dimension – the percentage explained of the total squared covariance between blocks – remained large (it changed from 63% to 94%), and the loading of temperature on LV 1 even increased. The pattern in macaque craniodental size thus can barely be explained by phylogenetic effects, suggesting that selection played an important role. Therefore, I interpret the variation in craniodental size – along with overall body size – as an adaptive response to variation in temperature along a latitudinal gradient, and argue that species differentiation in *Macaca* was associated with adaptive diversification in body size.

Some discrepancy exists between known ecogeographical gradients and the macaque findings. First, in many catarrhine primates, range size and habitat diversity increase with distance from the equator (Eeley and Foley, 1999; Harcourt, 2000). The opposite was found here along LV 1 in macaques, but which can be explained by the inflated geographical range sizes of tropical *M. fascicularis* and *M. nemestrina* due to the inclusion of ocean in their geographical range size that was derived from a published database (Jones et al., 2009). Northern *M. sylvanus* and *M. fuscata*, on the other hand, have comparatively small geographical ranges due to habitat contraction (Fooden, 2007) and insular isolation, respectively. Furthermore, although most broadleaf-evergreen-dwelling macaques occur around the equator, individual taxa that defy general trends have a relatively large statistical influence in the small sample (e.g., *M. nemestrina* occurs at a tropical latitude and has a preference for broadleaf-evergreen forests, but is also large in body size). Second, there was a small, negative effect of islands, with larger body size weakly associated with species occurring on islands. The island rule (also known as Foster's Rule; Foster, 1964) describes the tendency for large-bodied animals to evolve smaller body sizes on islands and for small-bodied animals to evolve larger body sizes (Foster, 1964; Lomolino et al., 2010). The effect of island occurrence observed among macaques was thus in the opposite direction from what is expected based on the pervasiveness of the island rule in vertebrates and mammals in general (Lomolino, 2005), and in primates in particular (Bromham and Cardillo, 2007; Welch, 2009). This can be explained by the small size of the macaque sample, as well as by the occurrence of the large-bodied Japanese macaque (*M. fuscata* in Japan and the relatively large pigtailed macaque (*M. nemestrina* from insular Southeast Asia.

The second factor discriminates between species with a relatively larger anterior dentition and a more prominent muzzle, and species with a relatively larger posterior dentition and longer skulls. (I point out that the dental contrast highlighted by LV 2 represents relative craniodental size, because differences due to overall size are captured primarily by LV 1.) The lower third premolar (P_3) is part of the CP_3 honing complex and indeed loaded in the same

direction as the canines rather than the posterior dentition. Regardless of whether phylogeny was accounted for or not, a larger anterior dentition is associated with tropical climates and increased habitat productivity, less variable habitats, small elevational, longitudinal and geographic ranges, and a high subsistence on fruits (e.g., in *M. nemestrina*, *M. silenus*, and the Sulawesi macaques). A larger posterior dentition, by contrast, is observed in taxa occupying more temperate regions. These include macaques that experience increased seasonality, occupy a larger variety of habitats and altitudes across larger geographic ranges, and which subsist on proportionally more leaves and highly variable amounts of fruit (e.g., *M. mulatta*, *M. sylvanus*, and *M. fuscata*). This environment-craniodental contrast coincides with a longitudinal gradient as long as phylogeny is not corrected for. In fact, in contrast to the first factor, the second pattern can be explained almost entirely in phylogenetic terms. The environment- and diet-related variance in craniodental morphology was greatly reduced following phylogenetic correction, resulting in a negligible effect size of LV 2. This is similar to the reduction in effect sizes of the relationships between climate, diet, and macaque craniofacial shape obtained by (Ito et al., 2014) after accounting for phylogeny. The pattern itself is similar to what has been found in capuchin monkeys, namely that relative tooth size (of primarily the postcanine dentition) is bigger in species living in relatively cooler, drier, and more seasonal climates (Cáceres et al., 2014). Cáceres and colleagues (2014) suggested that species with larger teeth for their body size are able to process a broader range of food items. However, the authors did not employ phylogenetic comparative methods and therefore it is unknown whether the relationship between tooth size and environment in capuchins mostly reflects the process of adaptation or 'merely' phylogenetic history.

Habitat productivity and rainfall patterns were not associated with variation in macaque body and craniodental size, in contrast to what has been found for baboons (Dunbar, 1990; Jolly, 2012), vervets (Cardini et al., 2007), and Malagasy sifakas (Lehman et al., 2005). This could mean that the relationship between rainfall and body size within vervet monkeys and baboons is due to environmental variation, or due to genetic variation in which case we may conclude that different environmental parameters were important in macaque evolution compared to their close cercopithecid relatives in Africa, as a result of different ecologies and environments occupied. For example, in the tropics and subtropics, patterns of rainfall are more variable than temperature (DeMenocal and Bloemendal, 1995). Also, many African monkeys may vary morphologically more with longitude than with latitude, because they have wider longitudinal distributions and are therefore subject to environmental variation mainly in that direction.

In addition to the species-level analyses, I also investigated the presence of environmental and spatial gradients as well as isolation by distance (IBD) patterns within species to be

able to infer what evolutionary processes are important in structuring intraspecific variation in macaques, and whether these processes can also explain the variation between species. Intraspecific phenotypic variation related to the environment or geography indicates phenotypic plasticity or, if gene flow is low, genetic differences due to local natural selection. An IBD pattern, by contrast, would result from strong genetic drift in the presence of reduced gene flow. IBD patterns can therefore reflect population history, an intraspecific equivalent to phylogenetic signal (Roseman and Auerbach, 2015). Intraspecific variation in body or skull length variation has previously been reported to correlate with latitude in *M. nemestrina* (Albrecht, 1980), *M. mulatta* (Fooden, 2000), and *M. fascicularis* (Schillaci et al., 2009). However, I found no relationships between craniodental variation, climate, and spatial geography within the three species, indicating low phenotypic plasticity in both absolute and relative craniodental size. These results also suggest that local environmental adaptation in the craniodental phenotype is either weak, perhaps due to relatively homogeneous environments, or that gene flow is strong, e.g., due to intensive migration. The absence of detectable plasticity supports the claim that the species differences along LV 1 are due to an evolved genetic basis.

Furthermore, no evidence for IBD was detected in craniodental size of *M. nemestrina*, *M. fascicularis*, or *M. mulatta*. The lack of an IBD pattern and spatial clines in these species is in contrast to the IBD found in recent modern humans (Betti et al., 2010) and the clinal variation observed in many African cercopithecid primates (Cardini et al., 2013; Dunn et al., 2013), respectively. This discrepancy with macaques may result from island effects in longtailed (*M. fascicularis*) and pigtailed macaques (*M. nemestrina*), such as the sea straits that act as barriers to gene flow between populations (Abegg and Thierry, 2002). The rhesus macaque (*M. mulatta*), on the other hand, unhindered by sea barriers and aided by their ability to move across a variety of habitats owing to their ecological flexibility, may exhibit strong male-mediated gene flow between populations in the sampled region (Figure 6.1c; Fooden, 2000; Morales and Melnick, 1998; Tosi et al., 2002, 2003).

Among the two ecogeographic gradients, the second (LV 2) is of particular interest. The depicted interspecific association between craniodental variation and diet is in agreement with early comparative work that has linked large incisors (relative to postcanine teeth) to frugivory, and smaller incisors to folivory (Hylander, 1975; Robinson, 1954). Likewise, there is a well-known and pervasive phenomenon among anthropoid primates that postcanine tooth size is often larger in folivores than in closely-related frugivores relative to body or facial size (e.g., Scott, 2011; Vinyard and Hanna, 2005). More recently, this diet-molar pattern has also been found in strepsirhines when adjusted for facial size (Scott, 2012). These two diet-related patterns of relative tooth size are often explained as an adaptive response to

masticatory challenges posed by the external properties of food items: large incisors are useful for the ingestion of large, husky, and fleshy fruits, whereas a large postcanine occlusal surface benefits the consumption of small and hard food items (e.g. nuts) or tough, fibrous foods (e.g. mature leaves; Lucas, 2004; Ungar, 2011). Even though this classic association was recovered between dental dimensions and diet in the present analysis, the interspecific differences along this pattern were strongly aligned with phylogenetic relatedness. When phylogeny is statistically accounted for, the pattern of association remains intact, but its magnitude diminishes: there is no longer conclusive support for an adaptive interpretation from the data.

While significant relationships between diet and dental size have been recovered after phylogenetic correction on higher taxonomic levels (e.g., Scott, 2011, 2012), the present results show that on lower taxonomic levels (like the genus level), phylogenetic relatedness alone may account for certain environment-phenotype associations. Neutral evolution by genetic drift can lead to phenotypic displacement in direct proportion to the amount of evolutionary time that has passed (the BM model of neutral evolution), which cautions against adaptive interpretations (Revell et al., 2008). This point is particularly relevant for palaeontological research where phylogenetic reconstruction is complicated due to the unresolved alpha taxonomy and the lack of genetic data, which in turn makes it difficult to assess the relative importance of adaptive and neutral evolutionary processes. The hominid fossil record is a notable example. In palaeoanthropology, the study of absolute and relative tooth size has been an important tool for the reconstruction of diets and adaptive zones of closely related species (Kay, 1985; Organ et al., 2011; Robinson, 1954; Wood and Collard, 1999, and reviewed in Ungar, 2011). My results offer a word of caution against overwhelmingly adaptive interpretations of craniodental morphometric variation when the phylogeny of the studied taxa is either not known or not explicitly take into account in the analysis.

Conclusion

The lack of ecogeographical signals within species and the phylogenetic effects between species show that the two macroevolutionary patterns present among macaque species are evolutionary in nature rather than non-genetic. The fact that the majority of the phenotypic dataset consists of measurements pertaining to the teeth, the plasticity of which is likely restricted to plastic responses of overall body size, supports this notion. Furthermore, the main ecogeographical pattern in macaques (a Bergmannian trend in overall body and craniodental size) differs from those found in other primate taxa, highlighting the fact that evolutionary changes in body size can evolve in response to a variety of environmental

factors, and what these are appears dependent on the geographical distribution of a taxonomic group. Moreover, historical contingency as a result of environmental vicariance seems to have played a significant role in interspecific variation between macaques. This may well apply to most comparisons of closely related taxa, i.e., groups at low taxonomic levels. Lastly, the analyses carried out in this chapter have demonstrated that it may be useful to inspect the (change in) effect size when controlling for phylogeny, rather than relying only on association patterns and correlations when interpreting results from comparative analyses.

Chapter 7

Phylogenetic Signal

7.1 Introduction

When studying macroevolutionary patterns in biology, various and numerous taxa are used that vary in their morphology, life history, behaviour, and/or ecology. Often, species' means (or means of higher-order taxa) are used as data points. At other times, individual specimen data are retained, but what species they belong to still matters. Regardless of the data format, genetic distances between species almost always vary within a taxonomic group, and some species are more closely related than others. Close relatives tend to resemble each other more due to shared ancestry, and this introduces phylogenetic effects in the data. This has important ramifications for the analysis and interpretation of patterns of phenotypic variation. Thus, it is important to take account of the non-independence between species in analyses of macroevolutionary patterns (e.g., environmental adaptation, or correlated character evolution). Furthermore, it can be useful to investigate which traits carry a (particularly) strong phylogenetic signal. The existence of phylogenetic signal can give insight into the underlying processes that have been important in morphological evolution.

Much of the work in this thesis relies on phenotype-environment and phenotype-phenotype correlations. With data derived from 13 species of macaques, which are hierarchically related, accounting for phylogeny is necessary for the purpose of statistical independence of observations. Earlier in this thesis, I have taken phylogeny into account by the phylogenetic comparative method of a phylogenetic regression, where necessary and relevant. But phylogenetic comparative methods are not only useful for the purpose of statistical independence; the identification of independent evolutionary events also helps reconstruct ancestral phenotypes and understand the pattern of phenotypic change (e.g., Harvey and Pagel, 1991; Losos, 2011b). Studying the correlation between the phylogenetic structuring of species and the pattern of species' phenotypic diversity is informative about the degree to

which shared descent influences phenotypic similarity. Here, I test for phylogenetic signal (defined below, in section 7.1.1) in all individual linear tooth measurements to locate which teeth or part(s) of the dentition show similarity between species as a function of genetic relatedness.

7.1.1 Phylogenetic Effects in Macroevolution

Comparative biology is the approach by which data from various different species is utilised to investigate the relationships between environments and phenotypes or to test hypotheses about correlated evolution between morphological characters. The ubiquity of phylogenetic effects in biological data complicates this method, however. Species used in comparative analyses rarely, if ever, constitute a so-called star phylogeny. In such a tree, there is no hierarchical structuring of species; they all share the same last common ancestor, and are therefore equally closely related to each other (Felsenstein, 1985). Moreover, the variances between all species pairs in a star phylogeny are temporally identically scaled (i.e., have the same branch lengths). In reality, however, species relationships are characterised by a hierarchical branching pattern (e.g., Felsenstein, 1985; Garland Jr. and Carter, 1994). For example, different species of pigs (the group Suidae) are more closely related to each other than they are to bovids (the group Bovidae; a diverse group including cattle, antelopes, and others) even though both groups are artiodactyls (even-toed ungulates). Humans and apes constitute a monophyletic group (the Hominoidea), but within this group, humans and great apes are the sister taxon to the gibbons. In turn, the genus *Homo* is more closely related to the genus *Pan* than either is to the other genera of *Gorilla* and *Pongo*. An important consequence of this hierarchical structuring is that species are not statistically independent, thus violating assumptions of many statistical techniques (Felsenstein, 1985; Harvey and Pagel, 1991; Martins and Hansen, 1997). It also means that obtained phenotype-phenotype (e.g., brain size and body size; Martin, 1981) and phenotype-environment (e.g., body size and population density; Damuth, 1981) correlations may be in whole or in part due to a confounding variable, namely common descent (Felsenstein, 1985; Harvey and Pagel, 1991). The implementation of phylogenetic comparative methods that take appropriate account of the phylogenetic relationships among data points (i.e. species or other operational taxonomic units, OTUs) have therefore become common practice.

What is phylogenetic signal?

'Phylogenetic signal' is defined as the tendency for closely related species to resemble each other behaviourally, morphologically, and/or ecologically (Blomberg and Garland, 2002).

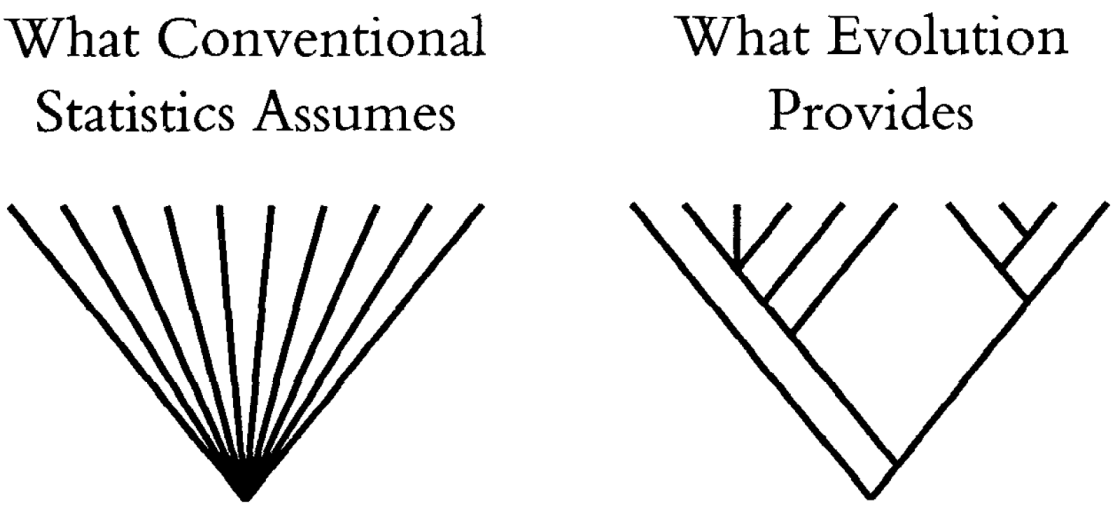


Fig. 7.1 Left: a star phylogeny in which species are statistically independent. Right: a hierarchical phylogeny, in which species are phylogenetically structured and thus statistically non-independent. Figure adapted from Garland, Jr. and Carter, 1994 (their figure 2).

The tendency for morphological/ecological similarity among phylogenetically close taxa has previously also been termed 'phylogenetic inertia' or 'phylogenetic constraint' (Blomberg and Garland, 2002; Blomberg et al., 2003). However, these concepts have been variously defined and operationalised by different workers, and refer to a process rather than a pattern that can be reliably measured (Blomberg and Garland, 2002; Kamilar and Cooper, 2013; Losos, 2008). Moreover, these concepts imply that some constraint on evolutionary change is at work, when in fact no assertions about underlying mechanisms (e.g., lack of genetic variation or developmental constraints, among others) can be confidently made based on statistical patterns in the data (Blomberg and Garland, 2002; Revell et al., 2008). The term 'phylogenetic signal' is thus defined as the *pattern* of statistical non-independence that exists when closely related taxa are more similar to each other than they are to taxa randomly drawn from the tree (Blomberg and Garland, 2002). Importantly, it does not make any reference to underlying processes (Blomberg et al., 2003). At present, this term is preferred by most workers to indicate a phylogenetic pattern comparative in data (e.g. Blomberg and Garland, 2002; Kamilar and Cooper, 2013; Losos, 2008; Revell et al., 2008). Phylogenetic signal is high when phenotypic similarity increases with phylogenetic relatedness: i.e., phenotypic *dis*similarity between species increases in a Brownian motion-like manner in proportion to the time since divergence (in a predominantly gradual and random manner) (Blomberg et al., 2003; Kamilar and Cooper, 2013; Losos, 2008). In contrast, traits possess low phylogenetic signal if distantly related species are phenotypically more similar (e.g., as

a result of convergent evolution) or when phenotypic resemblance is randomly distributed across a phylogeny (Blomberg et al., 2003; Kamilar and Cooper, 2013).

How is phylogenetic signal measured?

Although strong phylogenetic effects are common, there are some evolutionary processes that yield low phylogenetic signal (Hansen and Martins, 1996). Thus, it is worth to investigate and quantify the presence of phylogenetic signal before making *a priori* assumptions about the strength of phylogenetic signal present in the data (Blomberg et al., 2003) and applying a phylogenetic correction or transformation to the data (Blomberg et al., 2003; Revell et al., 2008).

Over the years various methods have been used or developed to detect and/or correct for phylogenetic signal, some of the most common of which include the Mantel test (Mantel, 1967; Mantel and Valand, 1970), phylogenetic independent contrasts (PICs; citealpFelsenstein1985), phylogenetic generalised least squares (PGLS; Grafen, 1989; Martins and Hansen, 1997), Moran's I (Moran, 1950), Abouheif's C_{mean} (Abouheif, 1999), Pagel's λ (Pagel, 1999), and Blomberg's K (Blomberg et al., 2003). A detailed review of these methods goes beyond the scope of this chapter (but for reviews see Hardy and Pavoine, 2012; Legendre and Fortin, 2010; Münkemüller et al., 2012; Pagel, 1999). However, many of these methods are permutation-based: a number of permutations (e.g., 1000) of randomly-drawn combinations from the original data are run to yield a simulated trait null distribution, against which the pattern in the original data is then compared and from which a test-statistic value and an associated p-value are derived. Some techniques (Moran's I) employ autocorrelation, whereas others assume an explicit model of trait evolution. The best-studied and most common model is that of Brownian motion (Revell et al., 2008). This model is relevant to the method that will be used here, and it is explained in some further detail below. The method used here for testing phylogenetic signal is Blomberg's K (Blomberg et al., 2003). This method will be discussed in more detail in Section 7.2.

A Brownian motion (BM) model of evolution assumes the magnitude and direction of character change to be random and independent of the character state (for example its size) (Kamilar and Cooper, 2013). It accommodates mechanisms of drift and random fluctuations in natural selection, such that characters undergo gradual and cumulative change proportional to time, in no particular direction (Revell et al., 2008). It is therefore a constant-variance model, with trait variance being directly proportional to branch length (Cavalli-Sforza and Edwards, 1967; Freckleton et al., 2002). Phylogenetic signal, then, is measured by the similarity of the data to the expectation of evolution by Brownian motion, because under BM the phenotypic covariance between species' trait values (i.e., their similarity) is proportional

to the sum of their shared branch lengths (i.e., their shared ancestry) (Blomberg et al., 2003; Revell et al., 2008).

The interpretation of phylogenetic signal: underlying causes

Phylogenetic signal is often used to make inferences about the underlying evolutionary process. This is not without problems, because different processes can give rise to the same phylogenetic pattern (e.g., Kamilar and Cooper, 2013; Revell et al., 2008). Low phylogenetic signal, for example, can arise as a result of several processes. One example is convergence (Losos, 2011a), which is a major focus in comparative biology. Convergence exists when distantly related taxa are phenotypically similar. The most common interpretation of convergence is that their similarity represent adaptations to similar environments, although explanations other than adaptation have also been proposed (e.g., evolutionary constraint in how phenotypic variation is produced at the genetic level; Losos, 2008, 2011a; Schluter, 2000. The discordance between phenotypic and phylogenetic similarity consequently yields a low phylogenetic signal (Blomberg et al., 2003; Kamilar and Cooper, 2013). Ecological character displacement is also associated with weak phylogenetic signal. Character displacement is the process by which closely related species diverge in phenotype and resource use so as to avoid ecological competition, for example in adaptive radiations (Brown and Wilson, 1956; Schluter and McPhail, 1992). Closely related species are then phenotypically more dissimilar than is expected on the basis of their phylogeny (Losos, 2000). In addition to the above examples of convergent and divergent selection, respectively, stabilising selection can also obscure phylogenetic signal by constraining the evolution of phenotypic variation in all branches of the tree (stasis) (Hansen, 1997; Hansen and Martins, 1996). Stasis can also be the result of other constraints (Hansen and Houle, 2004; Maynard Smith et al., 1985). Limited macroevolutionary variation in a trait can be the result of developmental limitations on the production or direction of variation (Blomberg and Garland, 2002; Losos, 2011a). Apart from the aforementioned systematic causes, the degree of phenotypic similarities between species can be randomly distributed along the phylogeny, corresponding to a scenario in which Blomberg's K approaches 0. Finally, if the assumptions of BM do not apply because evolutionary rates are faster and/or variable, then phylogenetic signal in a trait as compared to constant-rate BM evolution will also be low (Blomberg et al., 2003).

Strong or high phylogenetic signal, where Blomberg's K is higher than 1, can also have one of several underlying causes. An important example of evolutionary conservatism or phylogenetic niche conservatism (PNC) (Losos, 2008; Wiens et al., 2010). Phylogenetic niche conservatism refers to the process by which species diversify through time at a faster than expected rate and retain their niche and associated phenotypic traits (Wiens et al., 2010).

Closely related species are therefore *more* phenotypically similar than is expected on the basis of their phylogeny and Brownian-motion like evolution (Losos, 2008). This corresponds to a Blomberg's $K > 1$. A phylogenetic signal of $K > 1$ can also be obtained when the rate of genetic drift was in fact slower than assumed in the statistical model (Revell et al., 2008).

7.1.2 Questions and Hypotheses

First, I investigate whether any of the variation in tooth size between macaques carries a phylogenetic signal. Second, I inspect differences in phylogenetic signal between teeth and tooth dimensions. Variation in phylogenetic signal across the dental arcade would indicate that different genetic or developmental constraints vis-à-vis different evolutionary processes have shaped the various parts of the dentition in *Macaca*.

I also test for phylogenetic signal in dimensions of relative tooth size to appreciate whether the signal is concentrated in, or attenuated by differences in body size. To highlight the relevance of this exercise, consider cranial form as a hypothetical example. *Form* includes the aspects of size *and* shape (Mitteroecker et al., 2013). Cranial form in a certain primate group may carry a weak phylogenetic signal because it reflects, in part, differences in body size (often captured by the first principal component), which may have evolved by natural selection and therefore carry a weak phylogenetic signal. However, independent of overall size, cranial *shape* (captured in subsequent principal components, which are orthogonal to and independent of PC 1) may evolve in other directions, subject to different processes. Theoretically, it is therefore possible that size-free shape carries a stronger phylogenetic signal, for example due to genetic drift. The strength of the phylogenetic signal in cranial form would have previously been obscured due to the effect of size. In the present work, dental variation contains differences in absolute and relative tooth size. Similar to shape, relative size may carry stronger or weaker phylogenetic signals than does absolute size.

Evidence from quantitative genetics of baboon and mice dental variation suggests that the incisors are a genetically independent module from the postcanine dentition, and that within the latter premolars and molars are submodules (arising from incomplete pleiotropy) (Hlusko and Mahaney, 2009; Hlusko et al., 2011; addressed earlier in Chapter 4). Studies of tooth shape and morphological integration in baboons (Hlusko et al., 2011), other OWM genera (including *Macaca*; Grieco et al., 2013), and hominids (postcanine teeth only; Gomez-Robles and Polly, 2012) show that this pattern of genetic modularity also exists on the phenotypic level. The patterns of covariation reported in Chapter 4 support the notion that different tooth classes (i.e., incisors, canine/premolar complex, the non-P_3 premolars, and molars) likewise form at least partially independent morphological units in the macaque dentition – a pattern that likely characterises primates, or even mammals, in general. Therefore, the expectation

is that if there are differences in phylogenetic signal between teeth, that these most likely exist between the anterior (incisors, possibly including the canines) and postcanine dentition (premolars and molars). For if they are genetically independent, then they should (in theory) have been able to undergo independent evolution.

7.2 Materials and Methods

Dental mesiodistal lengths and labiolingual/buccolingual widths are the focus of analysis in this chapter. Phylogenetic signal is first tested in all craniodental data (except tooth heights; $k = 56$ variables) across all 13 species of macaque. Next, dental variables and calvarium length ($k = 40$) are tested for phylogenetic signal in the two main Asian subclades (illustrated in Figure 7.2). These are the *silenus* lineage ($N = 5$) and the *sinica-fascicularis* lineage ($N = 7$). *M. sylvanus* is the sister taxon to all Asian macaques and will be omitted at the latter level of analysis. Testing phylogenetic signal in the data at different phylogenetic levels has two purposes. First, phylogenetic signal in the dental phenotype may be strong in one subclade and absent in the other. Such a pattern would be masked when all 13 macaque species are considered together. Second, splitting the analysis by the main split among Asian macaques could give insight into whether different evolutionary processes have been influential in these two lineages. The interpretation of differences in phylogenetic signal with respect to processes follows below.

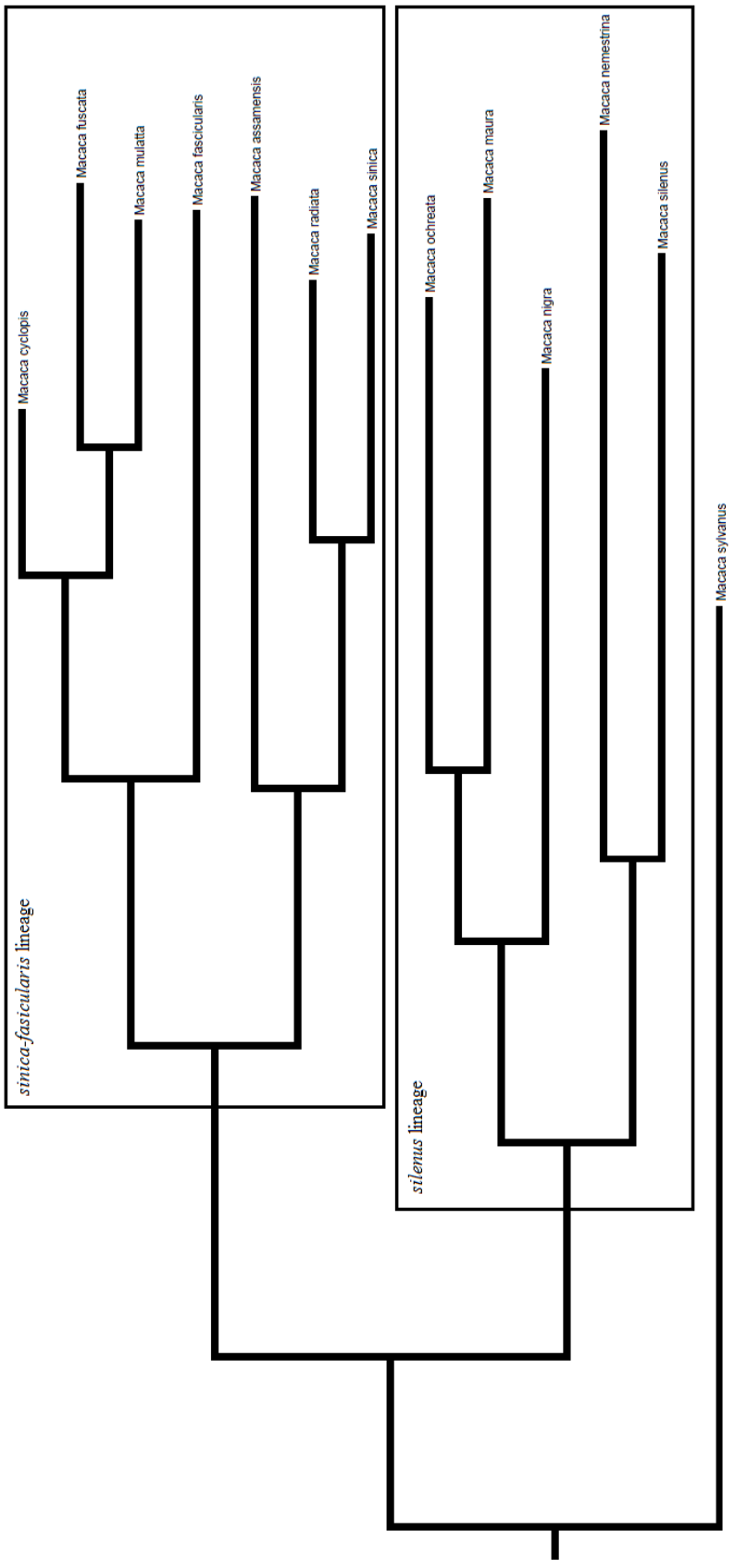


Fig. 7.2 Macaque phylogram comprising the 13 species represented in the sample. Rectangular boxes show the main split between the Asian lineages.

7.2.1 Blomberg's *K*

There are a number of indices that not only detect phylogenetic signal but also quantify its magnitude. They are standardised and thus allow for comparison between phylogenies and traits. Blomberg's *K* and Pagel's λ (Pagel, 1999) are two of the most commonly used metrics of phylogenetic signal in continuous traits (Kamilar and Cooper, 2013). Both have strengths and weaknesses depending on the nature of the data (e.g., Hardy and Pavoine, 2012; Harmon and Glor, 2010; Münkemüller et al., 2012), one of the main advantages of Blomberg's *K* is that the *K*-statistic not only has the potential to vary between the absence of signal and concordance with BM (explained in further detail below), but it can also assume values of phylogenetic signal that go beyond what is expected on the basis of BM, pointing to different processes still (Blomberg et al., 2003; Münkemüller et al., 2012). Furthermore, the number of tips (i.e., species) in the macaque phylogeny for the present sample is only 13, and is thus comparatively rather small. Blomberg's *K* is shown to have good power at a sample size of 20 or more (Blomberg et al., 2003; Kamilar and Cooper, 2013), whereas Pagel's λ performs well with a sample size of 30 and beyond (Freckleton et al., 2002; Kamilar and Cooper, 2013). Athough still not ideal, Blomberg's *K* is the preferred method because it is expected to have the best power out of these two methods.

Blomberg's *K* measures the strength of phylogenetic signal in a trait in the form of a ratio of two mean squared errors (MSE) (Blomberg et al., 2003). The mean squared error is a statistical measure of the average variability in the data (Field, 2009).

$$K = MSE_0/MSE \tag{7.1}$$

where the numerator is the mean squared error in the data relative to the 'phylogenetic mean' (the estimated ancestral value at the root node; Revell et al., 2008), and the denominator is the mean squared error derived in a generalised least squares (GLS) model that corrects for the phylogenetic variance-covariance matrix based on the candidate tree under the assumption of BM (Blomberg et al., 2003; Münkemüller et al., 2012). Thus, the trait variance that can be explained by the phylogenetic tree is factored out in *MSE*. Therefore, if phylogeny effectively predicts the observed data, then MSE will be small, and MSE_0, and *K* with it, will be relatively large. If phylogeny does not predict the observed data well, then MSE will be relatively large, and *K* relatively small (Blomberg et al., 2003; Kamilar and Cooper, 2013). *K* can vary continuously from 0, no phylogenetic signal, to 1 (phylogenetic signal consistent with BM), and beyond 1 to infinity. Values higher than 1 mean that closely related species are even more similar than may be expected under BM (Blomberg et al., 2003; Losos, 2008). Values below 1 indicate weak or no phylogenetic signal, and are consistent with a random

pattern or convergent evolution (e.g., environmental adaptation). No distinction can be made between randomness and convergence based on the K-statistic, however (Kembel et al., 2010). To make the K-statistic comparable across phylogenies and/or traits, its value is further standardised by the MSE ratio that would be expected given BM, and so

$$K = (MSE_0/MSE)_{observed}/(MSE_0/MSE)_{expected} \tag{7.2}$$

To generate a p-value assessing the statistical significance of K, the trait data are randomly permuted across the tips of the candidate phylogeny to obtain a null distribution against which the observed data can be compared (Blomberg et al., 2003). The null expectation as part of this procedure is thus that $K = 0$ (no signal), and can only be refuted when K reaches statistical significance (e.g., $p < 0.05$). The entire procedure is implemented in the package 'picante' (Kembel et al., 2010), function 'multiphylosignal', available for use in RStudio. Phylogenetic signal is tested in each individual variable, and the mean phylogenetic signal in dental modules separately: incisors, canine/premolar complex, and the postcanine dentition. The function 'multiphylosignal' computes K for individual traits or for sets of multiple traits.

Body size-adjustment

Relative tooth size may show different phylogenetic signal strength from absolute tooth size. Therefore, phylogenetic signal is also tested in the same measurements after they have been adjusted for overall body size (using calvarium length). There are several ways to adjust for tooth size, mainly related to whether one carries out an adjustment of isometric size (by obtaining a ratio; (Jungers et al., 1995)), or whether one partitions out all the size-related variance (Vinyard, 2008). In the present analysis, the residuals from a regression of tooth size on the body size proxy are used as the size-adjusted variables ($N = 39$). They are computed from log-transformed tooth size variables regressed onto the log-transformed body size proxy (calvarium length), and subsequently transformed back to raw data space. Whereas the raw tooth measurements include a large proportion of variation that is due to overall size, the residuals are size-free.

It is therefore also expected to mediate the relationship between dental variation and ecogeographical variation, for instance in the case of environmental gradients of morphology, through the effect of body size (e.g., Cope's rule postulating evolution towards larger body size over time, Stanley, 1973; the Bergmann effect of increasing size with latitude, Blackburn et al., 1999; the inverse relationship between population density and body size, Damuth, 1981; Foster's rule, also known as the island effect where species evolve to be smaller on islands, Foster, 1964). Body size will thus be adjusted for in those analyses in order to

investigate the relationship that exists between environmental variables and dental variation independently of body size. It is therefore necessary to know if there is phylogenetic signal in tooth size after removal of body size effects.

7.2.2 Multiple Comparisons

To compare the strength of phylogenetic signal in the different measurements, only the values of Blomberg's K are considered at first, without taking account of p-values, because the pattern is in the K-statistic, not the statistical significance. In order to subsequently determine whether the K-value for a particular measurement is significantly higher than 0 (the null hypothesis) a permutation is run to obtain a p-value. P-values are obtained for each Blomberg's K-statistic. Generating a p-value for a large bout of statistical tests creates the familiar problem of multiple comparisons.

When performing the same statistical test for multiple groups or variables at once, the family-wise error rate (Type I error) gets inflated. A Type I error is when one falsely rejects the null hypothesis when in fact the p-value suggesting statistical significance (commonly below 0.05) was obtained by chance (Field, 2009). The chances of such a false positive occurring increases the more comparisons are made, the higher the inflation (because the risk exists per individual test) (Gelman et al., 2012). Blomberg's K is tested for $\geq$39 variables, so the chances that the null hypothesis is falsely rejected in favour of accepting phylogenetic signal for at least one of the variables (and without knowing which one), are greatly increased. This constitutes a serious problem for the interpretation of the results.

One common way to keep the Type I error rate down, is to perform a Bonferroni correction. This correction adjusts the significance threshold to a new critical level: α/k, where α is the critical value and k is the number of comparisons (or tests). However, the problem with this approach is that it is often inappropriately conservative, for the strong control of the Type I error rate (false positives) comes at the expense of the Type II error rate (false negatives). That is, the power to detect a real effect (Field, 2009). For the Bonferroni correction the chances of failing to reject the null hypothesis when there is an effect are unreasonably high with a large number of comparisons (Gelman et al., 2012).

An alternative approach is called the 'false discovery rate' (FDR) adjustment, also known as the Benjamini-Hochberg (BH) method (Benjamini and Hochberg, 1995). It is particularly suitable for situations in which a large number of tests are conducted, only a few of which are expected to return significant results representing true effects (Gelman et al., 2012). It controls the proportion of false discoveries among the rejected hypotheses (incorrect rejections of the null hypothesis) at the usual α-level, rather than adjusting the critical value against which all results are measured (Benjamini and Hochberg, 1995). The FDR approach

thus maintains better statistical power to detect real effects. The method works as follows. First, all statistical tests are carried out to generate raw *p*-values. Next, the *p*-values are ranked from smallest to largest with the smallest *p*-value having a rank, *i*, of 1, the next smallest has $i = 2$, and so forth. A new, 'BH'-critical value is then computed for each *p*-value, defined by (i/m)Q, where *i* is the rank of the raw *p*-value, *m* is the number of comparisons, and Q is the false discovery rate (e.g., the usual 5%). If the raw *p*-value is smaller than its 'BH'-critical value, the result is considered statistically significant.

Here, I use the FDR method to adjust for the multiple comparisons, which is implemented in the default 'stats' package in RStudio, using function 'p.adjust' and method 'fdr'. This function returns adjusted *p*-values that can be interpreted in relation to a standard α-level of 0.05 (or any other value one chooses). The adjusted *p*-value is the raw *p*-value multiplied by m/i, or the adjusted *p*-value for the next higher raw *p*-value, whichever is smaller (Benjamini and Hochberg, 1995). The latter procedure means that some adjusted *p*-values may be identical.

Finally, which tests constitute one 'family' of multiple comparisons, and therefore how many tests the *p*-values need adjusting for, is usually left to the judgement of the researcher. Here, I consider all variables to be one such family in each group of species. Thus, all dental variables plus calvarium length (as a proxy for body size) constitute a single series of multiple comparisons ($k = 40$) when testing for phylogenetic signal across all macaques. The same test in the *silenus* and *sinica-fascicularis* lineages are two more 'families' of tests. Therefore, I adjust for multiple comparisons of $k = 40$ at a time. There is debate surrounding the need for adjustment against multiple comparisons, and also decisions regarding specific corrections are highly subjective (Gelman et al., 2012). Therefore, both the raw and the adjusted *p*-values are reported for the tests carried out in this chapter.

7.3 Results

7.3.1 The Pattern of Phylogenetic Signal

Variation in the pattern of phylogenetic signal exists between different parts of the skull and the dental arcade (Table 7.1). This variation is mainly driven by the CP_3 complex and the postcanine teeth, as they have the strongest and lowest phylogenetic signal, respectively (Table 7.1 and Figure 7.3). Although the anterior dentition carries overall stronger phylogenetic signal than the postcanine dentition, there is also variation in signal strength within each morphological unit (incisors, CP_3 complex, postcanine teeth, and skeletal measurements of the skull). For example, the upper lateral incisor (UI2) has among the lowest Blomberg's

Table 7.1 Phylogenetic signal, measured by Blomberg's K for the different parts of the skull and the dentition.

	Blomberg's K	p-value
Incisors	0.86	0.14
Canine/premolar (CP_3) complex	1.10	0.02
Postcanine teeth	0.69	0.32
Cranium	0.80	0.13
Mandible	0.83	0.18

The incisal 'module' comprises all the lengths and widths of the four incisors, plus the widths of the incisor rows (UIAW and LIAW). The CP_3 complex includes lengths and widths of the canines and the lower third premolar (P_3) and upper and lower bi-canine breadth (UBCB and LBCB). The postcanine dentition comprises lengths and widths of all the molars, fourth premolars, the upper third premolar, as well as the total length of the upper postcanine row (UpcRow). The cranium and mandible include the skeletal measurements taken on the cranium and mandible, respectively. For an overview and key to non-dental variables see Table B.13 in Appendix B.

K-values despite strong signal in the central incisors (UI1 and LI1; Figure 7.3. Moreover, several of the incisal and CP_3 measurements have K-values higher than 1.0. All molar dimensions have comparatively low K-values.

Figures 7.4 and 7.5 show the patterns of phylogenetic signal in the two Asian subclades separately. The two lineages show different patterns in strength as well as which part of the dentition carries the strongest phylogenetic signal. Members of the *silenus* lineage (*M. silenus*, *M. nemestrina*, and the Sulawesi macaques, *M. nigra*, *M. maura*, and *M. ochreata*) show strong phylogenetic signal across their entire dentition. The average Blomberg's K for all measurements is 1.039. The incisors, especially incisal mesiodistal lengths, carry the strongest signal and K even substantially exceeds the signal strength expected under Brownian motion (the dashed line in Figure 7.4). Furthermore, the premolars and second and third molar posterior widths stand out with high K-values. The CP_3 complex, and especially the upper canine (UC), have comparatively low signal among the *silenus* members.

Conversely, the dentition exhibits an overall phylogenetic signal that is much weaker in the *sinica-fascicularis* lineage (Figure 7.5). Blomberg's K has an average of 0.751 in this group. The strongest signal is found in the CP_3 complex, specifically the buccolingual width of the lower canine and the total length of P_3, which includes the honing facet. The weakest phylogenetic signal is found in the incisors (with the exception of the labiolingual width of the lower second incisor, LI2LL). The molars have intermediate values.

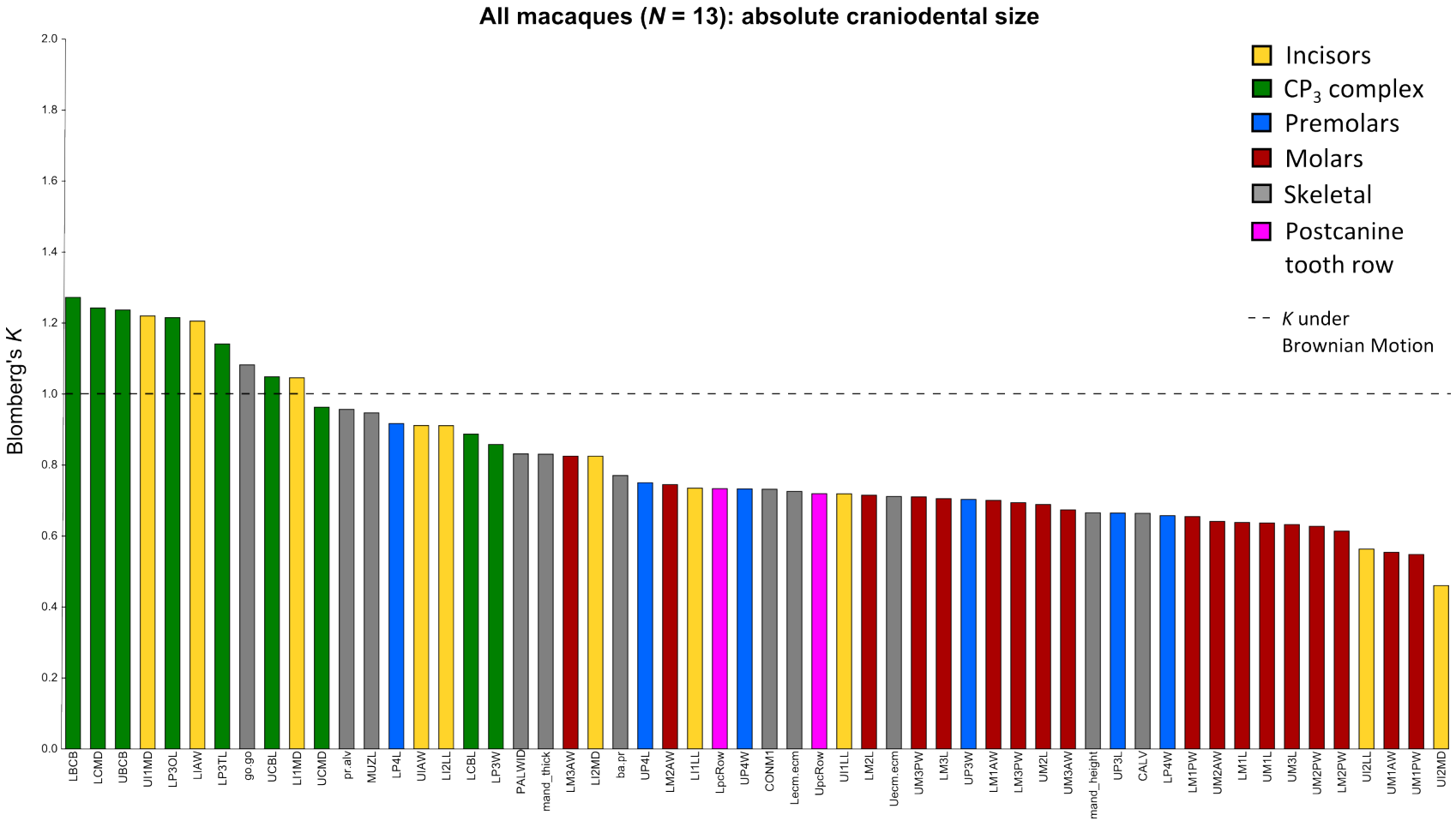


Fig. 7.3 Blomberg's *K* for 56 cranial, mandibular, and dental variables. Key to variable names can be found in Table B.13 and Table B.14 in Appendix B. The dashed reference line indicates the expected value (1.0) of *K* under Brownian motion (BM). The anterior dentition comprising the incisors and canine/premolar (CP_3) complex (yellow and green, respectively), stands out with relatively strong phylogenetic signal. The postcanine dentition (red and blue) carries comparatively weaker phylogenetic signal. Skeletal measurements taken on the cranium and mandible show a mixed pattern.

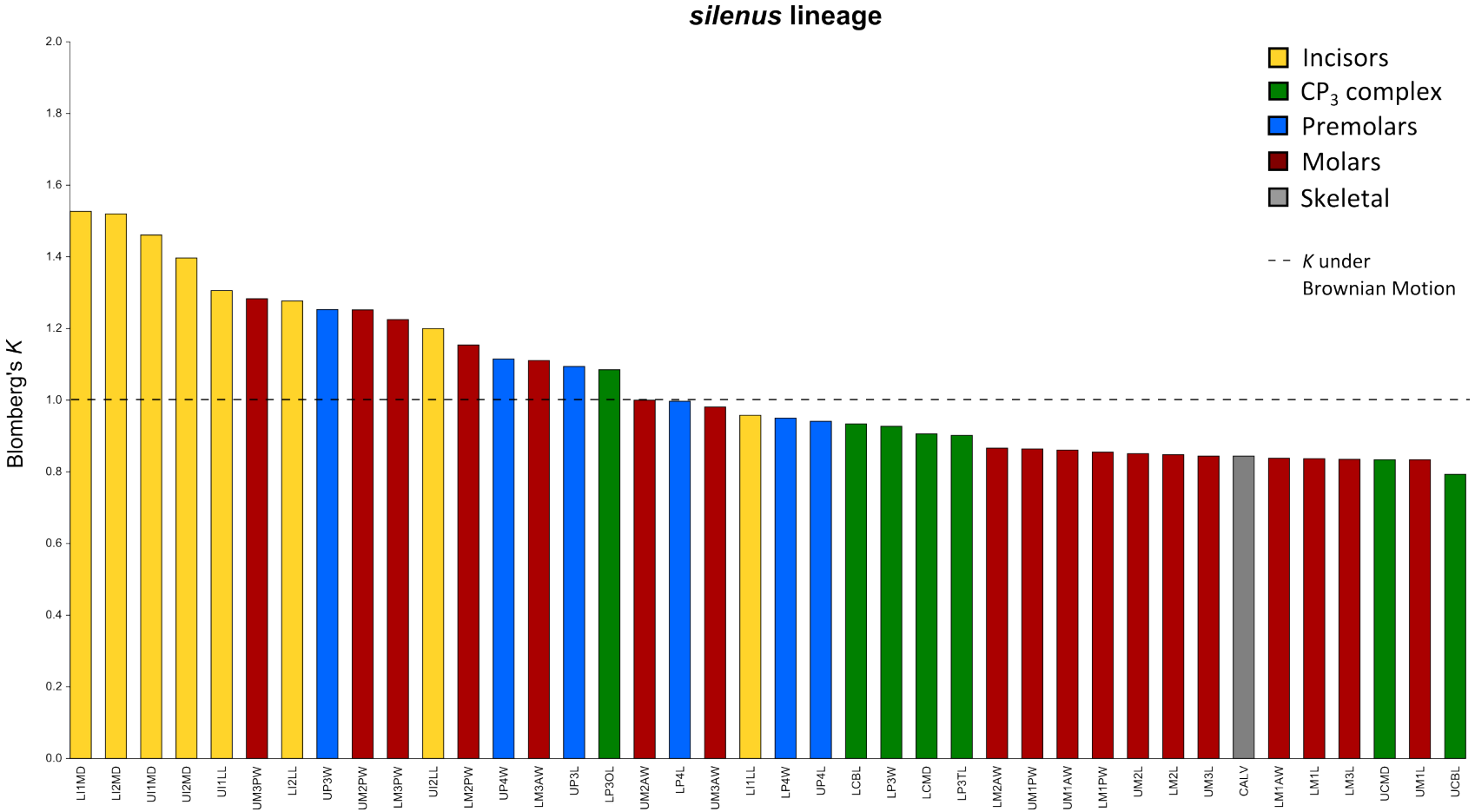


Fig. 7.4 Blomberg's *K* for 39 measurements of tooth mesiodistal lengths and labio-/buccolingual width, and calvarium length (a body size proxy) among species of the *silenus* lineage ($N = 5$). Key to variable names can be found in Table B.14 in Appendix B. The dashed reference line indicates the expected value (1.0) of *K* under Brownian motion (BM). All measurements carry relatively strong phylogenetic signal, yielding a mean *K* of 1.039. The incisors (yellow) stand out with especially high *K*-values. The canine/premolar (CP_3) complex (green) shows noticeably weaker phylogenetic signal in the *silenus* members than when the total study sample is considered (Figure 7.3). Premolars and the buccolingual widths of the second and third molars (M2 and M3, respectively) also have strong phylogenetic signal.

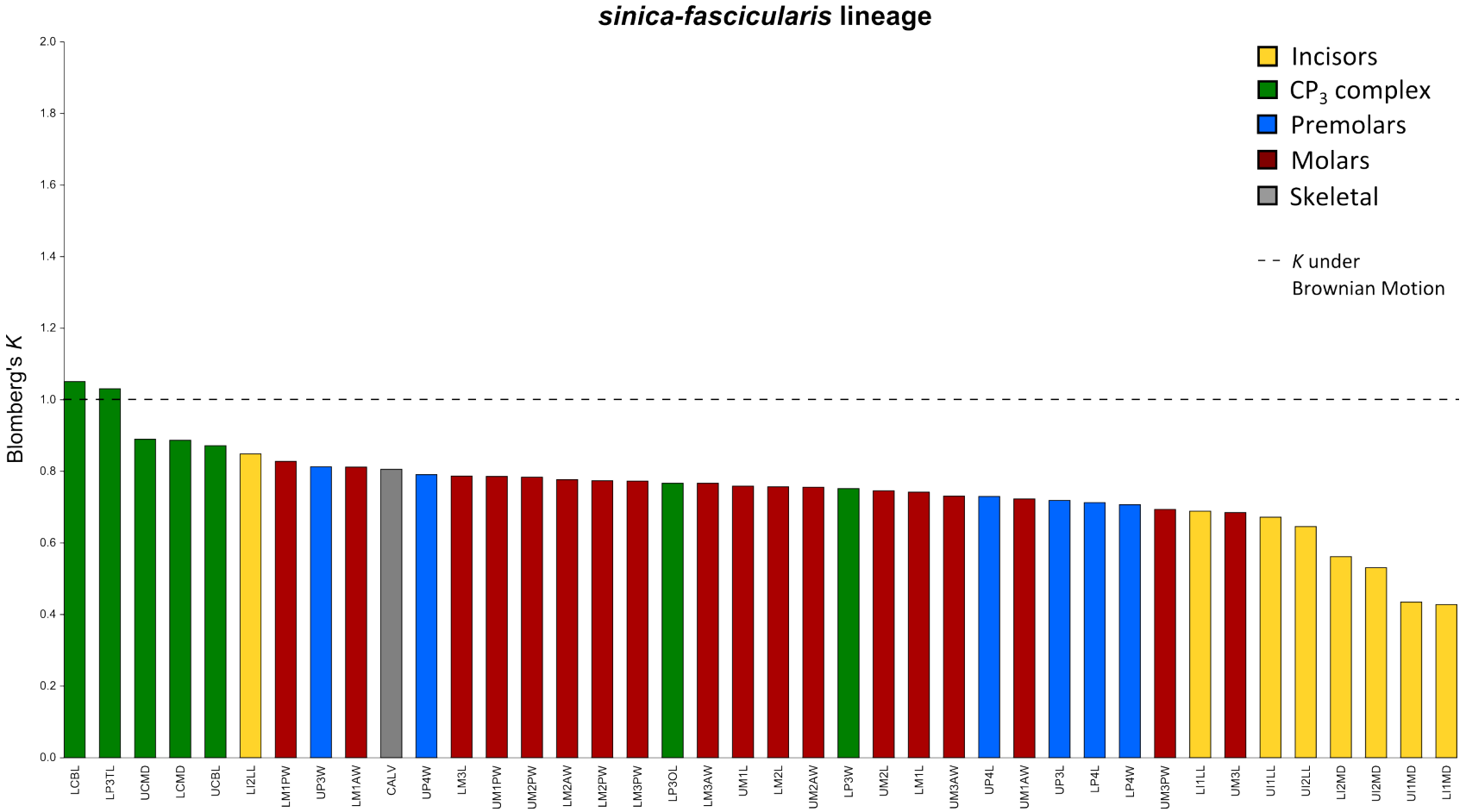


Fig. 7.5 Blomberg's *K* for 39 measurements of tooth mesiodistal lengths and labio-/buccolingual width, and calvarium length (a body size proxy) among species of the *sinica-fascicularis* lineage ($N = 7$). Key to variable names can be found in Table B.14 in Appendix B. The dashed reference line indicates the expected value (1.0) of *K* under Brownian motion (BM). Macaque species of this lineage, in contrast to the *silenus* members, exhibit overall weaker phylogenetic signal, with a mean *K* of 0.751. The strongest signal is present in the canine/premolar (CP_3) complex (green); the incisors (yellow) carry the weakest signal.

The exact values of Blomberg's K for all dental dimensions are listed in Tables G.1 to G.3 in Appendix G. The associated uncorrected and FDR-corrected p-values are also presented there. To limit the number of multiple comparisons, cranial and mandibular measurements were omitted from the calculation of adjusted p-values, since the main focus here is the phylogenetic signal in the macaque dentition. The exception is calvarium length (CALV), which was included as a body size proxy.

Table 7.2 shows the top ten dimensions with the highest Blomberg's K-values and the uncorrected p-values for the complete sample of macaques and the two Asian subclades separately. Tooth measurements are ranked here based on the value of Blomberg's K, not the p-values. However, because effect size and significance level are linked, many of the K-values listed also have among the lowest p-values. Although the strength of the phylogenetic signal depends on the value of K rather than the p-values, the p-value determines whether we can refute the null-hypothesis of $K = 0$. Based on the results of statistical significance, almost no dental dimension can be accepted to have a K-value > 0 (Table 7.2). The FDR correction for multiple comparisons removes almost any 'raw' statistical significance in the dental dimensions. Without such a correction, many more tooth dimensions exhibit K-values that reach statistical significance, so the penalty for multiple comparisons is quite strong, especially in our samples with small N. However, the pattern of dimensions with the lowest p-values matches the patterns of phylogenetic signal strength based on Blomberg's K presented in Figures 7.3 to 7.5: among all 13 species, the CP_3 complex and the incisors carry (significantly) strong phylogenetic signal, among *silenus* members the incisors and some postcanine tooth widths stand out, and in the *sinica-fascicularis* lineage the CP_3 complex has the highest K, although the latter is not statistically significant (not even the uncorrected p-values are smaller than 0.05).

Size-corrected data

The pattern of phylogenetic signal in the size-corrected tooth dimensions, i.e., in relative tooth size, can be seen in Figures 7.6 to 7.8 for the complete study sample, the *silenus* lineage, and the *sinica-fascicularis* lineage, respectively. The exact values of Blomberg's K and associated unadjusted and adjusted p-values can be found in Tables G.4 to G.6. Several measurements of relative tooth size – in fact, nearly identical to those of absolute tooth size – have K-values significantly higher than 1.0. That does not, however, mean that in those cases K is significantly larger than the K-value for absolute tooth size. Small sample size also means that small and individual differences should not be overinterpreted. Rather, I look for broad patterns of systematic and large differences in K-values between teeth.

Table 7.2 Top ten dental dimensions with the highest Blomberg's *K* for the complete study sample of macaques and species of the *silenus* and the *sinica-fascicularis* lineage separately.

All macaques			*silenus* lineage			*sinica-fascicularis* lineage		
	K-statistic	*p*-value		*K*-statistic	*p*-value		*K*-statistic	*p*-value
UI1MD	1.210	0.005	LI1MD	1.527	0.006	LCBL	1.051	0.081
LP3OL	1.123	0.002*	LI2MD	1.520	0.050	LP3TL	1.031	0.100
LCMD	1.076	0.001*	UI1MD	1.461	0.019	LM1PW	0.828	0.188
LP3TL	1.054	0.013	UI2MD	1.397	0.022	LCMD	0.887	0.192
LI1MD	1.034	0.013	UI1LL	1.306	0.036	UCBL	0.872	0.195
LI2LL	0.928	0.029	UM3PW	1.283	0.045	LM3L	0.787	0.198
LP4L	0.927	0.042	LI2LL	1.277	0.013	UP3W	0.813	0.204
LP3W	0.859	0.09	UP3W	1.253	0.010	CALV	0.806	0.207
LCBL	0.840	0.073	UM2PW	1.252	0.018	LP3W	0.752	0.209
LI2MD	0.837	0.051	LM3PW	1.225	0.074	UCMD	0.890	0.217

* Remains statistically significant at $p < 0.05$ after adjusting for multiple comparisons using the FDR correction.

Among all macaques, it is especially the relative tooth size of the CP_3 complex and the other premolars that stand out with higher phylogenetic signal than in absolute size (Figure 7.6). By contrast, the incisors and the molars show a similar strength of phylogenetic signal in relative and absolute size. Once again, the Asian sub-clades differ in the pattern of phylogenetic signal. While the dentition of the *silenus* members carries an overall strong phylogenetic signal, there is no difference in signal strength between absolute and relative tooth size (Figure 7.7). Conversely, in the *sinica-fascicularis* lineage the majority of dental dimensions show stronger phylogenetic signal in relative compared to absolute size (Figure 7.8). This contrast is most pronounced in the CP_3 complex and the buccolingual widths of the postcanine teeth.

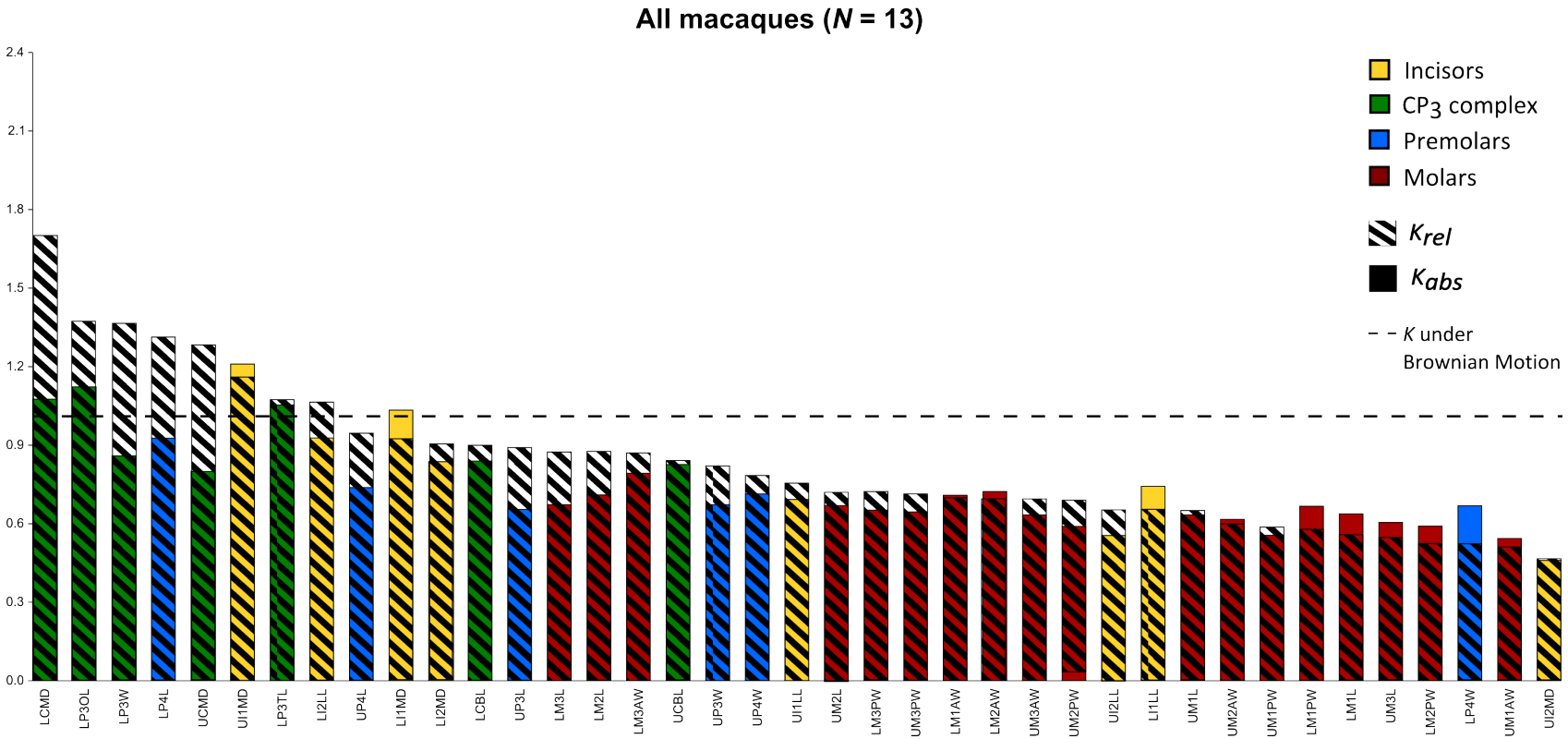


Fig. 7.6 Blomberg's K for the absolute (K_{abs}) and relative size (K_{rel}) of 39 measurements of tooth mesiodistal lengths and labio-/buccolingual width in the complete study sample. The key to variable abbreviations can be found in Table B.14 in Appendix B. The dashed reference line indicates the expected value (1.0) of K under Brownian motion (BM). Blomberg's K tends to be higher for relative tooth size (striped bars) than absolute tooth size (coloured bars), although this is most pronounced in the canine/premolar (CP_3) complex and the premolars.

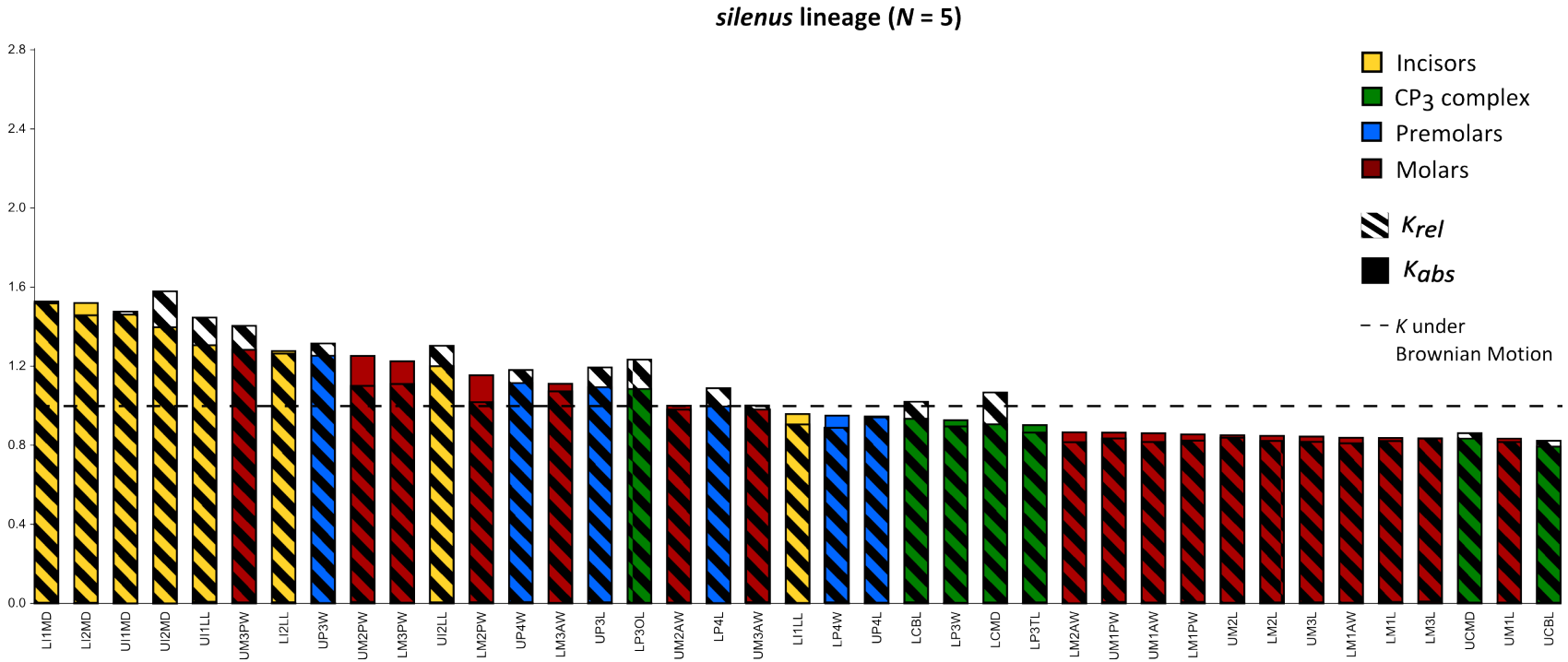


Fig. 7.7 Blomberg's K for the absolute (K_{abs}) and relative size (K_{rel}) of 39 measurements of tooth mesiodistal lengths and labio-/buccolingual width in the *silenus* lineage. Key to variable names can be found in Table B.14 in Appendix B. The dashed reference line indicates the expected value (1.0) of K under Brownian motion (BM). There is virtually no difference in the value of Blomberg's K between absolute tooth size (coloured bars) and relative tooth size (striped bars).

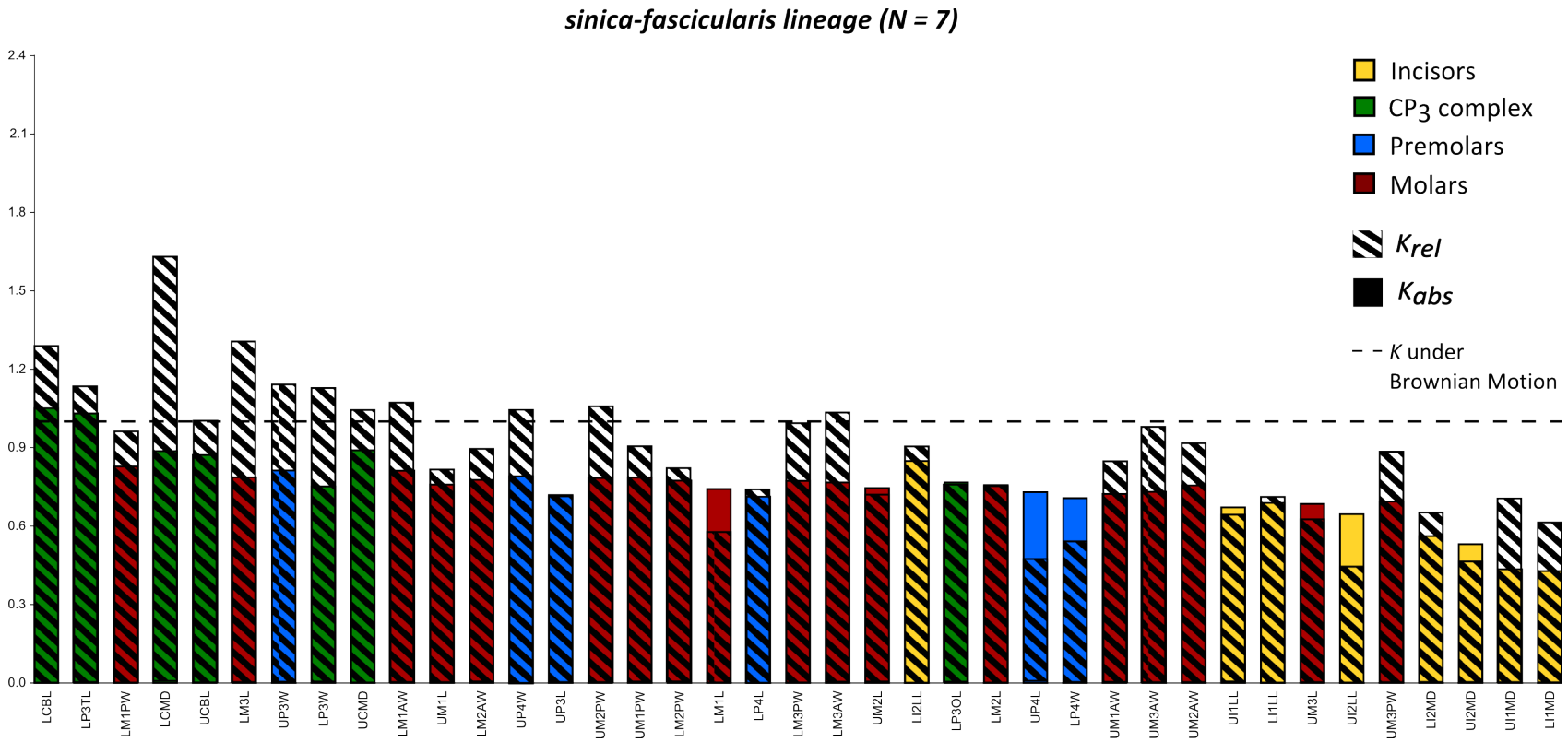


Fig. 7.8 Blomberg's *K* for the absolute (K_{abs}) and relative size (K_{rel}) of 39 measurements of tooth mesiodistal lengths and labio-/buccolingual width in the *sinica-fascicularis* lineage. Key to variable names can be found in Table B.14 in Appendix B. The dashed reference line indicates the expected value (1.0) of *K* under Brownian motion (BM). Blomberg's *K* tends to be higher for relative tooth size (striped bars) than absolute tooth size (coloured bars), and this is true for all tooth classes (although there are exceptions within these).

7.4 Discussion

The aim of this chapter was to investigate the pattern of phylogenetic signal in the macaque dentition. To this end, I measured phylogenetic signal by means of Blomberg's K in primarily tooth lengths and widths, expressed both in absolute and relative size. The pattern of phylogeny was analysed across all species as well as in the two Asian subclades separately (the *silenus* and *sinica-fascicularis* lineages). The mean strength of phylogenetic signal was also compared between dental classes and 'modules' to investigate if tooth classes that have been found to be genetically or developmentally more or less independent exhibit associated differences in phylogenetic signal, as a possible indication for different evolutionary processes.

Absolute tooth size

In general, the macaque dentition appears to carry relatively strong phylogenetic signal, as no K-value under 0.4 was observed. For comparison, some life history traits in primates yielded K-values as low as 0.25 (Kamilar and Cooper, 2013). Because teeth do not remodel following odontogensis, the expression of phenotypic plasticity in teeth is confined to the ontogenetic stage. Moreover, teeth develop inside the jaw where they are relatively well protected from environmental influences, and so their overall plasticity is likely low. Genetic variation may thus underlies most of the phenotypic variation in tooth size within and between species, and this can explain the generally high phylogenetic signal observed in the macaque dentition. It is important to note that there is no clear consensus among workers on what exactly constitutes 'high' (or strong) versus 'low' (or weak) phylogenetic signal (reviewed in Kamilar and Cooper, 2013). Nonetheless, teeth and tooth dimensions may be compared on the size of Blomberg's K relative to each other.

Within the dentition – and the rest of the skull – there is a mixed pattern of phylogenetic signal, both within and between 'trait units'. By trait units I mean different tooth classes that may serve different functions (e.g., the incisors are primarily involved in food ingestion, the molars in food mastication, and the canine/premolar complex primarily serves a sociosexual function in macaques), but also different bones of the skeleton (e.g., cranium versus mandible). Across all macaques, there was variation in the strength of phylogenetic signal among linear dimensions of both the mandible and the cranium. Similarly, incisal dimensions exhibited varying signal strength, with the mesiodistal dimensions of especially the central incisors (and as a result, total incisal tooth row length) carrying strong phylogenetic signal. Differences in phylogenetic signal strength within trait units indicate that different evolutionary constraints or pressures may be operating within them. Dimensions of the canine/premolar (CP_3)

complex and the postcanine dentition (the molars and the premolars, except for P_3) had similar K-values and thus exhibited a more consistent phylogenetic signal.

Overall, between-species variation in the size of the CP_3 complex in macaques corresponds well to the phylogenetic relatedness between species, because phylogenetic signal was relatively strong. By contrast, substantially lower phylogenetic signal in postcanine size highlights that interspecific variation in these traits is not well explained by phylogenetic relatedness. There is a degree of 'modularity' in phylogenetic signal in the dentition that corresponds well to tooth class. The mean value of Blomberg's K was the highest for the canine/premolar complex ($K = 1.10$), followed by the incisors ($K = 0.86$), and the postcanine dentition ($K = 0.69$). These results confirm that different parts of the dentition can and do undergo evolutionary change at least partially independently, insofar as differences in phylogenetic signal reflect differences in the relative importance of constraints, genetic drift, and selection (Blomberg et al., 2003).

The Asian subclades, the *silenus* and *sinica-fascicularis* lineages, showed different patterns of phylogenetic signal in the dentition. The *silenus* members analysed in the present work, which include the South Indian liontailed macaque (*M. silenus*), the southern pigtailed macaque on Sumatra and Borneo (*M. nemestrina*), and the Sulawesi macaques (*M. nigra*, *M. maura*, and *M. ochreata*), exhibited stronger overall phylogenetic signal than the remaining Asian macaques. Moreover, among the *silenus* members, the incisors showed a homogenously strong signal with $K > 1.0$. Conversely, the *sinica-fascicularis* clade, to which the Japanese macaque (*M. fuscata*), the rhesus macaque (*M. mulatta*), and the more elusive Assam macaque (*M. assamensis*) belong, showed a consistently low phylogenetic signal in the incisors. In this clade, the CP_3 complex carried the strongest phylogenetic signal relative to the other teeth. (The absolute values of Blomberg's K for the CP_3 complex were in fact quite similar in both clades.)

Relative tooth size

The phylogenetic signal was notably higher in relative than in absolute tooth size in the *sinica-fascicularis* group. Values of Blomberg's K for some anterior teeth (e.g., the lower canine and central incisors) and for most premolar and molar widths approached 1.0 following correction for overall size, whereas K was considerably lower in absolute size. Support for adaptation in response to temperature and latitude in macaque body size was obtained in Chapter 6. This adaptive signal is likely predominantly driven by the variation in environment and body size among the species of the *sinica* and *fascicularis* species groups, because it is these subclades that include the most variation in body size and whose geographical distribution includes tropical, subtropical, and more temperate (even subalpine) environments. The

adaptive variation in body and craniodental size in these macaques therefore likely accounts for the comparatively low phylogenetic signal in absolute tooth size measurements. This also explains why the strength of phylogenetic signal increased once the adaptive variation due to body size was factored out in the *sinica-fascicularis* lineage.

Conversely, such differences in the size of K were not observed in the *silenus* clade following size correction. It thus appears that overall size does not obscure the phylogenetic signal in the more tropical *silenus* lineage. In fact, the phylogenetic signal remained practically the same in every tooth dimension, indicating that variation in absolute and relative tooth size can be explained well, and equally well, by phylogenetic distance in the five *silenus* members.

In the complete sample of 13 species, Blomberg's K was markedly higher in relative tooth size (compared to absolute size) in the canine/premolar complex and some postcanine dimensions (mainly the premolars), while the rest of the dentition had similar K-values for relative and absolute tooth size (Figure 7.6). There is pronounced sexual dimorphism in the macaque canine/premolar complex, the socioecological underpinnings of which can only partially be explained by body size and are likely multifactorial (see Chapter 5). If sexual dimorphism in absolute canine size shows an adaptive pattern, it may explain the increase in phylogenetic signal strength when relative CP_3 size is considered. Calvarium length in macaques exhibit low phylogenetic signal ($K \approx 0.7$). Considering that calvarium length was found to be a good proxy for body size here and elsewhere [e.g.,][](Delson et al., 2000), this may explain why a larger number of dental variables show substantially stronger phylogenetic signal once they have been adjusted for overall size. Body size in mammals, and in the primate radiation separately, can best be explained by an early-burst (EB) model of evolution (Cooper and Purvis, 2010). This mode of evolution describes rapid phenotypic diversification early on in a lineage, after which diversification slows down markedly. There is a significant phylogenetic signal in body mass in primates in general (Kamilar and Cooper, 2013), but within genera comparatively little variation remains. Adaptive evolution is not necessarily inconsistent with phylogenetic signal (Losos, 2011b). However, if there is convergent evolution among distantly related taxa, then phylogenetic signal will be low. Strong phylogenetic signal, on the other hand, is at least consistent with constant-rate and heterogeneous-rate genetic drift (Revell et al., 2008).

The patterns of phylogenetic signal obtained in this chapter can then tentatively be explained in the following way: strong phylogenetic signal is detected in the incisors of the *silenus* lineage, to the extent that it seems to be largely responsible for the signal visible on the species level when all macaques are considered together and incisors also show Blomberg's K-values higher than 1.0. Strong phylogenetic signal in these anterior teeth may

be indicative of niche conservatism (Losos, 2008), as a result of a similar diet consisting of a large proportion of fruit relative to other plant material. This makes sense for the species of the *silenus* group, which all live in tropical, equatorial Asia, many of them in evergreen forest. However, it should be noted that a selection regime shared by all taxa in a clade is expected to result in low phylogenetic signal, because any phenotypic (dis)similarity within this clade as a result of phylogenetic distance would be erased by selection is moving species' phenotypes back towards the same selective optimum (Losos, 2011b). Therefore, the strong phylogenetic signal in the *silenus* clade, when only those species are considered relative to each other, is consistent with a BM pattern of genetic drift (Blomberg et al., 2003; Revell et al., 2008). The CP_3 complex is more related to social than to dietary behaviour (Plavcan, 2001, and references therein). Across the phylogeny of all 13 macaque species, dimensions of the CP_3 complex tend to show a signal that is indicative of phylogenetic niche conservatism (i.e., $K > 1$). The postcanine dentition, by contrast, consistently shows the weakest phylogenetic signal in the dentition, regardless of whether absolute or relative size is considered, and irrespective of which clade was inspected. Overall, the different patterns observed in macaque teeth suggest that different evolutionary processes have shaped different parts of the macaque dentition, corresponding (to some extent) to the varying functions of the teeth.

A phylogeny represented by a single genus, such as *Macaca*, have a relatively young last common ancestor and therefore tend to include fewer species than older lineages, making the former less suitable for conducting tests of phylogenetic signal due to their low sample size. One may argue that the tests carried out herein therefore lack statistical power, especially in the split sample ($N = 5$ and $N = 7$ for the *silenus* and the *sinica-fascicularis* lineage, respectively), resulting in uncertain estimates of phylogenetic signal for many of the dental variables. However, it is not unexpected to observe a lack of (strong) phylogenetic signal at the low taxonomic scale of a single genus, as the size and depth of the phylogenetic hierarchy as well as the extent of among-species variation are small compared to bigger-sized phylogenies.

Chapter 8

General Discussion and Conclusion

8.1 Introduction

In this chapter, the last part of the thesis, I will summarise and discuss the main findings of this work and how they connect to each other as well as to a broader evolutionary context. The results and the research questions they pertain to have already been discussed in each results chapter. Therefore, rather than recapitulate the findings chapter by chapter, I will structure the discussion around three main questions and themes that draw together the different elements of the research. These three themes will be addressed separately, and in doing so I will discuss how the outcomes of the analyses carried out in this work contribute to our knowledge of each of them. The three sections address related but slightly different topics. The first is on the evolvability of the macaque dentition and the relationship to the observed between-species patterns. The second question is about how the patterns of craniodental diversification connect to macaque evolutionary history and includes a discussion of possible underlying processes. The last section and topic evaluates whether macaques can be considered an adaptive radiation.

The first two questions are more specific with regard to the aims of this thesis and are addressed in the order that they were investigated, starting with how the dental phenotype appears to be developmentally and functionally patterned and how these patterns may have constrained or directed evolutionary change in macaques. This is followed by a discussion of how the present work has shed new light on macaque phenotypic and ecological diversity and the processes and conditions that have been relevant to their evolution. Here, a brief comparison with related primate taxa will be made. The last topic is relevant to evolutionary biology more widely and concerns the level at which we tend to identify, or are *able* to identify, adaptive radiations. Although the focus of this thesis has not directly been to formally test the prediction that macaques qualify as an adaptive radiation, the present

findings nevertheless allow this question to be considered. Directions for future research that will shed further light on the questions and issues raised in this thesis will be discussed as part of each overarching theme.

8.2 Evolvability of the Macaque Dentition and the Relationship to the Observed Between-Species Patterns

The translation of genetic into phenotypic variation is governed by the developmental system. As such, developmental mechanisms play an integral role in the production of phenotypic variation available for natural selection to act on, known as a system's evolvability (Müller, 2007; Wagner and Altenberg, 1996). Important, therefore, for understanding macroevolutionary patterns of variation between macaque species as well as evolutionary covariation between traits, is to know how craniodental variability is structured within species as a result of the developmental system, arising from properties such as canalisation and integration, but also due to growth processes underlying allometry. The first analysis chapter (Chapter 4) in this thesis was directed at understanding how individual teeth in the adult macaque dentition vary within and between species and how they covary. The second set of analyses (Chapter 5) was aimed at examining allometric patterns in the macaque dentition. The results of the latter yielded insight into the extent to which variation in tooth size within and between species are due to variation in body size. Here, I relate the properties of canalisation, plasticity, and integration, which are important determinants of evolvability (see Chapter 4), and allometry to the between-species patterns of variation retrieved in subsequent chapters (Chapters 6 and 7) in order to appreciate how the species patterns in macaque craniodental variation can be explained by developmental mechanisms and growth patterns.

Canalisation and Plasticity

Population and within-species levels of variation (e.g., variance, standard deviation, the coefficient of variation) are a common measure of canalisation, the ability of the developmental system to produce a stable phenotype that is minimally influenced by environmental perturbations or genetic mutations (Gibson and Wagner, 2000; Van Dongen, 2006). Where canalisation acts to constrain the phenotypic variation of a trait in the population, phenotypic plasticity results in increased phenotypic variation as a function of differences in the environment (Debat and David, 2001; Pigliucci, 2005). Since teeth do not remodel after odontogenesis, the phenotypic plasticity of teeth is limited to developmental plasticity (West-Eberhard, 2003).

In macaques, the pooled within-species variation for the 39 tooth lengths and breadths revealed that premolars (especially the two fourth premolars) and first molars (especially the lower) were the most canalised teeth in the dentition, followed by incisors and the other molars. On the other end of the spectrum, the canine/premolar (CP_3) complex had the largest intraspecific levels of variation. This pattern was consistent across different measures of variation (i.e., the pooled within-species variance weighted by sample size, MS_R, and the pooled standard deviation divided by the pooled mean, the CV; see also Table 4.3). The comparatively very high levels of variation in the CP_3 complex are most likely largely due to sexual dimorphism in canine and P_3 size, not due to phenotypic plasticity per se.

Integration

Macaque teeth were found to be highly phenotypically integrated as judged by pairwise phenotypic correlations. In both jaws, teeth tended to have the highest phenotypic correlations with other teeth of the same tooth class (incisors, canines, premolars and molars), although the canine and third premolar were much more strongly correlated in the mandible than in the maxilla. In all the analyses throughout this thesis, the lower third premolar (P_3) has been more strongly associated with the upper and lower canine than with the rest of the postcanine dentition. P_3 has the highest phenotypic correlations with the lower canine, shows the same strong sexual dimorphism in size, exhibits highly similar phylogenetic signal as the canines, and in its association with geographical and ecological variables, it behaved similarly to the anterior but not the postcanine dentition. By contrast, the other three premolars were most strongly associated with the postcanine dentition, and in fact showed phenotypic correlations with each other as strong as their correlations to the molars. Within species, this correlational pattern remained intact after all overall cranial size-related variation was regressed out. The magnitude of most dental correlations was reduced, demonstrating that allometry, through the effect of a shared duration of growth for example (Mitteroecker et al., 2012), acts as an integrating factor in the dentition. The result was particularly pronounced for incisal measurements, which, even before accounting for allometry, were only moderately correlated with each other, but weakly with other teeth. After allometric size adjustment, these correlations became even weaker. On the other hand, many correlations between premolars and molars were stronger after allometry was statistically removed, which offers strong support for a mechanism of developmental integration (Mitteroecker and Bookstein, 2007; Mitteroecker et al., 2012).

The patterns of phenotypic – and inferred underlying developmental – integration observed in macaques bear a strong resemblance to phenotypic integrative patterns observed in the dentition of Old World monkeys, including macaques, savannah baboons, blue mon-

keys, colobus monkeys, and surilis (Grieco et al., 2013; Hlusko and Mahaney, 2009) and hominins (Gomez-Robles and Polly, 2012). In turn, these patterns of phenotypic covariance are strongly congruent with the genetic covariance patterns derived for savannah baboons and mice (Hlusko and Mahaney, 2009; Hlusko et al., 2011). The genetic architecture of the baboon and mice dentition suggests genetic modularity between the incisors and the postcanine dentition (canines were omitted from these studies), with premolars and molars forming 'sub-modules' within the postcanine tooth rows due to shared genetic pleiotropy (Hlusko and Mahaney, 2009; Hlusko et al., 2011). It is therefore likely that the patterns of phenotypic integration within macaque species reflect developmental as well as genetic modularity. This supposition is further bolstered by the fact that the between-species patterns of dental integration also show allometric integration and a modular pattern and therefore seem to follow microevolutionary mechanisms. It is reasonable to assume, therefore, that the strong evolutionary correlations between molars are the result of developmental and genetic integration of these teeth. Genetic integration of traits leads to correlated responses to selection and evolutionary integration of these traits (Cheverud, 1996; Hallgrímsson et al., 2009; Hansen and Houle, 2008; Lande and Arnold, 1983). This explains why differences in canalisation and phenotypic plasticity between the molars do not correspond well to phenotypic differentiation of these teeth on the species level: molars are functionally linked (Lucas, 2004), are likely genetically and developmentally integrated, resulting in their evolutionary covariance and shared evolutionary trajectories.

The evolutionary effect of the modularity in the macaque dentition that separates the postcanine dentition from the anterior dentition (incisors but also canines) is reflected in the antero-posterior tooth size contrast observed in Chapters 4 and 6. Principal component (PC) 2 in the principal components analysis (PCA) of between-species craniodental variation, latent variable (LV) 2 in the two-block partial least squares (2B-PLS) analysis, and LV 2 in the reduced rank regression of ecogeographical associations with the craniodental phenotype were similar in showing a contrast in the relative size of the anterior and posterior teeth. In the PCA, with overall size variation accounted for in PC 1, macaque species were shown to differ in the size of their incisors and canines relative to their premolars (excluding P_3) and molars. In the 2B-PLS, virtually the same pattern showed up, but this time in association with a number of climatic and ecological variables. Because in both cases allometric variation was contained in the first dimension (PC 1 and LV 1, respectively), variation in allometric scaling between the anterior and posterior dentition cannot explain these patterns. Within species, PC 2 showed the same relative tooth size contrast (after variation due to sexual dimorphism and tooth wear was removed from the data). The congruence between intraspecific and interspecific patterns of dental integration support the conclusion that the macroevolutionary

craniodental variation in macaques has strongly been guided by the genetic and developmental patterning mechanisms underlying dental variation on a microevolutionary level.

Dental Allometry

Allometry, broadly defined as the relationship of overall size to the relative size or shape of traits, induces phenotypic covariation between traits. But it is also an important source of variation in individual traits. In the Huxlean sense, allometry refers to the disproportionate increase in trait size with overall size, characterised by a scaling coefficient smaller or larger than one. Isometry refers to an increase in trait size proportional to the increase in overall size and as a result the scaling coefficient is one (Jungers et al., 1995). Ontogenetic allometry refers to how shape or relative size of a trait changes with body size during development; static allometry refers to how trait shape or relative size varies with differences in body size within an ontogenetic stage (typically adults); and finally, evolutionary allometry describes how shape or relative size varies with body size across species (Cheverud, 1996; Strauss, 1993). Allometric scaling patterns in macaques were highly similar on the intraspecific and the interspecific level, with few exceptions, evincing the congruence between static and evolutionary dental allometry. Relative to the rest of the dentition, incisors, first molars and the upper fourth premolar had low scaling coefficients. Treating these as a baseline of negative allometry, second molars and the lower fourth premolar scaled with isometry, and third molars and the CP_3 complex with positive allometry (sexual size dimorphism was removed in the dental allometry study in Chapter 5). The allometric scaling patterns for the different teeth were consistent with previous findings for primates (Gingerich and Smith, 1985; Gingerich et al., 1982).

Differences in scaling coefficients between isomeres (teeth of opposing jaws) were found in the anterior dentition and the third premolars. This particular scaling pattern reflects the morphological differences that exist between jaws in this part of the dentition. Central upper incisors tend to be quite a bit larger than their lower counterparts in macaques and other papionin monkeys (Swindler, 2002). The upper and lower canine also differ markedly in size and shape (Swindler, 2002). Taken together however, anterior teeth have an average scaling coefficient of one in both the maxilla and mandible such that opposing tooth rows occlude well, reflecting phenotypic integration. Although integration patterns were not explored between jaws (e.g., by means of correlograms), isomeres are likely developmentally and genetically integrated to achieve such phenotypic coordination (isomeric pleiotropy; Stojanowski et al., 2017). By contrast, there were no large discrepancies in scaling coefficients between jaws with respect to the postcanine dentition; only the third premolar isomeres had differential scaling coefficients owing to the role of the lower third premolar in the

canine/premolar honing complex. For the rest of the postcanine dentition, the highly similar scaling pattern is not surprising given the similar size and shape of molars and fourth premolar isomeres. In order to optimise occlusion between isomeres, the genetic and developmental patterning mechanisms need to ensure that teeth that form an occluding pair vary with overall (cranial or body) size by the same proportion. Such coordinated tooth size scaling is integral to the masticatory function of the postcanine tooth row (Lucas, 2004).

Between molars in the same jaw, the differences in allometric scaling coefficients is described by an antero-posterior gradient: M1 < M2 < M3. This pattern corresponds to the gradient in macaque absolute molar size, with each posterior molar being larger than the one anterior to it, which is the typical papionin pattern (Swindler, 2002). Although the allometric scaling gradient describes the gradient in absolute molar size, allometry itself does not explain anything. Allometry itself requires an explanation.

The Inhibitory Cascade (IC) Model

Recent advances in experimental evolutionary developmental biology have identified a developmental mechanism of molar tooth size patterning, called the inhibitory cascade (IC) model (e.g., Bernal et al., 2013; Carter and Worthington, 2016; Evans et al., 2016; Kavanagh et al., 2007; Polly, 2007; Schroer and Wood, 2015a). Further discussed below, this mathematical model explains not only the proportional increase in molar occlusal size in an antero-posterior direction and the associated gradient in allometric scaling, but also the differences in intraspecific levels of variation between anterior and posterior molars (Kavanagh et al., 2007). The IC model has held up well in explaining large-scale macroevolutionary patterns of molar size variation across a wide range of extant taxa (Carter and Worthington, 2016; Kavanagh et al., 2007; Polly, 2007; Schroer and Wood, 2015a) and extinct taxa (Halliday and Goswami, 2013; Polly, 2007; Wilson et al., 2012) and has been argued to be the plesiomorphic condition in mammals (Halliday and Goswami, 2013).

The inhibitory cascade model is so named after an experimentally derived model that defines how the dynamic balance of signalling molecules determines relative lower molar size (Kavanagh et al., 2007). During ontogeny, molars develop consecutively in an anterior-posterior direction in the dental lamina, a band of epithelial tissue parallel to the jaw (Jernvall and Thesleff, 2000). Employing cell culture techniques on mice, Kavanagh and colleagues discovered that mandibular molar initiation and growth rate, and thus ultimately size, was determined by the ratio of activator and inhibitor molecules (*a/i*) diffusing through the dental lamina. Comparing *in vivo* and *in vitro* molar development, they discovered that the activator molecules are released by the surrounding mesenchymal tissue, as *in vitro* explants that had been removed from the mesenchyme following M_1 initiation, exhibited a delayed

development of the posterior molars M_2 and M_3 (but not M_1). Cutting the epithelium at the posterior tail of the M_1 tooth bud seemed to alleviate the inhibitory impact of M_1 and lead to normal or even accelerated tooth development (initiation and growth rate) of successive molars (Kavanagh et al., 2007). The effect of the activator/inhibitor ratio is cumulative along the tooth row, however, with the inhibitory effect on M_3 arising from M_1 as well as M_2. Based on their experimental manipulation of the levels of activators and inhibitors and the resulting variation in measured posterior molar size, Kavanagh and colleagues derived the following empirical relationship of the dynamic balance of activator and inhibitor signalling molecules and the relative size of the molars at different positions in the molar row:

$$y = 1 + [(a - i)/i](x - 1) \tag{8.1}$$

where y is relative molar size (occlusal area), a is the strength of activation, i the strength of inhibition, and x indicates the position in the molar row (1, 2, or 3). According to this model, relative molar size increases or decreases linearly along the tooth row. Kavanagh and colleagues subsequently performed a macroevolutionary test of their model by applying it to 29 species of murine rodents of different ecological adaptations. They found it had very good explanatory power of between-species molar size variation, a finding that has been corroborated in many other taxonomic groups since then (e.g. Bernal et al., 2013; Carter and Worthington, 2016; Halliday and Goswami, 2013; Polly, 2007; Schroer and Wood, 2015a). The large-scale pattern shows a strong link between diet and the relative strength of a/i molecules. Herbivorous mammals often have molars that increase in size in a posterior direction ($M_1 < M_2 < M_3$) and are thus inferred to have relatively reduced inhibition levels, whereas carnivorous species, like the murine condition, show the opposite trend with larger anterior molars, and which thus have relatively increased inhibition levels (Polly, 2007).

One of the outcomes of the IC model is that molar size can be predicted on the basis of the size of the other two molars (Evans et al., 2016; Kavanagh et al., 2007). Support for the inhibitory cascade has been found in platyrrhine and catarrhine taxa (Bernal et al., 2013; Carter and Worthington, 2016; Polly, 2007; Schroer and Wood, 2015a), including in macaques (Schroer and Wood, 2015a). Although the dental inhibitory cascade was not tested in the present sample of macaques, but given that the IC model seems to explain relative molar size in macaques, it likely also explains the allometric scaling gradient in molars (M1: negative allometry, M2: isometry, and M3: positive allometry) both within and between species.

Another predicted outcome of the IC model is that the level of phenotypic variation increases in an antero-posterior direction along the molar row as a result of the cumulative impact of the a/i ratio of earlier developing molars (Kavanagh et al., 2007). As such, third

molars are predicted to be more variable than second molars, which are predicted to be more variable than first molars, as a direct outcome of the cascade effect. Let us assume that there are two sources of variation in tooth size: A) independent variation in the size of each tooth (including M1), and B) variation in the precise a/i ratio (the slope of the inhibitory cascade) from the first molar through to the second and the third molars. The final variation in M1 will only be due to A (assuming it is itself not affected by previously developing teeth), that of M2 will be due to both A and B, while for M3 it will be A and 2*B (A.R. Evans, pers.comm.). The final size of M3 is thus affected by independent influences (e.g., developmental instability only affecting the developmental system at the time of third molar odontogenesis), by the activation/inhibition balance at the time of M2 odontogenesis as well as by the activation/inhibition balance at the time of M3 odontogenesis. On a population level, this would result in exactly the kind of gradient of an increase in phenotypic variance from anterior to posterior molars that was observed in macaques in this work. According to the IC model, molar phenotypic variance arises predominantly as the result of variation in the previously developing molars, and therefore the independent variation – the phenotypic variation that is available for natural selection to act on independently from adjacent molars – is in fact small. It also supports the notion that – at least among the molars – first molars truly are more canalised (or less plastic) than the posterior molars, as ostensibly the latters' heightened variation levels are the result of a ratchet effect from the developmental mechanism governing the relative molar size, and thus that they reflect developmental plasticity as a special case of phenotypic plasticity (West-Eberhard, 2003).

Whether the differences in levels of variation between the three molars within and between species of macaques can be adequately explained by the IC model needs to be tested in future analyses. Additional research could expand on this and test the 'variance gradient' against the IC model in a wider range of taxa, including those taxa for which the IC model fails to explain relative molar size, such as in extant guenons (Carter and Worthington, 2016; Schroer and Wood, 2015a), canids (Asahara, 2013), arvicoline rodents (Renvoise et al., 2009), and fossil ungulates (Halliday and Goswami, 2013; Wilson et al., 2012). In canids, for example, the IC model does not explain relative molar size and moreover, the first lower molar was found to be more variable than the consecutive molars. It would be interesting and worthwhile to investigate whether there is a link between deviations from the plesiomorphic IC mechanism of mammalian molar development and the observed levels of variation in molar size. This might identify taxa in which molar variability is independent of (or less dependent on) variation in adjacent molars, identifying lineages in which phenotypic variation has been available for natural selection to act on change the genetic and phenotypic patterning of molars from the plesiomorphic mammalian condition.

8.3 Ecogeographical and Phylogenetic Associations with Craniodental Diversity: A Window into Macaque Evolutionary History?

In this work, several ecological, geographical, and phylogenetic patterns were detected in the interspecific craniodental variation of the thirteen macaque species studied. Evolutionary signals, even if they are often 'mere' statistical associations pertaining to the sample and variables analysed, can, in combination with knowledge of the past and present biogeography, provide useful insight into the past conditions that have been relevant to the evolution of diversity, as well as into the role of natural selection vis-á-vis neutral processes. In this section, I will discuss what the present work has contributed to our knowledge about the evolutionary history of macaques on the basis of the detected macroevolutionary patterns of morphology, ecogeography, and phylogeny.

Macaque Phenotypic Diversity

The genus *Macaca* is well known for its speciosity (Groves, 2001; Mittermeier et al., 2013; Thierry, 2007b) and its successful occurrence across a wide range of environments and a broad geographical range (Fa, 1989; Fleagle, 2013; Fooden, 1980). The latter is not merely a between-species pattern in this group; several species also occupy large ranges, a variety of environments, or both (Fooden, 2006). These include most obviously the rhesus macaque (*M. mulatta*) and the longtailed macaque (*M. fascicularis*), but also the bonnet (*M. radiata*), and Japanese macaques (*M. fuscata*). One of the main findings of the present work, however, is that macaques are phenotypically not very differentiated as might be expected on the basis of their ecological diversity, at least insofar as observed in the dentition and in several associated craniofacial and mandibular measurements. Both the PCA and the ecogeographical analysis (2B-PLS and the reduced rank regression) yielded only two meaningful dimensions of variation and covariation describing between-species diversity. In all three analyses, more than 90 percent of the variance or covariance was explained by PC 1 and PC 2 (PCA) and LV 1 and LV 2 (2B-PLS and reduced rank regression), respectively, thus leaving little remaining interspecific (co)variation unexplained. All analyses were consistent in showing that the main separation between macaques pertained to variation in body size. PC 1 represented allometric size in the craniodental phenotype (Chapter 4). The 2B-PLS analysis (Chapter 6) included body mass data in the block of environmental variables, and the main axis of covariance between the latter and the block of craniodental variables showed high positive loadings for all craniodental measurements (morphological block) as well

as body mass (environmental block), confirming that allometric size in the skull and teeth is positively associated with body size. As expected then, the PCA showed a separation between small, medium, and large-bodied species, and an overlap of species of similar body size (see Figure 4.5 and Table B.1). When evolutionary divergence has occurred along the direction of greatest within-population genetic variance, it has occurred along the line of least evolutionary resistance (Schluter, 1996a). This is expected under neutral evolution – in the absence of natural selection – or when the selection gradient is in line with this direction of maximum variance ($\mathbf{g}_{max}$; Lande, 1979; Schluter, 1996a. Although it is the genetic covariance pattern (**G**) that is relevant for evolutionary change (Lande, 1979), the phenotypic covariance pattern (**P**) may be used as a proxy (Marroig and Cheverud, 2005). Figure 4.8 showed that the direction and orientation of the maximum within-species phenotypic variance among craniodental traits was similar to the direction of maximum between-species variance. The greatest direction of phenotypic (and assumed genetic) variance is necessarily PC 1, which was represented by size. Thus, adaptive differentiation in body size seems to have occurred along an LLER trajectory.

PC 2 showed an antero-posterior tooth size contrast between, on the one hand, the pigtailed macaque (*M. nemestrina*), the liontailed macaque (*M. silenus*), and the black crested macaque (*M. nigra*) with a relatively larger anterior dentition (incisors and CP_3 complex), and the Japanese (*M. fuscata*) and Barbary macaques (*M. sylvanus*) with a relatively larger posterior dentition on the other. The other macaques fell somewhere in between. The same pattern of a relative tooth size contrast was retrieved in association with an ecological factor of rainfall, dietary and habitat specialisation, and a northwest-to-southeast cline. Together, they describe the differences between frugivorous macaques living in wet, tropical environments where they occupy small ranges, such as the pigtailed and the Sulawesi macaques, and more omnivorous macaques living in temperate climates, some of which also occupy a broad range of habitats, such as the Japanese, Barbary, and rhesus macaques (*M. mulatta*).

That the latter pattern is to a large extent a phylogenetic phenomenon can be observed in Figure 8.1. Members of the tropical *silenus* clade (lower right quadrant) are all highly frugivorous and also have a relatively enlarged anterior dentition evinced by the negative PC 2 scores. On the other end of the spectrum, however, the closely related rhesus and Japanese macaques but also the relatively distantly related Barbary macaque contribute to the dental contrast. The pattern of the PLS scores for LV 2 in the 2B-PLS analysis of ecogeography showed a very similar distribution of species along the PLS scores (not presented here).

Before discussing possible underlying evolutionary processes, we may inspect where in the dentition the phylogenetic and potentially adaptive pattern is situated. Are the incisors and the canines driving the pattern, or the postcanine tooth row? In Chapter 5, no differences

in postcanine occlusal area (PCOA) relative to body size were found in relation to dietary differences between the macaque species: PCOA scaled highly similarly with body size irrespective of dietary composition (Chapter 5). If there had been a correlation between relative PCOA and diet, then, retrospectively, we would expect to see a phylogenetic pattern, considering that most of the predominantly frugivorous macaques form a clade to the exclusion of the other species. But no such effect of diet – mediated by phylogeny – was observed in the data (Figure 5.5). The lack of a phylogenetic pattern in relative PCOA corresponds to the low phylogenetic signal observed in the relative (but also absolute) size of the postcanine dentition in Chapter 7. By contrast, strong phylogenetic signals were detected in the absolute and relative size of the incisors and the canines (plus the lower third premolar) (Figure 7.6). From this, it appears that the relative tooth size contrast is largely due to the phylogenetic signal present in the anterior dentition, at least based on a study of the macaque species analysed in this work.

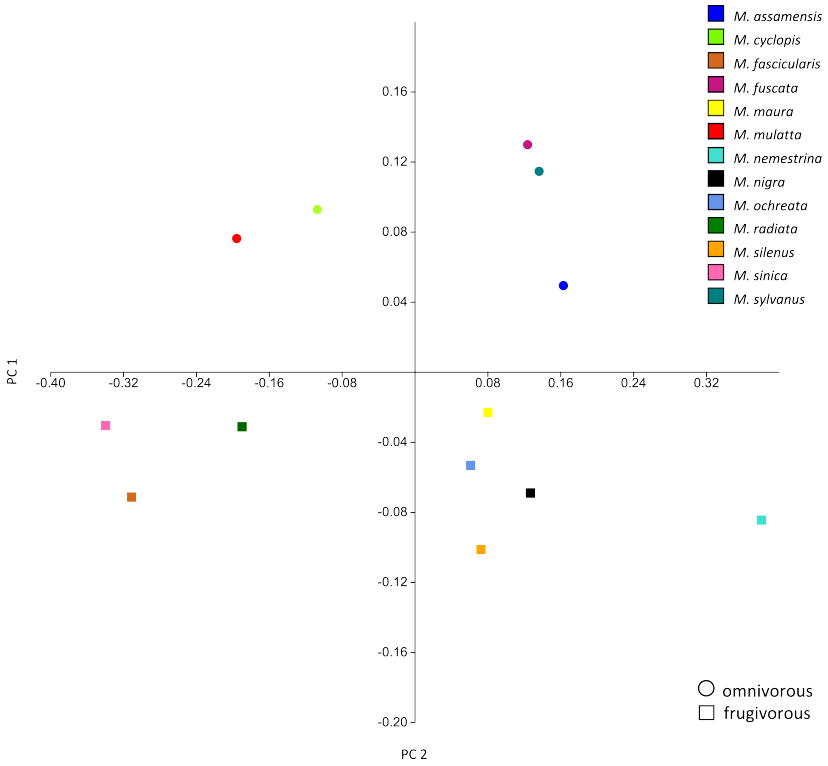


Fig. 8.1 Principal component plot of the first (PC 1) and second principal component (PC 2) of between-species craniodental variation in all 13 macaque species. This PC plot is based on species means of all 72 craniodental variables (omitting cranial, mandibular, or tooth height measurements did not change the results). PC 2 was demonstrated elsewhere (Chapter 4) to reflect the antero-posterior gradient of relative tooth size. Negative scores on PC 2 denote a relatively larger anterior dentition; positive scores a relatively larger posterior dentition. PC 2 scores are strongly associated with the percentage fruit included in the diet. (The dietary classification was presented in Table 5.1.)

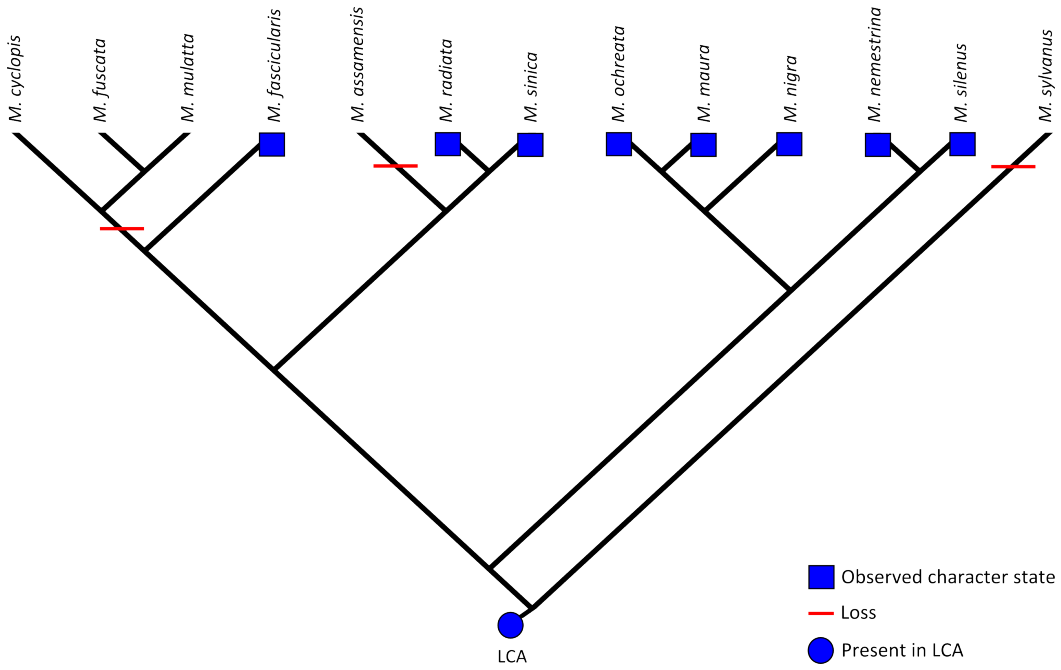
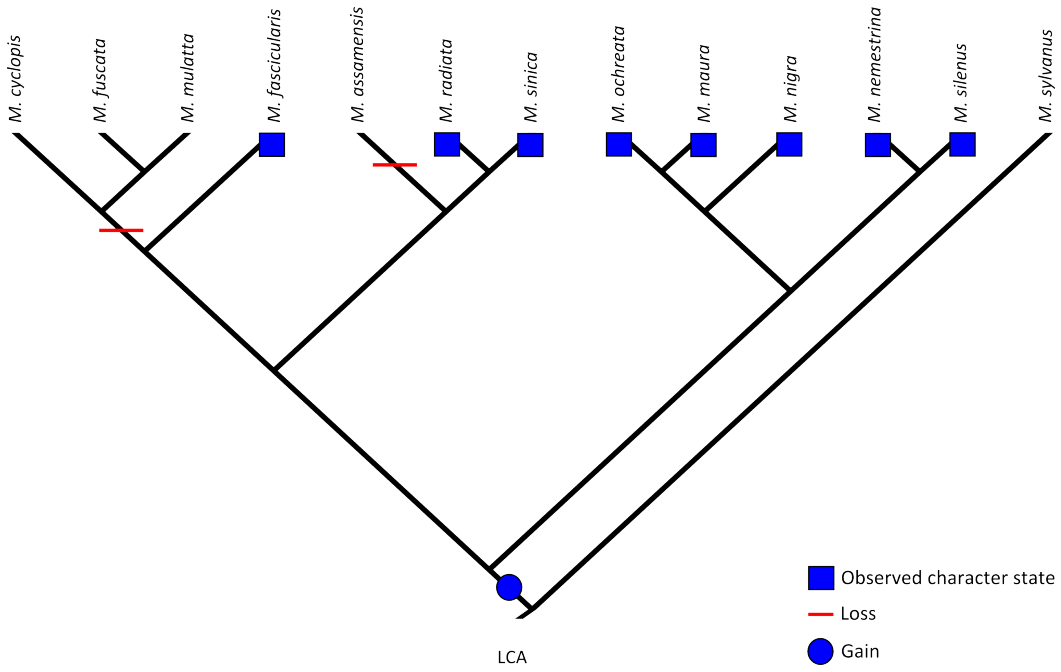


Fig. 8.2 Evolutionary scenario 1: a large anterior dentition (blue trait) was present in the last common ancestor (LCA) to all macaques, and subsequently independently lost three times.

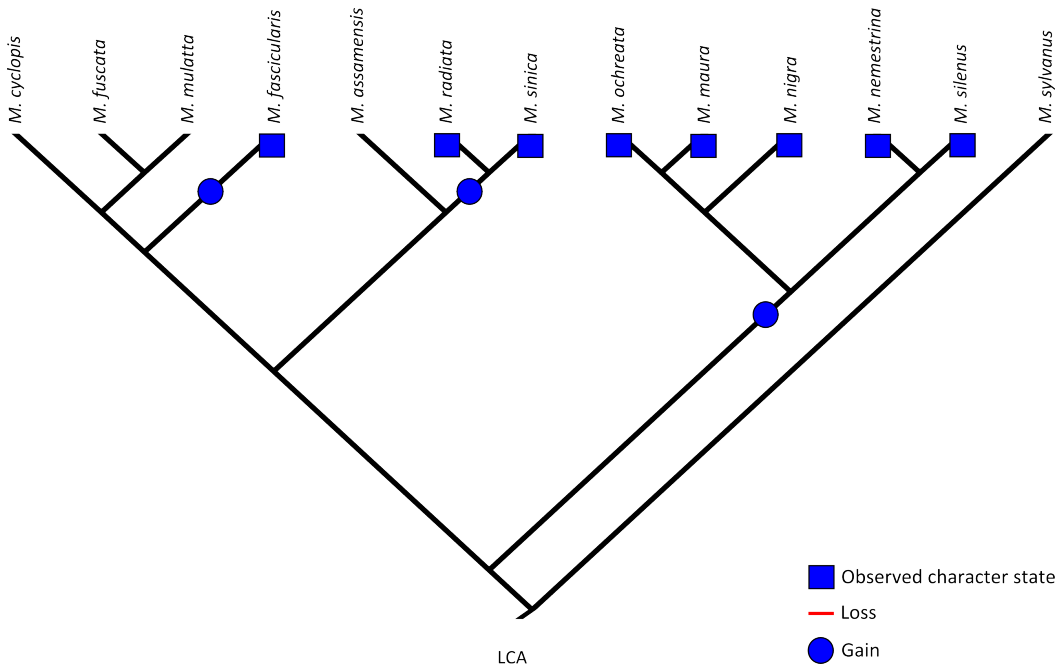
Figures 8.2 and 8.3 show different scenarios of character evolution in a cladistic framework. The character state (blue) represents the condition of larger anterior teeth relative to the posterior teeth (after both are adjusted for overall size variation). Although it is a continuous multivariate trait, Figure 8.1 showed good separation between macaques with respect to PC 2 scores and diet, and so it is treated here as a trait with two character states for a cladistic discussion. Moreover, as discussed previously, there is evidence for functional and genetic independence of the anterior from the posterior dentition, and so their evolution may be uncoupled. In the absence of information on relative tooth sizes (anterior vs. posterior) in the macaque's sister group, the African papionins, it cannot be deduced whether presence or absence of the blue state in the macaque ground pattern is more parsimonious. I will therefore consider both of these cases separately. Scenario one in Figure 8.2 assumes presence in the last common ancestor (LCA) of all macaques. The trait would then have been lost three times independently – on the branch leading to the extant Barbary macaque, and an additional two times in *M. assamensis* and the common ancestor to the rhesus, Taiwanese, and Japanese macaques. If the blue state was absent in the macaques' LCA (Figure 8.3), two equally parsimonious scenarios result. It could either have evolved in the LCA to all Asian macaques and subsequently been lost twice (scenario 2a, Figure 8.3a); or, alternatively, it would have evolved three times independently (scenario 2b, Figure 8.3b) in the three frugivorous lineages:

once (and probably first given the age of this node, see Figure 2.3) in the common ancestor of the *silenus* group, and then again in the *sinica* and the *fascicularis* species groups separately.



(a) Evolutionary scenario 2a: a large anterior dentition evolved in the common ancestor to all Asian macaques and was subsequently independently lost twice.

Under scenario 2a the presence of the blue state in the eight extant species could be due to common ancestry alone, irrespective of whether the trait originally evolved as an adaptation or not. If, however, it evolved three times independently in the frugivorous lineages (scenario 2b), then an adaptive origin seems likely. A well-known empirical relationship exists between diet and tooth size in primates. Large incisors are argued to be beneficial for the consumption of large, fleshy, and husky fruits, while small incisors are associated with folivory (Hylander, 1975). Conversely, an enlarged postcanine dentition is linked to folivory, explained by the advantage of a large occlusal surface for the mastication of large quantities of low-quality, fibrous food (Lucas et al., 1986; Scott, 2011, and references therein). If scenario 2b is correct, there would thus be both empirical and theoretical evidence making it plausible that dietary ecology has driven the adaptive evolution of relative size in the anterior and posterior part of the dental arcade in macaques. However, further research incorporating craniodental morphometric data from baboons (*sensu lato*) and mangabeys (and potentially further outgroups) is needed to test the underlying hypothesis that a large anterior dentition is not the ground pattern in macaques. Still, even if the LCA to all macaques did have a relatively large anterior dentition, this would not rule out an adaptive advantage and concomitant selection pressure in the frugivorous species. A well-known and important



(b) Evolutionary scenario 2b: a larger anterior dentition is a relatively recent trait in macaques that evolved independently three times.

Fig. 8.3 Scenario 2 for the evolution of a large anterior dentition relative to the postcanine tooth row after accounting for overall body size (blue trait).

caveat to any adaptive scenario is the possibility of exaptation (Gould and Vrba, 1982). 'Exaptation' refers to the process whereby an existing trait has been 'co-opted' for its present purpose, for which the trait is adaptive, although it originally evolved for a different purpose or no purpose at all (e.g., genetic drift). This famous critique of the adaptationist programme stresses that often only the current utility of a trait is known but that this is insufficient evidence as the reason for its evolution. Gould and Vrba (1982) thereby cautioned against the default assumption that traits evolved as an adaptation for their present purpose. The possibility that a relatively large anterior dentition is an exaptation is most likely in scenarios 1 and 2a.

Therefore, irrespective of whether large anterior teeth presently confer an adaptive advantage to fruit-eating macaques, the origin of the trait may be due to adaptive or non-adaptive evolution. Much of the phylogenetic pattern arises from the *silenus* clade. As they all share a common ancestor, their manifestation of enlarged incisors as well as a frugivorous and tropical ecology could simply be explained by shared ancestry without the need to invoke adaptation. Additionally, in a restricted morphospace, the chance that distantly related taxa randomly exhibit similar trait values (i.e., homoplasies) is not unlikely (Losos, 2011b). Furthermore, the effect of genetic drift on within- and between-population variance can be comparatively large in the absence of strong selection, particularly when effective population sizes are low (Hamilton, 2009). Incisors may only be under moderate selection owing to their limited role in food processing, namely the ingestion of certain food items (e.g., large fruits) more than others (e.g., seeds, most leaves). The conditions and possible mechanisms by which neutral evolution may have played a role in macaque evolution in general, and in the aforementioned relative tooth size trait in particular, is discussed further on as part of the next sections on phylogenetic comparative methods and macaque evolutionary history.

A Note on Phylogenetic Comparative Methods

Phylogeny plays a central role in comparative studies of biological diversity and it must therefore also form part of the explanation of any comparative pattern (Harvey and Pagel, 1991; Paradis, 2014). In this thesis, strong phylogenetic signal was detected in the incisors and the canines across all macaques and in the two Asian subclades separately (*silenus* clade: incisors, *sinica-fascicularis* clade: canine/premolar complex). The postcanine dentition, by comparison, showed low phylogenetic signal. This discrepancy between the anterior and posterior dentition is noteworthy and indicates that different processes have operated on these two parts of the dental arcade. Further interpretation of this finding is hampered, however, by the fact that phylogeny is more pattern than process and therefore itself requires an explanation. Ultimately, molecular phylogenetic relationships reflect the historical pattern

of speciation, and speciation events and population divergence may have variable underlying causes. What, then, is the utility of measured phylogenetic patterns and how can or should they inform our interpretation of macroevolutionary patterns?

Phylogenetic signal is the statistical association of phenotypic similarity among species with the species' phylogenetic affinity (Blomberg et al., 2003; Kamilar and Cooper, 2013; Münkemüller et al., 2012; Revell et al., 2008). Additional phylogenetic patterns occur, for example, when the phylogenetic relatedness between species (or other operational taxonomic units, OTU's) biases the relationship between two traits, such that closely related species are similar to each other but not to distantly related species. Accounting for phylogeny by a weighting of the data so that data points (e.g., OTU's) are phylogenetically and statistically independent can change several statistical properties of the observed relationship, such as the correlation, regression slope and intercept (Rohlf, 2001), which may warrant a different interpretation of the data. This applies to bivariate and multivariate relationships alike (Adams and Felice, 2014). However, statistical phylogenetic patterns may be consistent with more than one underlying evolutionary process, namely drift as well as selection (Revell et al., 2008). In phylogenetic regression, measurement of phylogenetic signal, and certain other estimation techniques, a Brownian motion model of evolution is the underlying null model against which the data are explicitly tested in statistical applications (Adams and Felice, 2014; Blomberg et al., 2003; Revell et al., 2008; Rohlf, 2001). Nonetheless, the detection of phylogenetic statistical patterns need not be inconsistent with adaptive evolution. When adaptive evolution drives phyletic divergence, the phylogenetic and adaptive signals overlap (Losos, 2011b). In cases where phylogenetic signal is assessed by means of a single test statistic (e.g., Blomberg's K or Pagel's λ), or a strong phylogenetic effect is deduced by comparing the results before and after phylogenetic correction (both of which apply to the present work), the more conservative conclusion is that the data are at least consistent with a Brownian motion (BM) model of neutral evolution such as drift and that there is no conclusive support for a case of adaptation. The caveat is, however, that adaptation cannot be ruled out under these circumstances. Clearly, such a conclusion is unsatisfying and leaves an important question unanswered: are we observing adaptation or not?

In recent years, there has been a rapid and continuous increase in the design and use of more powerful phylogenetic comparative modelling (PCM) techniques that provide more insight into both the patterns and underlying processes of trait evolution (Butler and King, 2004; Hansen, 1997; Ingram and Mahler, 2013; Khabbazian et al., 2016; Smaers et al., 2016; Uyeda and Harmon, 2014). Recent, popular methods incorporate molecular phylogenetic information onto which macroevolutionary phenotypic variation is mapped, visualising the most likely pattern of trait evolution using ancestral state estimation, with the possibility of

testing for phenotypic reversals, convergence, parallelism, or accelerated evolution, among other things (Beaulieu et al., 2012; Khabbazian et al., 2016; Smaers et al., 2016). Some of these methods have been designed to accommodate fossil data (Beaulieu et al., 2012; Clavel et al., 2015; Ingram and Mahler, 2013; Uyeda and Harmon, 2014), handle multivariate data (Bartoszek et al., 2012; Clavel et al., 2015), or carry out explicit hypothesis-testing (Khabbazian et al., 2016; Uyeda and Harmon, 2014). But the main improvement of recent PCM methods is that they can explicitly test trait evolution in an adaptive landscape framework (Bartoszek et al., 2012; Butler and King, 2004; Martins et al., 2002; Paradis, 2014). The underlying evolutionary model used in this approach is called the Ornstein-Uhlenbeck (OU) model, a generalisation of the BM model, which allows traits to evolve towards optima, i.e., an adaptive landscape (Bartoszek et al., 2012; Hansen, 1997; O'Meara and Beaulieu, 2014). With these more recent PCM methods, which are developing very rapidly, researchers can compare hypotheses about the process and rate of evolution, and study evolutionary patterns in more detailed ways, including where evolutionary shifts occurred in a given phylogeny. Many of these methods have been applied to large-scale patterns of evolutionary variation, such as genome size evolution in flowering plants (Beaulieu et al., 2012), brain size evolution in primates (Smaers et al., 2017; Smaers and Soligo, 2013), or evolutionary rate changes in the carnivoran skull (Jones et al., 2015), in part because the capacity to estimate best-fit models from among a range of hypothesised evolutionary scenarios requires large sample sizes to meet the demand for statistical power. Nevertheless, these techniques are also useful for investigating patterns of trait evolution on lower taxonomic and therefore shorter time scales (e.g., the evolution of hand proportions in apes and humans: Almecija et al., 2015; the relationship between brain and tooth size evolution in hominins: Gómez-Robles et al., 2017).

Whereas phylogenetic signal and removing phylogenetic effects from the data provide little if any insight into which taxa are driving the signal and where (e.g., at deeper or more recent splits), phylogenetic models of trait evolution indicate exactly which lineages (if any) show a deviation from the assumed null model. Among anthropoid primates, for example, hand evolution is characterised by so-called adaptive regime shifts (Almecija et al., 2015). Adaptive regimes refer to groups of OTU's (or a single taxon) with a similar phenotype. The model finds the configuration of phenotypic shifts on a phylogenetic tree with the most statistical support (often in the form of an information criterion, e.g., AICc). An analysis of the evolution of anthropoid hand proportions (measured by the relative size of the hand bones) shows regime shifts between major clades: platyrrhines differ from the catarrhines, and within the catarrhines, the Old World monkeys (OWM) possess the inferred plesiomorphic catarrhine condition, while the best-fit regime configuration also shows that, among apes and hominins, hominins retain the plesiomorphic state, while the hylobatid,

orangutan, gorilla, and chimpanzee lineages represent different regimes, with chimpanzees and orangutans showing convergent evolution (Almecija et al., 2015). While the data on anthropoid hand proportions show adaptive shifts, it is also clear that at the same time they bear a strong phylogenetic signal. The advantage of trait mapping techniques in an explicit evolutionary context is that one gains substantially more insight into the process (mode) and rate (tempo) of evolution underlying the phylogenetic signal in the trait(s) of interest. In future analyses, I aim to investigate the possibly adaptive origin of macaque dental variation employing more sophisticated PCM methods such as those mentioned above. This will be briefly discussed in more detail further on.

Macaque Evolutionary History

Molecular genetic data places the split between the macaque lineage and its sister taxon, the African papionins, at approximately 10 MYA (Liedigk et al., 2014; Raaum et al., 2005). The first diversification of the genus *Macaca* subsequently occurred in northern Africa during the late Miocene, as indicated by fossil evidence (Delson, 1975, 1980). African macaques further spread around the Mediterranean basin and into Europe during the Pliocene and Pleistocene (Delson, 1980; Szalay and Delson, 1979). Except for the extant Barbary macaque, however, all the Mediterranean macaques were extinct by the late Pleistocene (Delson, 1980). The Asian macaque fossil record is very sparse, but the present distribution of macaques across large parts of Asia demonstrates their evolutionary success in this part of the world. The question is which evolutionary processes were particularly important for the spread and speciation of macaques: phenotypic differentiation driven by dispersal into novel and different environments, ecological competition and adaptation, or drift as a result of environmental vicariance, isolation and allopatry, and a large component of historical contingency? The former is consistent with adaptation by natural selection, competition, and phenotypic homoplasies. The latter is more indicative of the role of nonadaptive processes and chance events, such as the separation between populations by geographical barriers or a lack of ecological competition encountered by ancestral populations during range expansion facilitated by environmental change. Such a scenario would have resulted in less evolutionary convergence and perhaps overall phenotypic differentiation between macaque species than if they had been subject to strong directional or divergent selection.

The traditional view is that macaques diversified through competition, at least in mainland Asia. Fooden (1976, 1980, 1982a) favoured a competitive scenario for macaque diversification, which has found traction due to the vast geographical range and diversity of environments that macaques occupy until today. Early waves of macaque radiation are held to have been replaced through competition by later waves of dispersing macaques. The

macaque clades with the more disjunct distribution were argued to be descendants of the earlier wave(s), with the gaps in the distribution representing ancestral populations that had been replaced, and the clades with the more continuous ranges are the descendants of more recent dispersal waves (Fooden, 1976, 1980). The aforementioned clades correspond to the heavily 'insularised', tropical *silenus* group, the less geographically disjunct *sinica* group that occurs predominantly in mainland Asia, and the *fascicularis* group with the most continuous and widest-ranging distribution across continental and insular Southeast Asia, respectively (see also Table 2.3). The second piece of evidence for competitive exclusion among macaques comes from the ecological segregation between macaque species in continental Southeast Asia and India. By Fooden's (1982a) account (and references therein), the eight species that occur in this region are sympatric in various combinations, and they can be divided into one of two groups based on their habitat preferences: broad-leaf evergreen (BE) forests, or non-BE forests. Sympatric species were found to belong to different ecological groups, the outcome of competition (Fooden, 1982a).

An alternative view is that contingency played a more prominent role in the evolution of macaques than previously acknowledged (Abegg, 2004; Abegg and Thierry, 2002; Brandon-Jones, 1996; Eudey, 1980). The Pliocene and Pleistocene saw extensive and repeated climatic changes (Morley, 2000), which had a major impact on the biogeography in Southeast Asia of mammals in general (e.g., Hall and Holloway, 1998; Meijaard, 2003), and primates in particular (Brandon-Jones, 1996, 1998; Eudey, 1980). During cool and dry glacials, forest cover contracted, forcing forest-dwelling primates such as the colobines (Brandon-Jones, 1996), but likely also ancestral macaques (Abegg and Thierry, 2002), into forest refugia. Moreover, cooling trends coincided with eustatic changes of lowered sea levels and the exposure of land bridges from the Thai-Malay Peninsula to islands on the continental Sunda Shelf in Southeast Asia (Eudey, 1980; Voris, 2000; Woodruff, 2003), which maintained wet, tropical climates (Hall and Morley, 2004) for considerable periods of time (Voris, 2000). Conversely, during the warm and wet interglacials, tropical forest cover expanded, sea levels rose, and the few remaining mainland ancestral primate populations were able to disperse out of their refugia, encountering little or no ecological competition (Abegg, 2004; Brandon-Jones, 1996). That the land around the refugia was void of competition from other primates, a chance event, has been argued to explain the wide geographical distribution of extant pigtailed macaques (*M. nemestrina* and *M. leonina*; Abegg, 2004). Island populations, on the other hand, became geographically isolated after sea levels rose (Voris, 2000; Woodruff, 2003). Populations on oceanic islands, which were not reconnected to surrounding landmasses in subsequent glacials, soon became genetically isolated from other populations. Evidence that eustatic changes and the physiography of islands (deep-water, oceanic vs. shallow-water,

continental) have affected primate distributions in Southeast Asia, comes from the fact that presently, the continental islands on the Sunda Shelf are stocked with multiple macaque and colobine species, hylobatids, lorises, and tarsiers (Mittermeier et al., 2013), – many of which are present on several islands. Conversely, oceanic islands, such as the Mentawai islands and Sulawesi, have much higher degrees of endemism, because they have been much more difficult to reach and have therefore been colonised by fewer species. (For a detailed review of the palaeogeographical and genetic evidence of the temporal relationship of major climatic and geographical changes to macaque cladogenetic events, see Section 2.3).

The longtailed macaque (*M. fascicularis*) presents a rare primate case of having successfully colonised both shallow-water and deep-water islands, west and east of Wallace's line (Fooden, 1996). Longtailed macaques are often found in riverine habitats, near the mouths of rivers, and thus the ancestral dispersal may have occurred by chance success of rafting (Abegg and Thierry, 2002). Additional support for the role of chance comes from the observation that longtailed macaques, obviously successful colonisers of other oceanic islands, are not present on the Mentawai islands or on Sulawesi, which had already been stocked by earlier arrivals of macaques (the progenitors of *M. pagensis*, *M. siberu*, and the Sulawesi macaques). Selection could subsequently have become more relevant again if genetic introgression or the inability to establish themselves through competition prevented longtailed macaques from obtaining a foothold on these islands (Abegg, 2004; Abegg and Thierry, 2002). Less is known about the dispersal and colonisation of the remaining macaque species belonging to the *sinica* and *fascicularis* groups. However, considering the greater diversity of environments and climatic conditions these species occur in, it is likely that dispersal and dispersal ability conferred by some degree of adaptation to environmental variability played a bigger role than environmental vicariance in explaining their present distribution – at least more so than compared to their sister clade, the *silenus* group.

The findings in the present work provide support for adaptive differentiation in macaque body size in relation to the environment. 2B-PLS revealed a significant association between overall craniodental size, body size, and temperature: larger-bodied species occur in colder, more seasonal environments. Additional correlates of this pattern are a reduction in the percentage fruit in the diet, increased dietary breadth, and a weak tendency to occur at higher altitudes. The reduced rank regression showed that this pattern is associated with a latitudinal cline. It thus represents a classic Bergmann effect, the evolutionary response in body size to the pressure of thermoregulation in cold environments (Bergmann, 1847; Meiri and Dayan, 2003). After adjusting for phylogeny, the pattern remained, supporting its adaptive interpretation. These findings match the convergent pattern in craniofacial allometric size observed among macaques by Ito et al. (2014). Unfortunately, based on the present

results it is not possible to evaluate whether sympatric species in the Indochinese region diversified in allometric size through competitive exclusion and adaptive diversification by niche differentiation. Several of the eight species that co-occur in this region were either not (*M. arctoides*, *M. thibetana*, *M. leonina*) or not adequately (*M. assamensis*, *M. mulatta*) sampled in the present work. However, there is evidence of character displacement in the fourth premolars of the pigtailed (*M. nemestrina*) and longtailed macaque (*M. fascicularis*) from Borneo, Sumatra, and the Malay peninsula (Schroer and Wood, 2015b). Future work should focus on additional sampling of all the aforementioned eight species and test specific hypotheses of character displacement in sympatric pairs. The pattern of phenotypic differentiation can then also be compared with the pattern found among the allopatric species in insular Southeast Asia.

As discussed in detail above, the contrast in relative tooth size between the anterior and the posterior dentition, which explained the remaining covariance between macaque phenotypic and ecogeographical variation, is at least in accordance with an adaptive interpretation as well, in the light of the well-known, and evolutionarily relevant, link between tooth morphology and diet (Hillson, 2005; Ungar, 2010). Additional correlates of this pattern are restricted geographical ranges, narrow habitat breadth, low temperature and rainfall seasonality, high habitat productivity, a small percentage of leaves in the diet, and a strong association with an insular distribution. This strongly points to a larger anterior dentition associated with a tropical ecology, dominated by species that occur on islands and have small geographical ranges. From a cladistic point of view, scenarios 2a and 2b are equally parsimonious. 2b is more indicative of an adaptive origin, while 2a can also accommodate contingency. Based on the review above, chance events are likely to have played an important part in macaque evolution, especially during the first wave that gave rise to the *silenus* lineage. This clade counts 11 species, many of which are confined to deep-water islands (all Sulawesi macaques, and another two species from the Mentawai islands), suggesting a strong link between this clade's speciosity and the geographic and genetic isolation afforded by islands. The liontailed macaque (*M. silenus*) occurs in mainland India, but is postulated to have had a very restricted range during Plio-Pleistocene glaciations (Abegg, 2004). It is well known in population genetics that genetic drift is a powerful mechanism of changes in allele frequencies in small and isolated populations, even in the presence of selection (Hamilton, 2009; Hartl and Clark, 2007). Moreover, loss of genetic variance due to founder effects and the lack of gene flow with adjacent populations facilitate drift (Hamilton, 2009; Mayr, 1942; Slatkin, 1985). The ancestors of the liontailed macaque, the black crested (*M. nigra*), moor (*M. maura*), and booted macaques (*M. ochreata*), and possibly even of the pigtailed macaque (*M. nemestrina*)

in the present sample are likely to have experienced strong genetic drift relative to selection, leaving its mark on phenotypic variation.

Future research is needed to elucidate when a relatively larger anterior dentition evolved in macaque history and whether a scenario of adaptive or neutral evolution is more compatible with the data. It will be necessary to include data on dental measurements and dietary composition from *Mandrillus*, *Cercocebus*, *Lophocebus*, *Papio*, *Theropithecus*, and *Rungwecebus* in order to establish whether the trait is ancestral or derived in macaques. Incorporating data on European fossil macaques that are part of the African macaque lineage (represented by the extant Barbary macaque) will also be valuable in this exercise. The African papionins are well-known for their morphological homoplasies (e.g., Collard and Wood, 2000; Delson, 1975; Jolly, 1970; Szalay and Delson, 1979), and therefore further outgroup data (e.g., from the sister group to papionins, the cercopithecins) would also improve the analysis. Morphometric data such as the type collected in the present work is freely available in the PRIMO database (a NYCEP morphometric database). Ornstein-Uhlenbeck (OU) modelling and trait mapping will subsequently allow ancestral character states to be visualised, providing insight into ancestral and derived conditions of this trait in papionins (or even cercopithecines as a whole). Explicit hypotheses about trait evolution, such as the scenarios described above and any other that may follow from ancestral trait mapping techniques, can be tested by means of comparing a standard BM model (constant-rate evolution), a multivariate BM model (different rates of evolution on different branches; Smaers et al., 2016), and OU models of selection towards adaptive optima. The latter can incorporate an analysis of parallelism vs. convergence, which would be of interest here. Which model, and thus scenario, best describes the trait variation can be determined on the basis of information criteria (e.g., AIC, BIC). The proposed analysis will not only answer whether relatively large anterior teeth are likely to have an adaptive origin – exaptations are difficult to rule out –, it will elucidate regime shifts where they are likely to exist, which may include a pattern consistent with neutral evolution in the tropical *silenus* clade and a convergent pattern in the *sinica-fascicularis* clade, for example.

Overall, only limited phenotypic differentiation was detected between macaque species in relation to the diverse ecogeographical parameters in the dataset. More dimensions of phenotypic differentiation may have been expected, given the widespread view that macaques are ecologically diverse and show niche differentiation (Fa, 1989; Pan and Oxnard, 2004; Thierry, 2004). However, these results match previous morphological studies of macaque cranial variation, which have found similar results of limited to no differentiation between macaque species in cranial or craniofacial ontogenetic (e.g., Collard and O'Higgins, 2001;

Rook and O'Higgins, 2005; Singleton, 2012) and allometric patterns (e.g., Ito et al., 2014; Pan and Oxnard, 2002, 2004).

There are several, mutually non-exclusive possible explanations. First of all, evolutionary divergence and differentiation are not independent of time, and there may thus have been insufficient evolutionary time for macaques to differentiate to the extent that is observed in other, older mammalian lineages (discussed further in Section 8.4). Secondly, in this work I have focused only on the craniodental phenotype, which I have shown to be a strongly integrated and canalised phenotype in macaques (and likely all primates or indeed mammals). There are therefore only limited ways in which the dentition can vary, which affects the number of independent ecogeographical patterns that can statistically be detected. Apparently, the fact that additional cranial and mandibular measurements were included did not make a difference, but this is not surprising given the highly similar ontogenetic patterns of craniometric and craniofacial shape variation among macaques. However, an inspection of the contextual data of geographical distributions and ecological diversity shows a similar lack of differentiation. Without the need for any formal analysis, one can observe that considerable environmental (but not necessarily geographical) variation exists *within* species, not only *between* species. Of particular relevance here are those parameters that measure some range of variation, such as dietary and habitat breadth. Indeed, many macaque species are observed to occur in a similar range of different habitats, even if some of them tend to prefer a particular habitat. The same applies to the range of food items eaten. It seems, therefore, that a tendency to disproportionately use a particular resource (e.g., fruit, or primary forest) should not be confused with ecological specialisation and niche differentiation compared to other congeners. Such a tendency may simply reflect opportunism. Broadly speaking, across time and space, macaques have similar enough diets, habitats, and social behaviour for them to be under similar selection and therefore posses one and the same adaptive repertoire. The fact that no associations between craniodental variation and climate, altitude, longitude, latitude, and geographical distance were observed *within* macaques (see Chapter 6), is consistent with this idea. Further tentative support for this possibility comes from the low phylogenetic signal that was detected in macaque molars. Phylogenetic signal was comparatively low in both absolute and relative size of the molars. As discussed in Chapter 7, low phylogenetic signal may arise from phenotypic convergence (distantly related taxa share adaptations) or by chance (closely related taxa are no more phenotypically similar than they are to distantly related taxa). If, however, only very little phenotypic variation exists between taxa, phylogenetic signal will also be low. In future research, it would be interesting to investigate if macaques are under stabilising selection for a generalised phenotype that specifically enables these species to be so ecologically successful.

The present work primarily analysed interspecific variation by means of species averages. Another way to investigate differences between species is to analyse and compare the within-species patterns of variation. A detailed multivariate ecogeographical analysis *within* species was only possible for three out of the 13 species due to insufficient sample sizes for the remaining species, and inadequate geographical sampling across the full species' ranges. However, differences in the *levels* of intraspecific phenotypic variation may be related to specific environmental conditions (e.g., island occurrence, or diet), or the level of environmental variation itself may predict the range of phenotypic variation observed within species. We may ask if phenotypic variance accumulates with geographical range size, climatic variability, or the number of habitats occupied. The absence of an association between environmental and phenotypic variation would be consistent with the hypothesis that a morphologically generalised phenotype, which affords ecological flexibility and evolutionary success, is under stabilising selection.

Nevertheless, the limited number of associations between craniodental and detailed ecogeographical variation retrieved in this thesis, combined with previous findings about morphological growth patterns in macaques, so far suggest that there is less adaptation to different niches in macaques than previously assumed. This does not mean that selection and adaptation were not important at all in macaque evolution, but rather that neutral processes and chance may have had a more significant impact on the present taxonomic and phenotypic diversity of macaques than previously held. In macaques, diversity (species richness) is high compared to disparity (differentiation in morphospace).

A Comparison with Other Primate Groups

Macaques, together with the African papionins (baboons, gelada, mangabeys, crested mangabeys, kipunji, mandrills, and drills), form the tribe Papionini. Together with the guenons (*sensu lato*), tribe Cercopithecini, they constitute the Cercopithecinae, or cheek-pouch monkeys. To help interpret the macaque patterns of variation in geography, ecology, and morphology, a comparison with these other groups may be insightful.

The African papionins – as the name implies – are here referred to as all non-macaque, sub-Saharan papionin species. These include the 'baboon' genera *Mandrillus*, *Papio*, and *Theropithecus*, and the 'mangabey' genera *Cercocebus*, *Lophocebus*, and *Rungwecebus* (Mittermeier et al., 2013). They are the sister taxon to all macaques (Liedigk et al., 2014; Raaum et al., 2005), which means that they are directly comparable as the two lineages are equally old. As a group, African papionins are spread across sub-Saharan Africa (Jolly, 2007, and references therein). All mangabeys and *Mandrillus* species are reported to prefer closed, moist, evergreen or semi-deciduous forest across West-Central Africa (Jolly, 2007).

The gelada is confined to the grasslands of the Ethiopian highlands (Rowe, 1996), whereas savannah baboons (genus *Papio*) are spread across almost all of sub-Saharan Africa and occur in the widest range of habitats of all African papionins, including tropical, subtropical, and temperate forests, savannah, and even semidesert (Jolly, 2007, and references therein). *Papio* is regarded as the most omnivorous papionin (including macaques), whereas *Lophocebus* prefers to forage on fruits in the forest canopy and hardly descends to the forest floor (Rowe and Myers, 2011, and references therein). Its fallback foods include hard-shelled fruits and seeds (ibid.). *Mandrillus* and *Cercocebus* – sister taxa – are described as "forest-floor gleaners" because they specialise in fallen fruit, bark, fungi, small animals, and hard nuts, among others (Jolly, 1970). Lastly, gelada are specialised grazers of grasses, bulbs, roots, and rhizomes (ibid.).

It is well known that the African papionins show homoplasies in their morphology, obscuring their phylogenetic relationships (e.g., Collard and Wood, 2000; Delson, 1975; Jolly, 1970; Szalay and Delson, 1979), which, in the skull, can partly be explained by allometric effects (Collard and O'Higgins, 2001; Singleton, 2002) and developmental heterochrony (Leigh et al., 2003). These homoplasies are argued to be the result of convergent evolution for larger gapes, larger male canine size, and increased incisal bite forces in the savannah baboons and *Mandrillus*; and increased relative bite force and mechanical advantage at smaller body sizes to accommodate hard-object feeding in mangabeys (e.g., Ravosa, 1990; Singleton, 2005).

The cercopithecins, sister to African and Asian papionins, comprise the genera *Allenopithecus*, *Cercopithecus*, *Allochrocebus*, *Erythrocebus*, *Chlorocebus*, and *Miopithecus* (Mittermeier et al., 2013). The species that have 'guenon' in their common name are nowadays known to constitute a paraphyletic group, so instead I refer to all cercopithecins as guenons *sensu lato*, and the clade comprising *Cercopithecus*, *Allochrocebus*, *Erythrocebus*, and *Chlorocebus* as the guenons *sensu stricto* for the purpose of the present discussion. Guenons *sensu lato* are small to medium-sized monkeys and are taxonomically very rich (Groves, 2001; Mittermeier et al., 2013). All taxa are endemic to sub-Saharan Africa, although there are marked differences in range sizes (Mittermeier et al., 2013, and references therein). Cercopithecins predominantly occur in West-Central sub-Saharan Africa, although *Chlorocebus* extends into southern Africa (Mittermeier et al., 2013). Except for *Erythrocebus* and *Chlorocebus*, which occur in open or wooded savannah, all cercopithecins are forest-dwelling, albeit forests of different vegetation types (Enstam and Isbell, 2007, and references therein). Moreover, all are frugivorous, although there is considerable variation between and within taxa with respect to the proportion of fruit that makes up the diet (Enstam and Isbell, 2007), an indication of dietary flexibility. The talapoin monkey (genus *Miopithecus*)

for example, includes many insects and other arthropods in its diet (Rowe and Myers, 2011, and references therein). *Erythrocebus* and *Chlorocebus*, conversely, rely very little on fruit (Enstam and Isbell, 2007).

Guenons *sensu lato*, but especially guenons *sensu stricto*, are thus ecologically quite similar to each other. With regard to phenotypic diversity, they are best known for their marked differentiation in pelage colour and vocalisations (Enstam and Isbell, 2007; Kingdon, 1997), but also for their apparent homogeneity in skull form and craniodental characters (Verheyen, 1962 in Cardini and Elton, 2008a). Cardini and Elton (2008a) carried out a detailed geometric morphometric study of guenon cranial shape variation and found that guenon cranial shape varied almost exclusively along the line of allometry. Allometry was also found to be highly conserved in guenons (Cardini and Elton, 2008a,b), similar to New World monkeys (Marroig and Cheverud, 2005), and within macaques (Singleton, 2012), but unlike among the African papionins (Collard and O'Higgins, 2001; Singleton, 2002). Guenons *sensu stricto*, comprising the arboreal (*Cercopithecus*) and terrestrial (*Allochrocebus*, *Erythrocebus*, and *Chlorocebus*) subclades, are of similar age as *Macaca* (Tosi et al., 2005) and they are therefore comparable. Although the traits analysed differ between this thesis and the study carried out by Cardini and Elton (2008a), the main axis of phenotypic differentiation was represented by allometry in both groups (Cardini and Elton, 2008a; this thesis). Furthermore, only a small amount of size-free variation remained between species in both groups (Cardini and Elton, 2008a; this thesis). Guenon and macaque hard tissue differentiation may thus have primarily followed lines of least evolutionary resistance (LLER; Schluter, 1996a) defined by allometric variation, as in New World monkeys (Marroig and Cheverud, 2005). Limited observed change in directions orthogonal to the LLER may point to the role of genetic or developmental constraints (Marroig and Cheverud, 2005; Schluter, 1996a). However, such a constraint requires an explanation in itself. A lack of evolutionary time to overcome genetic or developmental constraints is not a plausible explanation. New World monkeys (NWM), which are separated by approximately 30 million years of evolution, certainly had enough time to diverge along non-LLER lines but only showed limited variation in those directions (Marroig and Cheverud, 2005). Furthermore, if natural selection in a direction away from the LLER is strong enough, it will succeed in pushing the phenotype in that direction (Hunt, 2007; Lande, 1979; Mitteroecker et al., 2012). The African papionins, which have an evolutionary history the length of that of macaques and comparable to that of guenons *sensu stricto* (i.e., 8 million years; Tosi et al., 2005), show dissociation of their allometric trajectories despite a shorter evolutionary history than NWM (Collard and O'Higgins, 2001; Singleton, 2002), but likely due to convergent evolution and therefore directional selection. Compared to the African papionins, guenons (*sensu stricto* but possibly also *sensu lato*) and

macaques may have experienced weak directional selection other than on body size, and instead been subject to drift or stabilising selection. The possibility of stabilising selection on a generalised phenotype in both guenons and macaques poses an interesting avenue for future research.

8.4 Macaques as an Adaptive Radiation: A Re-evaluation

Macaques are a successful radiation and are well known for their wide geographical distribution and ability to thrive in almost any environment, but might they qualify as an adaptive radiation? Although this question was not formally tested in this work, it is still possible to evaluate here. Taxonomic, ecological, and adaptive or phenotypic diversity are three classic hallmarks of adaptive radiations (Futuyma, 2013; Givnish, 1997). Macaques are taxonomically rich: there are up to 24 species of macaque recognised (depending on the classification), which is many for a young lineage (<10 MYA) of species with relatively long generation times. In fact, macaques are the most speciose group of that age among all primates (Arnold et al., 2010). Next, all macaques are semi-terrestrial. Although they encompass a wide range of niches and habitats, ecological diversity is greater within than between species, because many macaques occupy a range of similar habitats (Table B.2 in Appendix B). The main difference in habitat that exists between species was identified by Fooden (1982a) and is probably still the best classification of habitat differences between macaques: there are those macaques that mainly occur in and prefer broadleaf-evergreen (BE) forests, and those species that occur mainly in non-BE environments, with no obvious preference. This difference is especially pronounced in 'heartland' (continental Southeast) Asia where many macaque species are sympatric (but not sister taxa). However, the ecological segregation appears limited to those two broad habitat categories; within those groups there are no pronounced differences between species. As discussed, even when the two patterns that explain nearly all of macaque interspecific craniodental variation both reflect adaptive evolution, taxonomic diversity in macaques is not mirrored in their ecological and phenotypic differentiation. A study of other traits, such as pelage colour or sexually selected traits, may yield additional evidence of adaptive phenotypic diversification in macaques.

Gavrilets and Losos (2009) identified ten criteria that characterise adaptive radiations, the following of which can be (qualitatively) considered here for macaques: 1) an early burst of diversification, 2) decelerating rates of diversification ("overshooting"), and 3) nonallopatric speciation. Whether the macaque diversification pattern fits that of an explosive radiation or an early-burst pattern can be evaluated based on the macaque phylogeny in Figure 2.3 (Chapter 2). Dividing the history of the macaque lineage into time bands yields insight into

changes in diversification rates through time. From 9-7 MYA, there is an increase from two to three branches, from 7-5 MYA there is an increase from three to five branches, from 5-3 MYA the number of lineages increases from five to 15, and between 3 MYA and the present another six branching events occur (a total of 21 species in the phylogeny presented in Figure 2.3). At present, the pattern of speciation of macaques rather fits a late-burst model of evolution instead of an early-burst pattern. This also suggests that the rate of diversification has not decelerated throughout time, but rather accelerated until at least 3 MYA. This point in time matches fossil evidence for the arrival of macaques in Asia (Delson, 1980). Macaques are a young lineage and therefore the time scale inspected for evolutionary rate shifts may be too short. It is possible that macaques are still in the early stage of explosive radiation.

Another way to evaluate the rate of a taxon's radiation is to compare the diversification pattern of the sister taxon, because sister taxa share an exclusive common ancestor and are of equal age (Glor, 2010). When two sister groups consist of a species-poor clade and a species-rich clade, this can be a sign that the latter radiated extensively. A good example are the rodents (Rodentia) versus the lagomorphs (Lagomorpha: rabbits, hares, and pikas) (Blanga-Kanfi et al., 2009). With close to 2500 species recognised, rodents make up approximately 40% of all mammal species. Their sister taxon, lagomorphs, is very species-poor by comparison with only 92 species currently recognised (Wilson et al., 2016). The sister clade of macaques comprises the rest of the papionin tribe, the baboons, gelada, mangabeys, mandrills and drills (Arnold et al., 2010; Perelman et al., 2011; Springer et al., 2012).

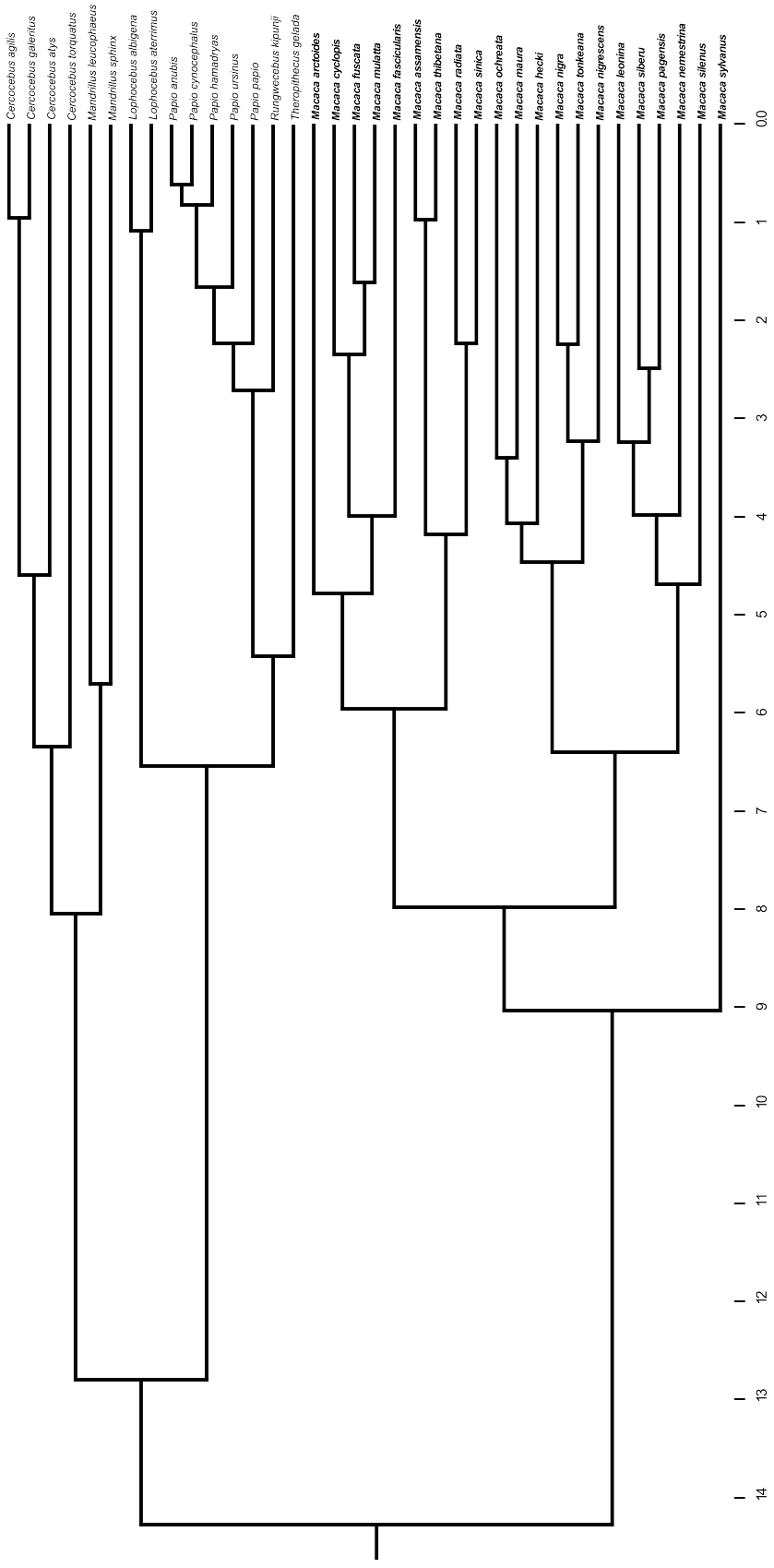


Fig. 8.4 Phylogenetic tree (chronogram) of the tribe Papionini (Arnold et al., 2010). Taxa in bold are *Macaca* (the bottom clade). Its sister taxon are all remaining African papionins (the top clade). The number of macaque species is a conservative estimate because it does not recognise recently discovered species as full species (*M. munzala* and *M. leucogenys*). The number of species in the papionin sister clade may be a more liberal estimate with each *Papio* 'morphospecies' recognised at the species level. Nonetheless, *Macaca* is more speciose than its sister clade, although not by much. The contrast becomes much greater when comparing the African macaque to the Asian macaque lineage.

Figure 8.4 shows that macaques are somewhat more speciose with 21 species (or as many as 24 depending on whether *M. brunnescens*, *M. munzala*, and *M. leucogenys* are valid species), compared to their sister taxon. The African, non-macaque papionins comprise 15 species. The latter is a generous estimate of African papionin diversity, as all the baboons are counted as individual species, even though some evidence suggests they are perhaps more appropriately classified as subspecies of a single species, *Papio hamadryas* (Zinner et al., 2009). Possibly then, the difference in taxonomic richness between macaques and the rest of the papionins is a bit larger still. But this is not such a striking difference to count as compelling evidence that macaques are exceptionally speciose. If, however, we compare the Asian macaques ($N = 20$) to the Barbary macaque (a single species) the discrepancy is pronounced. (The fact that all these species are commonly referred to as macaques does not preclude a comparison between sister clades within the group, as what we call groups is arbitrary; monophyly is not.) Fossil taxa complicate this picture. There are several known fossil macaques from the circum-Mediterranean region dating to the Pliocene and Pleistocene that are considered part of the *sylvanus* lineage (Delson, 1980). First of all, however, they are considered part of an anagenetic lineage leading up to *M. sylvanus* (Delson, 1980). Secondly, even if they should be considered separate species, the Asian macaque clade also included fossil taxa, albeit they are not as well known (Delson, 1980). Regardless of which node is used for the comparison between sister taxa, the time scale of papionin history is short and it is likely that sufficient time has not passed for stark macroevolutionary patterns to play out like those that can be detected at much larger time scales.

Geographical speciation, also known as allopatric speciation (Mayr, 1942), involves reproductive isolation coinciding with geographical isolation without the need for ecological differentiation, in contrast to ecological speciation (Rundell and Price, 2009; Schluter, 2000). First of all, it is reasonable to say that most (if not all) macaques occupy more or less the same ecological niche, namely that of a semi-terrestrial generalist primate. Furthermore, a review of the past biogeography of macaques revealed that much of the speciation in macaques has occurred in insular Southeast Asia where processes of chance (genetic drift, but also colonisation events that were likely successful by chance), disruption of gene flow, geographical isolation on islands and in habitat refugia due to environmental vicariance, have all likely had a major influence (Abegg, 2004; Abegg and Thierry, 2002; Eudey, 1980). The traditional view, however, was that macaque evolution was characterised by ecological competition (Fooden, 1976, 1980). As referenced above, the present sample of 13 macaques did not include enough species from mainland Asia where many of the species are sympatric and so mechanisms of competition and character displacement could not be tested here. The analyses carried out in this work do not provide conclusive support for adaptive differentiation

beyond the variation in body size. Although the relative tooth size contrast appears to be an adaptation to function, the observed phylogenetic signal may be the result of neutral evolution. Genetic drift is likely to have been a powerful mechanism in contracted or founder populations of macaques in refugia and on islands. It is plausible that geographical speciation has played an important role in at least part of macaque evolution. Geographical speciation has been proposed to be the dominant mode of speciation in nonadaptive radiations (Losos and Miles, 2002; Rundell and Price, 2009).

Thus, by these criteria there is not good evidence to suggest that macaques form an adaptive radiation. A few general but relevant points about identifying adaptive radiations are worth considering, however. The first point relates to age. Young radiations that have had comparatively little time to evolve and diversify may still be in the early stage of rapid diversification. Moreover, this may coincide with the stage of radiation that involves adaptation to the 'macrohabitat', whereas, by the narrow definition of adaptive radiation, adaptation to the 'microhabitat' should already have occurred (Gavrilets and Losos, 2009). If a clade is a true adaptive radiation (pattern), or it evolved by true adaptive radiation (process), then the time scale at which we inspect this clade (or part of it) should not affect it being a true adaptive radiation. Our ability to *identify* it as such, however, is clearly not independent of the evolutionary time scale. Time contributes to our *retrospective* ability to detect adaptive radiations by making the broad pattern stand out from a noisy background, but also by providing more opportunity for environments to change, ecological niches to open up, organisms to respond, and evolution to take place. Furthermore, after sufficient time and fine-tuning of the microhabitat and attendant phenotypic adaptations, sympatry may follow rather than precede it (Rundell and Price, 2009). In an ontological sense, however, whether something is an adaptive radiation or not should not depend on our ability to recognise it. This point can be illustrated with a thought experiment: take a known example of an adaptive radiation, such as the genus *Anolis*, a group of iguanian lizards (Losos, 2010). Anoles diverged from their last common ancestor between 125 and 65 MYA and currently consist of nearly 400 species (Nicholson et al., 2012). Imagine we had perfect knowledge of anole fossil taxa, including their ecology and phenotypes, and we knew the 'true' phylogenetic tree with accurate times of divergence. If we then were to move back in time across the tree towards the last common ancestor, regularly evaluating taxonomic diversity, ecological and phenotypic differentiation, sympatry, and changes in diversification rate, what would happen if we reached a point in the past (closer to the clade's origin in fact) where the anole radiation no longer satisfied the criteria for adaptive radiation? It could not have turned into a nonadaptive radiation. If a group is truly an adaptive radiation at present, it must have been so in the past, from the moment of the first divergence from the last common ancestor

onwards, and this must be true independent of our ability to recognise it. The other side of the coin is that there may be adaptive radiations that are presently undetected, because they can only be identified after the fact, when enough time has passed after an explosive burst of evolution, a subsequent deceleration in the diversification rate, and after successive stages of adaptation to the macrohabitat and choice of microhabitat.

The concept of adaptive radiation thus bears a strong resemblance to the species problem. It is obvious that Asian and African elephants are two different species, because they are separated by several millions of years, but going further and further back in time it will be increasingly difficult to recognise the two lineages as separate species, even though we presently know that the speciation process has taken place (Zachos, 2016). A crucial point in the species debate, one that is often overlooked, is that what makes a species is different from how a species can be identified (Zachos, 2016). The same applies to adaptive radiations.

Another point relates to species biology and ecological adaptation. By species biology, I mainly refer to body size and life history. Larger animals have slower life histories due to longer generation times and small litter size (Stearns, 1992). All things being equal, the tempo of evolution will be slower in larger animals compared to smaller animals. Moreover, larger animals take up more space. Due to their size and energy requirements larger animals, like catarrhine primates, occupy multiple parts of a macrohabitat; smaller animals, like anole lizards, may be able to colonise only a very particular structure (e.g., tree trunk, twigs, or undergrowth; Losos, 2010) that is large enough to sustain them, but this is not possible for many larger-bodied animals. This size effect is compounded by sociality and patchiness of food resources that require travel. Sociality is an adaptation to predation pressure (van Schaik, 1983) and resource defensibility (Wrangham, 1980) in primates, but group-living entails larger home ranges. Patchiness of resource distribution in time and space also leads to the occupation of a larger proportion of the macrohabitat. Such lifestyles are common among mammals but impede specialisation of and adaptation to microhabitats within a larger (macro)habitat. This may have a cascading effect on the likelihood that future descendants are able to differentiate and diversify in the way predicted by adaptive radiation theory (Gavrilets and Losos, 2009).

Ecological specialisation and generalisation can both be successful adaptive strategies, but the success rate of either strategy is probably not equally distributed among small and large-bodied taxa. For example, many small primates are able to specialise on an insectivorous diet, something that is energetically not sustainable for large-bodied primates (Kay, 1975; Lucas, 2004). Being able to subsist on a varied diet is an important contributing factor to the ability to persist in a variety of environments, which promotes dispersal ability and curbs extinction risk (Harcourt et al., 2002; Hernández Fernández and Vrba, 2005). Having

a more generalised digestive system (which the dentition is a part of) enables individuals to successfully subsist on fallback foods during times of resource scarcity, which can have important evolutionary relevance (Marshall and Wrangham, 2007). The same argument applies to other phenotypic traits (e.g., skeletal size and shape) that enable species to be ecologically flexible. More generalised phenotypes beget ecological versatility and the ability to exploit a variety of ecological niches. While there is a wide range of possible ecological specialisations, even between closely related taxa, the range of generalised ecological strategies and attendant adaptations is, by definition, much smaller because there is no or limited resource partitioning. Thus, placing emphasis on a pattern of adaptive diversification between closely related species might favour old lineages of specialised, small-bodied taxa. Many primates (especially monkeys, apes, and humans), but also members of the mammalian families Canidae (especially the genera *Canis* and *Vulpes*, that include wolves and red foxes), Ursidae (bears), and Muridae (*Rattus* and *Mus*, rats and mice) are very widespread, extremely ecologically flexible and successful. Within these groups, however, individual species are lacking in apomorphies. According to adaptive radiation theory, such groups probably do not qualify as adaptive, but as nonadaptive radiations due to the lack of niche and phenotypic differentiation (Gavrilets and Losos, 2009; Losos and Miles, 2002; Rundell and Price, 2009).

Furthermore, the criteria devised to detect adaptive radiations may in themselves be based on, and therefore biased towards, the traditional examples of adaptive radiations. Classic examples such as *Anolis* lizards, Darwin's finches, East African cichlids have been well-studied, but are all examples of small-bodied animals.

On the one hand, defining what constitutes an adaptive radiation and what does not seems useful as it helps disentangle an otherwise very broad and muddy concept that either applies to the entire tree of life or to none of it. Within the framework of adaptive radiation theory (which propagates the narrowly defined view of adaptive radiations), it is not implied that nonadaptive radiations have not undergone adaptive evolution, or that 'allospecies' do not differ phenotypically in relation to small variations (e.g., climatic) in their habitat (Losos and Miles, 2002; Rundell and Price, 2009). As a result of this 'allowance', the distinction between adaptive and nonadaptive radiations may seem like a semantic one, but it is not (Losos and Miles, 2002). Adaptive radiations are argued to have evolved by a special set of processes, notably natural selection and ecological (sympatric) speciation, to produce a specific pattern of diversity (Gavrilets and Losos, 2009; Glor, 2010; Losos and Miles, 2002; Rundell and Price, 2009; Schluter, 2000). As I have tried to argue, however, is that what this specific pattern of diversity looks like is biased (or at risk of being biased) by a number of factors, namely evolutionary time passed, body size, and ecological specialisation (and possibly there are more). This bias is exacerbated by the fact that as workers in a historical

science we must work backwards and infer processes from patterns, but in doing so, we easily conflate detection – and criteria to enable detection – of the pattern as the relevant set of evolutionary processes and conditions that we are trying to uncover in the first place. In other words, we would be reifying adaptive radiations. The following quote provides a case in point: "The definition that we use here emphasizes allopatry [...] as the criterion of nonadaptive radiation, because it is unambiguous" (Rundell and Price, 2009, p. 396). Finally, usage of the terms 'adaptive' and 'nonadaptive radiations', as well as the underlying processes implied by these terms, creates a false dichotomy out of a continuum of complex combinations of evolutionary processes and conditions and accompanying macroevolutionary patterns. As discussed, they appear to be rate and/or time-dependent phenomena and are better used as a classificatory tool.

8.5 Conclusion

The aim of the present work was to investigate the impact of the varying environmental conditions on the taxonomic and phenotypic diversification of a geographically widespread and ecologically successful Old World primate genus, the macaques (Cercopithecidae: *Macaca*). To this end, the relationship between geography, ecology, and evolutionary phenotypic variation among macaques was investigated. The dentition, as a functionally relevant and heritable phenotype, served as the analytical proxy for the evolutionary outcome of a complex combination of evolutionary constraints, conditions, and causes. In order to better understand the effect of past environmental conditions, developmental constraints to phenotypic variation – and thus evolution – were analysed, as were allometric effects. These were investigated within and between species in order to compare and understand how population-level processes govern evolutionary divergence. Where relevant, phylogeny was statistically accounted for or specifically discussed in relation to the observed evolutionary variation.

The findings in this work support five broad conclusions. First, the dentition is a strongly phenotypically integrated structure inside the cranium and mandible. Allometry is a major integrating factor and dominates the variance of, and covariance between, teeth, within as well as between species. Evolutionary diversification of the macaque craniodental phenotype has first and foremost occurred along what is likely a common allometric trajectory, the line of least evolutionary resistance (LLER).

Second, this axis of main phenotypic divergence reflects adaptive differentiation in macaque body size, which occurred mainly in response to temperature and seasonality. A latitudinal cline in craniodental size accompanies this ecological pattern. The present findings

thus corroborate the existence of a classic Bergmann effect on the evolution of macaque body size. Furthermore, it cannot be explained by a pattern of common descent, which provides support for adaptation and convergent evolution driven by climatic conditions in macaque body size.

Third, compared to climate, macaques exhibit a lesser degree of phenotypic differentiation in response to resource ecology. An antero-posterior tooth size contrast exists in the relative size of the macaque dentition. Relative to body size, the anterior dentition (consisting of the incisors and the canines) is large in macaques that are mostly frugivorous and which live in less variable, tropical habitats. Relative to body size, and relative to the anterior dentition, postcanine teeth (the premolars and the molars) are larger in macaques that are comparatively more folivorous, and which live in more variable, temperate habitats, with larger geographical ranges. The differentiation between macaques appears to be concentrated in the relative size of the anterior dentition; relative postcanine occlusal area did not differ between frugivorous and more folivorous macaques. The above association provides a link between the functional properties of the dentition and primate resource ecology. However, it also bears a resemblance to the pattern of common descent in macaques, complicating its interpretation in an adaptive context.

Fourth, the strong phylogenetic signal in the incisors and the canines drives the correlation between phylogeny and the pattern associating relative tooth size and diet. Different evolutionary scenarios exist with respect to the origin of a large anterior dentition and with regard to the underlying processes responsible for its evolution. Whether it is characterised by adaptation, neutral evolution, or a combination of both will have to be resolved in future research using additional data and specialised methodologies testing hypotheses of trait evolution.

Finally, underlying the relative tooth size contrast is a modular pattern of integration in the macaque dentition. The postcanine dentition forms a strongly integrated module to the exclusion of the anterior teeth, which form a separate (albeit less strongly integrated) module of their own. A comparison of the phenotypic integration pattern in macaques with the genetic integration pattern in baboons suggests that this modularity is genetic and that the two parts of the dentition may therefore be partly uncoupled during evolution. Uncoupled evolution, at least along the non-LLER trajectory, is evinced by the macroevolutionary antero-posterior tooth size contrast (discussed above) as well as by the stark differences in phylogenetic signal detected in the anterior versus the posterior teeth. The latter observation further supports that different processes may have operated in the anterior and the posterior dentition during the evolution of *Macaca*.

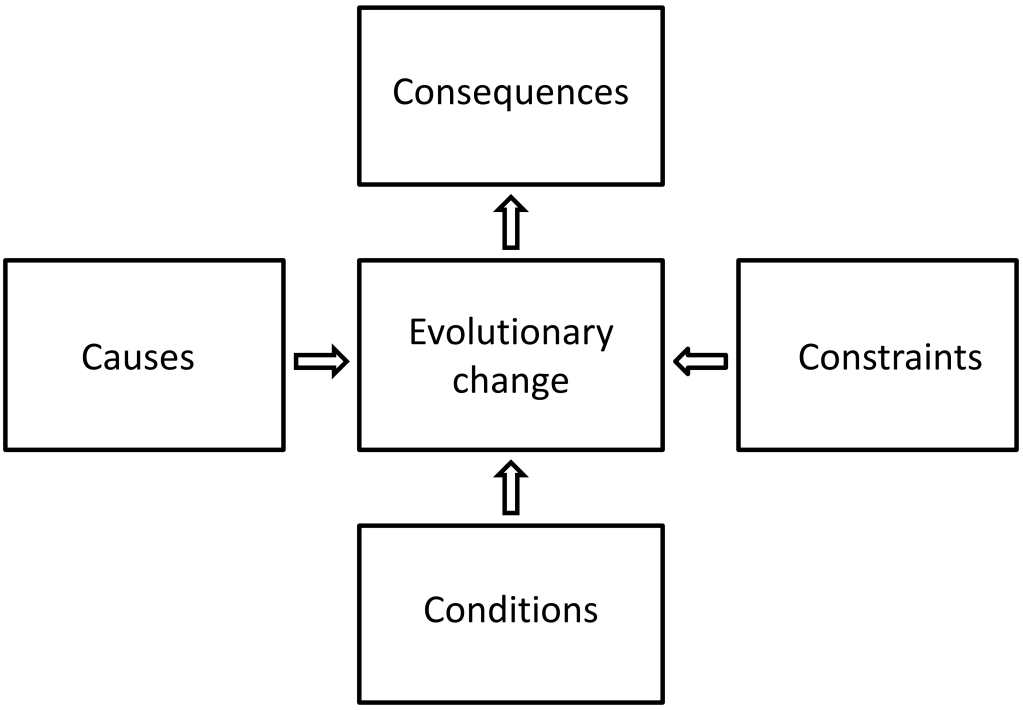


Fig. 8.5 Diagrammatic illustration of the different levels of explanation, or components, of the evolution of diversity (the 4 C's). One or several *causal mechanisms*, such as drift or natural selection, bring about the change in allelic frequency and adjust the phenotypic distribution of a trait in the population; *constraints* channel evolutionary change in a particular direction and help determine its magnitude; and the environmental *conditions* determine the impetus for change. Evolutionary *change* is the result of the complex interplay of these three components, and they have *consequences* for the organism, which in time will influence the conditions, causes, and constraints underlying further evolutionary change. Adapted from Foley (1995).

It is generally difficult to ascertain the exact contribution of natural selection versus neutral processes on the origin of phenotypic diversity. But the underlying causes (i.e., evolutionary mechanisms) are only part of understanding patterns of diversity (see Figure 8.5). In the present work, I have shown how macaque evolutionary craniodental variation is structured by population-level constraints arising from the genotype and the developmental system, as well as from possible phylogenetic constraints due to common descent. I have also elucidated the role of various environmental conditions in explaining variation in macaque craniodental morphology. Future research should be aimed at broadening the taxonomic scope to include craniodental variation of the African papionins and cercopithecins in order to put the observed macaque patterns in a broader evolutionary context.

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Appendix A

Specimen Catalogue

Table A.1 Abbreviations of museum names, including number of specimens measured (in parentheses), and associated accession prefixes.

Abbreviation	Museum	Accession prefix
MNB	Museum für Naturkunde, Berlin (95)	BZM_MAM_
MNHN	Muséum National d'Histoire Naturelle , Paris (65)	MNHN/ZM/
NHM	The Natural History Museum, London (202)	ZD. or ZE.
NMNH	National Museum of Natural History, Washington, DC (129)	USNM.
NMW	Naturhistorisches Museum, Vienna (47)	NMW.
RCS	Royal College of Surgeons of England, London (57)	RCSOM/
RMNH	Naturalis Biodiversity Center, Leiden (103)	RMNH.MAM. or ZMA.MAM.
SMF	Naturmuseum Senckenberg, Frankfurt (46)	SMF.

Table A.2 Catalogue of specimens used in this study.

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. assamensis	*assamensis*	ZD. 1950.384	Ad	M	1	Taron Valley, Upper Burma
M. assamensis	*assamensis*	ZD. 1950.385	Ad	M	1	Htingnan, Triangle, Upper Burma
M. assamensis	*assamensis*	ZD. 1950.386	Ad	M	1	Goletu, Upper Burma
M. assamensis	*assamensis*	ZD.1862.8.18.1	Sub-ad	M	1	Lao Mountains, Laos
M. assamensis	*assamensis*	ZD.1921.8.2.3	Ad	M	1	Mokokchung, Naga Hills, India
M. assamensis	*assamensis*	ZD.1921.8.2.4	Ad	F	1	Mokokchung, Naga Hills, India
M. assamensis	*assamensis*	ZD.1933.4.1.18	Ad	F	1	Chapa, Tonkin, N. Vietnam
M. assamensis	*assamensis*	ZD.1955.1507	Sub-ad	F	1	H'me Kom, Me Puan, Thailand
M. assamensis	*pelops*	ZD.1845.1.8.4	Ad	M	1	Nepal
M. assamensis	*pelops*	ZD.1879.11.21.303	Ad	F	1	Nepal
M. assamensis	*pelops*	ZD.1915.9.1.2	Ad	M	1	Chunthang, Sikkim, India
M. assamensis	*pelops*	ZD.1915.9.1.3	Ad	M	1	Sukiapokhri, Darjeeling, W. Bengal, India
M. assamensis	*pelops*	ZD.1915.9.1.4	Ad	M	1	Sukiapokhri, Darjeeling, W. Bengal, India
M. assamensis	*pelops*	ZD.1915.9.1.5	Juv	F	1	Sukiapokhri, Darjeeling, W. Bengal, India

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. assamensis	*pelops*	ZD.1925.1.1.1	Ad	F	1	Gopaldhara, Rungbong Valley, Darjeeling, W. Bengal, India
M. assamensis	*pelops*	ZD.1937.3.24.10	Ad	M	1	R. Tebang, Mishmi Hills, Assam, India
M. assamensis	*pelops*	ZD.1937.3.24.11	Ad	M	1	R. Tebang, Mishmi Hills, Assam, India
M. assamensis	*pelops*	ZD.1937.3.24.8	Ad	M	1	Balasia, Tonglu, Darjeeling, W. Bengal, India
M. assamensis	*pelops*	ZD.1937.3.24.9	Ad	M	1	Pashok, Darjeeling, W. Bengal, India
M. cyclopis		BZM_MAM_48984	Sub-ad	F	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_48985	Ad	F	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_48986	Ad	M	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_48987	Sub-ad	F	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_48990	Ad	F	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_48991	Sub-ad	F	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_48992	Ad	M	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_48993	Ad	F	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_48994	Ad	M	1	Teraso, Formosa, Taiwan

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. cyclopis		BZM_MAM_48995	Ad	M	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_48996	Ad	M	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_48997	Ad	M	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_48998	Ad	M	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_48999	Ad	F	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_49000	Sub-ad	F	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_49076	Ad	F	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_49077	Ad	F	1	Teraso, Formosa, Taiwan
M. cyclopis		BZM_MAM_49078	Ad	F	1	Teraso, Formosa, Taiwan
M. fascicularis	*fascicularis*	USNM.141145	Ad	F	1	Tarussan Bay, Sumatra
M. fascicularis	*fascicularis*	USNM.141371	Ad	M	1	Samasama Island, Nias Islands, off N.W. Sumatra
M. fascicularis	*fascicularis*	USNM.141372	Ad	M	1	(Le) Lafau, Nias Island, off W. Sumatra
M. fascicularis	*fascicularis*	USNM.143582	Ad	M	1	Rupat Tinggi, Bengkalis Island, off E. Sumatra
M. fascicularis	*fascicularis*	USNM.143583	Ad	M	1	Padang Island, E. Sumatra

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. fascicularis	*fascicularis*	USNM.144419	Ad	M	1	Bulan Island, Riau Archipelago, Kepulauan Riau, off Sumatra
M. fascicularis	*fascicularis*	USNM.175896	Ad	F	1	Sebatik Island, East Kalimantan, off N.E. Borneo
M. fascicularis	*fascicularis*	USNM.196813	Ad	M	1	Mahakam River, East Kalimantan, Borneo
M. fascicularis	*fascicularis*	USNM.196815	Ad	M	1	Lo Bon Bon, Borneo
M. fascicularis	*fascicularis*	USNM.196816	Ad	F	1	Karang Mumus River, Kampung Selili, Borneo
M. fascicularis	*fascicularis*	USNM.196817	Ad	F	1	Berau River (n. Bank), Borneo
M. fascicularis	*fascicularis*	USNM.196818	Juv	M	1	Berau River (n. Bank), Borneo
M. fascicularis	*fascicularis*	USNM.196819	Sub-ad	F	1	Berau River (n. Bank), Borneo
M. fascicularis	*fascicularis*	USNM.196822	Juv	M	1	Berau River (n. Bank), Borneo
M. fascicularis	*fascicularis*	USNM.196824	Ad	F	1	Karang Tigan River, Bulungang, N. Kalimantan, Borneo
M. fascicularis	*fascicularis*	USNM.196826	Ad	M	1	Mahakam River, East Kalimantan, Borneo

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. fascicularis	*fascicularis*	USNM.196827	Ad	F	1	Gusong Djerong, Borneo
M. fascicularis	*fascicularis*	USNM.198300	Ad	M	1	Sungai Karangan, Borneo
M. fascicularis	*fascicularis*	USNM.198301	Ad	M	1	Sungai Karangan, Borneo
M. fascicularis	*fascicularis*	USNM.199183	Ad	M	1	Sungai Djambajan, Kalimantan Timur, Borneo
M. fascicularis	*fascicularis*	USNM.292555	Ad	M	1	Mt. Kinabalu, Bundu Tuhan, Sabah, Borneo
M. fascicularis	*fascicularis*	USNM.292558	Ad	M	1	Mt. Kinabalu, Bundu Tuhan, Sabah, Borneo
M. fascicularis	*fascicularis*	USNM.317191	Ad	M	1	Ranau, Borneo
M. fascicularis	*fascicularis*	USNM.344989	Sub-ad	F	2	Captive (but wild-caught in Sabah, Borneo)
M. fascicularis	*fascicularis*	USNM.344990	Ad	M	2	Captive (but wild-caught in Sabah, Borneo)
M. fascicularis	*fascicularis*	USNM.521837	Ad	M	1	Hantakan, Kalimantan Selatan, Borneo
M. fascicularis	*fascicularis*	USNM.521838	Sub-ad	M	1	Telang, S. Kalimantan, Borneo
M. fascicularis	*fascicularis*	BZM_MAM_38543	Ad	M	1	S.E. Borneo, Indonesia

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. fascicularis	*fascicularis*	BZM_MAM_48465	Ad	F	1	La Datu, Borneo
M. fascicularis	*fascicularis*	BZM_MAM_48486	Ad	M	1	Zamboanga, Mindanao, Philippines
M. fascicularis	*fascicularis*	BZM_MAM_48494	Ad	M	1	Kari Orang, S.E. Borneo
M. fascicularis	*fascicularis*	BZM_MAM_48497	Ad	F	1	Luzon, Philippines
M. fascicularis	*fascicularis*	BZM_MAM_49090	Ad	F	1	Pagansan, E. Sumatra
M. fascicularis	*fascicularis*	BZM_MAM_49091	Sub-ad	F	1	Pagansan, E. Sumatra
M. fascicularis	*fascicularis*	BZM_MAM_49098	Sub-ad	F	1	Pagansan, E. Sumatra
M. fascicularis	*fascicularis*	BZM_MAM_49099	Ad	F	1	Siak (Copatta?), Sumatra
M. fascicularis	*fascicularis*	BZM_MAM_49100	Ad	F	1	Pap-ka, E. Sumatra
M. fascicularis	*fascicularis*	BZM_MAM_5442	Ad	M	1	Luzon, Philippines
M. fascicularis	*fascicularis*	BZM_MAM_92132	Sub-ad	M	1	Moltis, Timor, Lesser Sunda Islands
M. fascicularis	*fascicularis*	BZM_MAM_92309	Ad	F	1	Wawo, Sapeh, Soembawa, Lesser Sunda Islands, Indonesia
M. fascicularis	*fascicularis*	SMF.1026	Ad	F	1	Sumbawa (island), Nusa Tenggara Barat, Indonesia
M. fascicularis	*fascicularis*	SMF.1043	Sub-ad	F	1	Bengal, N.E. India

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. fascicularis	*fascicularis*	SMF.16629	Ad	M	1	Nusa Tenggara Barat, Indonesia
M. fascicularis	*fascicularis*	SMF.16630	Ad	F	1	Nusa Tenggara Timur, Indonesia
M. fascicularis	*fascicularis*	SMF.16631	Ad	M	1	Nusa Tenggara Barat, Indonesia
M. fascicularis	*fascicularis*	SMF.16632	Sub-ad	F	1	Gitgit, Bali
M. fascicularis	*fascicularis*	SMF.2501	Ad	F	3	Zool. Soc. Frankfurt
M. fascicularis	*fascicularis*	SMF.47977	Ad	F	1	Marak Island, off W. Sumatra
M. fascicularis	*fascicularis*	USNM.19192	Sub-ad	M	1	Kinabatangan River, Sabah, Borneo
M. fascicularis	*fascicularis*	USNM.19193	Ad	F	1	Kinabatangan River, Sabah, Borneo
M. fascicularis	*fascicularis*	USNM.83944	Ad	M	1	Mount Salikan, Sarawak, Borneo
M. fascicularis	*fascicularis*	USNM.101638	Juv	F	1	Benua Island, Tambelan Islands, Kepulauan Riau, Indonesia
M. fascicularis	*fascicularis*	USNM.101666	Ad	F	1	Benua Island, Tambelan Islands, Kepulauan Riau, Indonesia
M. fascicularis	*fascicularis*	USNM.113169	Ad	M	1	Indragiri River, E. Sumatra
M. fascicularis	*fascicularis*	USNM.114408	Ad	M	1	Tuangku Island (Pulo), Banjak Islands, Aceh, off W. Sumatra

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. fascicularis	*fascicularis*	USNM.114410	Ad	M	1	Tuangku Island (Pulo), Banjak Islands, Aceh, off W. Sumatra
M. fascicularis	*fascicularis*	USNM.114411	Ad	M	1	Tuangku Island (Pulo), Banjak Islands, Aceh, off W. Sumatra
M. fascicularis	*fascicularis*	USNM.114505	Ad	M	1	Tapanuli Bay, N. Sumatra
M. fascicularis	*fascicularis*	USNM.114506	Ad	M	1	Tapanuli Bay, N. Sumatra
M. fascicularis	*fascicularis*	USNM.114643	Sub-ad	M	1	Tuangku Island (Pulo), Banjak Islands, Aceh, off W. Sumatra
M. fascicularis	*fascicularis*	USNM.121802	Sub-ad	F	1	Tana Bala Island (Tahnabala), Batu Islands, N. Sumatra
M. fascicularis	*fascicularis*	USNM.121803	Ad	M	1	Tana Bala Island (Tahnabala), Batu Islands, N. Sumatra
M. fascicularis	*fascicularis*	USNM.121836	Ad	M	1	Tana Masa Island (Tanahmasa), Batu Islands, N. Sumatra
M. fascicularis	*fascicularis*	USNM.121868	Ad	M	1	Nias Island, off W. Sumatra
M. fascicularis	*fascicularis*	USNM.121869	Ad	F	1	Nias Island, off W. Sumatra
M. fascicularis	*fascicularis*	USNM.121872	Ad	M	1	Siaba Bay, Nias Island, off W. Sumatra

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. fascicularis	*fascicularis*	USNM.121873	Ad	M	1	Siaba Bay, Nias Island, off W. Sumatra
M. fascicularis	*fascicularis*	USNM.121874	Ad	F	1	Siaba Bay, Nias Island, off W. Sumatra
M. fascicularis	*fascicularis*	USNM.122848	Ad	F	1	Great Karimun Island, off E. Sumatra
M. fascicularis	*fascicularis*	USNM.122849	Ad	M	1	Great Karimun Island, off E. Sumatra
M. fascicularis	*fascicularis*	USNM.123147	Sub-ad	M	1	Kateman River, E. Sumatra
M. fascicularis	*fascicularis*	USNM.123990	Ad	F	1	Pulo Terutao, Thailand
M. fascicularis	*fascicularis*	USNM.123991	Ad	M	1	Pulo Terutao, Thailand
M. fascicularis	*fascicularis*	USNM.123992	Ad	F	1	Pulo Terutao, Thailand
M. fascicularis	*fascicularis*	USNM.124710	Ad	M	1	Tanjong Rensam, Bangka Island, off E. Sumatra
M. fascicularis	*fascicularis*	USNM.124969	Ad	M	1	Tanjung Batu, Belitung, E. Sumatra
M. fascicularis	*fascicularis*	USNM.124970	Ad	M	1	Tanjung Batu, Belitung, E. Sumatra
M. fascicularis	*fascicularis*	USNM.125102	Ad	M	1	Telok Pai, Karimata Island, West Kalimantan, off Borneo
M. fascicularis	*fascicularis*	ZD.1894.6.12.13	Ad	F	1	Mouth of R. Baram, Sarawak, Borneo

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. fascicularis	*fascicularis*	ZD.1910.4.5.20	Ad	F	1	Moera Tewe (Muaratewe), R. Barito, S. Borneo, Kalimantan
M. fascicularis	*fascicularis*	ZD.1910.4.5.23	Ad	F	1	Boentok (Buntok), R. Barito, S. Borneo
M. fascicularis	*fascicularis*	ZD.1951.66	Ad	F	1	Kulalong or Belaga, Sarawak, Borneo
M. fascicularis	*fascicularis*	ZD.1951.68	Ad	F	1	Kulalong or Belaga, Sarawak, Borneo
M. fascicularis	*fascicularis*	ZD.1951.70	Sub-ad	F	1	Kulalong or Belaga, Sarawak, Borneo
M. fascicularis	*fascicularis*	ZD.1955.710	Sub-ad	M	1	Entawa, Samarahan, Sarawak, Borneo
M. fascicularis	*fusca*	USNM.114162	Ad	F	1	Simeulue, Aceh, off W. Sumatra
M. fascicularis	*fusca*	USNM.114163	Ad	M	1	Simeulue, Aceh, off W. Sumatra
M. fascicularis	*fusca*	USNM.114165	Ad	F	1	Simeulue, Aceh, off W. Sumatra
M. fascicularis	*fusca*	USNM.114166	Ad	F	1	Simeulue, Aceh, off W. Sumatra
M. fascicularis	*fusca*	USNM.121511	Ad	M	1	Simeulue, Aceh, off W. Sumatra
M. fascicularis	*fusca*	USNM.121512	Ad	M	1	Simeulue, Aceh, off W. Sumatra
M. fascicularis	*fusca*	USNM.121513	Ad	F	1	Simeulue, Aceh, off W. Sumatra
M. fuscata	?	BZM_MAM_12957	Ad	F	3	Zoo (Japan)
M. fuscata	?	BZM_MAM_135	Ad	M	1	Japan

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. fuscata	?	BZM_MAM_25548	Sub-ad	F	3	Japan
M. fuscata	?	BZM_MAM_32430	Ad	F	2	Zoo (but wild-caught)
M. fuscata	?	BZM_MAM_48925	Ad	M	1	Nikko, Japan
M. fuscata	?	BZM_MAM_7739	Ad	M	3	Japan
M. fuscata	?	BZM_MAM_84817	Ad	F	3	Japan
M. fuscata	?	BZM_MAM_84820	Ad	M	3	Japan
M. fuscata	?	BZM_MAM_84821	Sub-ad	M	3	Japan
M. fuscata	?	MNHN/ZM/AC-1995-287	Ad	M	3	Menagerie
M. fuscata	?	MNHN/ZM/MO-1886-101	Ad	M	0	
M. fuscata	?	MNHN/ZM/MO-1962-1440	Ad	M	0	
M. fuscata	?	NMW.52357	Ad	F	1	Japan
M. fuscata	?	NMW.52360	Sub-ad	F	1	Japan
M. fuscata	?	NMW.52361	Ad	F	1	Japan
M. fuscata	?	RMNH.MAM.1726	Ad	M	3	Rotterdam zoo
M. fuscata	?	RMNH.MAM.3893	Juv	F	1	Japan
M. fuscata	?	RMNH.MAM.493	Ad	M	3	Rotterdam zoo

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. fuscata	?	ZD.1842.1.19.95	Ad	M	1	Japan
M. fuscata	?	ZD.1850.8.15.2	Sub-ad	F	1	Japan
M. fuscata	?	ZD.1873.11.5.9	Sub-ad	F	1	Japan
M. fuscata	?	ZMA.MAM.2277	Ad	M	0	
M. fuscata	?	ZMA.MAM.2340	Ad	M	0	
M. fuscata	*fuscata*	BZM_MAM_48926	Ad	F	1	Yedo, Japan
M. fuscata	*fuscata*	BZM_MAM_48927	Ad	F	1	Nikko, Japan
M. fuscata	*fuscata*	BZM_MAM_48928	Ad	F	1	Nikko, Japan
M. fuscata	*fuscata*	BZM_MAM_48929	Ad	F	1	Yedo, Japan
M. fuscata	*fuscata*	BZM_MAM_48930	Ad	F	1	Yedo, Japan
M. fuscata	*fuscata*	BZM_MAM_48932	Ad	M	1	Nikko, Japan
M. fuscata	*fuscata*	BZM_MAM_48933	Ad	M	1	Nikko, Japan
M. fuscata	*fuscata*	BZM_MAM_48934	Ad	M	1	Nikko, Japan
M. fuscata	*fuscata*	BZM_MAM_48936	Ad	M	1	Yedo, Japan
M. fuscata	*fuscata*	BZM_MAM_48937	Ad	M	1	Nikko, Japan
M. fuscata	*fuscata*	BZM_MAM_48938	Ad	F	1	Yedo, Japan

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. fuscata	*fuscata*	BZM_MAM_5982	Ad	M	1	Yedo, Japan
M. fuscata	*fuscata*	MNHN/ZM/MO-1887-16	Ad	M	1	Fuji-Yama, Japan
M. fuscata	*fuscata*	ZD.1906.1.4.1	Juv	M	1	Jinrio, Tokushima Ken, Shikoku, Japan
M. fuscata	*fuscata*	ZD.1906.1.4.2	Ad	F	1	Jinrio, Tokushima Ken, Shikoku, Japan
M. fuscata	*fuscata*	ZD.1906.1.4.3	Ad	F	1	Jinrio, Tokushima Ken, Shikoku, Japan
M. fuscata	*fuscata*	ZD.1939.1050	Ad	M	1	Japan
M. fuscata	*yakui*	ZD.1905.11.3.1	Ad	M	1	Yakushima, Osumi Is., Liu Kiu Is., Japan
M. fuscata	*yakui*	ZD.1905.11.3.2	Ad	M	1	Yakushima, Osumi Is., Liu Kiu Is., Japan
M. fuscata	*yakui*	ZD.1905.11.3.3	Ad	M	1	Yakushima, Osumi Is., Liu Kiu Is., Japan
M. fuscata	*yakui*	ZD.1905.11.3.4	Ad	F	1	Yakushima, Osumi Is., Liu Kiu Is., Japan
M. fuscata	*yakui*	ZD.1905.11.3.5	Ad	F	1	Yakushima, Osumi Is., Liu Kiu Is., Japan
M. maura		BZM_MAM_13016	Ad	M	2	Zoo (but wild-caught)
M. maura		BZM_MAM_13257	Ad	F	2	Zoo (but wild-caught)
M. maura		BZM_MAM_15660	Ad	M	2	Zoo (but wild-caught)
M. maura		BZM_MAM_15909	Ad	M	2	unknown, wild-caught
M. maura		BZM_MAM_20406	Juv	F	2	Zoo (but wild-caught)

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. maura		BZM_MAM_26246	Juv	M	2	Aquarium (but wild-caught)
M. maura		BZM_MAM_26247	Sub-ad	M	3	Hamburg Zoo
M. maura		BZM_MAM_26248	Juv	M	2	Aquarium (but wild-caught)
M. maura		BZM_MAM_26249	Sub-ad	F	2	Aquarium (but wild-caught)
M. maura		BZM_MAM_26251	Juv	M	2	Zoo (but wild-caught)
M. maura		BZM_MAM_48921	Ad	M	0	
M. maura		BZM_MAM_7735	Ad	M	2	Zoo (but wild-caught)
M. maura		MNHN/ZM/AC-1894-24	Juv	M	3	Menagerie
M. maura		NMW.737/B.4039	Ad	F	3	Vienna zoo
M. maura		NMW.739	Ad	F	3	Vienna zoo
M. maura		NMW.770	Ad	M	1	Sulawesi, Indonesia
M. maura		RMNH.MAM.1009	Ad	M	1	Makassar, S.W. Sulawesi
M. maura		RMNH.MAM.1580	Ad	F	1	Makassar, S.W. Sulawesi, Indonesia
M. maura		RMNH.MAM.3383	Sub-ad	M	1	Borneo
M. maura		RMNH.MAM.3398	Ad	M	0	
M. maura		RMNH.MAM.53194	Sub-ad	M	1	Borneo

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. maura		RMNH.MAM.53195	Ad	F	1	Borneo
M. maura		RMNH.MAM.53196	Juv	M	0	
M. maura		RMNH.MAM.53198	Sub-ad	M	0	
M. maura		RMNH.MAM.53200	Sub-ad	F	0	
M. maura		RMNH.MAM.53201	Sub-ad	M	2	Rotterdam zoo (but wild-caught in Makassar, S.W. Sulawesi)
M. maura		RMNH.MAM.53202	Ad	M	0	
M. maura		RMNH.MAM.53203	Ad	M	3	
M. maura		RMNH.MAM.53204	Ad	M	0	
M. maura		RMNH.MAM.53205	Sub-ad	M	2	Rotterdam zoo (but wild-caught in Makassar, S.W. Sulawesi)
M. maura		RMNH.MAM.53209	Ad	M	0	
M. maura		RMNH.MAM.810	Ad	F	1	Makassar, S.W. Sulawesi
M. maura		RMNH.MAM.855	Sub-ad	F	2	Rotterdam zoo (but wild-caught in Makassar, S.W. Sulawesi)
M. maura		SMF.1038	Ad	M	1	Sulawesi

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. maura		SMF.1039	Juv	F	1	Sulawesi
M. maura		SMF.1040	Ad	M	0	
M. maura		SMF.16636	Juv	F	2	Captive (but wild-caught on S. Sulawesi)
M. maura		SMF.16638	Ad	M	0	
M. maura		SMF.38361	Ad	M	0	
M. maura		ZD.1862.3.19.17	Sub-ad	F	1	Sulawesi
M. maura		ZD.1872.3.5.1	Ad	F	1	Aroe (Aru Island) (+ waterfall near Bantimurung), New Guinea
M. maura		ZD.1934.1.1.1	Ad	M	2	Sulawesi (died in captivity, Kent)
M. maura		ZD.1938.3.14.3	Ad	F	1	Sulawesi (Sourabaya
M. maura		ZD.1939.1057	Ad	M	1	Sulawesi
M. maura		ZD.1973.24	Sub-ad	M	1	Sulawesi
M. maura		ZMA.MAM.116	Sub-ad	F	1	Kendari Bay, SE. Sulawesi, Indonesia
M. maura		ZMA.MAM.117	Ad	M	1	Sulawesi
M. maura		ZMA.MAM.118	Juv	M	1	Sulawesi
M. maura		ZMA.MAM.119	Ad	M	0	

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. maura		ZMA.MAM.120	Sub-ad	M	1	Sulawesi
M. maura		ZMA.MAM.12435	Juv	F	1	Maros, S.W. Sulawesi
M. maura		ZMA.MAM.12436	Ad	F	1	Maros, S.W. Sulawesi
M. maura		ZMA.MAM.12437	Ad	F	1	Pare Pare, S. Sulawesi
M. maura		ZMA.MAM.5765	Ad	F	0	
M. mulatta		BZM_MAM_125	Juv	F	1	Bengalen, India
M. mulatta		BZM_MAM_28919	Ad	M	1	Sechuan, China
M. mulatta		BZM_MAM_43500	Ad	F	2	Hainan, China (bought in Canton)
M. mulatta		BZM_MAM_48974	Juv	F	1	Pi-sui, Loi, Hainan, China
M. mulatta		BZM_MAM_48976	Juv	F	1	Kuang-si, Canton, China
M. mulatta		BZM_MAM_48977	Juv	F	1	Tenasserim
M. mulatta		BZM_MAM_5811	Ad	F	1	N. China
M. mulatta		MNHN/ZM/MO-1891-387	Ad	M	1	Olongche, Tibet, China
M. mulatta		MNHN/ZM/MO-1891-389	Ad	F	1	Olongche, Tibet, China
M. mulatta		MNHN/ZM/MO-1892-1357	Sub-ad	M	1	border of Nam-(H)ou, Laos

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. mulatta		MNHN/ZM/MO-1899-54	Ad	F	1	Song-Ta-Voy, Huong-Binh, Huon-Him, Vietnam
M. mulatta		MNHN/ZM/MO-1929-456	Ad	F	1	Back-Kau, Tonkin, Vietnam
M. mulatta		RCSOM/A 84.27	Juv	M	0	
M. mulatta		RCSOM/A 84.41	Juv	M	2	Captive (but wild-caught in India)
M. mulatta		RCSOM/A 84.42	Juv	M	2	Captive (but wild-caught in India)
M. mulatta		RCSOM/A 84.43	Juv	M	2	Captive (but wild-caught in India)
M. mulatta		RCSOM/A 84.44	Sub-ad	M	2	Captive (but wild-caught in India)
M. mulatta		RCSOM/A 84.51	Sub-ad	F	2	Captive (but wild-caught in India)
M. mulatta		RCSOM/G 68.415	Ad	F	2	Captive (but wild-caught in India)
M. mulatta		ZD.1843.5.27.2	Ad	M	1	India
M. mulatta		ZD.1845.1.8.222	Ad	M	1	Nepal
M. mulatta		ZD.1845.1.8.223	Sub-ad	M	1	Nepal
M. mulatta		ZD.1858.6.24.144	Sub-ad	M	1	Nepal
M. mulatta		ZD.1870.7.18.19	Juv	M	1	Yaich'eng, S. Hainan, Hainan, China
M. mulatta		ZD.1897.6.5.2	Sub-ad	F	1	Kuatun, N.W. Fukien, Fukien, China

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. mulatta		ZD.1898.11.1.29	Juv	M	1	Kuatun, N.W. Fukien, Fukien, China
M. mulatta		ZD.1909.7.11.1	Juv	M	1	Mt. Wu-chih, Hainan, China
M. mulatta		ZD.1910.10.19.5	Ad	M	1	Kindat, (Upper R. Chindwin), Upper Burma
M. mulatta		ZD.1911.9.8.1	Ad	F	1	Kia-ting-fu (Omei), Szechwan, China
M. mulatta		ZD.1914.7.19.1	Ad	M	1	Mingun, Sagaing District, Burma
M. mulatta		ZD.1914.7.19.2	Ad	F	1	MountPopa, Myingyan District, Burma
M. mulatta		ZD.1915.4.3.2	Sub-ad	F	1	Luia, Chaibassa, Singbhum District, Bihar, India
M. mulatta		ZD.1915.5.5.3	Ad	M	1	Homalin, Upper R. Chindwin, West bank, Burma
M. mulatta		ZD.1915.5.5.5	Ad	F	1	Hkamti, (Upper R. Chindwin), Burma
M. mulatta		ZD.1915.5.5.6	Ad	M	1	Tatkon, West bank (upper) R. Chindwin, Burma
M. mulatta		ZD.1915.5.5.7	Sub-ad	F	1	Yin, East bank lower R. Chindwin, Burma
M. mulatta		ZD.1915.9.1.1	Ad	F	1	Narbon, Darjeeling, W. Bengal, India

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. mulatta		ZD.1916.7.29.1	Ad	M	1	Hasimara, Bhutan Duars, (W. Bengal), India
M. mulatta		ZD.1916.7.29.2	Ad	F	1	Hasimara, Bhutan Duars, W. Bengal, India
M. mulatta		ZD.1921.5.1.1	Ad	F	1	Nagarcot, Nepal
M. mulatta		ZD.1921.7.9.3	Ad	M	1	Rajapara, S. Kamrup, (Assam), India
M. mulatta		ZD.1921.7.9.4	Ad	F	1	Lamsakhang, Cachar Hills, Assam, India
M. mulatta		ZD.1922.5.16.2	Ad	M	1	Hazaria Patherghatta, (N. Of Bairaglia), Nepal
M. mulatta		ZD.1926.10.8.7	Ad	M	1	Chittagong Hill Tracts, Burma
M. mulatta		ZD.1926.10.8.8	Sub-ad	F	1	Bijnor, Uttar Pradesh, India
M. mulatta		ZD.1927.11.18.1	Ad	F	1	N. of Toungoo, (E. Bank of R. Sittang), Burma
M. mulatta		ZD.1927.12.1.18	Ad	F	1	Bac-kan, Tonkin, N. Vietnam
M. mulatta		ZD.1927.12.1.20	Ad	F	1	Bac-kan, Tonkin, N. Vietnam
M. mulatta		ZD.1928.7.1.11	Ad	F	1	Phu Qui, Annam, N. Vietnam
M. mulatta		ZD.1931.1.11.10	Juv	F	1	Bouzini, (Nepal Terai), Nepal

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. mulatta		ZD.1931.1.11.11	Juv	M	1	Chengli, west of Gorkha (Gurkha), N.W. Nepal
M. mulatta		ZD.1931.1.11.12	Ad	F	1	Golaghat, Sibsagar, Assam, India
M. mulatta		ZD.1931.1.11.13	Ad	F	1	Dening, Mishmi Hills, N.E. Frontier Province, India
M. mulatta		ZD.1931.1.11.14	Ad	F	1	Dening, Mishmi Hills, N.E. Frontier Province, India
M. mulatta		ZD.1931.1.11.18	Ad	F	1	Toungoo, Burma
M. mulatta		ZD.1931.1.11.19	Ad	F	1	Toungoo (E. Bank of R. Sittang), Burma
M. mulatta		ZD.1931.1.11.2	Ad	F	1	The Dangs, Surat, Gujerat, India
M. mulatta		ZD.1931.1.11.21	Ad	F	1	S.E. Of Prome, Burma
M. mulatta		ZD.1931.1.11.22	Ad	M	1	Ali Cha, S.W. Of Kindat, Chin Hills, Burma
M. mulatta		ZD.1931.1.11.24	Ad	F	1	Hiswet, West bank R. Tuzu, upper R. Chindwin, Burma
M. mulatta		ZD.1931.1.11.25	Ad	M	1	Hkamti, N. Chindwin, Burma
M. mulatta		ZD.1931.1.11.26	Ad	F	1	N.W. Kindat, Chin Hills, Burma

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. mulatta		ZD.1931.1.11.29	Sub-ad	M	1	Se'en, Hsipaw State, North Shan States, Burma
M. mulatta		ZD.1931.1.11.3	Ad	F	1	The Dangs, Surat, Gujerat, India
M. mulatta		ZD.1931.1.11.30	Ad	F	1	Pyaunggang, (e. Of Gokteik), North Shan States, Burma
M. mulatta		ZD.1931.1.11.8	Ad	M	1	Bharnabari, Bhutan Duars, W. Bengal, India
M. mulatta		ZD.1931.1.11.9	Sub-ad	F	1	Hasimara, Bhutan Duars, W. Bengal, India
M. mulatta		ZD.1936.12.26.3	Ad	F	1	Ledhan hla, Maymo F.D., (Mandalay District), Burma
M. mulatta		ZD.1937.12.3.75	Ad	F	1	Karen Chaung, Pidaung Reserve, Myitkyina District, Burma
M. mulatta		ZD.1937.12.3.76	Ad	M	1	Kokhoanig, Morit Forest, Mandalay District, Burma
M. mulatta		ZD.1943.60	Sub-ad	M	1	Bishenpur, Manipur, India
M. mulatta		ZD.1943.61	Ad	F	1	Bishenpur, Manipur, India

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. mulatta		ZD.1950.372	Ad	M	1	Htingnan, Upper Burma
M. mulatta		ZD.1950.373	Sub-ad	M	1	Bawmwang, Upper Burma
M. mulatta		ZD.1950.377	Ad	M	1	Upper Burma
M. mulatta		ZD.1972.1013	Ad	F	1	Nepal
M. nemestrina		USNM.141143	Ad	M	1	Tarussan Bay, Sumatra
M. nemestrina		USNM.141144	Ad	F	1	Tarussan Bay, Sumatra
M. nemestrina		USNM.142227	Ad	M	1	Sakaiam River, Borneo
M. nemestrina		USNM.142228	Ad	M	1	Sakaiam River, Borneo
M. nemestrina		USNM.154367	Ad	M	1	Pamuk(l)any Bay, Borneo
M. nemestrina		USNM.198299	Juv	F	1	Sungai Karangan, Borneo
M. nemestrina		USNM.199165	Sub-ad	F	1	Sungai Djambajan, Kalimantan Timur, Borneo
M. nemestrina		USNM.300919	Ad	F	2	Poring, Sabah, Borneo
M. nemestrina		USNM.305069	Ad	F	1	Penang Island, Pinang, Malaysia
M. nemestrina		USNM.399506	Ad	F	1	Puroi, Borneo
M. nemestrina		BZM_MAM_48948	Ad	F	1	Sagamama river, N. Borneo

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. nemestrina		BZM_MAM_7868	Ad	F	1	Castelan
M. nemestrina		BZM_MAM_8241	Ad	M	1	Castelan
M. nemestrina		BZM_MAM_84822	Ad	M	1	Palembang, E. Sumatra
M. nemestrina		BZM_MAM_84823	Ad	M	1	Langkat, Sumatra
M. nemestrina		MNHN/ZM/AC-1906-544	Sub-ad	M	1	N. Sumatra
M. nemestrina		MNHN/ZM/AC-A3896	Ad	M	1	Sumatra
M. nemestrina		MNHN/ZM/MO-1959-211	Ad	M	1	Borneo
M. nemestrina		NMW.49802	Ad	M	1	Medan, Sumatera Utara (=N. Sumatra), Sumatra
M. nemestrina		NMW.725/B.542	Ad	M	3	Vienna zoo
M. nemestrina		NMW.728	Sub-ad	F	3	Vienna zoo
M. nemestrina		NMW.846	Ad	F	3	Vienna zoo
M. nemestrina		RCSOM/G 82.15	Ad	M	0	
M. nemestrina		RCSOM/OH 275	Ad	M	0	
M. nemestrina		RMNH.MAM.1066	Ad	M	2	Rotterdam zoo (but wild-caught in Palembang, S. Sumatra)

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. nemestrina		RMNH.MAM.1721	Ad	F	3	
M. nemestrina		RMNH.MAM.1725	Ad	F	0	
M. nemestrina		RMNH.MAM.34366	Ad	M	1	Bengkulen, W. Sumatra
M. nemestrina		RMNH.MAM.43381	Ad	F	0	
M. nemestrina		RMNH.MAM.43385	Juv	F	1	Deli Serdang, N. Sumatra
M. nemestrina		RMNH.MAM.4656	Ad	M	2	unknown (collected by Eugene Dubois)
M. nemestrina		RMNH.MAM.4657	Ad	F	1	Bengkulen, W. Sumatra
M. nemestrina		RMNH.MAM.5035	Ad	F	1	Pajakombo, W. Sumatra
M. nemestrina		RMNH.MAM.513	Ad	M	1	Solok, W. Sumatra
M. nemestrina		RMNH.MAM.53159	Sub-ad	F	1	Borneo
M. nemestrina		RMNH.MAM.53162	Ad	M	1	Tanjung Morawa, Deli Serdang, Sumatra
M. nemestrina		RMNH.MAM.53170	Ad	M	1	Tanjung Morawa, Deli Serdang, Sumatra
M. nemestrina		RMNH.MAM.53181	Ad	F	0	
M. nemestrina		RMNH.MAM.53182	Ad	F	1	Padang, W. Sumatra
M. nemestrina		RMNH.MAM.53189	Ad	F	2	Rotterdam zoo (but wild-caught on Sumatra)

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. nemestrina		RMNH.MAM.53191	Ad	F	1	Tanjung Morawa, Deli Serdang, Sumatra
M. nemestrina		RMNH.MAM.975	Sub-ad	M	3	
M. nemestrina		SMF.1031	Sub-ad	M	2	Zool. Soc. Frankfurt (but wild-caught on Sumatra)
M. nemestrina		SMF.16640	Ad	M	1	Deli, Sumatra, Indonesia
M. nemestrina		SMF.6751	Ad	M	1	Sumatra, Indonesia
M. nemestrina		ZD.1879.11.21.304	Juv	M	1	Pinang (Penang Island), Malaysia
M. nemestrina		ZD.1893.4.29.1	Sub-ad	F	1	Long Salai, R. Baram, E. Sarawak, Sarawak, Borneo
M. nemestrina		ZD.1893.6.2.2	Ad	M	1	Mt. Kalulong, E. Sarawak, Sarawak, Borneo
M. nemestrina		ZD.1938.11.30.6	Ad	M	1	Palembang, S.E. Sumatra
M. nemestrina		ZD.1947.447	Ad	M	1	Sumatra
M. nemestrina		ZD.1947.448	Ad	M	1	Sumatra
M. nemestrina		ZD.1955.1501	Ad	M	1	Rungkup, near Bagan Datoh, Perak, Malaysia
M. nemestrina		ZD.1955.1502	Ad	M	1	Benton, Pahang, Malaysia

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. nemestrina		ZD.1955.1503	Ad	M	1	Sungai Rengam, Selangor, Malaysia
M. nemestrina		ZD.1955.1504	Ad	M	1	Chong, Trang, Thailand
M. nemestrina		ZD.1955.707	Ad	M	1	Pulo Paku, Betong, Sarebas, Sarawak, Borneo
M. nemestrina		ZD.1955.708	Sub-ad	M	1	Pulo Paku, Betong, Sarebas, Sarawak, Borneo
M. nemestrina		ZD.1955.709	Ad	M	1	Entawa, Samarahan, W. Sarawak, Sarawak, Borneo
M. nemestrina		USNM.123143	Ad	M	1	Kateman River, E. Sumatra
M. nemestrina		USNM.123144	Ad	M	1	Kateman River, E. Sumatra
M. nemestrina		USNM.123145	Ad	M	1	Kateman River, E. Sumatra
M. nemestrina		USNM.123146	Ad	F	1	Kateman River, E. Sumatra
M. nigra		USNM.175893	Sub-ad	M	1	Limbe Strait (Limbe = Lembeh), N.E. Sulawesi
M. nigra		USNM.216994	Ad	F	1	Teteamoet (= Likupang), Sulawesi
M. nigra		USNM.216995	Ad	F	1	Teteamoet (= Likupang), Sulawesi
M. nigra		USNM.216996	Sub-ad	M	1	Teteamoet (= Likupang), Sulawesi

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. nigra		USNM.216997	Ad	F	1	Teteamoet (= Likupang), Sulawesi
M. nigra		USNM.217001	Ad	F	1	Teteamoet (= Likupang), Sulawesi
M. nigra		USNM.217002	Ad	F	1	Teteamoet (= Likupang), Sulawesi
M. nigra		USNM.217003	Ad	M	1	Teteamoet (= Likupang), Sulawesi
M. nigra		USNM.217004	Sub-ad	M	1	Teteamoet (= Likupang), Sulawesi
M. nigra		USNM.217142	Juv	F	1	Likupang, Sulawesi
M. nigra		USNM.217560	Sub-ad	F	1	Koeala Prang, Sulawesi
M. nigra		USNM.217561	Ad	F	1	Pulo Lembeh, Sulawesi
M. nigra		USNM.217562	Juv	M	1	Pulo Lembeh, Sulawesi
M. nigra		USNM.217563	Ad	M	1	Lembeh Prang, Sulawesi
M. nigra		USNM.217564	Sub-ad	M	1	Batoe Hangoes, Baroe, Sulawesi
M. nigra		USNM.217565	Juv	M	1	Batoe Hangoes, Baroe, Sulawesi
M. nigra		USNM.217566	Ad	F	1	Lembeh, Sulawesi
M. nigra		USNM.217567	Ad	M	1	Lembeh, Sulawesi
M. nigra		USNM.217568	Ad	F	1	Lembeh, Sulawesi
M. nigra		USNM.217569	Ad	F	1	Lembeh, Sulawesi

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. nigra		USNM.217570	Ad	F	1	Lembeh, Sulawesi
M. nigra		USNM.217571	Ad	M	1	Temboan, N. Sulawesi
M. nigra		USNM.217572	Ad	F	1	Lembeh, Sulawesi
M. nigra		USNM.305070	Sub-ad	M	3	
M. nigra		USNM.308873	Juv	M	3	Smithsonian National Zoo
M. nigra		USNM.588432	Ad	F	0	
M. nigra		BZM_MAM_12118	Ad	F	2	Sulawesi (but wild-caught)
M. nigra		BZM_MAM_12119	Ad	M	1	Sulawesi
M. nigra		BZM_MAM_12121	Ad	F	1	Batjan, Sulawesi
M. nigra		BZM_MAM_21039	Ad	M	1	Sulawesi
M. nigra		BZM_MAM_48923	Ad	M	1	Batjan, Sulawesi
M. nigra		BZM_MAM_8247	Sub-ad	F	1	S. Sulawesi, Indonesia
M. nigra		MNHN/ZM/MO-1904-131	Sub-ad	F	1	Sulawesi
M. nigra		MNHN/ZM/MO-1974-135	Ad	F	1	Sulawesi
M. nigra		NMW.31559	Ad	F	3	Vienna zoo
M. nigra		NMW.742	Juv	F	3	Vienna zoo

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. nigra		NMW.B.5395	Juv	F	3	Vienna zoo
M. nigra		RCSOM/A 87.38	Sub-ad	M	3	
M. nigra		RCSOM/A 87.381	Juv	F	0	
M. nigra		RMNH.MAM.2210	Sub-ad	M	0	
M. nigra		RMNH.MAM.2613	Ad	M	3	
M. nigra		RMNH.MAM.53119	Juv	F	3	
M. nigra		RMNH.MAM.53120	Ad	F	1	Manado, N.E. Sulawesi
M. nigra		RMNH.MAM.53121	Sub-ad	M	1	Manado, N.E. Sulawesi
M. nigra		RMNH.MAM.53122	Ad	M	1	Manado, N.E. Sulawesi
M. nigra		RMNH.MAM.53124	Sub-ad	M	1	Bacan Island (Batjan), E. off N. Sulawesi
M. nigra		RMNH.MAM.53125	Sub-ad	F	1	Bacan Island (Batjan), E. off N. Sulawesi
M. nigra		RMNH.MAM.53127	Ad	M	1	Sulawesi
M. nigra		RMNH.MAM.53128	Ad	F	1	Bacan Island (Batjan), E. off N. Sulawesi
M. nigra		RMNH.MAM.53129	Ad	M	1	Bolaang, Mongondo(w), N. Sulawesi
M. nigra		RMNH.MAM.53130	Ad	M	1	Bolaang, Mongondo(w), N. Sulawesi
M. nigra		RMNH.MAM.53131	Ad	F	1	Bolaang, Mongondo(w), N. Sulawesi

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. nigra		RMNH.MAM.53132	Sub-ad	F	1	Bacan Island (Batjan), E. off N. Sulawesi
M. nigra		RMNH.MAM.53138	Sub-ad	M	1	N. Sulawesi
M. nigra		RMNH.MAM.53139	Sub-ad	M	0	
M. nigra		RMNH.MAM.53140	Ad	M	1	Bacan Island (Batjan), E. off N. Sulawesi
M. nigra		RMNH.MAM.53141	Ad	M	1	Manado, N.E. Sulawesi
M. nigra		RMNH.MAM.53142	Ad	M	1	Bacan Island (Batjan), E. off N. Sulawesi
M. nigra		SMF.1015	Ad	M	1	Bacan, Bacan Islands, N. Maluka, Indonesia
M. nigra		SMF.1016	Ad	M	1	Maluka Utara (N. Maluka), Indonesia
M. nigra		SMF.12539	Ad	M	2	Captive (but wild-caught on Sulawesi)
M. nigra		SMF.1550	Ad	F	3	Frankfurt zoo
M. nigra		ZD.1845.4.2.5	Ad	M	1	Sulawesi
M. nigra		ZD.1858.5.4.208	Sub-ad	F	1	Sulawesi
M. nigra		ZD.1860.8.27.0	Sub-ad	F	1	Menado (Manado), Sulawesi
M. nigra		ZD.1867.4.12.76	Sub-ad	F	1	Sulawesi
M. nigra		ZD.1896.6.24.5	Ad	M	1	Likupang, Sulawesi

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. nigra		ZD.1920.1.26.4	Ad	M	1	Batchian (Pulau Batjan Island), Sulawesi
M. nigra		ZD.1940.360	Ad	F	1	Gerian (Girian), Minahassa, N.E. Sulawesi
M. nigra		ZD.1940.361	Ad	F	1	Gerian (Girian), Minahassa, N.E. Sulawesi
M. nigra		ZD.1940.362	Sub-ad	F	1	Gerian (Girian), Minahassa, N.E. Sulawesi
M. nigra		ZE.1966.5.18.1	Ad	F	1	Sulawesi
M. nigra		ZMA.MAM.121	Sub-ad	M	1	Sulawesi
M. nigra		ZMA.MAM.12434	Sub-ad	M	1	Sulawesi
M. ochreata	*brunnescens*	MNHN/ZM/AC-1912-338	Sub-ad	F	3	Menagerie
M. ochreata	*brunnescens*	SMF.1017	Ad	M	1	Raha, Muna Island, off S.E. Sulawesi
M. ochreata	*brunnescens*	SMF.1018	Ad	M	1	Raha, Muna Island, off S.E. Sulawesi
M. ochreata	*brunnescens*	SMF.1019	Ad	M	1	Raha, Muna Island, off S.E. Sulawesi
M. ochreata	*brunnescens*	SMF.1020	Ad	M	1	Bau Bau, Buton, off S.E. Sulawesi
M. ochreata	*brunnescens*	SMF.1021	Sub-ad	F	1	Raha, Muna Island, off SE. Sulawesi

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. ochreata	*ochreata*	SMF.1022	Ad	M	1	Yendoke, S.E. Sulawesi, Indonesia
M. ochreata	*ochreata*	SMF.1023	Juv	M	1	Kolaka, S.E. Sulawesi, Indonesia
M. ochreata	*ochreata*	SMF.1024	Ad	F	1	Kolaka, S.E. Sulawesi, Indonesia
M. radiata	?	USNM.334797	Ad	M	0	
M. radiata	?	USNM.398463	Ad	F	0	
M. radiata	?	MNHN/ZM/AC-1844-196	Juv	F	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1868-124	Ad	F	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1870-470	Juv	?	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1871-117	Sub-ad	M	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1871-21	Juv	F	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1871-21bis	Sub-ad	F	0	
M. radiata	?	MNHN/ZM/AC-1873-28	Ad	F	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1875-196	Juv	?	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1880-1305	Sub-ad	M	0	
M. radiata	?	MNHN/ZM/AC-1889-250	Sub-ad	M	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1890-1	Sub-ad	M	3	Menagerie

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. radiata	?	MNHN/ZM/AC-1892-23	Sub-ad	F	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1903-637	Juv	F	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1906-131	Sub-ad	F	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1906-323	Sub-ad	F	0	
M. radiata	?	MNHN/ZM/AC-1907-88	Ad	M	0	
M. radiata	?	MNHN/ZM/AC-1909-489	Juv	M	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1912-314	Sub-ad	M	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1912-320	Ad	M	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1912-581	Ad	M	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1920-158	Juv	M	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1920-164	Ad	F	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1927-108	Sub-ad	M	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1930-337	Sub-ad	F	3	Menagerie
M. radiata	?	MNHN/ZM/AC-1971-186	Sub-ad	F	3	Menagerie
M. radiata	?	MNHN/ZM/AC-A1371	Ad	F	0	
M. radiata	?	MNHN/ZM/AC-A1422	Ad	M	0	

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. radiata	?	MNHN/ZM/AC-A1423	Ad	M	0	
M. radiata	?	MNHN/ZM/AC-A1459	Juv	M	0	
M. radiata	?	MNHN/ZM/MO-2009-295	Sub-ad	M	0	
M. radiata	?	NMW.2851/B.3846	Sub-ad	M	3	Vienna zoo
M. radiata	?	NMW.5271/B.5037	Ad	M	3	Vienna zoo
M. radiata	?	RCSOM/A 83.1	Juv	F	3	
M. radiata	?	RCSOM/A 83.3	Sub-ad	F	3	
M. radiata	?	RCSOM/A 83.4	Sub-ad	F	3	
M. radiata	?	RCSOM/G 107.1	Ad	M	3	
M. radiata	?	RCSOM/G 140.311	Juv	F	3	
M. radiata	?	RCSOM/G 68.43	Juv	F	3	
M. radiata	?	RCSOM/G 68.431	Sub-ad	F	3	
M. radiata	?	RCSOM/G 68.432	Ad	F	1	unknown (but wild-shot)
M. radiata	?	RCSOM/G 96.6	Juv	?	3	
M. radiata	?	SMF.16642	Ad	M	0	
M. radiata	?	ZD.1850.11.22.60	Ad	M	1	India

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. radiata	?	ZD.1853.7.12.4	Juv	?	1	India
M. radiata	?	ZD.1855.12.26.46	Sub-ad	M	3	Zool. Soc. London
M. radiata	?	ZD.1855.12.26.47	Ad	M	3	Zool. Soc. London
M. radiata	?	ZD.1855.12.26.49	Sub-ad	M	3	Zool. Soc. London
M. radiata	?	ZD.1855.12.26.50	Sub-ad	M	3	Zool. Soc. London
M. radiata	?	ZD.1855.12.26.53	Sub-ad	M	3	Zool. Soc. London
M. radiata	?	ZD.1858.5.4.198	Sub-ad	M	1	India
M. radiata	?	ZD.1858.5.4.204	Sub-ad	M	1	India
M. radiata	?	ZD.1858.5.4.250	Sub-ad	M	3	Zool. Soc. London
M. radiata	?	ZMA.MAM.23966	Juv	?	0	
M. radiata	?	USNM.16362	Sub-ad	M	3	Zool. Soc. Philadelphia
M. radiata	?	USNM.122171	Sub-ad	F	1	India
M. radiata	*diluta*	ZD.1845.8.12.3	Ad	F	1	Travancore, S. India, Kerala
M. radiata	*diluta*	ZD.1930.11.1.31	Ad	F	1	Boothapaundy, Travancore, (Kerala), India
M. radiata	*diluta*	ZD.1937.5.26.1	Ad	F	1	Boothapaundy, Travancore, Kerala, India

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. radiata	*radiata*	ZD.1888.2.5.17	Ad	M	1	Nilghiris (Nilghiri Hills), Madras, India
M. radiata	*radiata*	ZD.1919.6.2.1	Ad	M	1	Rookery Estate, Kil Kotagiri, Nilgiri Hills, (Madras), India
M. radiata	*radiata*	ZD.1919.6.2.2	Ad	F	1	Rookery Estate, Kil Kotagiri, Nilgiri Hills, (Madras), India
M. radiata	*radiata*	ZD.1921.11.5.2	Juv	M	1	Shernelly, (Palghat, Nelliampathy Plateau), (Madras), India
M. radiata	*radiata*	ZD.1925.10.1.1	Sub-ad	M	1	23 miles from Kodaikanal, Palni Hills, (Madras), India
M. radiata	*radiata*	ZD.1930.11.1.12	Sub-ad	F	1	Gersoppa, Kanara, Mysore, India
M. radiata	*radiata*	ZD.1930.11.1.13	Ad	M	1	Dharwar, S. Mahratta, Mysore, India
M. radiata	*radiata*	ZD.1930.11.1.14	Ad	F	1	Dharwar, S. Mahratta, Mysore, India
M. radiata	*radiata*	ZD.1930.11.1.15	Ad	M	1	Samasgi, S. Mahratta, S.W. Dharwar, Mysore, India
M. radiata	*radiata*	ZD.1930.11.1.16	Sub-ad	M	1	Samasgi, S. Mahratta, S.W. Dharwar, Mysore, India

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. radiata	*radiata*	ZD.1930.11.1.17	Ad	F	1	Samasgi, S. Mahratta, S.W. Dharwar, Mysore, India
M. radiata	*radiata*	ZD.1930.11.1.18	Ad	M	1	Haleri (Estate), N. Coorg, (Mysore), India
M. radiata	*radiata*	ZD.1930.11.1.19	Ad	M	1	Haleri (Estate), N. Coorg, (Mysore), India
M. radiata	*radiata*	ZD.1930.11.1.20	Ad	M	1	Haleri (Estate), N. Coorg, (Mysore), India
M. radiata	*radiata*	ZD.1930.11.1.21	Ad	F	1	Haleri (Estate), N. Coorg, (Mysore), India
M. radiata	*radiata*	ZD.1930.11.1.22	Ad	F	1	Wotekolli, S. Coorg, (Mysore), India
M. radiata	*radiata*	ZD.1930.11.1.23	Sub-ad	M	1	Kolar Town, East Mysore, Mysore, India
M. radiata	*radiata*	ZD.1930.11.1.24	Ad	M	1	Vijayanagar (Hampi), Bellary, Mysore, India
M. radiata	*radiata*	ZD.1930.11.1.25	Juv	M	1	Vijayanagar (Hampi), Bellary, Mysore, India
M. radiata	*radiata*	ZD.1930.11.1.26	Ad	M	1	Malakondapenta, Kurnool District, India
M. radiata	*radiata*	ZD.1930.11.1.27	Ad	M	1	Malakondapenta, Kurnool District, India
M. radiata	*radiata*	ZD.1930.11.1.30	Ad	F	1	Palni Hills, northern slopes, (Madras), India
M. radiata	*radiata*	ZD.1930.5.24.1	Ad	M	1	Shevaroy Hills, (Madras), India

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. radiata	*radiata*	ZD.1930.5.24.2	Ad	F	1	Kurumbapatti, Eastern Ghats, Madras, India
M. silenus		USNM.173046	Sub-ad	M	3	Smithsonian National Zoo
M. silenus		USNM.268917	Juv	M	3	Smithsonian National Zoo
M. silenus		USNM.271177	Sub-ad	F	3	Smithsonian National Zoo
M. silenus		USNM.364993	Juv	M	3	Calcutta Zoo
M. silenus		USNM.574135	Ad	M	0	
M. silenus		BZM_MAM_13276	Ad	M	2	Zoo (but wild-caught)
M. silenus		BZM_MAM_45063	Juv	?	1	Aramboli, Travancore, India
M. silenus		BZM_MAM_48905	Juv	F	3	Zool. Garten
M. silenus		BZM_MAM_48906	Ad	F	0	
M. silenus		BZM_MAM_48907	Ad	M	2	Zoo (but wild-caught)
M. silenus		BZM_MAM_4944	Sub-ad	F	2	Zoo (but wild-caught from Malabar, India)
M. silenus		BZM_MAM_5895	Juv	F	2	unknown, wild-caught
M. silenus		BZM_MAM_7733	Juv	M	2	Zoo (but wild-caught)

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. silenus		MNHN/ZM/AC-1852-518	Ad	M	0	
M. silenus		MNHN/ZM/AC-1880-1131	Juv	M	3	Menagerie
M. silenus		MNHN/ZM/MO-1925-8	Ad	M	1	Hilghirries
M. silenus		MNHN/ZM/MO-1939-1119	Sub-ad	M	3	Menagerie
M. silenus		MNHN/ZM/MO-1962-1745	Ad	M	1	India
M. silenus		MNHN/ZM/MO-2009-294	Ad	F	0	
M. silenus		NMW.12379	Ad	M	3	Vienna zoo
M. silenus		NMW.20403	Juv	F	3	Vienna zoo
M. silenus		NMW.31558	Sub-ad	F	3	Vienna zoo
M. silenus		NMW.33992	Sub-ad	F	3	Vienna zoo
M. silenus		NMW.33993	Ad	M	3	Vienna zoo
M. silenus		NMW.5	Juv	M	2	amusement park Vienna wild-caught in Ceylon)
M. silenus		RCSOM/A 87.11	Ad	M	1	Annamalais, Mysore, India
M. silenus		RMNH.MAM.1308	Ad	M	3	Rotterdam zoo
M. silenus		RMNH.MAM.1314	Ad	F	2	Rotterdam zoo (but wild-caught in India)

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. silenus		RMNH.MAM.2122	Sub-ad	M	3	Rotterdam zoo
M. silenus		RMNH.MAM.324	Sub-ad	F	3	Rotterdam zoo
M. silenus		RMNH.MAM.53116	Juv	M	0	
M. silenus		RMNH.MAM.53117	Ad	F	0	
M. silenus		RMNH.MAM.53118	Ad	F	3	Rotterdam zoo
M. silenus		SMF.1035	Juv	F	2	Zool. Soc. Frankfurt (but wild-caught in Malabar, India)
M. silenus		SMF.16641	Juv	F	2	Zool. Soc. Frankfurt (but wild-caught in Malabar, India)
M. silenus		ZD.10a	Sub-ad	F	1	India
M. silenus		ZD.10b	Ad	F	1	India
M. silenus		ZD.1841.1.15.1	Sub-ad	M	1	India
M. silenus		ZD.1855.12.26.45	Sub-ad	F	1	India
M. silenus		ZD.1857.4.9.3	Juv	F	1	India
M. silenus		ZD.1858.5.4.237	Ad	F	1	India
M. silenus		ZD.1921.11.5.1	Juv	M	1	Cotengady Estate, Cochin, Kerala, India

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. silenus		ZD.1937.4.2.1	Ad	M	1	Cochin, S. India
M. silenus		ZD.1976.271	Juv	M	1	S.W. India
M. silenus		ZMA.MAM.23967	Ad	F	1	India
M. silenus		ZMA.MAM.5766	Sub-ad	M	3	Rotterdam zoo
M. sinica	?	USNM.256728	Ad	F	1	Nikeweratiya, Sri Lanka
M. sinica	?	USNM.256729	Ad	M	1	Nikeweratiya, Sri Lanka
M. sinica	?	MNHN/ZM/AC-1845-271	Sub-ad	F	0	
M. sinica	?	MNHN/ZM/MO-1907-845	Sub-ad	F	0	
M. sinica	?	NMW.2756	Sub-ad	F	3	Vienna zoo
M. sinica	?	NMW.3951/B.4052	Juv	M	1	Eastern India
M. sinica	?	NMW.694	Sub-ad	F	3	Vienna zoo
M. sinica	?	NMW.695	Juv	M	3	Vienna zoo
M. sinica	?	NMW.696	Sub-ad	F	1	Sri Lanka
M. sinica	?	NMW.732/B.630	Sub-ad	M	2	Vienna zoo (wild-caught in Sri Lanka)
M. sinica	?	NMW.741	Ad	F	3	Vienna zoo
M. sinica	?	NMW.852	Ad	M	3	Vienna zoo

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. sinica	?	RCSOM/A 82.2	Ad	M	1	Ceylon
M. sinica	?	RCSOM/A 82.32	Juv	M	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/A 82.33	Sub-ad	M	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/A 82.331	Ad	M	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/A 82.34	Sub-ad	F	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/A 82.341	Ad	F	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/A 82.5	Ad	M	1	Monoragala, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/A 82.51	Ad	M	1	Monoragala, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 140.21	Ad	F	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 169.4	Ad	M	1	Monoragala, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 169.41	Ad	M	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 169.411	Ad	F	1	Monoragala, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 169.42	Ad	F	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 169.421	Ad	M	1	Monoragala, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 169.43	Ad	F	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 169.45	Ad	M	1	Monoragala, Ceylon (Sri Lanka)

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. sinica	?	RCSOM/G 169.47	Ad	F	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 68.31	Ad	M	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 68.33	Ad	M	1	Monoragala, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 68.34	Ad	F	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 68.35	Ad	F	1	Monoragala, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 8.2	Ad	F	1	Polgahawela, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 8.6	Ad	M	1	Monoragala, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/G 82.1441	Ad	M	1	Monoragala, Ceylon (Sri Lanka)
M. sinica	?	RCSOM/OH 298	Ad	M	0	
M. sinica	?	RMNH.MAM.1326	Sub-ad	F	3	Rotterdam zoo
M. sinica	?	RMNH.MAM.1475	Sub-ad	M	2	English India
M. sinica	?	RMNH.MAM.1743	Juv	M	3	
M. sinica	?	RMNH.MAM.53171	Sub-ad	F	1	Sri Lanka
M. sinica	?	RMNH.MAM.53173	Juv	F	0	
M. sinica	?	RMNH.MAM.53174	Ad	M	2	Reunion, E. of Madagascar, S.W. of Mauritius

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. sinica	?	RMNH.MAM.53176	Sub-ad	F	1	Sri Lanka
M. sinica	?	RMNH.MAM.53177	Ad	M	2	Pondichery, India
M. sinica	?	RMNH.MAM.53178	Juv	F	1	Sri Lanka
M. sinica	?	RMNH.MAM.53185	Ad	M	2	Rotterdam zoo (but wild-caught)
M. sinica	?	RMNH.MAM.53186	Sub-ad	F	0	
M. sinica	?	RMNH.MAM.565	Juv	F	3	Rotterdam zoo
M. sinica	?	SMF.1032	Ad	F	3	Zool. Soc. Frankfurt
M. sinica	?	SMF.1033	Sub-ad	F	3	Zool. Soc. Frankfurt
M. sinica	?	SMF.3092	Sub-ad	M	0	
M. sinica	?	SMF.3093	Juv	M	3	Zool. Soc. Frankfurt
M. sinica	?	SMF.59133	Ad	M	0	
M. sinica	?	SMF.59134	Juv	M	0	
M. sinica	?	SMF.59135	Juv	M	0	
M. sinica	?	SMF.59136	Juv	F	0	
M. sinica	?	SMF.59137	Juv	M	0	
M. sinica	?	ZD.1858.5.4.225	Ad	M	1	Ceylon, Sri Lanka

Continued on next page

Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. sinica	?	ZD.1949.515	Ad	M	1	Ohiya, Horton Plains, Ceylon, Sri Lanka
M. sinica	?	ZD.1976.270	Ad	M	2	Sri Lanka (but wild-caught)
M. sinica	?	ZMA.MAM.23959	Juv	?	1	Sri Lanka
M. sinica	?	ZMA.MAM.23961	Sub-ad	M	0	
M. sinica	?	USNM.15259	Ad	M	0	
M. sinica	*aurifrons*	RMNH.MAM.53179	Juv	M	1	Colombo, Sri Lanka
M. sinica	*aurifrons*	ZD.1920.2.8.2	Ad	M	1	Kotiyagalla, Ceylon, Sri Lanka
M. sinica	*aurifrons*	ZD.1920.5.1.2	Ad	F	1	Anasigalla, Matugama, W.P., Ceylon, Sri Lanka
M. sinica	*aurifrons*	ZD.1930.11.1.38	Ad	M	1	Rayigam Korale, Ceylon, Sri Lanka
M. sinica	*sinica*	RCSOM/A 82.41	Juv	F	1	Nitre Cave District, Ceylon (Sri Lanka)
M. sinica	*sinica*	RCSOM/A 82.43	Ad	M	1	Nitre Cave District, Ceylon (Sri Lanka)
M. sinica	*sinica*	RCSOM/A 82.6	Juv	F	1	Kumbukkan, Ceylon (Sri Lanka)
M. sinica	*sinica*	RCSOM/G 169.44	Ad	F	1	Kumbukkan, Ceylon (Sri Lanka)
M. sinica	*sinica*	RCSOM/G 169.46	Ad	F	1	Kumbukkan, Ceylon (Sri Lanka)
M. sinica	*sinica*	RCSOM/G 169.48	Ad	F	1	Nitre Cave District, Ceylon (Sri Lanka)

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. sinica	*sinica*	RCSOM/G 169.49	Ad	F	1	Kumbukkan, Ceylon (Sri Lanka)
M. sinica	*sinica*	RCSOM/G 36.3	Ad	F	1	Kumbukkan, Ceylon (Sri Lanka)
M. sinica	*sinica*	RCSOM/G 68.32	Ad	M	1	Nitre Cave District, Ceylon (Sri Lanka)
M. sinica	*sinica*	RCSOM/G 82.61	Ad	F	1	Kumbukkan, Ceylon (Sri Lanka)
M. sinica	*sinica*	ZD.1879.9.5.6	Juv	F	1	Hambantota District, S.P., Ceylon, Sri Lanka
M. sinica	*sinica*	ZD.1915.3.1.1	Ad	M	1	Mankeni, Ceylon, Sri Lanka
M. sinica	*sinica*	ZD.1915.3.1.2	Sub-ad	M	1	Mankeni, Ceylon, Sri Lanka
M. sinica	*sinica*	ZD.1915.3.1.3	Ad	M	1	Cheddikulam, Ceylon, Sri Lanka
M. sinica	*sinica*	ZD.1915.3.1.4	Ad	M	1	Maha Oya, Ceylon, Sri Lanka
M. sinica	*sinica*	ZD.1928.7.18.2	Ad	F	1	Telulla, Uva, Ceylon, Sri Lanka
M. sinica	*sinica*	ZD.1930.11.1.33	Juv	M	1	Mankeni, Ceylon, Sri Lanka
M. sinica	*sinica*	ZD.1930.11.1.34	Ad	F	1	Wellawaya, Uva, Ceylon, Sri Lanka
M. sinica	*sinica*	ZD.1930.11.1.37	Juv	M	1	Tammannewa, N.C.P., Ceylon, Sri Lanka
M. sinica	*sinica*	ZD.1937.5.26.3	Sub-ad	M	1	Cheddikulam, N.P., Ceylon, Sri Lanka

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. sinica	*sinica*	ZD.1971.776	Ad	M	1	Meda Maha, Nuwara, C.P., Ceylon, Sri Lanka
M. sinica	*sinica*	ZD.1971.777	Juv	M	1	Telulla, Uva, Ceylon, Sri Lanka
M. sinica	*sinica*	ZD.1972.1011	Juv	M	1	Cheddikulam, Ceylon, Sri Lanka
M. sylvanus		USNM.196984	Ad	F	1	Morocco
M. sylvanus		USNM.255979	Ad	M	2	Smithsonian National Zoo (but wild-caught from Gibraltar)
M. sylvanus		USNM.476780	Ad	M	1	Azrou, Meknes, Morocco
M. sylvanus		USNM.476781	Sub-ad	M	1	Azrou, Meknes, Morocco
M. sylvanus		USNM.476782	Ad	F	1	Azrou, Meknes, Morocco
M. sylvanus		USNM.476783	Ad	F	1	Azrou, Meknes, Morocco
M. sylvanus		USNM.476784	Ad	M	1	Azrou, Meknes, Morocco
M. sylvanus		USNM.476785	Ad	M	1	Azrou, Meknes, Morocco
M. sylvanus		USNM.476786	Ad	F	1	Azrou, Meknes, Morocco
M. sylvanus		USNM.476787	Ad	F	1	Azrou, Meknes, Morocco
M. sylvanus		USNM.476790	Sub-ad	F	1	Khenifra, Meknes, Morocco

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. sylvanus		USNM.476791	Ad	M	1	Khenifra, Meknes, Morocco
M. sylvanus		USNM.543429	Juv	F	3	Smithsonian National Zoo
M. sylvanus		BZM_MAM_13756	Juv	F	2	Zoo (but wild-caught)
M. sylvanus		BZM_MAM_49082	Ad	M	2	Zoo (but wild-caught)
M. sylvanus		BZM_MAM_566	Juv	M	2	Gibraltar (but captive)
M. sylvanus		BZM_MAM_70003	Ad	F	2	Zoo (but wild-caught from Morocco)
M. sylvanus		BZM_MAM_92913	Sub-ad	M	1	Berber country (N. Africa)
M. sylvanus		MNHN/ZM/AC-1872-449	Juv	F	0	
M. sylvanus		MNHN/ZM/AC-1874-343	Sub-ad	M	0	
M. sylvanus		MNHN/ZM/AC-1900-244	Ad	F	0	
M. sylvanus		MNHN/ZM/AC-1926-251	Ad	M	1	Algeria
M. sylvanus		MNHN/ZM/MO-1931-835	Ad	M	1	Morocco
M. sylvanus		MNHN/ZM/MO-1939-1118	Ad	M	0	
M. sylvanus		MNHN/ZM/MO-1962-1469	Sub-ad	M	1	Aif Isherq, Morocco
M. sylvanus		MNHN/ZM/MO-1962-1473	Sub-ad	M	0	
M. sylvanus		MNHN/ZM/MO-1962-1474	Ad	F	1	Bekrit, Middle Atlas, Morocco

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. sylvanus		MNHN/ZM/MO-1995-1252	Ad	M	1	Massif de l'Akouker, Algeria
M. sylvanus		MNHN/ZM/MO-2009-364	Ad	M	1	Gorge de la Chiffa, Algeria
M. sylvanus		NMW.22718	Juv	F	3	Vienna zoo
M. sylvanus		NMW.23990	Ad	M	3	Vienna zoo
M. sylvanus		NMW.2519	Juv	F	2	Vienna zoo (wild-caught in Kabylie, E. Algeria)
M. sylvanus		NMW.2614/B.3976	Ad	M	2	Vienna zoo (wild-caught in Kabylie, E. Algeria)
M. sylvanus		NMW.2615	Ad	F	2	Vienna zoo (wild-caught in Kabylie, E. Algeria)
M. sylvanus		NMW.2616	Ad	F	2	Vienna zoo (wild-caught in Kabylie, E. Algeria)
M. sylvanus		NMW.34222	Ad	F	3	Vienna zoo
M. sylvanus		NMW.38395	Ad	F	3	Vienna zoo
M. sylvanus		NMW.4405	Juv	F	2	Vienna zoo (wild-caught in Kabylie, E. Algeria)

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. sylvanus		NMW.4406	Ad	F	2	Vienna zoo (wild-caught in Kabylie, E. Algeria)
M. sylvanus		NMW.4407	Ad	F	2	Vienna zoo (wild-caught in Kabylie, E. Algeria)
M. sylvanus		NMW.4408	Sub-ad	M	2	Vienna zoo (wild-caught in Kabylie, E. Algeria)
M. sylvanus		NMW.52528	Ad	F	3	Vienna zoo
M. sylvanus		NMW.57466	Ad	F	3	Safaripark Gaenserndorf
M. sylvanus		NMW.62198	Ad	F	3	Vienna zoo
M. sylvanus		NMW.68140	Ad	F	3	unknown (Vienna zoo)
M. sylvanus		NMW.730	Juv	M	3	Vienna zoo
M. sylvanus		NMW.B.3849	Ad	F	2	Vienna zoo (wild-caught in Kabylie, E. Algeria)
M. sylvanus		RCSOM/G 99.11	Ad	M	3	
M. sylvanus		RMNH.MAM.24578	Ad	F	0	
M. sylvanus		RMNH.MAM.24579	Sub-ad	F	1	Barbary, N. Africa
M. sylvanus		RMNH.MAM.24580	Juv	F	0	

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. sylvanus		RMNH.MAM.24585	Ad	M	1	Barbary, N. Africa
M. sylvanus		RMNH.MAM.4153	Juv	M	3	Rotterdam zoo
M. sylvanus		RMNH.MAM.53112	Juv	F	0	
M. sylvanus		RMNH.MAM.53113	Juv	F	3	Rotterdam zoo
M. sylvanus		SMF.1036	Juv	M	0	
M. sylvanus		SMF.1037	Juv	F	3	Zool. Soc. Frankfurt
M. sylvanus		SMF.1551	Ad	M	3	Menagerie
M. sylvanus		SMF.1552	Juv	M	3	Menagerie
M. sylvanus		SMF.1621	Juv	M	3	Zool. Soc. Frankfurt
M. sylvanus		ZD.1854.3.20.1	Ad	F	0	
M. sylvanus		ZD.1858.4.5.1	Sub-ad	M	0	
M. sylvanus		ZD.1858.5.4.247	Sub-ad	M	0	
M. sylvanus		ZD.1911.11.4.1	Ad	F	0	
M. sylvanus		ZD.1919.8.19.1	Ad	M	1	Azrou, Jebel Hebri Plateau, Moyen Atlas, Morocco
M. sylvanus		ZD.1939.3470	Ad	F	0	

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Table A.2 – *continued*

Species	Subspecies	Accession no.	Age[a]	Sex	Captivity[b]	Locality
M. sylvanus		ZD.1939.3471	Ad	M	1	Gargide Chiffa (Gorges de la Chiffa), Algeria
M. sylvanus		ZD.1939.3471	Juv	M	1	Algeria
M. sylvanus		ZD.1943.5.27.1	Ad	M	0	
M. sylvanus		ZD.1975.569	Ad	M	0	
M. sylvanus		ZD.1976.1398	Ad	F	1	Setti Fatma, Ourika Valley, S.S.E. of Marrakesh, Morocco
M. sylvanus		ZD.1977.3119	Ad	M	0	
M. sylvanus		ZD.84.1734	Sub-ad	M	0	
M. sylvanus		ZMA.MAM.934	Ad	F	0	

[a]Age: Juv = juvenile, Sub-ad = sub-adult, Ad = adult. [b]Captivity: 0 = unknown, 1 = wild-shot, 2 = wild-caught but then captive, 3 = captive.

Appendix B

Materials and Methods: Data and Supporting Information

Table B.1 Macaque body size data.

Species	BM	HB	References
M. sylvanus	M: 14500 F: 9900	M: 634.3 F: 556.8	a, b, c
M. silenus	M: 8000 F: 5000	M: 546 F: 469	d, e, b, c
M. nemestrina	M: 11800 F: 6500	M: 635 F: 455	d, b, c
M. nigra	M: 9890 F: 5470	M: 545 F: 497	b, c
M. maura	M: 8000 F: 5565	M: 656.7 F: 542.5	b, c
M. ochreata	M: 10140 F: 6388	M: 590 F: 500	b, c
M. sinica	M: 5500 F: 3300	M: 468 F: 413	f, b, c
M. radiata	M: 7000 F: 4000	M: 527 F: 455	g, b, c
M. assamensis	M: 11200 F: 7300	M: 624 F: 525	h, b, c
M. fascicularis	M: 5500 F: 3600	M: 460 F: 400	i, b, c
M. mulatta	M: 9000 F: 6500	M: 535 F: 475	j, b, c
M. cyclopis	M: 8120 F: 5360	M: 540 F: 472	k, b
M. fuscata	M: 11800 F: 8800	M: 580.1 F: 528.2	l, b

BM = adult body mass (g); HB = adult head-body length (mm). Data from a) Fooden (2007); b) Mittermeier et al. (2013); c) data compiled by Rowe and Myers (2011); d) Fooden (1975); e) Ross (2003); f) Fooden (1979); g) Fooden (1981); h) Fooden (1982b); i) Fooden (1996); j) Fooden (2000); k) Fooden and Wu (2001); l) Fooden and Aimi (2005).

Table B.2 Macaque dietary and habitat data.

Species	Ecological group	Diet breadth (categories)	Frugivory (%)	Folivory (%)	Range in % fruit	Habitat breadth (layers)	References
M. sylvanus	2	9	2.55	13.45	4	6	b, c, d, e, f, aa
M. silenus	1	8	70	0	16	2	a, c, g, h, ab
M. nemestrina	1	9	74.6	8.25	9	5	a, c, e, i
M. nigra	1	10	66	5	11	2	j, c, ac
M. maura	2	6	71	8.4	10	3	k, c, ad
M. ochreata	1	6	66	12	?	2	l, c
M. sinica	2	9	70	11	9	3	b, m, c, n, ae
M. radiata	2	10	53.5	13.6	23	8	a, c, g, o, p, ae-af
M. assamensis	1	8	40	38.85	53	2	a, c, q, r, ag-ak
M. fascicularis	2	7	74.35	9.4	23	7	a, c, e, s, t, ae, al-am
M. mulatta	2	12	28.65	50	71	12	a, c, u, v, an-aq
M. cyclopis	2	9	50.5	26.95	8	3	c, w, e, x
M. fuscata	2	13	22.9	58.3	22	3	b, c, y, e, z, aa, ar

Ecological group (after Fooden (1982a)): 1 = Broadleaf evergreen (BE) forest, 2 = non-BE forest; dietary breadth: number of dietary categories in diet (see Table B.3); frugivory: % of diet consisting of fruits; folivory: % of diet consisting of leaves; range in % fruit: intra-annual range of proportion of fruit in diet (averaged across populations when data for more than one population were known); habitat breadth: number of habitat layers that are of major importance. Habitat layers are identified following the habitats classification scheme by the International Union for Conservation of Nature and Natural Resources (IUCN) (IUCN Red List, 2007). Human-made (artificial) habitats taken together count once. Data from a) Fooden (1982a); b) Ross (1992); c) data compiled by Rowe and Myers (2011); d) Fooden (2007); e) Ménard (2004); f) Butynski et al. (2008); g) Roy et al. (2012); h) Kumar et al. (2008a); i) Richardson et al. (2008); j) Supriatna and Andayani (2008); k) Supriatna et al. (2008); l) Supriatna (2008); m) Fooden (1979); n) Dittus et al. (2008); o) Fooden (1981); p) Singh et al. (2008); q) Heesen et al. (2013); r) Boonratana et al. (2008); s) Fooden (1996); t) Ong and Richardson (2008); u) Fooden (2000); v) Timmins et al. (2008); w) Fooden and Wu (2001); x) Hai Yin and Richardson (2008); y) Fooden and Aimi (2005); z) Watanabe and Tokita (2008); aa) Hanya et al. (2011); ab) Kumar (1987); ac) O'Brien and Kinnaird (1997); ad) Sagnotti (2013); ae) Rowe (1996); af) Krishnamani (1994); ag) Schülke et al. (2011); ah) Huang et al. (2015); ai) Kaewpanus et al. (2015); aj) Koirala and Chalise (2014); ak) Zhou et al. (2011); al) Yeager (1996); am) Mittermeier et al. (2013); an) Richard et al. (1989); ao) Sarker et al. (2008); ap) Lindburg (1977); aq) Sengupta et al. (2014); ar) Tsuji (2010).

Table B.3 Definition of dietary categories.

Category	Food types
1	Fruits and seeds
2	Leaves and stems
3	Flowers, nectar, and pollen
4	Other plant material: roots, bamboo, corms, tubers, grasses, herbs, buds and shoots
5	Bark, lichen, or sap
6	Insects, spiders, and scorpions
7	Invertebrates: e.g. snails, molluscs, crabs and other crustaceans
8	Vertebrates: e.g., fish, birds, small reptiles, amphibians and mammals
9	Eggs
10	Honey
11	Fungi
12	Soil
13	Other, e.g. charcoal, human trash

Table B.4 Geographical data for macaques.

Species	Latitude (DD)	Longitude (DD)	Geo range (km^2)	Island
M. sylvanus	34.21 (31.5 – 36.92)	-0.62 (-6.93 – 5.67)	95,331	2
M. silenus	13.19 (10.21 – 16.17)	76.12 (74.55 – 77.69)	56,995	2
M. nemestrina	3.04 (-4.89 – 10.98)	108.07 (96.87 – 119.26)	1,033,483	3
M. nigra	1.01 (0.27 – 1.75)	124.26 (123.28 – 125.24)	13,015	1
M. maura	-4.98 (-5.70 – 4.25)	1.11 (119.35 – 120.46)	13,648	1
M. ochreata	-4.93 (-5.71 – 3.70)	122.54 (121.07 – 123.22)	26,330	1
M. sinica	7.87 (5.91 – 9.83)	80.78 (79.69 – 81.88)	66,627	1
M. radiata	14.59 (8.06 – 21.12)	77.06 (72.65 – 81.47)	679,816	2
M. assamensis	23.01 (14.93 – 31.08)	97.19 (83.42 – 110.95)	1,383,530	2
M. fascicularis	4.13 (-10.37 – 18.65)	111.24 (95.18 – 127.30)	2,197,587	3
M. mulatta	25.07 (13.69 – 36.45)	96.67 (71.21 – 122.13)	6,566,547	2[a]
M. cyclopis	23.91 (22.96 – 24.86)	121.04 (120.63 – 121.45)	12815	1
M. fuscata	35.88 (30.22 – 41.54)	135.51 (129.55 – 141.47)	177,386	1

Latitude and longitude (in decimal degrees) denote mid-point coordinates with ranges indicated in (). Geo range = geographical range size (km^2). Data from Jones et al. (2009). Island/continent: 1 = island species, 2 = continental species, 3 = mixed.

[a]*M. mulatta* also occurs on Hainan island (China), but this is a single and recent population that only colonised the island following the bridge constructed to connect with mainland China.

Table B.5 Elevational distribution of macaques.

Species	Median altitude (m)	Alt. range (m)	References
M. sylvanus	1900	2200	a
M. silenus	900	1200	b
M. nemestrina	300	1700	b
M. nigra	400	2000	c
M. maura	250	2000	c
M. ochreata	?	800	c
M. sinica	500	2300	d, e, f
M. radiata	1250	2600	d, e, g, h
M. assamensis	1200	2750	d, e, i
M. fascicularis	200	2000	j, k
M. mulatta	500	4000	j, l
M. cyclopis	1250	3300	j, m
M. fuscata	600	3180	j, n, o

These are species-level data as they are known from the literature, rather than values derived based on the present sample of specimens, because the goal of this work is to analyse the association between environment and phenotype in evolved species differences, which all members of the same species are assumed to share. The spatial distribution of the sample may not be representative of the species. The median altitude was computed from altitudes reported for individual localities, or estimated based on locality data in combination with www.elevationmap.net. Altitudinal ranges are calculated from minimum and maximum recorded altitudes, collated by www.alltheworldsprimates.org (Rowe and Myers, 2011). Data are from species accounts in Rowe and Myers (2011) and the following additional publications: a) Fooden (2007); b) Fooden (1975); c) Fooden (1969); d) Fooden (1986); e) Fooden (1988); f) Fooden (1979); g) Fooden (1981); h) Molur et al. (2003); i) Fooden (1982b); j) Fooden (2006); k) Fooden (1996); l) Fooden (2000); m) Fooden and Wu (2001); n) Fooden and Aimi (2005); o) Muroyama and Yamada (2010).

Table B.6 Climate data for macaques.

Species	Temperature (°C * 10)				Precipitation (mm)			
	Mean	Maximum	Minimum	Seasonality	Annual	Maximum	Minimum	Seasonality
M. sylvanus	147	323	13	6124	708	108	5	59
M. silenus	245	320	178	1286	2589	784	11	101
M. nemestrina	260	311	211	325	2888	343	145	27
M. nigra	258	310	212	338	2710	368	119	33
M. maura	253	309	195	376	2565	448	53	61
M. sinica	256	316	201	921	2047	339	56	55
M. radiata	231	312	152	1670	1542	372	12	79
M. assamensis	177	264	49	4149	2260	538	8	95
M. fascicularis	259	308	212	356	2742	331	141	29
M. mulatta	226	322	96	3986	1933	438	9	93
M. cyclopis	240	302	162	2619	2717	594	46	89
M. fuscata	106	256	-42	7663	2234	336	77	46

Mean temperature is the annual mean; minimum temperature is the coldest temperature of the coldest month; maximum temperature is the warmest temperature of the warmest month; temperature seasonality is the standard deviation across months in a year (*100); annual precipitation is the total amount of precipitation across a year; minimum precipitation is the precipitation of the driest month; maximum precipitation is the precipitation of the wettest month; precipitation seasonality is the coefficient of variation across months in a year. Data extracted from Hijmans et al. (2005) at a resolution of 2.5 arc-minutes. Data were not extracted for *M. ochreata* because all nine specimens come from the same locality.

Table B.7 Dental inventory categories.

Score	Definition
1	In occlusion
2	Damaged
3	Ante-mortem loss
4	Post-mortem loss
5	Erupting
6	Unerupted

Table B.8 Dental wear scoring system for macaques (*Macaca*), excluding canines.[a]

Tooth	Score	Description
Incisors	1	Unworn, small wear facets, and/or a small dentine line.
	2	Dentine oval with enamel still encircling the occlusal plateau.
	3	Enamel lost from incisal edge down to lingual CEJ or tubercle.
	4	Enamel lost on two sides.
	5	Reduction in crown size and pulp cavity exposed, and/or roots function in occlusion.
Premolars	1	Unworn, small wear facets, and/or slight cusp blunting and pinprick dentine.
	2	Severe cusp blunting with clear dentine exposure.
	3	One cusp removed (with large dentine patch), other cusp blunted.
	4	Two large dentine areas with possible coalescence.
	5	Complete dentine exposure but enamel rim intact.
Lower P3	1	Unworn, small wear facets, and/or slight cusp blunting with pinprick dentine.
	2	Cusp blunting with dentine exposure.
	3	Large dentine patch distal to the protoconid, mesial basin still present.
	4	Two large dentine areas (mesial and distal to the protoconid) with possible coalescence.
	5	Severe crown reduction, extensive wear facet on sectoral face, and enamel rim intact.
Molars	1	Unworn, small wear facets, and/or slight cusp blunting with pinprick dentine.
	2	Severe cusp blunting with clear dentine exposure.
	3	Cusps removed on one side (with large dentine patches), cusps blunted on opposite side.
	4	Cusps removed and coalescence of dentine patches.
	5	Complete dentine exposure, enamel rim intact, and severe crown reduction.

[a] A score 0 ‘unobservable’ was assigned for any tooth that was missing, damaged or otherwise unable to be assessed for dental wear.

Table B.9 Dental wear scoring system for macaques (*Macaca*), canines only (by sex).[a]

Sex	Jaw	Score	Description
Males	Upper	1	Unworn, small wear facets, and/or small dentine exposure on (disto)lingual surface.
		2	Moderate dentine exposure on (disto)lingual surface and enamel thinning on other surfaces.
		3	Dentine exposed from tip to CEJ on distolingual surface, enamel lost on/around mesial groove.
		4	A distal basin may be created, enamel lost on lingual surface (incl. mesiolingual border).
		5	Severe crown reduction, pulp cavity exposed, mesial groove (nearly) erased.
	Lower	1	Unworn, small wear facets, and/or small dentine exposure on distolingual surface.
		2	Dentine exposure from tip to distal heel along distolingual border/edge.
		3	As per '2' but wear facet extending onto lingual surface, possible transverse cut in distal heel.
		4	As per '3' but enamel thinning/dentine exposure on mesiolingual surface, possible secondary dentine.
		5	Pulp cavity exposed (or secondary dentine), severe crown reduction and enamel loss.
Females	Upper	1	Unworn, small wear facets, and/or small dentine exposure on distolingual surface.
		2	Large dentine patch on distolingual surface.
		3	As per '2' but cusp blunting and dentine extending onto lingual surface.
		4	As per '3' but dentine exposure on mesiolingual surface, with possible coalescence between mesio- & distolingual dentine.
		5	Severe crown reduction, secondary dentine, and possible 'hollowing out' of lingual surface.
	Lower	1	Unworn, small wear facets, and/or small dentine exposure (worn enamel)on lingual surface.
		2	Large dentine patch (from CEJ up) and well-etched facet on distolingual surface.
		3	As per '2' but cusp blunting and possible coalescence between mesial and distal dentine.
		4	As per '3' but enamel absent on lingual surface.
		5	Severe crown reduction, pulp cavity or secondary dentine exposed.

[a] A score 0 'unobservable' was assigned for any tooth that was missing, damaged or otherwise unable to be assessed for dental wear.

Table B.10 Definition of mesiodistal tooth length measurements.[a]

Tooth	Jaw	Measurement description
Incisors	Upper	From most mesial to most distal corner along incisal edge (measured on labial side).
	Lower	As per upper.
Canines	Upper	From most mesial point on mesial edge (at the cemento-enamel junction, CEJ) to distolingual border/corner, parallel to the jaw.
	Lower	From mesial to distolabial surface at level of mesial alveolar margin (viewed mesiolabially).
Premolars	Upper	From mesial (contact) point to distal contact point.
	Lower	P4: As per upper.
		P3 (2x): (1) occlusal length, from mesio-occlusal corner to distal contact point; (2) total length, from mesiobuccal CEJ to distal contact point on occlusal surface.
Molars	Upper	From mesial to distal contact point, appr. in the middle (buccolingually) between cusps.
		M3: from mesial contact point to distal margin.
	Lower	As per upper.

[a] All measurements captured maximum length and were taken irrespective of tooth orientation in the jaw.

Table B.11 Definition of buccolingual tooth width measurements.[a]

Tooth	Jaw	Measurement description
Incisors	Upper	I1: from lingual cemento-enamel junction (CEJ) to labial CEJ.
		I2: from lingual CEJ to labial CEJ at mesiolabial corner.
	Lower	As per upper.
Canines	Upper	From lingual CEJ to labial CEJ.
	Lower	As per upper.
Premolars	Upper	From most convex point on lingual to most convex point on buccal surface, measured mid-crown.
	Lower	P4: as per upper.
		P3: as per upper, but at distal (non-honing face) part of crown.
Molars	Upper	From most convex point on lingual to most convex point on buccal surface, measured mid- crown (2x), at (1) mesial and (2) distal cusps.
	Lower	As per upper.

[a]All measurements captured maximum width, at the most bulbous part of the crown, and were taken at a right angle of the tooth length measurement (except in the case of the incisors).

Table B.12 Definition of crown height measurements.[a]

Tooth	Jaw	Measurement description
Incisors	Upper	From cemento-enamel junction (CEJ) to occlusal edge.
	Lower	As per upper.
Canines	Upper	From CEJ on mesiolabial edge/groove to cusp apex.
	Lower	As per upper.
Premolars	Upper	From buccal CEJ to cusp apex.
	Lower	P4: as per upper.
		P3: from mesiobuccal CEJ to cusp apex.
Molars	Upper	From CEJ to cusp apex on buccal side.
	Lower	As per upper.

[a]All measurements captured maximum height, and were taken at a right angle to the jaw (except in the case of the canines).

Table B.13 Dentocranial measurements

Variable	Measurement description[a]
CALV	Calvarium length, from nasion to occipital protuberance.
BA-PR	Distance from basion to prosthion.
MUZL	Muzzle length, from mesial orbital margin to alveolar margin at I^1.
UIAW	Tooth row length of upper incisors, from distal border of left I^2 to distal border of right I^2.[b]
UBCB	Width at upper canines, from left to right canine (buccal surface).[b]
UPC_ROW	Length of upper postcanine tooth row, from mesial border of P^3 to distal border of M^3.[b]
UECM-ECM	Maxillo-alveolar width, from left to right ectomolare.
PR-ALV	Maxillo-alveolar length, from prosthion to alveolon.
PAL_WID	Palatal width, from left lingual M^2 to right lingual M^2.
LIAW	Tooth row length of lower incisors, from distal border of left I^2 to distal border of right I^2.[b]
LBCB	Width at lower canines, from left to right canine (buccal surface).[b]
LPC_ROW	Length of lower postcanine tooth row, from mesial border of P_3 to distal border of M_3.[b]
LECM-ECM	Width of lower dental arcade, from left to right ectomolare.
MAND_HGHT	Mandible height, from mesiobuccal cusp of M_2 at a right angle down to inferior surface of mandibular body.
MAND_THICK	Mandible thickness, from medioposterior mandibular symphysis to point on anterior mandibular body at right angle to dental arcade.
MAND_WID	Mandibular width, from gonion to gonion.
CON_M1	Distance from tip of mandibular condyle to mesial border of first molar.

[a]All measurements were taken on the bone unless stated otherwise. [b]Measured at the cemento-enamel junction (CEJ) on the tooth.

Table B.14 Key to dental variable names.

	Abbreviations
Prefix/jaw	U = upper (maxillary), L = lower (mandibular)
Tooth class	I = incisor
	C = canine
	P = premolar
	M = molar
Tooth position	incisors (1 = central, 2 = lateral)
	canines (number n/a)
	premolars (3 = mesial, 4 = distal)
	molars (1 = mesial, 2 = central, 3 = distal)
Dimension	MD = mesiodistal length of incisors and canines
	LL = labiolingual width of incisors
	H = height of all teeth
	BL = buccolingual width of canines
	L = mesiodistal length of premolars and molars (except P_3)
	OL and TL = occlusal and total length of P_3
	W = buccolingual width of premolars
	AW and PW = anterior and posterior buccolingual width of molars

E.g., UI1MD is the mesiodistal length of the upper central incisor, LM3PW is the posterior width (at the distal loph) of the lower third molar.

Appendix C

Descriptive Statistics

All macaques
Male:
Mean: 6.39
SD: 0.91
N: 336
Female:
Mean: 6.05
SD: 0.83
N: 280
M. assamensis
Male:
Mean: 6.22
SD: 0.68
N: 8
Female:
Mean: 5.59
SD: 0.33
N: 4
M. cyclopis
Male:
Mean: 5.92
SD: 0.53
N: 6
Female:
Mean: 5.68
SD: 0.28
N: 11
M. fascicularis
Male:
Mean: 5.83
SD: 0.59
N: 45
Female:
Mean: 5.93
SD: 0.72
N: 35
M. fuscata
Male:
Mean: 6.51
SD: 0.59
N: 20
Female:
Mean: 6.24
SD: 0.38
N: 18
M. maura
Male:
Mean: 6.75
SD: 0.59
N: 30
Female:
Mean: 6.35
SD: 0.56
N: 16
M. mulatta
Male:
Mean: 5.52
SD: 0.54
N: 31
Female:
Mean: 5.31
SD: 0.58
N: 32
M. nemestrina
Male:
Mean: 7.52
SD: 0.95
N: 34
Female:
Mean: 7.28
SD: 0.84
N: 20
Frequency N
U1MD
Female
Male
Female
Male

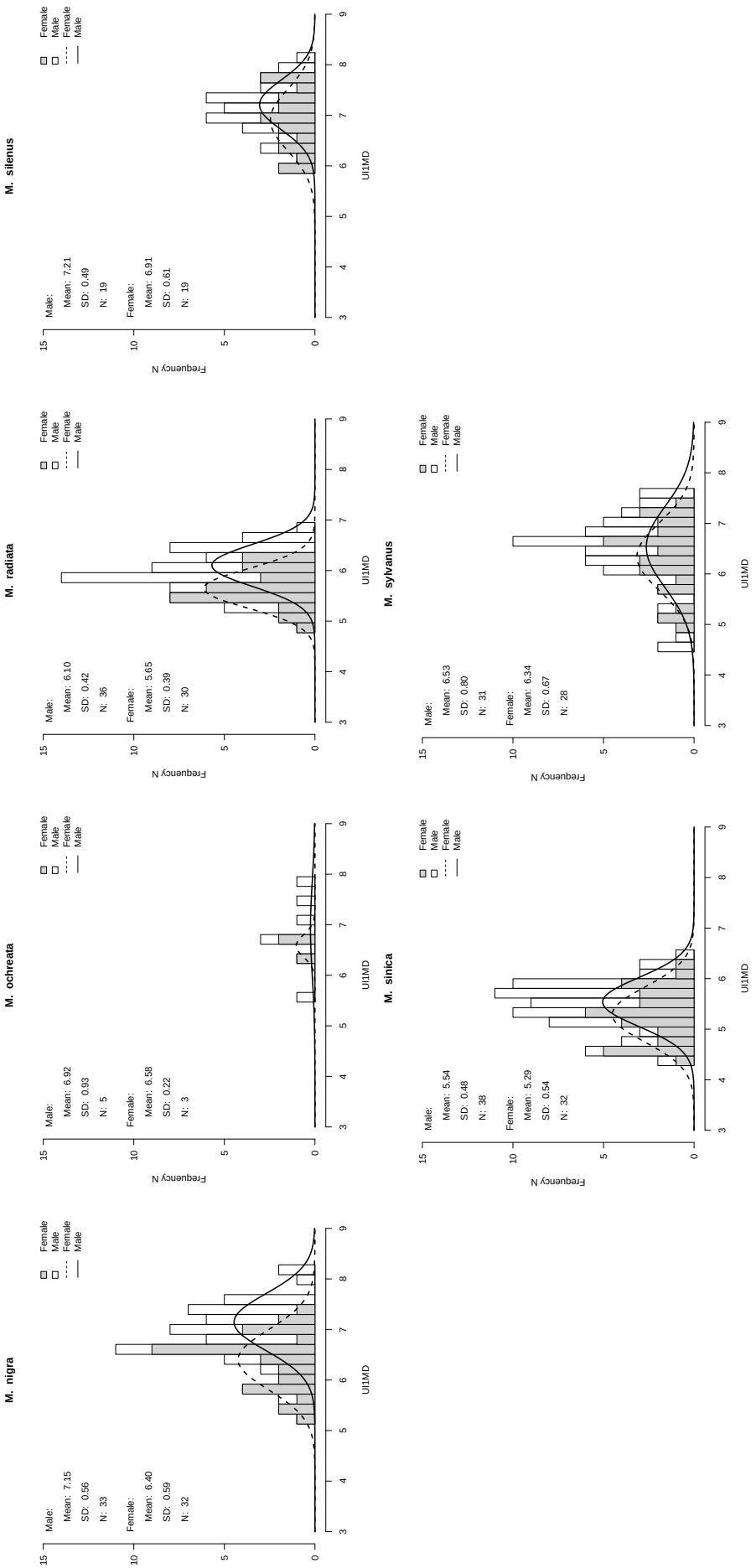

M. nigra
Male:
Mean: 7.15
SD: 0.56
N: 33
Female:
Mean: 6.40
SD: 0.59
N: 32
M. ochreata
Male:
Mean: 6.92
SD: 0.93
N: 5
Female:
Mean: 6.58
SD: 0.22
N: 3
M. radiata
Male:
Mean: 6.10
SD: 0.42
N: 36
Female:
Mean: 5.65
SD: 0.39
N: 30
M. silenus
Male:
Mean: 7.21
SD: 0.49
N: 19
Female:
Mean: 6.91
SD: 0.61
N: 19
M. sinica
Male:
Mean: 5.54
SD: 0.48
N: 38
Female:
Mean: 5.29
SD: 0.54
N: 32
M. sylvanus
Male:
Mean: 6.53
SD: 0.60
N: 31
Female:
Mean: 6.34
SD: 0.67
N: 28
Female
Male
Female
Male
Frequency N
UI1MD

Fig. C.1 UI1MD

All macaques
Male:
Mean: 5.75
SD: 0.54
N: 337
Female:
Mean: 5.49
SD: 0.51
N: 283
M. assamensis
Male:
Mean: 6.22
SD: 0.35
N: 8
Female:
Mean: 5.88
SD: 0.17
N: 4
M. cyclopis
Male:
Mean: 5.36
SD: 0.25
N: 6
Female:
Mean: 5.16
SD: 0.23
N: 11
M. fascicularis
Male:
Mean: 5.63
SD: 0.46
N: 47
Female:
Mean: 5.49
SD: 0.33
N: 36
M. fuscata
Male:
Mean: 5.88
SD: 0.36
N: 19
Female:
Mean: 5.68
SD: 0.39
N: 18
M. maura
Male:
Mean: 5.83
SD: 0.44
N: 27
Female:
Mean: 5.58
SD: 0.43
N: 15
M. mulatta
Male:
Mean: 5.53
SD: 0.36
N: 31
Female:
Mean: 5.33
SD: 0.45
N: 35
M. nemestrina
Male:
Mean: 6.55
SD: 0.43
N: 35
Female:
Mean: 6.38
SD: 0.54
N: 22
Frequency N
UI1LL
Female
Male
Female
Male

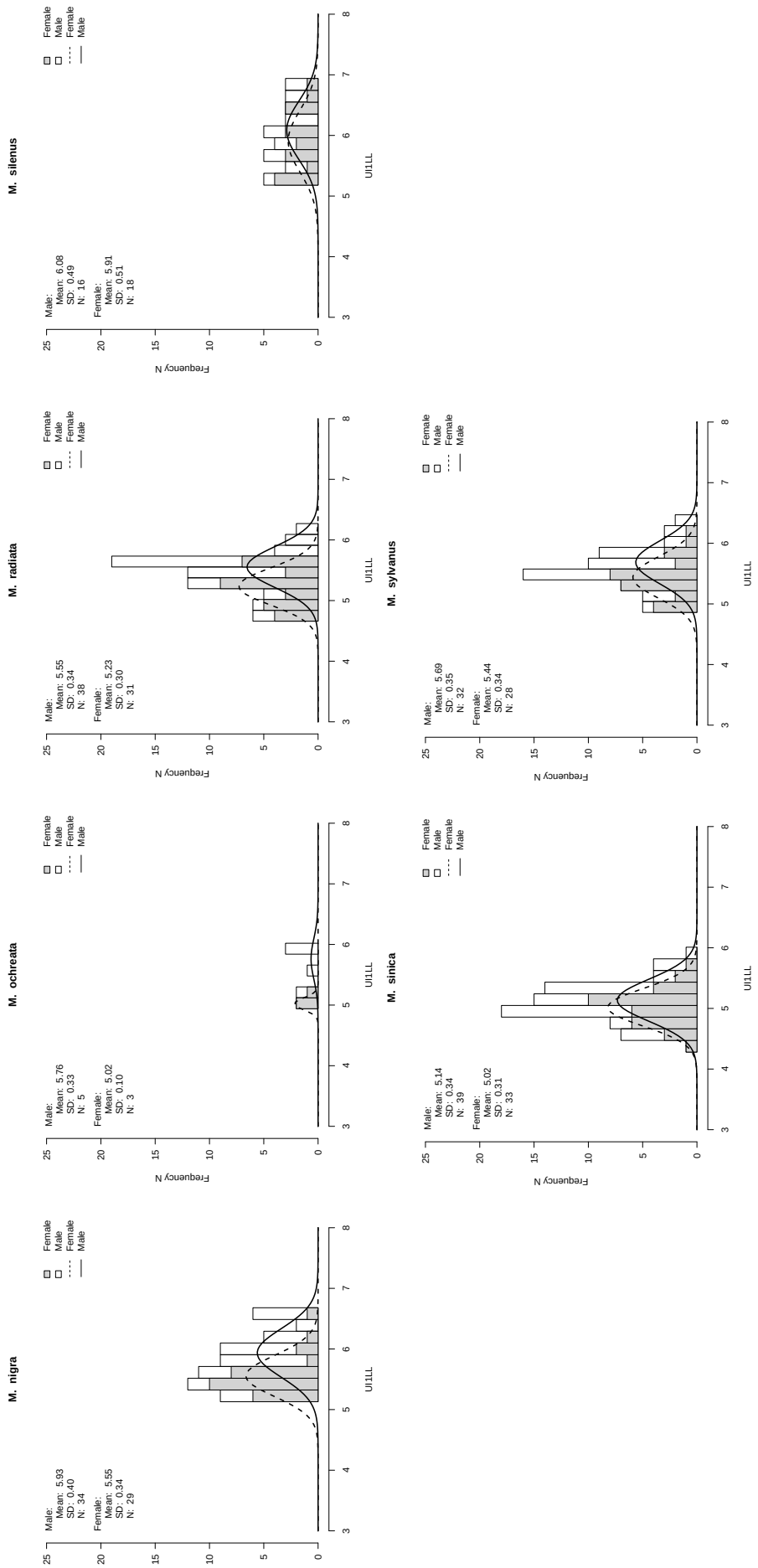

M. silenus
Male:
Mean: 6.08
SD: 0.49
N: 16
Female:
Mean: 5.91
SD: 0.51
N: 18
M. radiata
Male:
Mean: 5.55
SD: 0.34
N: 38
Female:
Mean: 5.23
SD: 0.30
N: 31
M. sylvanus
Male:
Mean: 5.69
SD: 0.35
N: 32
Female:
Mean: 5.44
SD: 0.34
N: 28
M. ochreata
Male:
Mean: 5.76
SD: 0.33
N: 5
Female:
Mean: 5.02
SD: 0.10
N: 3
M. sinica
Male:
Mean: 5.14
SD: 0.34
N: 39
Female:
Mean: 5.02
SD: 0.31
N: 33
M. nigra
Male:
Mean: 5.93
SD: 0.40
N: 34
Female:
Mean: 5.55
SD: 0.34
N: 29
Female
Male
Female
Male
Frequency N
UI1LL

Fig. C.2 UI1LL

All macaques
Male:
Mean: 4.00
SD: 0.66
N: 337
Female:
Mean: 3.92
SD: 0.54
N: 295
M. assamensis
Male:
Mean: 4.05
SD: 0.60
N: 8
Female:
Mean: 4.21
SD: 0.11
N: 5
M. cyclopis
Male:
Mean: 3.62
SD: 0.22
N: 6
Female:
Mean: 3.43
SD: 0.18
N: 10
M. fascicularis
Male:
Mean: 3.50
SD: 0.38
N: 49
Female:
Mean: 3.63
SD: 0.39
N: 39
M. fuscata
Male:
Mean: 4.91
SD: 0.42
N: 21
Female:
Mean: 4.79
SD: 0.59
N: 19
M. maura
Male:
Mean: 3.96
SD: 0.47
N: 28
Female:
Mean: 4.01
SD: 0.44
N: 16
M. mulatta
Male:
Mean: 3.79
SD: 0.49
N: 33
Female:
Mean: 3.77
SD: 0.42
N: 37
M. nemestrina
Male:
Mean: 4.94
SD: 0.68
N: 35
Female:
Mean: 4.68
SD: 0.41
N: 22
Frequency N
UI2MD
Female
Male
Female
Male

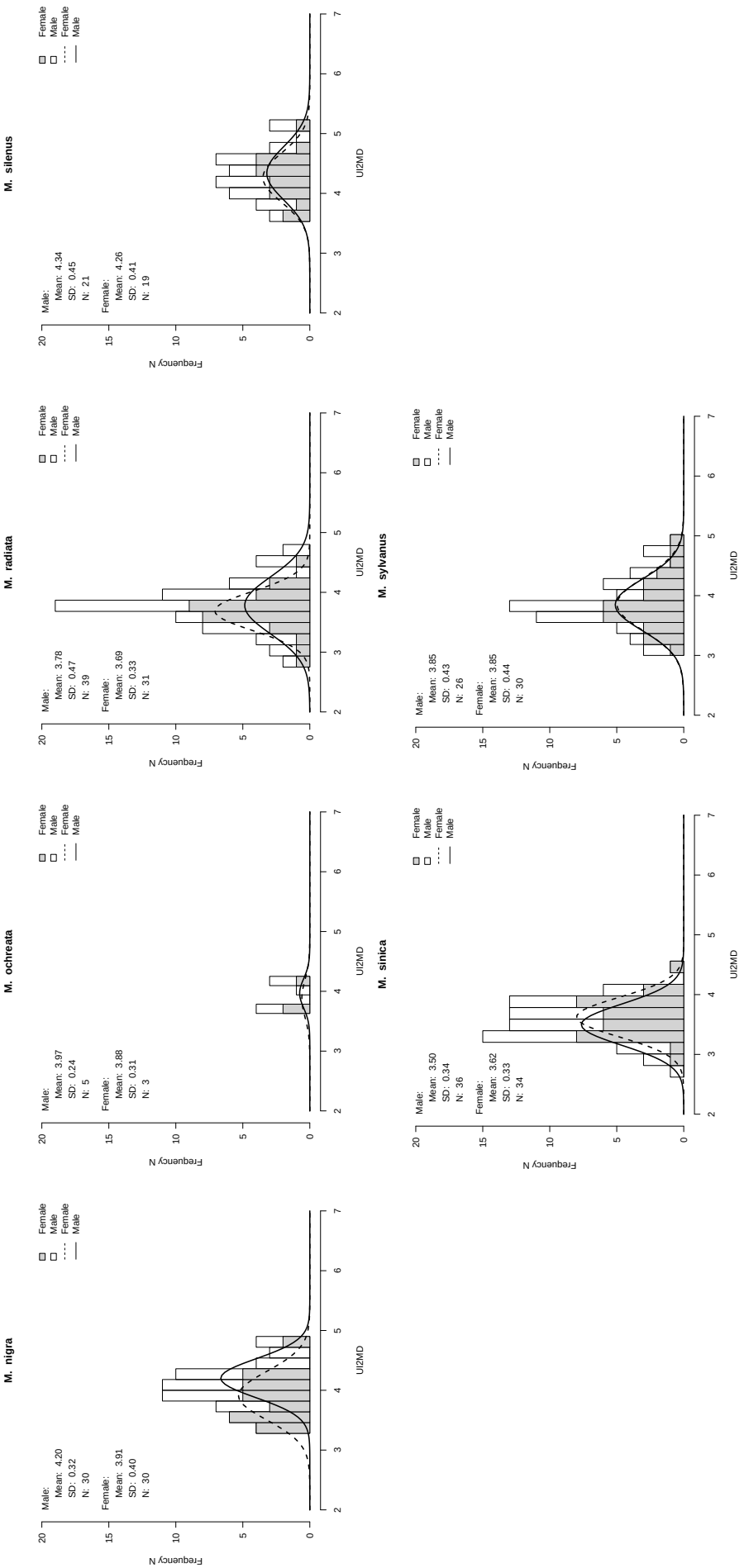

M. silenus
Male:
Mean: 4.34
SD: 0.45
N: 21
Female:
Mean: 4.26
SD: 0.41
N: 19
M. radiata
Male:
Mean: 3.78
SD: 0.47
N: 39
Female:
Mean: 3.69
SD: 0.33
N: 31
M. sylvanus
Male:
Mean: 3.85
SD: 0.43
N: 26
Female:
Mean: 3.85
SD: 0.44
N: 30
M. ochreata
Male:
Mean: 3.97
SD: 0.24
N: 5
Female:
Mean: 3.88
SD: 0.31
N: 3
M. sinica
Male:
Mean: 3.50
SD: 0.34
N: 36
Female:
Mean: 3.62
SD: 0.33
N: 34
M. nigra
Male:
Mean: 4.20
SD: 0.32
N: 30
Female:
Mean: 3.91
SD: 0.40
N: 30
Female
Male
Female
Male
Frequency N
UI2MD

Fig. C.3 UI2MD

All macaques
Male:
Mean: 5.12
SD: 0.57
N: 336
Female:
Mean: 4.76
SD: 0.44
N: 288
M. assamensis
Male:
Mean: 5.45
SD: 0.37
N: 9
Female:
Mean: 5.16
SD: 0.20
N: 5
M. cyclopis
Male:
Mean: 4.86
SD: 0.29
N: 6
Female:
Mean: 4.62
SD: 0.20
N: 10
M. fascicularis
Male:
Mean: 4.54
SD: 0.40
N: 48
Female:
Mean: 4.49
SD: 0.33
N: 39
M. fuscata
Male:
Mean: 5.61
SD: 0.38
N: 21
Female:
Mean: 5.38
SD: 0.36
N: 19
M. maura
Male:
Mean: 5.12
SD: 0.39
N: 28
Female:
Mean: 4.83
SD: 0.42
N: 15
M. mulatta
Male:
Mean: 4.99
SD: 0.39
N: 32
Female:
Mean: 4.66
SD: 0.34
N: 36
M. nemestrina
Male:
Mean: 5.95
SD: 0.40
N: 34
Female:
Mean: 5.49
SD: 0.32
N: 21
Frequency N
UI2LL
Female
Male
Female
Male

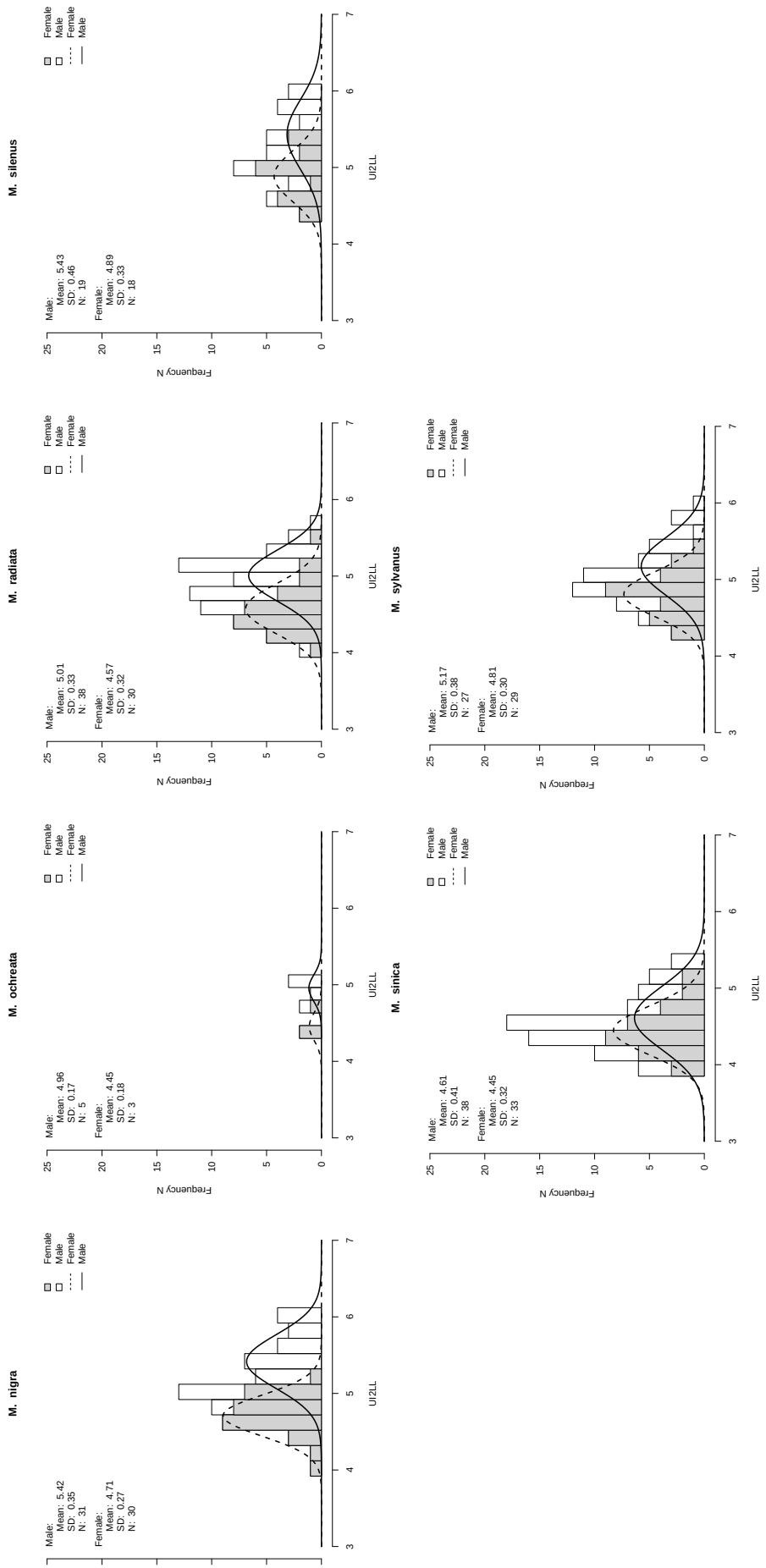

M. nigra
Male:
Mean: 5.42
SD: 0.35
N: 31
Female:
Mean: 4.71
SD: 0.27
N: 30
M. ochreata
Male:
Mean: 4.96
SD: 0.17
N: 5
Female:
Mean: 4.45
SD: 0.18
N: 3
M. radiata
Male:
Mean: 5.01
SD: 0.33
N: 38
Female:
Mean: 4.57
SD: 0.32
N: 30
M. silenus
Male:
Mean: 5.43
SD: 0.46
N: 19
Female:
Mean: 4.89
SD: 0.33
N: 18
M. sinica
Male:
Mean: 4.61
SD: 0.41
N: 38
Female:
Mean: 4.45
SD: 0.32
N: 33
M. sylvanus
Male:
Mean: 5.17
SD: 0.38
N: 27
Female:
Mean: 4.81
SD: 0.30
N: 29
Female
Male
Female
Male
Frequency N
UI2LL

Fig. C.4 UI2LL

All macaques
Male:
Mean: 4.43
SD: 0.57
N: 343
Female:
Mean: 4.24
SD: 0.54
N: 295
M. assamensis
Male:
Mean: 4.24
SD: 0.60
N: 8
Female:
Mean: 3.92
SD: 0.26
N: 5
M. cyclopis
Male:
Mean: 3.83
SD: 0.19
N: 6
Female:
Mean: 3.88
SD: 0.21
N: 11
M. fascicularis
Male:
Mean: 4.28
SD: 0.35
N: 44
Female:
Mean: 4.24
SD: 0.42
N: 40
M. fuscata
Male:
Mean: 4.53
SD: 0.50
N: 21
Female:
Mean: 4.36
SD: 0.34
N: 20
M. maura
Male:
Mean: 4.60
SD: 0.35
N: 31
Female:
Mean: 4.41
SD: 0.31
N: 15
M. mulatta
Male:
Mean: 3.90
SD: 0.30
N: 32
Female:
Mean: 3.76
SD: 0.35
N: 37
M. nemestrina
Male:
Mean: 5.10
SD: 0.67
N: 32
Female:
Mean: 5.07
SD: 0.51
N: 21
Frequency N
L1LMD
Female
Male
Female
Male

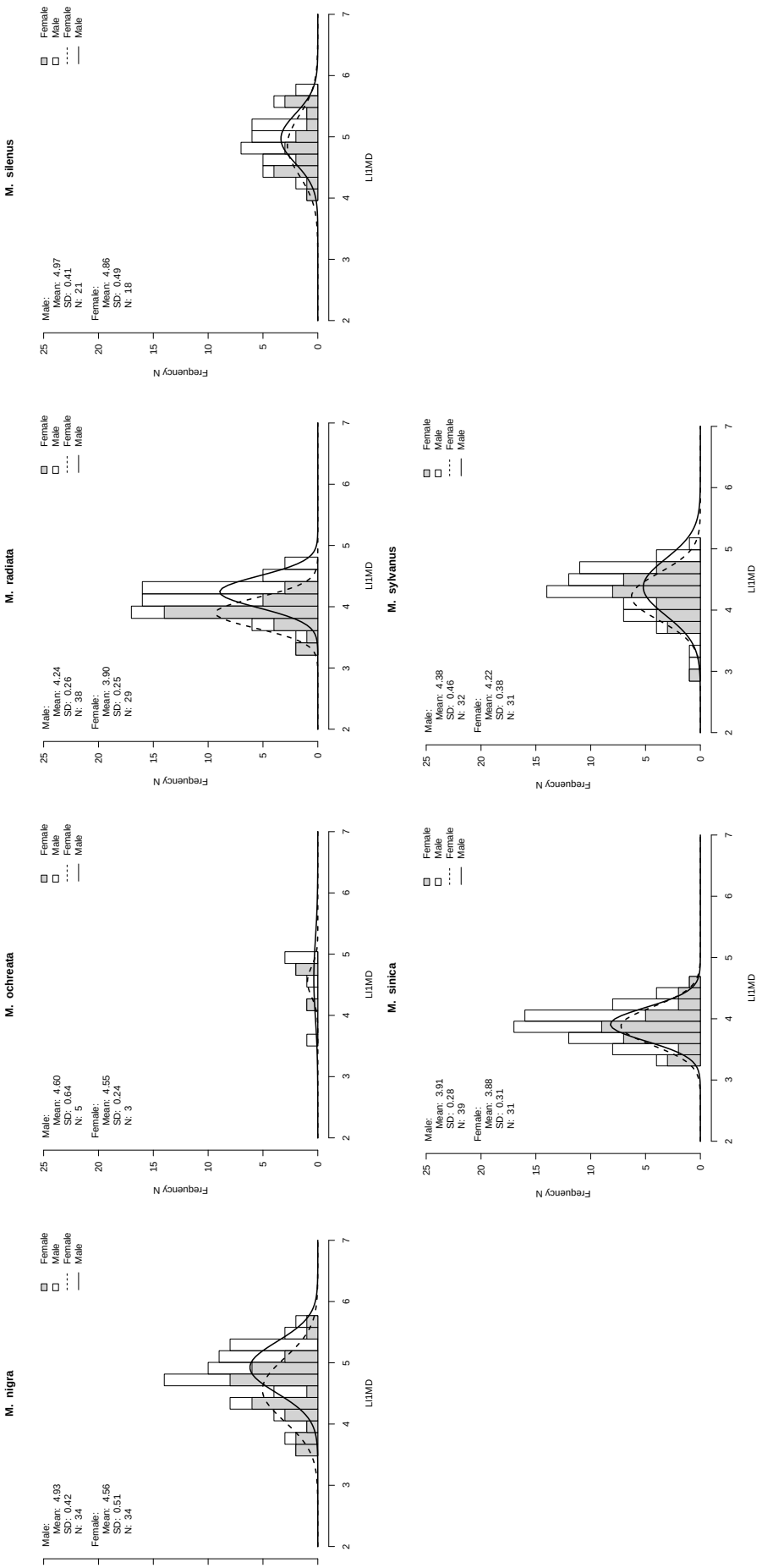

M. silenus
Male:
Mean: 4.97
SD: 0.41
N: 21
Female:
Mean: 4.86
SD: 0.49
N: 18
M. radiata
Male:
Mean: 4.24
SD: 0.26
N: 38
Female:
Mean: 3.90
SD: 0.25
N: 29
M. sylvanus
Male:
Mean: 4.38
SD: 0.46
N: 32
Female:
Mean: 4.22
SD: 0.38
N: 31
M. ochreata
Male:
Mean: 4.60
SD: 0.64
N: 5
Female:
Mean: 4.55
SD: 0.24
N: 3
M. sinica
Male:
Mean: 3.91
SD: 0.28
N: 39
Female:
Mean: 3.88
SD: 0.31
N: 31
M. nigra
Male:
Mean: 4.93
SD: 0.42
N: 34
Female:
Mean: 4.56
SD: 0.51
N: 34
Female
Male
Female
Male
Frequency N
LI1MD

Fig. C.5 LI1MD

All macaques
Male:
Mean: 5.45
SD: 0.57
N: 337
Female:
Mean: 5.09
SD: 0.49
N: 294
M. assamensis
Male:
Mean: 5.78
SD: 0.35
N: 7
Female:
Mean: 5.60
SD: 0.08
N: 4
M. cyclopis
Male:
Mean: 4.83
SD: 0.22
N: 5
Female:
Mean: 4.60
SD: 0.16
N: 11
M. fascicularis
Male:
Mean: 5.39
SD: 0.53
N: 44
Female:
Mean: 5.21
SD: 0.47
N: 39
M. fuscata
Male:
Mean: 5.46
SD: 0.36
N: 20
Female:
Mean: 5.09
SD: 0.34
N: 20
M. maura
Male:
Mean: 5.58
SD: 0.34
N: 31
Female:
Mean: 5.26
SD: 0.30
N: 15
M. mulatta
Male:
Mean: 4.95
SD: 0.35
N: 31
Female:
Mean: 4.74
SD: 0.40
N: 38
M. nemestrina
Male:
Mean: 6.17
SD: 0.45
N: 33
Female:
Mean: 5.75
SD: 0.44
N: 22
Frequency N
LILLL
Female
Male
Female
Male

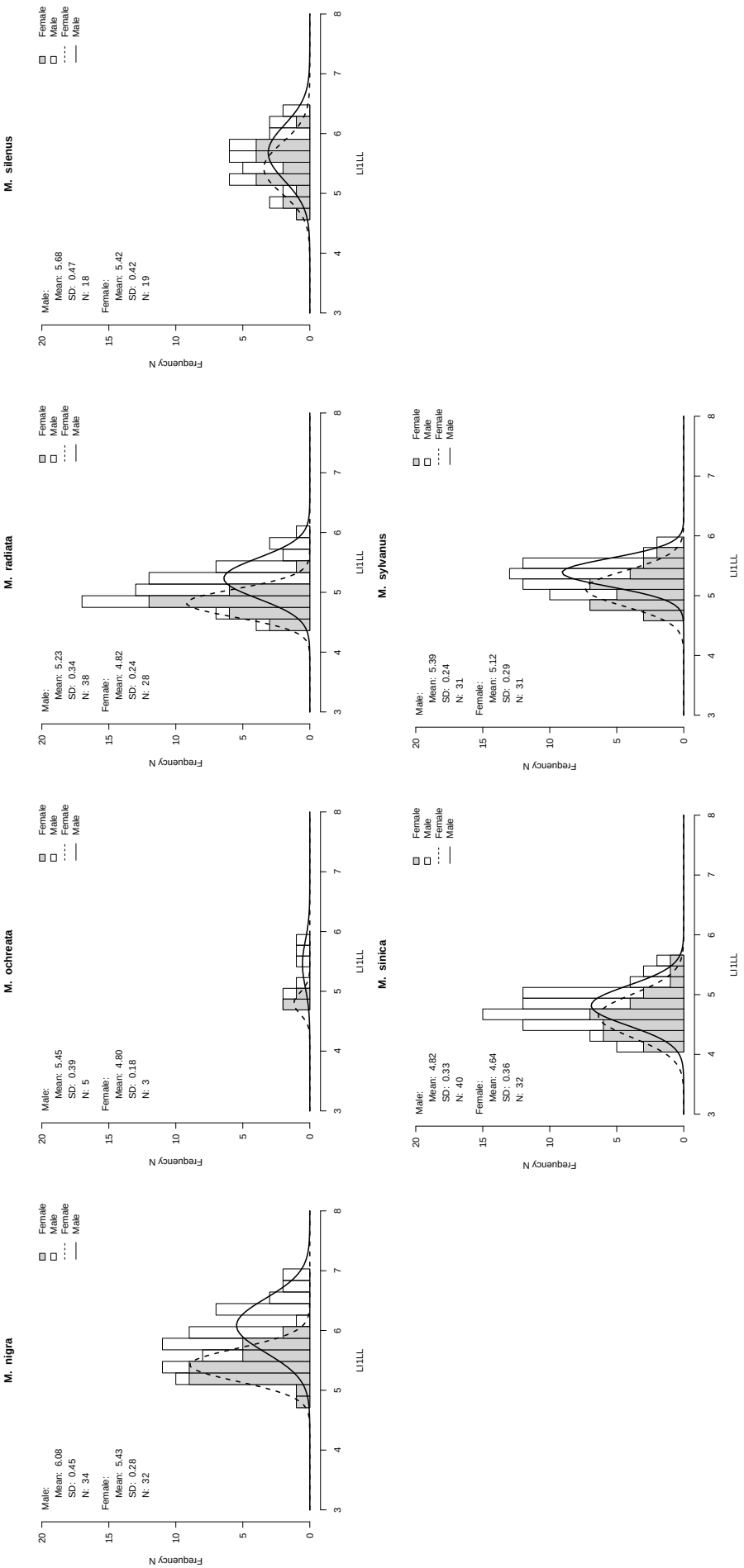

M. silenus
M. radiata
M. sylvanus
M. ochreata
M. sinica
M. nigra
Female
Male
Female
Male
Male:
Mean: 6.08
SD: 0.45
N: 34
Female:
Mean: 5.43
SD: 0.28
N: 32
Male:
Mean: 5.45
SD: 0.39
N: 5
Female:
Mean: 4.80
SD: 0.18
N: 3
Male:
Mean: 5.23
SD: 0.34
N: 38
Female:
Mean: 4.82
SD: 0.24
N: 28
Male:
Mean: 4.82
SD: 0.33
N: 40
Female:
Mean: 4.64
SD: 0.36
N: 32
Male:
Mean: 5.39
SD: 0.24
N: 31
Female:
Mean: 5.12
SD: 0.29
N: 31
Male:
Mean: 5.68
SD: 0.47
N: 18
Female:
Mean: 5.42
SD: 0.42
N: 19
Frequency N
LI1LL

Fig. C.6 LI1LL

All macaques
Male:
Mean: 4.40
SD: 0.69
N: 335
Female:
Mean: 4.07
SD: 0.61
N: 295
M. assamensis
Male:
Mean: 4.09
SD: 0.66
N: 8
Female:
Mean: 4.08
SD: 0.40
N: 5
M. cyclopis
Male:
Mean: 4.19
SD: 0.43
N: 6
Female:
Mean: 4.18
SD: 0.46
N: 11
M. fascicularis
Male:
Mean: 3.89
SD: 0.57
N: 44
Female:
Mean: 3.76
SD: 0.56
N: 41
M. fuscata
Male:
Mean: 4.75
SD: 0.45
N: 20
Female:
Mean: 4.50
SD: 0.47
N: 19
M. maura
Male:
Mean: 4.62
SD: 0.30
N: 31
Female:
Mean: 4.39
SD: 0.35
N: 14
M. mulatta
Male:
Mean: 4.09
SD: 0.56
N: 29
Female:
Mean: 3.68
SD: 0.41
N: 35
M. nemestrina
Male:
Mean: 5.15
SD: 0.64
N: 32
Female:
Mean: 4.69
SD: 0.53
N: 20
Frequency N
LI2MD
Female
Male
Female
Male

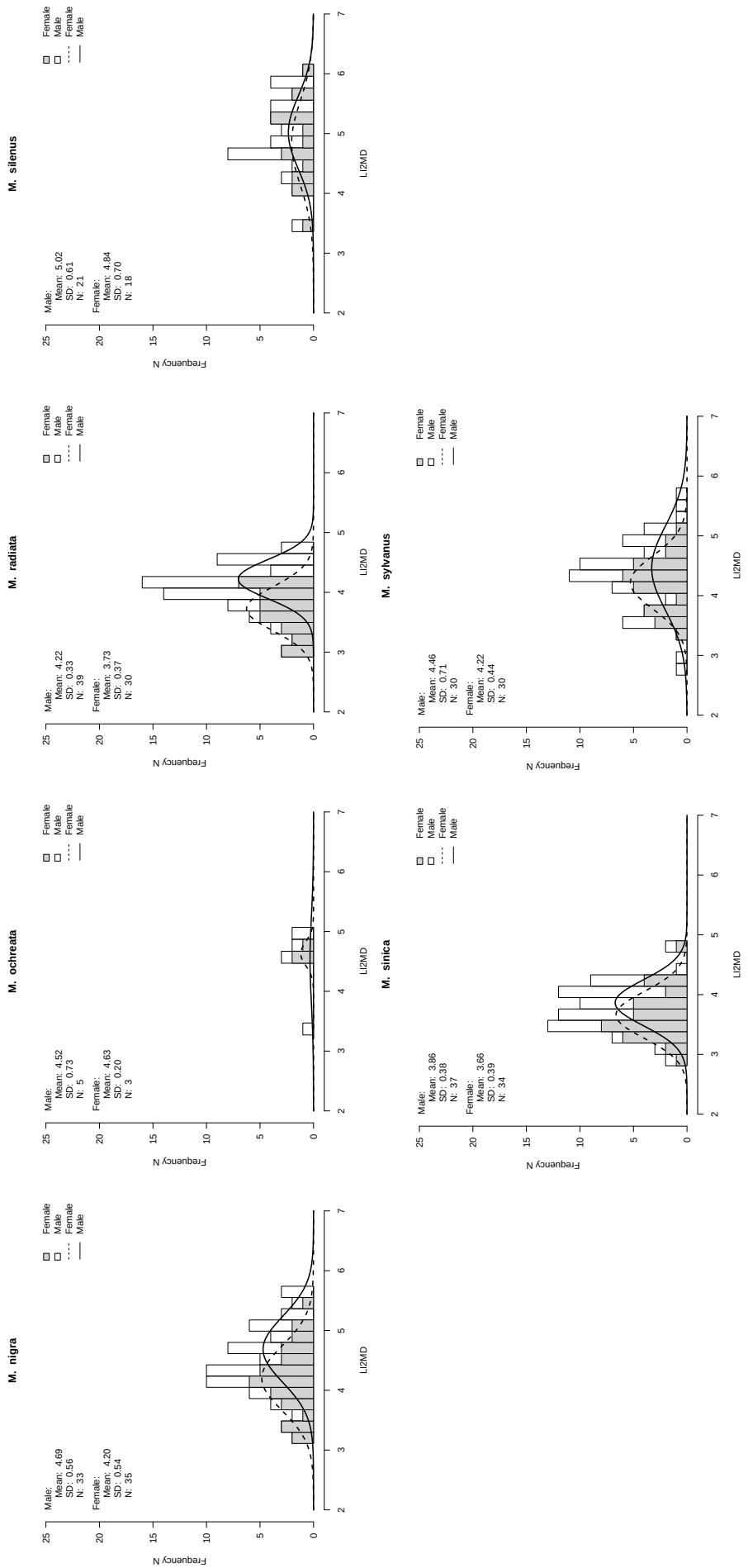

M. silenus
Male:
Mean: 5.02
SD: 0.61
N: 21
Female:
Mean: 4.84
SD: 0.70
N: 18
M. radiata
Male:
Mean: 4.22
SD: 0.33
N: 39
Female:
Mean: 3.73
SD: 0.37
N: 30
M. sylvanus
Male:
Mean: 4.46
SD: 0.71
N: 30
Female:
Mean: 4.22
SD: 0.44
N: 30
M. ochreata
Male:
Mean: 4.52
SD: 0.73
N: 5
Female:
Mean: 4.63
SD: 0.20
N: 3
M. sinica
Male:
Mean: 3.86
SD: 0.38
N: 37
Female:
Mean: 3.66
SD: 0.39
N: 34
M. nigra
Male:
Mean: 4.69
SD: 0.56
N: 33
Female:
Mean: 4.20
SD: 0.54
N: 35
Female
Male
Female
Male
Frequency N
LI2MD

Fig. C.7 LI2MD

All macaques
Male:
Mean: 5.08
SD: 0.63
N: 330
Female:
Mean: 4.71
SD: 0.53
N: 299
M. assamensis
Male:
Mean: 5.80
SD: 0.33
N: 8
Female:
Mean: 5.40
SD: 0.23
N: 6
M. cyclopis
Male:
Mean: 4.69
SD: 0.25
N: 6
Female:
Mean: 4.45
SD: 0.19
N: 11
M. fascicularis
Male:
Mean: 4.55
SD: 0.47
N: 43
Female:
Mean: 4.47
SD: 0.52
N: 41
M. fuscata
Male:
Mean: 5.16
SD: 0.27
N: 19
Female:
Mean: 4.78
SD: 0.35
N: 19
M. maura
Male:
Mean: 5.32
SD: 0.35
N: 31
Female:
Mean: 4.88
SD: 0.24
N: 16
M. mulatta
Male:
Mean: 4.60
SD: 0.37
N: 28
Female:
Mean: 4.36
SD: 0.44
N: 37
M. nemestrina
Male:
Mean: 6.00
SD: 0.39
N: 32
Female:
Mean: 5.60
SD: 0.43
N: 20
Frequency N
LI2LL
Female
Male
Female
Male

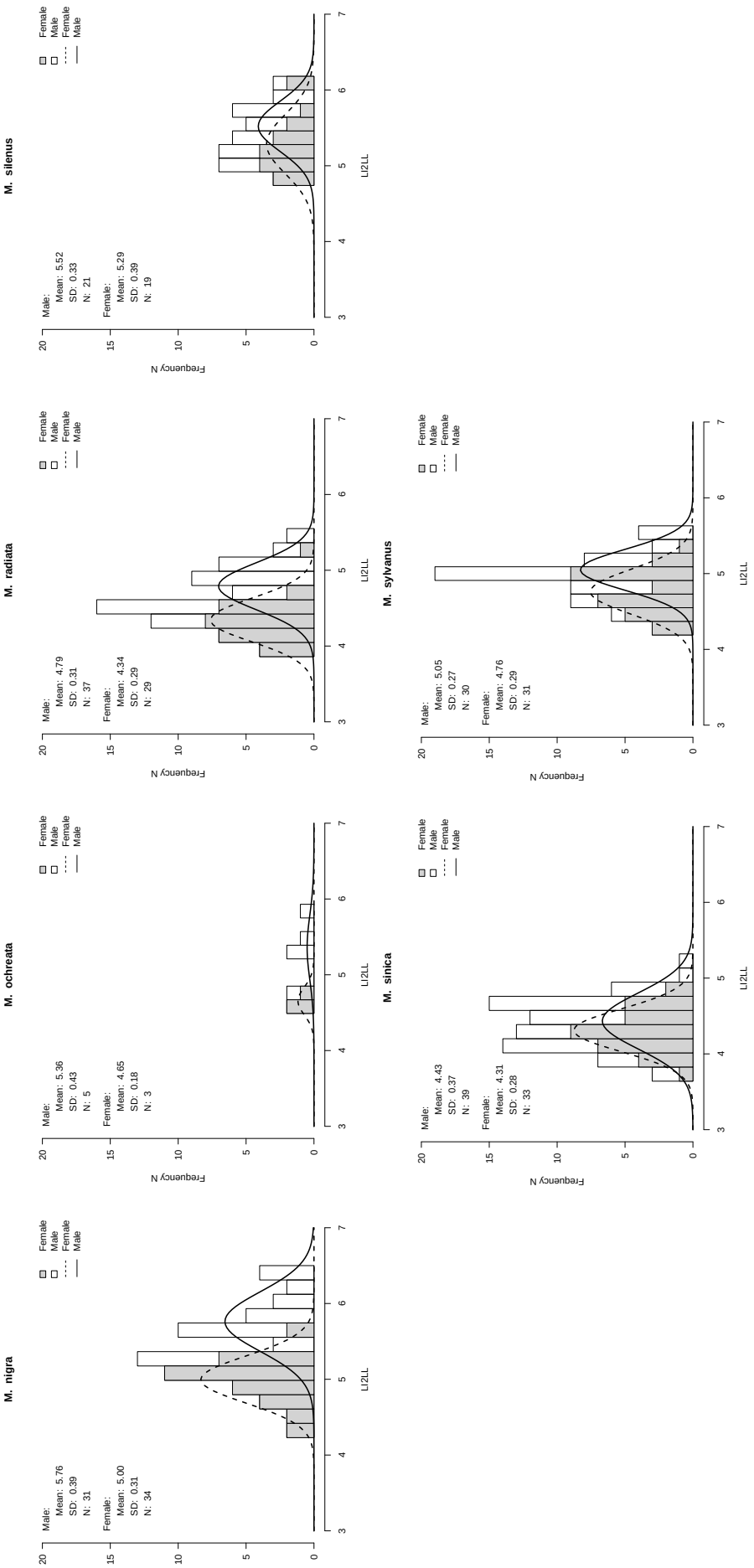

M. silenus
M. radiata
M. sylvanus
M. ochreata
M. sinica
M. nigra
Female
Male
Female
Male
Male:
Mean: 5.52
SD: 0.33
N: 21
Female:
Mean: 5.29
SD: 0.39
N: 19
Male:
Mean: 4.79
SD: 0.31
N: 37
Female:
Mean: 4.34
SD: 0.29
N: 29
Male:
Mean: 5.05
SD: 0.27
N: 30
Female:
Mean: 4.76
SD: 0.29
N: 31
Male:
Mean: 5.36
SD: 0.43
N: 5
Female:
Mean: 4.65
SD: 0.18
N: 3
Male:
Mean: 4.43
SD: 0.37
N: 39
Female:
Mean: 4.31
SD: 0.28
N: 33
Male:
Mean: 5.76
SD: 0.39
N: 31
Female:
Mean: 5.00
SD: 0.31
N: 34
Frequency N
LI2LL

Fig. C.8 LI2LL

All macaques
Male:
Mean: 9.34
SD: 1.72
N: 208
Female:
Mean: 6.01
SD: 0.72
N: 277
M. assamensis
Male:
Mean: 10.40
SD: 1.31
N: 11
Female:
Mean: 6.93
SD: 0.59
N: 5
M. cyclopis
Male:
Mean: 9.34
SD: 0.93
N: 4
Female:
Mean: 5.99
SD: 0.57
N: 10
M. fascicularis
Male:
Mean: 7.80
SD: 1.06
N: 34
Female:
Mean: 5.39
SD: 0.59
N: 37
M. fuscata
Male:
Mean: 8.97
SD: 1.39
N: 15
Female:
Mean: 6.16
SD: 0.43
N: 19
M. maura
Male:
Mean: 10.06
SD: 1.09
N: 18
Female:
Mean: 6.59
SD: 0.41
N: 15
M. mulatta
Male:
Mean: 8.31
SD: 1.04
N: 11
Female:
Mean: 5.41
SD: 0.64
N: 34
M. nemestrina
Male:
Mean: 11.58
SD: 1.66
N: 23
Female:
Mean: 7.01
SD: 0.62
N: 21
Frequency N
UCMD
Female
Male
Female
Male

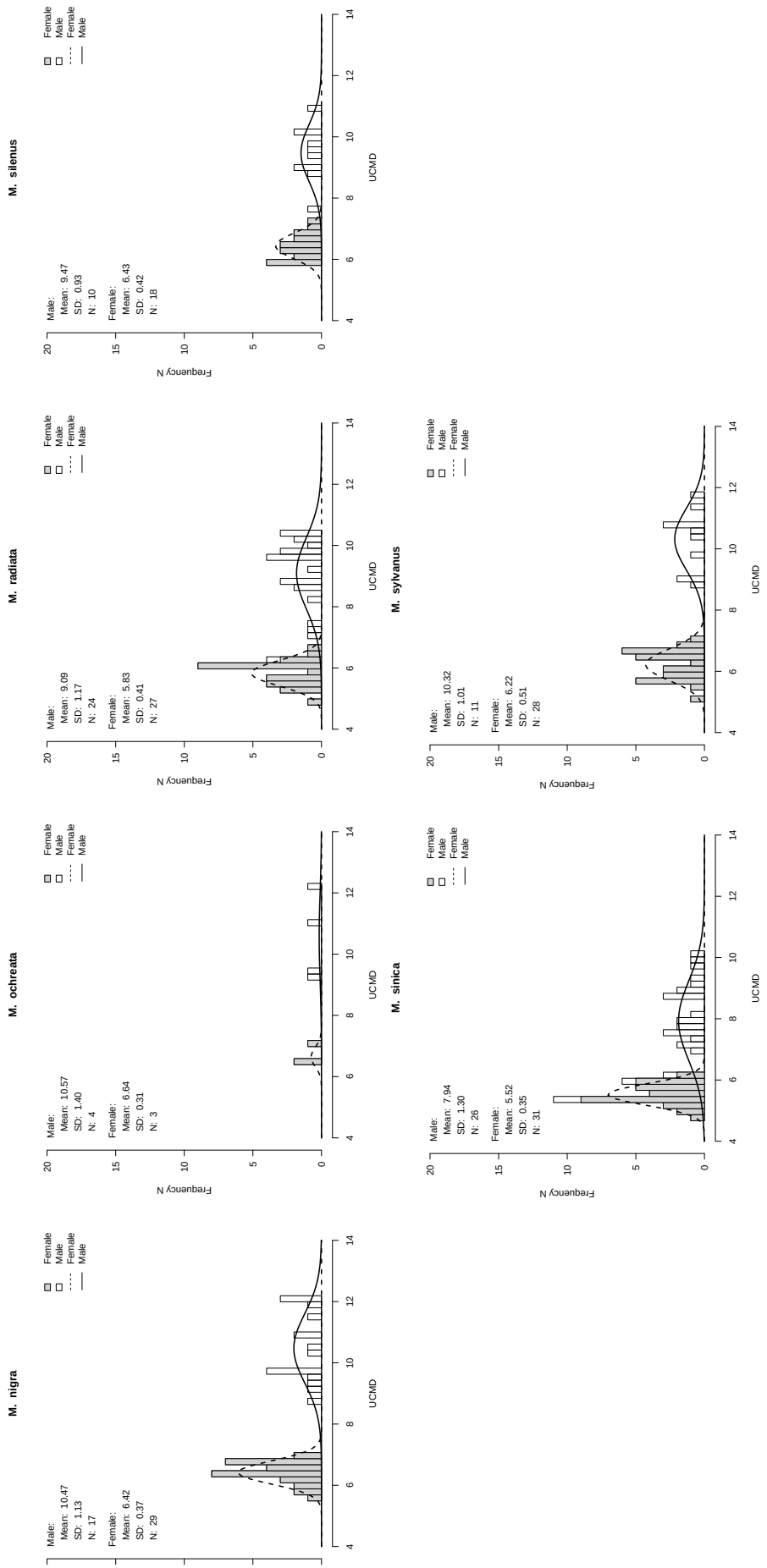
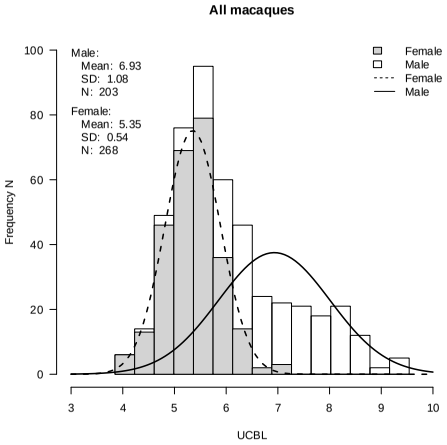
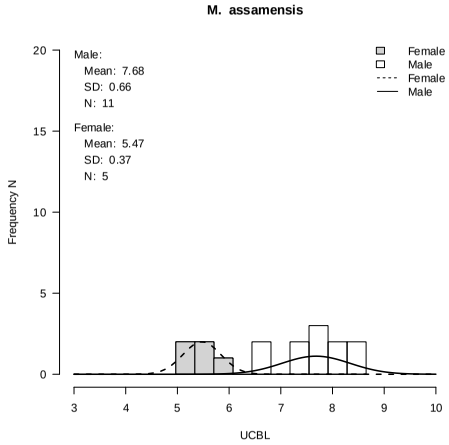
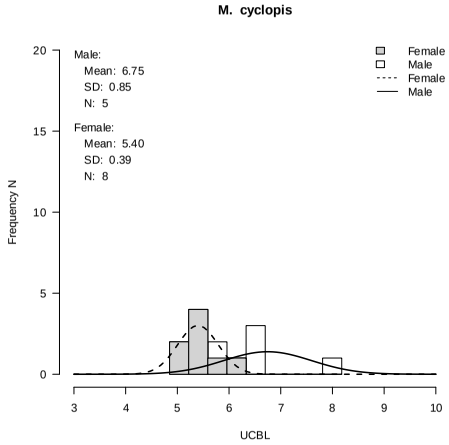
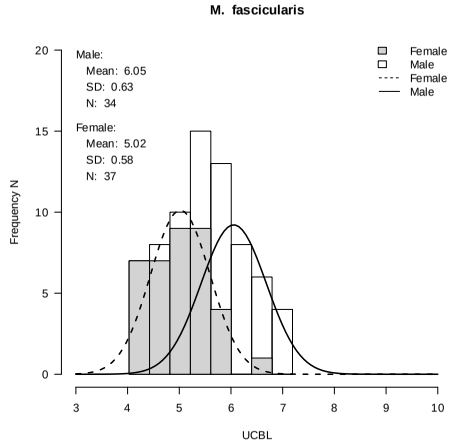

M. nigra
Male:
Mean: 10.47
SD: 1.13
N: 17
Female:
Mean: 6.42
SD: 0.37
N: 29
M. ochreata
Male:
Mean: 10.57
SD: 1.40
N: 4
Female:
Mean: 6.64
SD: 0.31
N: 3
M. radiata
Male:
Mean: 9.09
SD: 1.17
N: 24
Female:
Mean: 5.83
SD: 0.41
N: 27
M. silenus
Male:
Mean: 9.47
SD: 0.93
N: 10
Female:
Mean: 6.43
SD: 0.42
N: 18
M. sinica
Male:
Mean: 7.94
SD: 1.30
N: 26
Female:
Mean: 5.52
SD: 0.35
N: 31
M. sylvanus
Male:
Mean: 10.32
SD: 1.01
N: 11
Female:
Mean: 6.22
SD: 0.51
N: 28
Female
Male
Female
Male
Frequency N
UCMD

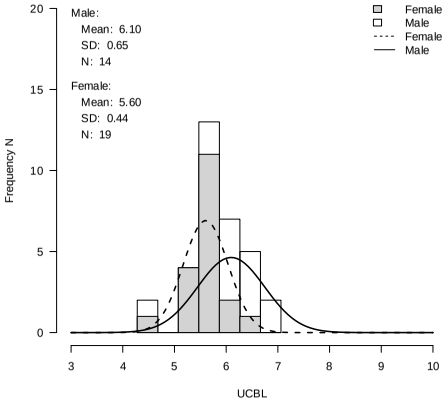
Fig. C.9 UCMD

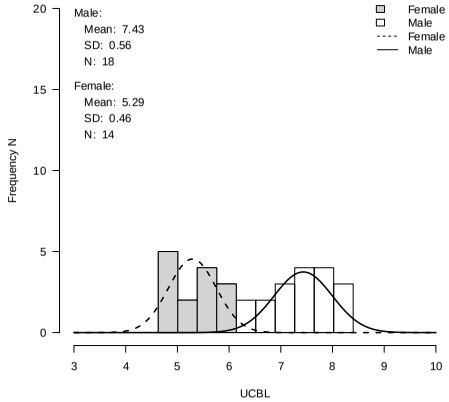

All macaques
Male:
Mean: 6.93
SD: 1.08
N: 203
Female:
Mean: 5.35
SD: 0.54
N: 268
Female
Male
Female
Male
Frequency N
UCBL

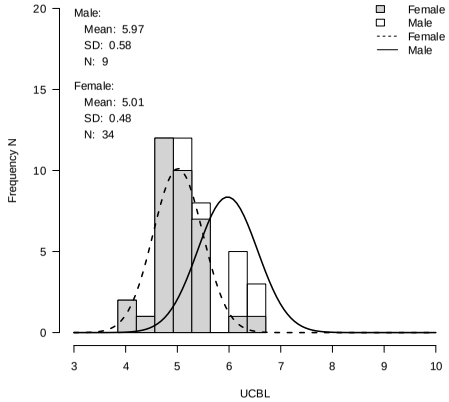

M. assamensis
Male:
Mean: 7.68
SD: 0.66
N: 11
Female:
Mean: 5.47
SD: 0.37
N: 5
Female
Male
Female
Male
Frequency N
UCBL

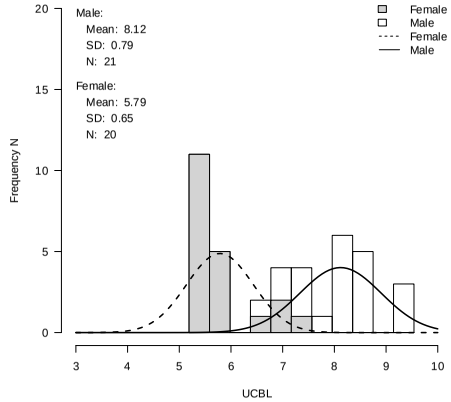

M. cyclopis
Male:
Mean: 6.75
SD: 0.85
N: 5
Female:
Mean: 5.40
SD: 0.39
N: 8
Female
Male
Female
Male
Frequency N
UCBL


M. fascicularis
Male:
Mean: 6.05
SD: 0.63
N: 34
Female:
Mean: 5.02
SD: 0.58
N: 37
Female
Male
Female
Male
Frequency N
UCBL


M. fuscata
Male:
Mean: 6.10
SD: 0.65
N: 14
Female:
Mean: 5.60
SD: 0.44
N: 19
Female
Male
Female
Male
Frequency N
UCBL


M. maura
Male:
Mean: 7.43
SD: 0.56
N: 18
Female:
Mean: 5.29
SD: 0.46
N: 14
Female
Male
Female
Male
Frequency N
UCBL


M. mulatta
Male:
Mean: 5.97
SD: 0.58
N: 9
Female:
Mean: 5.01
SD: 0.48
N: 34
Female
Male
Female
Male
Frequency N
UCBL


M. nemestrina
Male:
Mean: 8.12
SD: 0.79
N: 21
Female:
Mean: 5.79
SD: 0.65
N: 20
Female
Male
Female
Male
Frequency N
UCBL

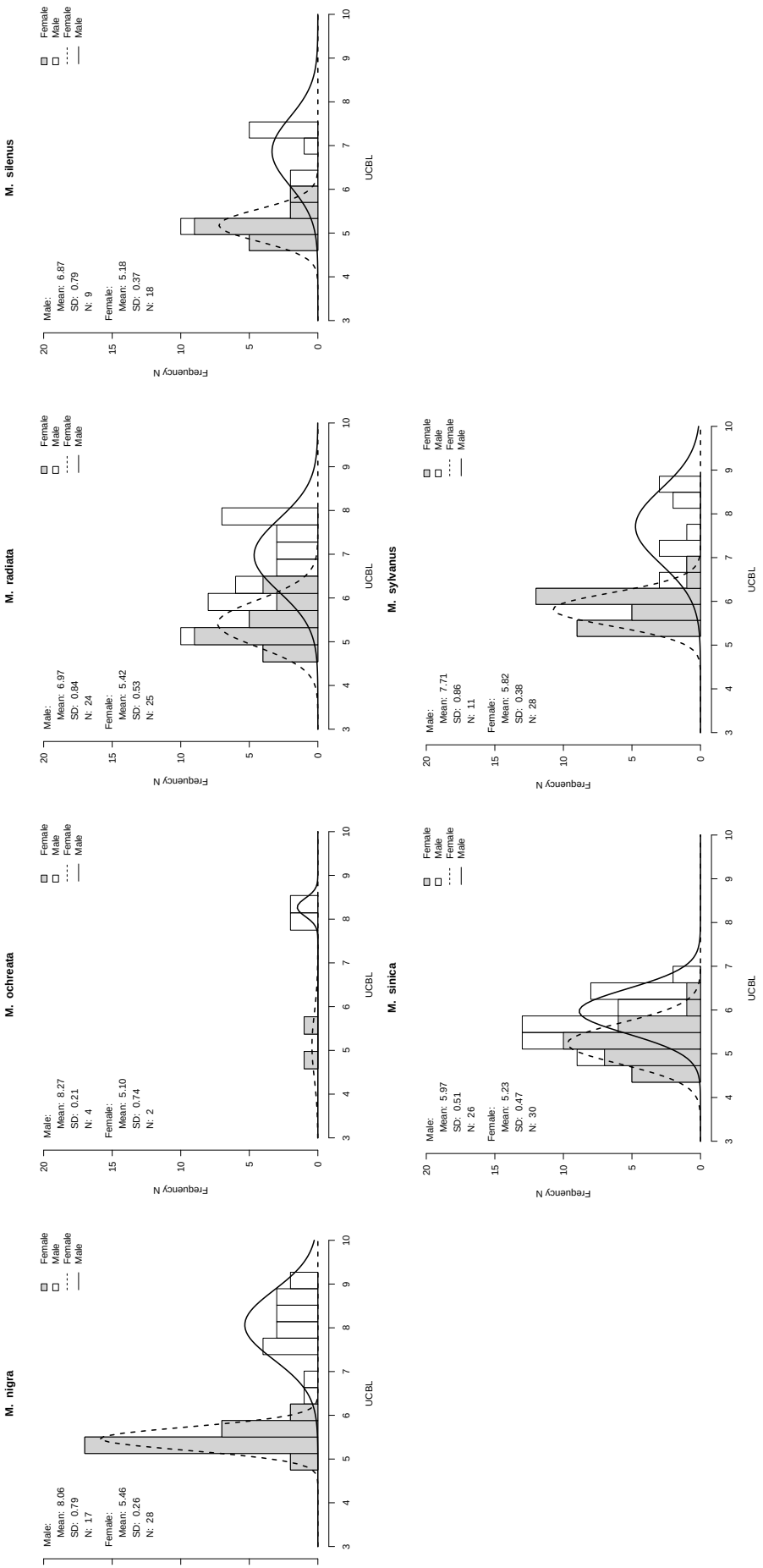

M. silenus
Male:
Mean: 6.87
SD: 0.79
N: 9
Female:
Mean: 5.18
SD: 0.37
N: 18
M. radiata
Male:
Mean: 6.97
SD: 0.84
N: 24
Female:
Mean: 5.42
SD: 0.53
N: 25
M. sylvanus
Male:
Mean: 7.71
SD: 0.86
N: 11
Female:
Mean: 5.82
SD: 0.38
N: 28
M. ochreata
Male:
Mean: 8.27
SD: 0.21
N: 4
Female:
Mean: 5.10
SD: 0.74
N: 2
M. sinica
Male:
Mean: 5.97
SD: 0.51
N: 26
Female:
Mean: 5.23
SD: 0.47
N: 30
M. nigra
Male:
Mean: 8.06
SD: 0.79
N: 17
Female:
Mean: 5.46
SD: 0.26
N: 28
Female
Male
Female
Male
Frequency N
UCBL

Fig. C.10 UCBL

All macaques
Male:
Mean: 5.10
SD: 0.77
N: 290
Female:
Mean: 3.59
SD: 0.44
N: 279
M. assamensis
Male:
Mean: 5.41
SD: 0.30
N: 11
Female:
Mean: 4.11
SD: 0.14
N: 6
M. cyclopis
Male:
Mean: 4.73
SD: 0.25
N: 7
Female:
Mean: 3.33
SD: 0.09
N: 9
M. fascicularis
Male:
Mean: 4.40
SD: 0.37
N: 43
Female:
Mean: 3.19
SD: 0.32
N: 37
M. fuscata
Male:
Mean: 4.98
SD: 0.55
N: 19
Female:
Mean: 3.58
SD: 0.24
N: 18
M. maura
Male:
Mean: 5.50
SD: 0.46
N: 23
Female:
Mean: 4.00
SD: 0.26
N: 17
M. mulatta
Male:
Mean: 4.52
SD: 0.41
N: 24
Female:
Mean: 3.33
SD: 0.38
N: 37
M. nemestrina
Male:
Mean: 6.44
SD: 0.55
N: 32
Female:
Mean: 4.25
SD: 0.42
N: 21
Frequency N
LCMD
Female
Male
Female
Male

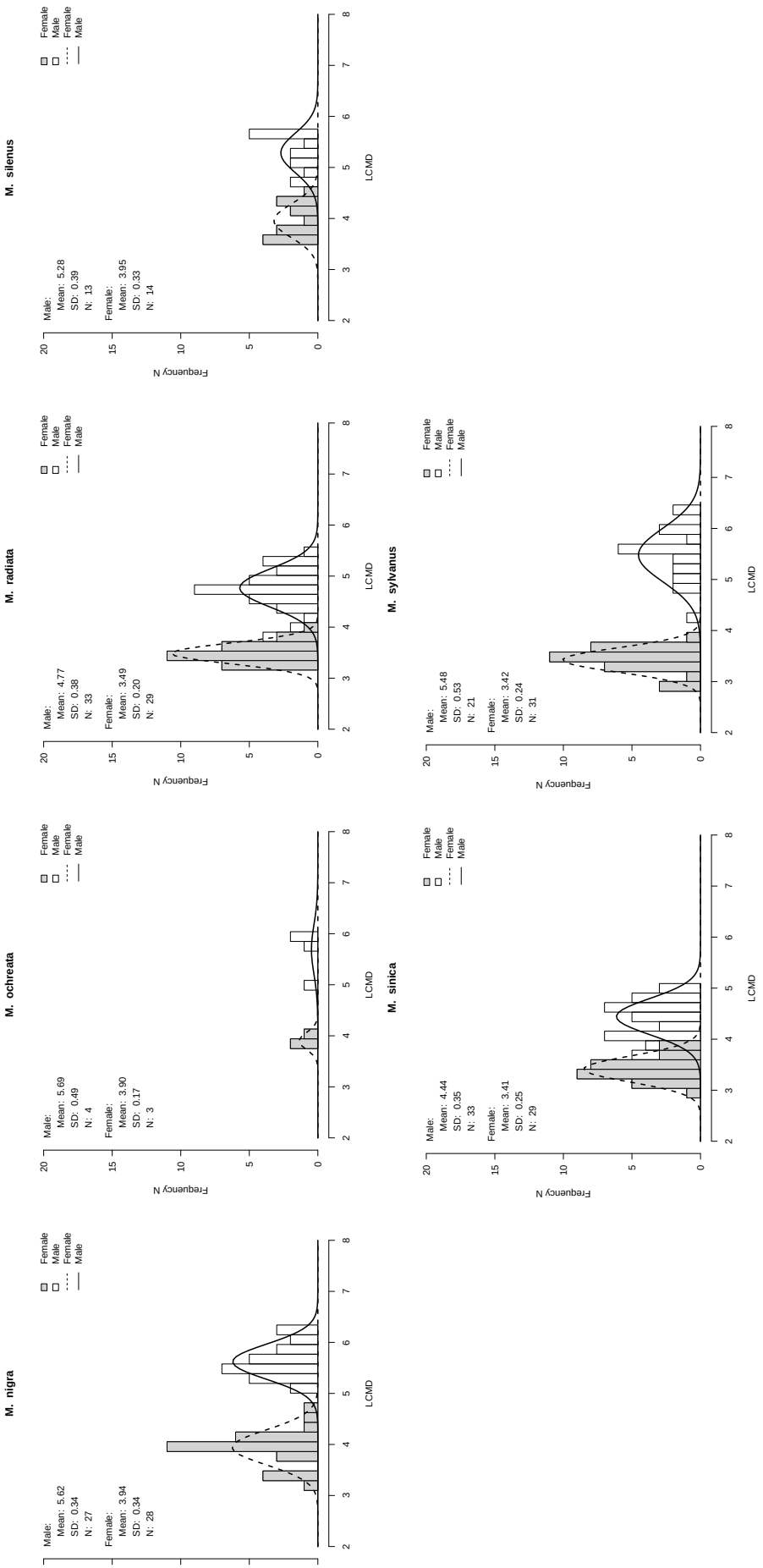

M. silenus
Male:
Mean: 5.28
SD: 0.39
N: 13
Female:
Mean: 3.95
SD: 0.33
N: 14
M. radiata
Male:
Mean: 4.77
SD: 0.38
N: 33
Female:
Mean: 3.49
SD: 0.20
N: 29
M. sylvanus
Male:
Mean: 5.48
SD: 0.53
N: 21
Female:
Mean: 3.42
SD: 0.24
N: 31
M. ochreata
Male:
Mean: 5.69
SD: 0.49
N: 4
Female:
Mean: 3.90
SD: 0.17
N: 3
M. sinica
Male:
Mean: 4.44
SD: 0.35
N: 33
Female:
Mean: 3.41
SD: 0.25
N: 29
M. nigra
Male:
Mean: 5.62
SD: 0.34
N: 27
Female:
Mean: 3.94
SD: 0.34
N: 28
Female
Male
Female
Male
Frequency N
LCMD

Fig. C.11 LCMD

All macaques
Male:
Mean: 8.89
SD: 1.23
N: 279
Female:
Mean: 5.92
SD: 0.65
N: 281
M. assamensis
Male:
Mean: 10.03
SD: 0.77
N: 11
Female:
Mean: 7.60
SD: 0.63
N: 6
M. cyclopis
Male:
Mean: 8.37
SD: 0.62
N: 7
Female:
Mean: 6.07
SD: 0.46
N: 9
M. fascicularis
Male:
Mean: 7.89
SD: 0.73
N: 41
Female:
Mean: 5.52
SD: 0.49
N: 38
M. fuscata
Male:
Mean: 8.32
SD: 0.75
N: 19
Female:
Mean: 5.64
SD: 0.41
N: 19
M. maura
Male:
Mean: 9.30
SD: 0.67
N: 23
Female:
Mean: 6.35
SD: 0.45
N: 17
M. mulatta
Male:
Mean: 8.04
SD: 0.70
N: 20
Female:
Mean: 5.46
SD: 0.56
N: 37
M. nemestrina
Male:
Mean: 11.04
SD: 0.81
N: 32
Female:
Mean: 6.79
SD: 0.57
N: 21
Frequency N
LCBL
Female
Male
Female
Male

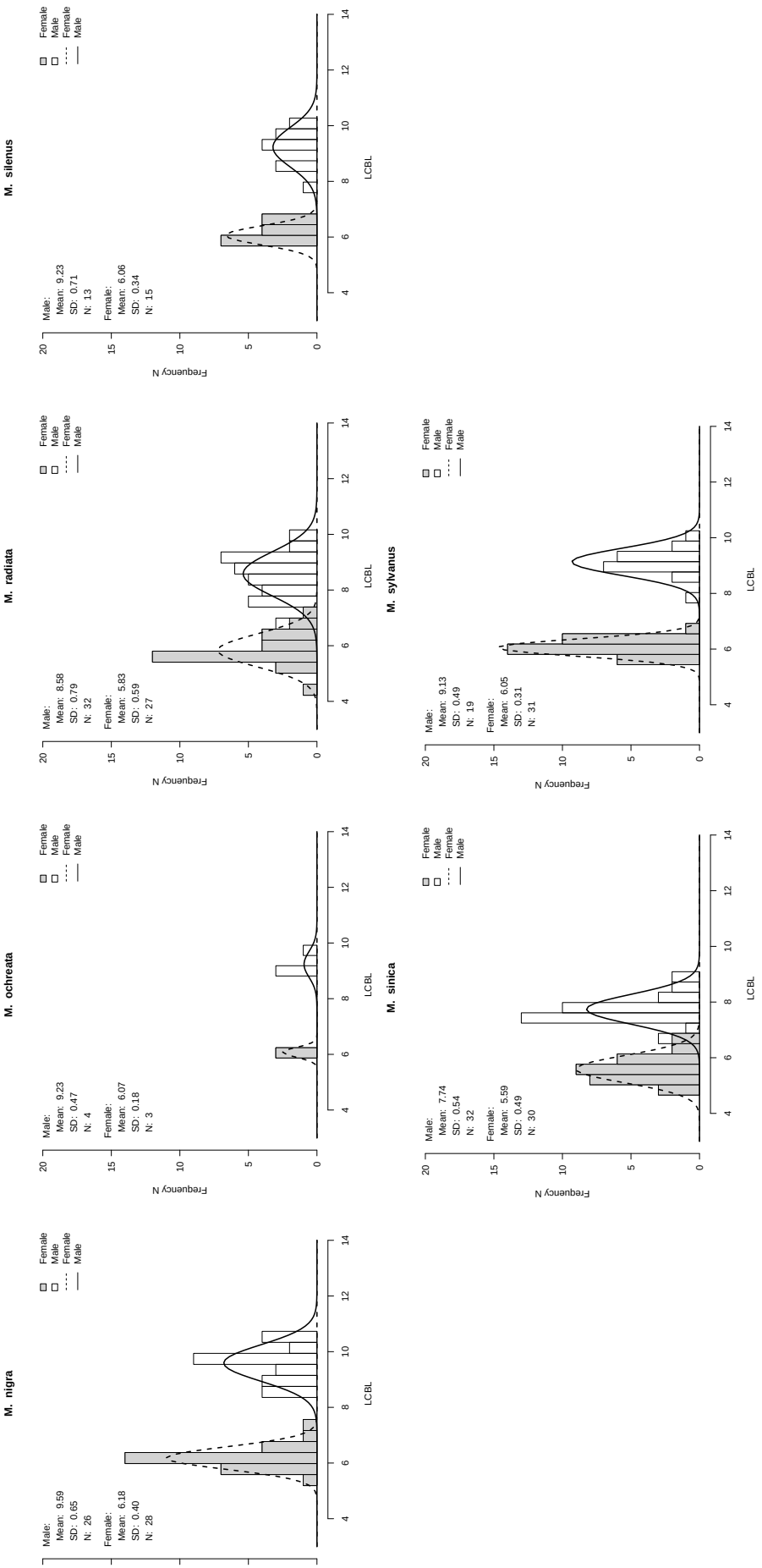

M. nigra
Male:
Mean: 9.59
SD: 0.65
N: 26
Female:
Mean: 6.18
SD: 0.40
N: 28
M. ochreata
Male:
Mean: 9.23
SD: 0.47
N: 4
Female:
Mean: 6.07
SD: 0.18
N: 3
M. radiata
Male:
Mean: 8.58
SD: 0.79
N: 32
Female:
Mean: 5.83
SD: 0.59
N: 27
M. silenus
Male:
Mean: 9.23
SD: 0.71
N: 13
Female:
Mean: 6.06
SD: 0.34
N: 15
M. sinica
Male:
Mean: 7.74
SD: 0.54
N: 32
Female:
Mean: 5.59
SD: 0.49
N: 30
M. sylvanus
Male:
Mean: 9.13
SD: 0.49
N: 19
Female:
Mean: 6.05
SD: 0.31
N: 31
Female
Male
Female
Male
Frequency N
LCBL

Fig. C.12 LCBL

All macaques
Male:
Mean: 5.13
SD: 0.58
N: 340
Female:
Mean: 4.75
SD: 0.51
N: 285
M. assamensis
Male:
Mean: 5.38
SD: 0.30
N: 12
Female:
Mean: 5.21
SD: 0.19
N: 5
M. cyclopis
Male:
Mean: 5.32
SD: 0.34
N: 6
Female:
Mean: 4.99
SD: 0.29
N: 11
M. fascicularis
Male:
Mean: 4.43
SD: 0.29
N: 48
Female:
Mean: 4.27
SD: 0.31
N: 38
M. fuscata
Male:
Mean: 5.63
SD: 0.50
N: 22
Female:
Mean: 5.21
SD: 0.35
N: 19
M. maura
Male:
Mean: 5.32
SD: 0.30
N: 29
Female:
Mean: 5.11
SD: 0.23
N: 15
M. mulatta
Male:
Mean: 5.00
SD: 0.35
N: 29
Female:
Mean: 4.54
SD: 0.38
N: 39
M. nemestrina
Male:
Mean: 5.94
SD: 0.30
N: 33
Female:
Mean: 5.54
SD: 0.35
N: 20
Frequency N
UP3L
Female
Male
Female
Male

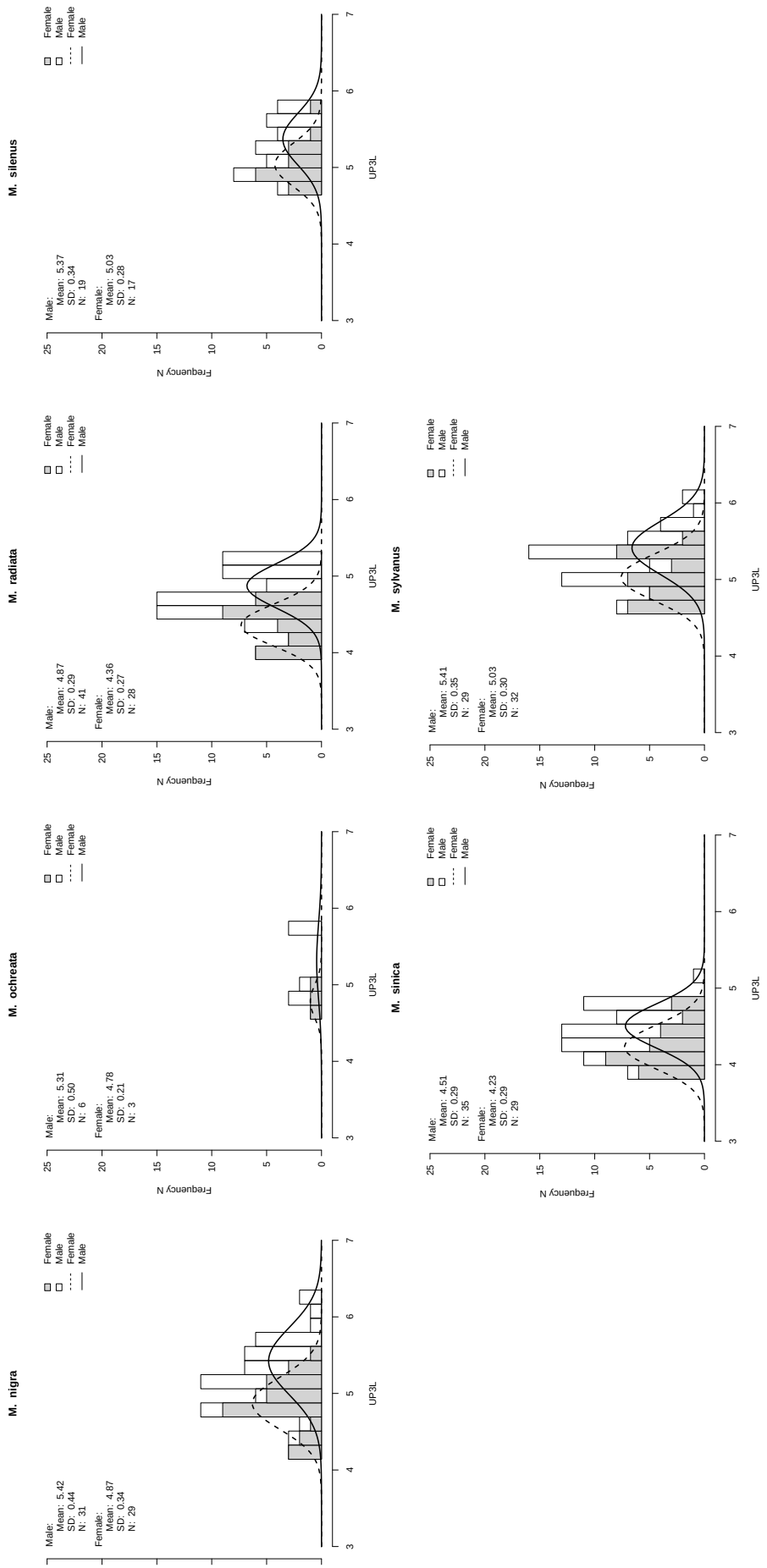

M. nigra
Male:
Mean: 5.42
SD: 0.44
N: 31
Female:
Mean: 4.87
SD: 0.34
N: 29
M. ochreata
Male:
Mean: 5.31
SD: 0.50
N: 6
Female:
Mean: 4.78
SD: 0.21
N: 3
M. radiata
Male:
Mean: 4.87
SD: 0.29
N: 41
Female:
Mean: 4.36
SD: 0.27
N: 28
M. silenus
Male:
Mean: 5.37
SD: 0.34
N: 19
Female:
Mean: 5.03
SD: 0.28
N: 17
M. sinica
Male:
Mean: 4.51
SD: 0.29
N: 35
Female:
Mean: 4.23
SD: 0.29
N: 29
M. sylvanus
Male:
Mean: 5.41
SD: 0.35
N: 29
Female:
Mean: 5.03
SD: 0.30
N: 32
Female
Male
Female
Male
Frequency N
UP3L

Fig. C.13 UP3L

All macaques
Male:
Mean: 5.92
SD: 0.62
N: 345
Female:
Mean: 5.65
SD: 0.57
N: 292
M. assamensis
Male:
Mean: 6.30
SD: 0.25
N: 12
Female:
Mean: 6.08
SD: 0.25
N: 5
M. cyclopis
Male:
Mean: 6.07
SD: 0.35
N: 7
Female:
Mean: 5.75
SD: 0.29
N: 11
M. fascicularis
Male:
Mean: 5.23
SD: 0.38
N: 47
Female:
Mean: 5.11
SD: 0.31
N: 38
M. fuscata
Male:
Mean: 6.61
SD: 0.51
N: 23
Female:
Mean: 6.36
SD: 0.36
N: 19
M. maura
Male:
Mean: 5.81
SD: 0.34
N: 30
Female:
Mean: 5.71
SD: 0.35
N: 17
M. mulatta
Male:
Mean: 5.94
SD: 0.39
N: 27
Female:
Mean: 5.64
SD: 0.44
N: 40
M. nemestrina
Male:
Mean: 6.66
SD: 0.41
N: 37
Female:
Mean: 6.30
SD: 0.48
N: 22
Frequency N
UP3W
Female
Male
Female
Male

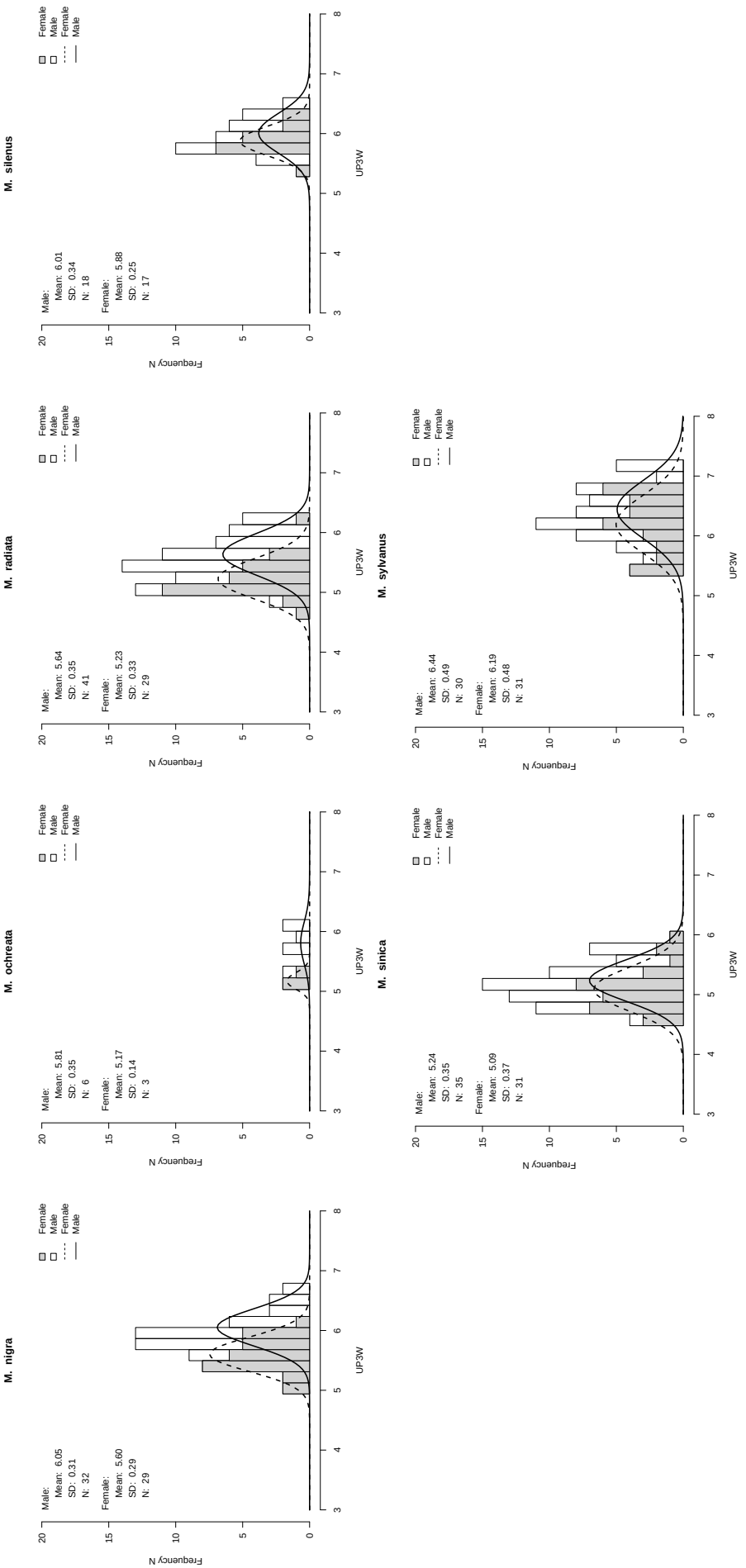
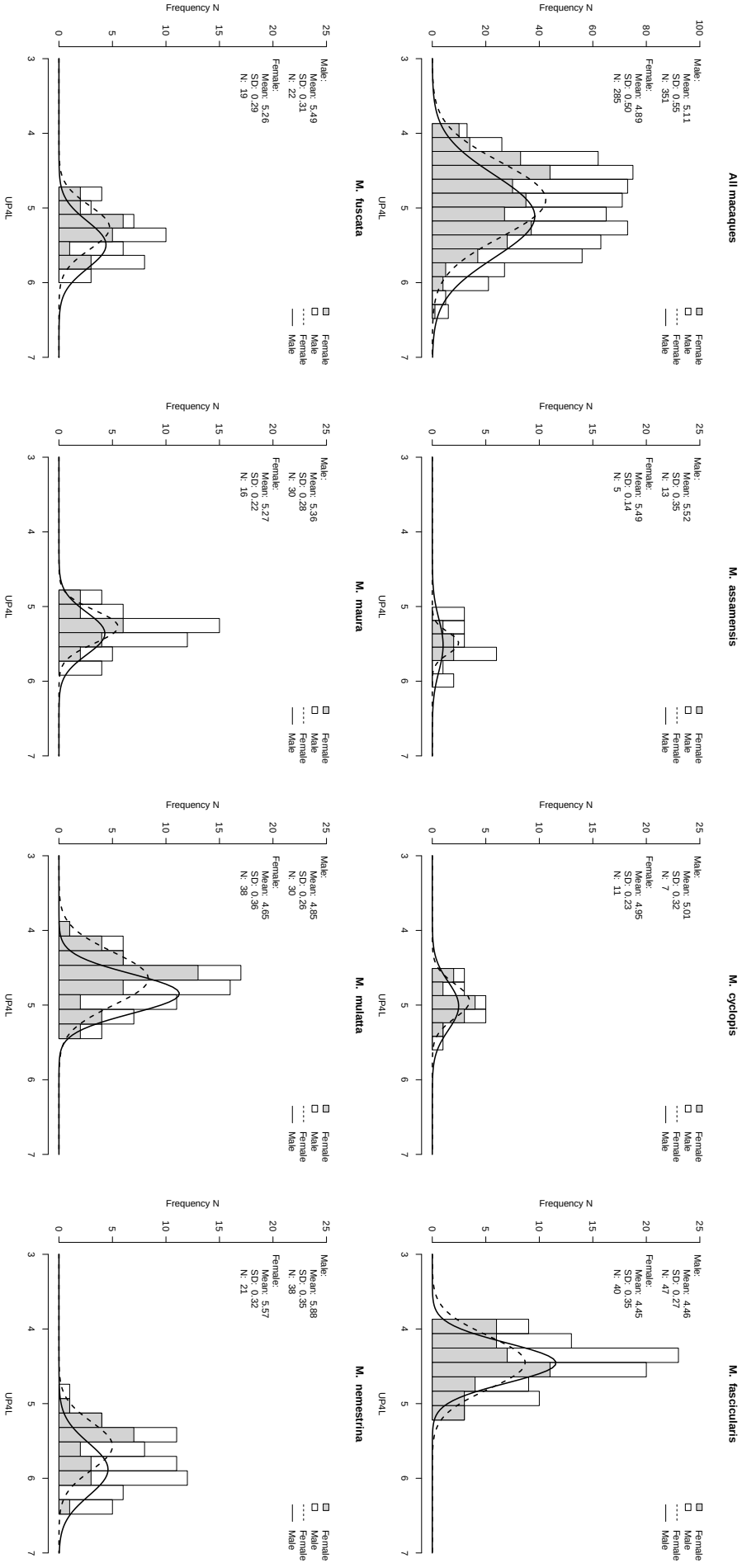

M. silenus
M. radiata
M. sylvanus
M. ochreata
M. sinica
M. nigra
Female
Male
Female
Male
Male:
Mean: 6.01
SD: 0.34
N: 18
Female:
Mean: 5.88
SD: 0.25
N: 17
Male:
Mean: 5.64
SD: 0.35
N: 41
Female:
Mean: 5.23
SD: 0.33
N: 29
Male:
Mean: 6.44
SD: 0.49
N: 30
Female:
Mean: 6.19
SD: 0.48
N: 31
Male:
Mean: 5.81
SD: 0.35
N: 6
Female:
Mean: 5.17
SD: 0.14
N: 3
Male:
Mean: 5.24
SD: 0.35
N: 35
Female:
Mean: 5.09
SD: 0.37
N: 31
Male:
Mean: 6.05
SD: 0.31
N: 32
Female:
Mean: 5.60
SD: 0.29
N: 29
Frequency N
UP3W

Fig. C.14 UP3W


All macaques
Male:
Mean: 5.11
SD: 0.55
N: 351
Female:
Mean: 4.89
SD: 0.50
N: 285
M. assamensis
Male:
Mean: 5.52
SD: 0.35
N: 13
Female:
Mean: 5.49
SD: 0.14
N: 5
M. cyclopis
Male:
Mean: 5.01
SD: 0.32
N: 7
Female:
Mean: 4.95
SD: 0.23
N: 11
M. fascicularis
Male:
Mean: 4.46
SD: 0.27
N: 47
Female:
Mean: 4.45
SD: 0.35
N: 40
M. fuscata
Male:
Mean: 5.49
SD: 0.31
N: 22
Female:
Mean: 5.26
SD: 0.29
N: 19
M. maura
Male:
Mean: 5.36
SD: 0.28
N: 30
Female:
Mean: 5.27
SD: 0.22
N: 16
M. mulatta
Male:
Mean: 4.85
SD: 0.26
N: 30
Female:
Mean: 4.65
SD: 0.36
N: 38
M. nemestrina
Male:
Mean: 5.88
SD: 0.35
N: 38
Female:
Mean: 5.57
SD: 0.32
N: 21
Frequency N
UP4L
Female
Male
Female
Male

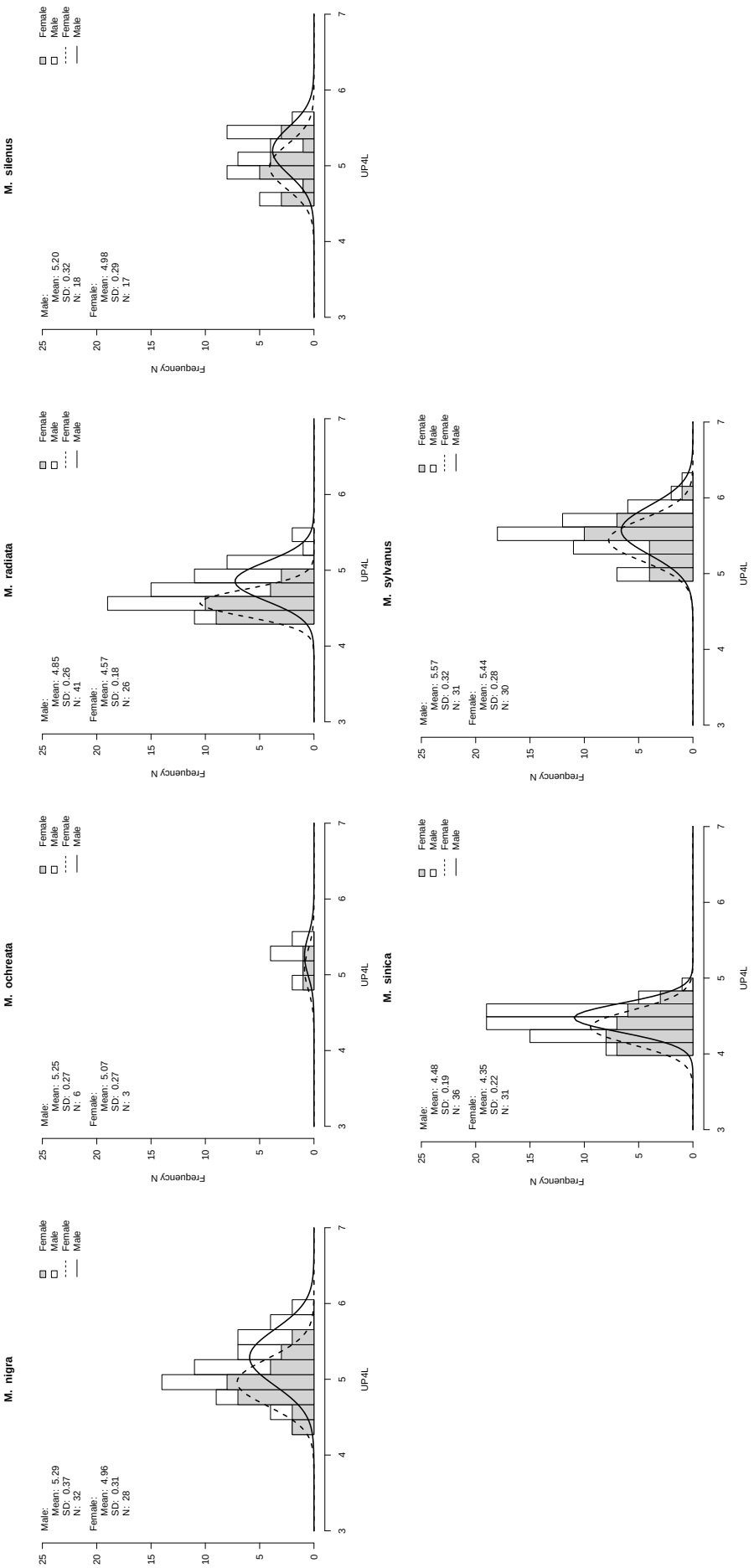
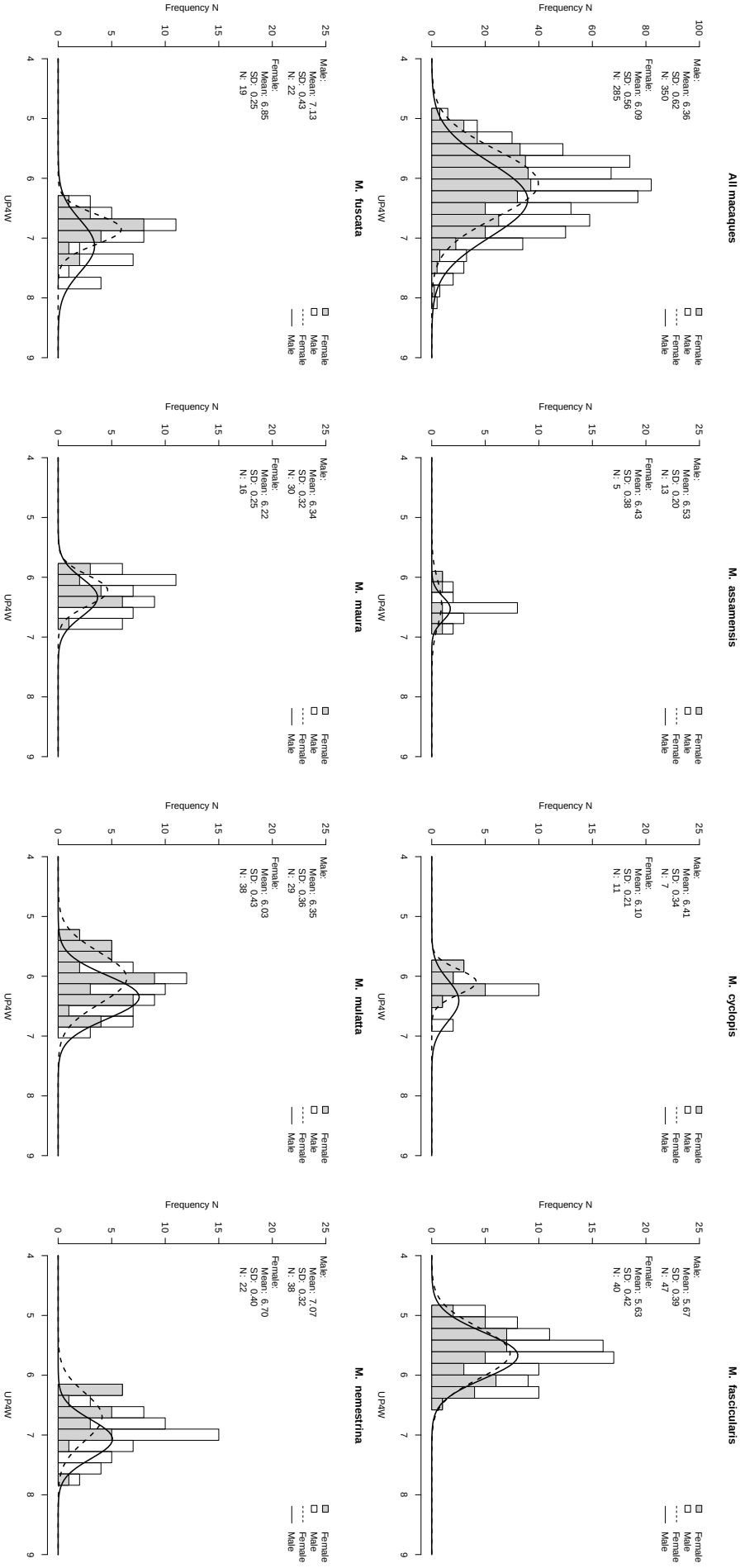

M. nigra
Male:
Mean: 5.29
SD: 0.37
N: 32
Female:
Mean: 4.96
SD: 0.31
N: 28
M. ochreata
Male:
Mean: 5.25
SD: 0.27
N: 6
Female:
Mean: 5.07
SD: 0.27
N: 3
M. radiata
Male:
Mean: 4.85
SD: 0.26
N: 41
Female:
Mean: 4.57
SD: 0.18
N: 26
M. silenus
Male:
Mean: 5.20
SD: 0.32
N: 18
Female:
Mean: 4.98
SD: 0.29
N: 17
M. sinica
Male:
Mean: 4.48
SD: 0.19
N: 36
Female:
Mean: 4.35
SD: 0.22
N: 31
M. sylvanus
Male:
Mean: 5.57
SD: 0.32
N: 31
Female:
Mean: 5.44
SD: 0.28
N: 30
Female
Male
Female
Male
Frequency N
UP4L

Fig. C.15 UP4L


All macaques
Male: Mean: 6.36 SD: 0.62 N: 350
Female: Mean: 6.09 SD: 0.56 N: 285
M. assamensis
Male: Mean: 6.53 SD: 0.20 N: 13
Female: Mean: 6.43 SD: 0.38 N: 5
M. cyclopis
Male: Mean: 6.41 SD: 0.34 N: 7
Female: Mean: 6.10 SD: 0.21 N: 11
M. fascicularis
Male: Mean: 5.67 SD: 0.39 N: 47
Female: Mean: 5.63 SD: 0.42 N: 40
M. fuscata
Male: Mean: 7.13 SD: 0.43 N: 22
Female: Mean: 6.85 SD: 0.25 N: 19
M. maura
Male: Mean: 6.34 SD: 0.32 N: 30
Female: Mean: 6.22 SD: 0.25 N: 16
M. mulatta
Male: Mean: 6.35 SD: 0.36 N: 29
Female: Mean: 6.03 SD: 0.43 N: 38
M. nemestrina
Male: Mean: 7.07 SD: 0.32 N: 38
Female: Mean: 6.70 SD: 0.40 N: 22
Frequency N
UP4W
Female
Male
Female
Male

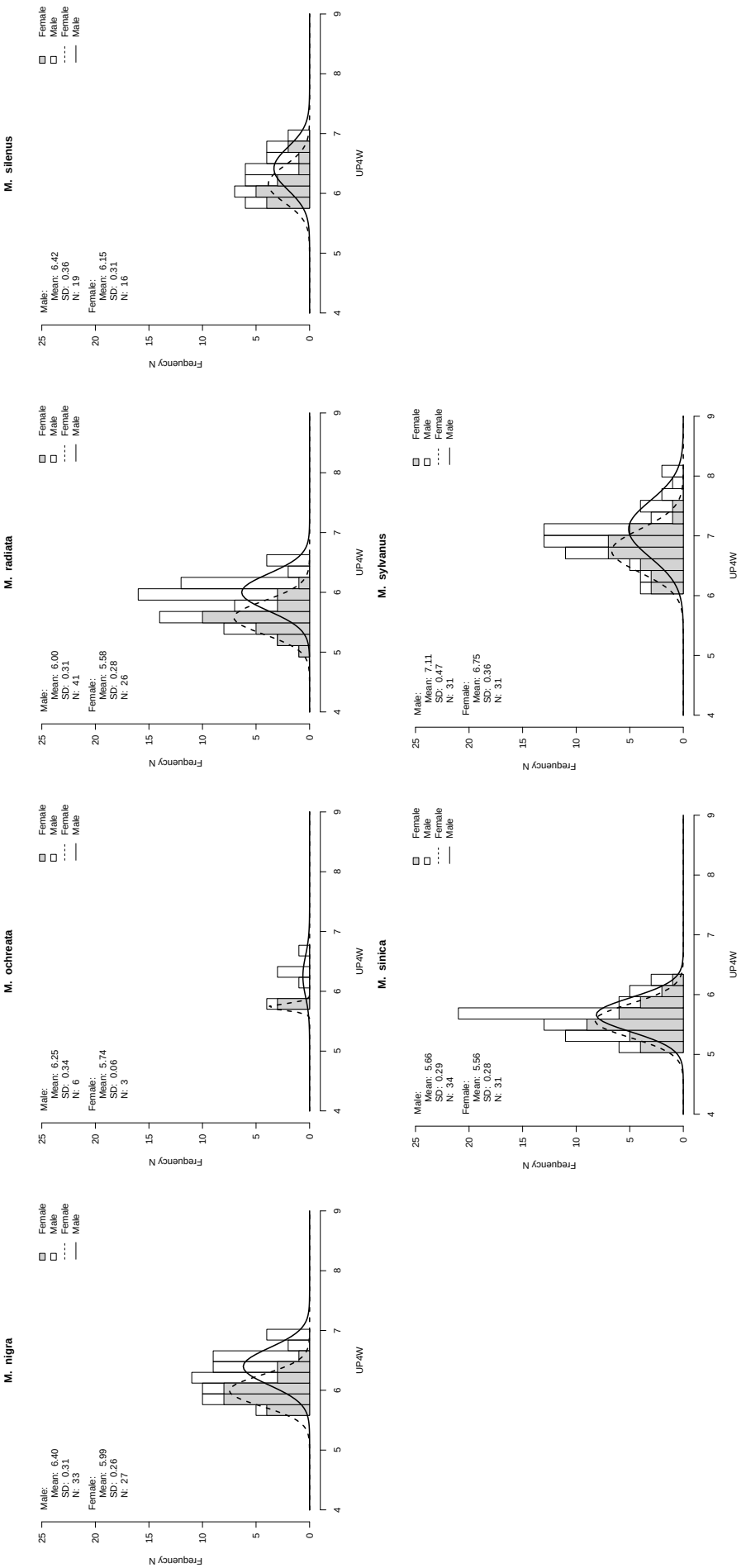
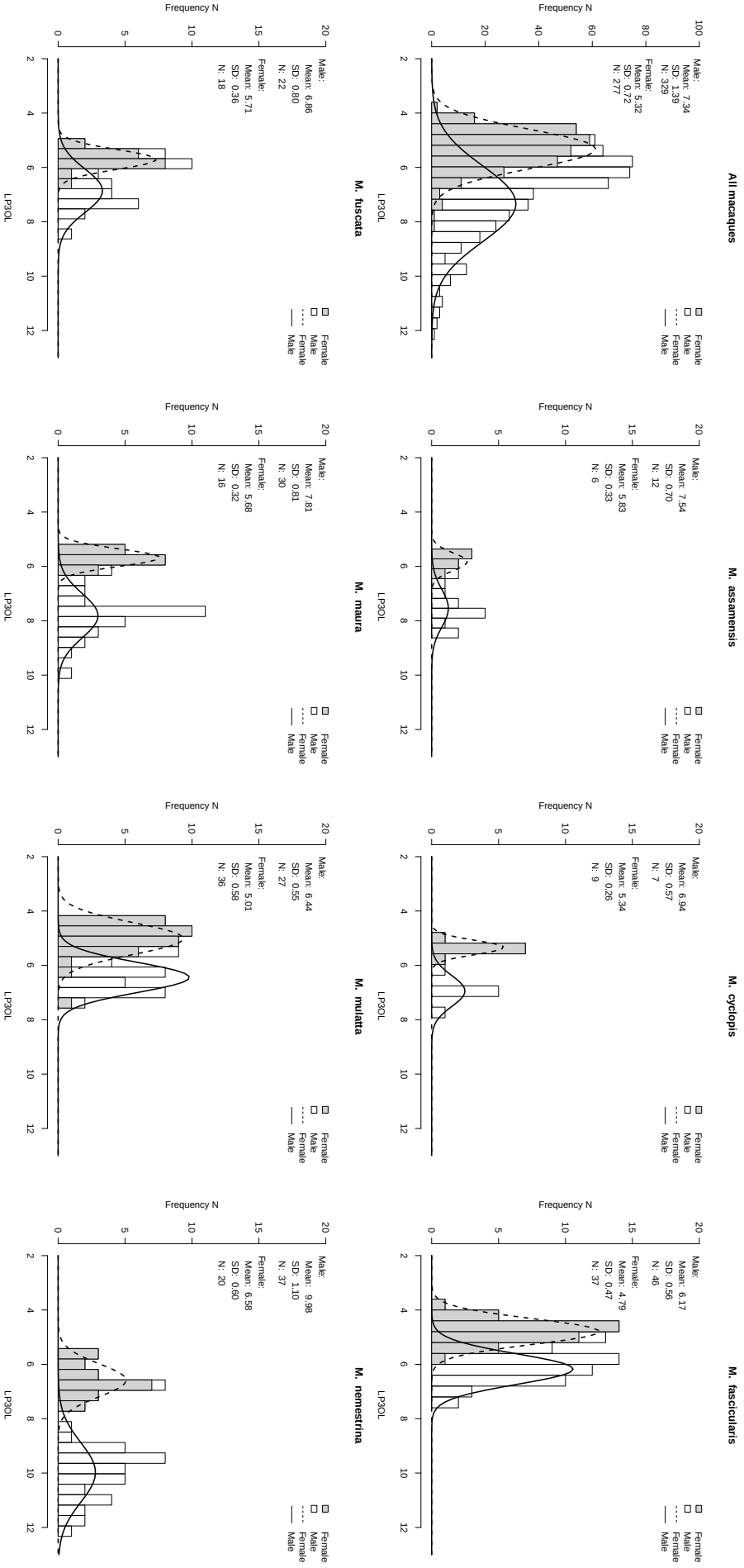

M. nigra
Male:
Mean: 6.40
SD: 0.31
N: 33
Female:
Mean: 5.99
SD: 0.26
N: 27
M. ochreata
Male:
Mean: 6.25
SD: 0.34
N: 6
Female:
Mean: 5.74
SD: 0.06
N: 3
M. radiata
Male:
Mean: 6.00
SD: 0.31
N: 41
Female:
Mean: 5.58
SD: 0.28
N: 26
M. silenus
Male:
Mean: 6.42
SD: 0.36
N: 19
Female:
Mean: 6.15
SD: 0.31
N: 16
M. sinica
Male:
Mean: 5.66
SD: 0.29
N: 34
Female:
Mean: 5.56
SD: 0.28
N: 31
M. sylvanus
Male:
Mean: 7.11
SD: 0.47
N: 31
Female:
Mean: 6.75
SD: 0.36
N: 31
Female
Male
Female
Male
Frequency N
UP4W

Fig. C.16 UP4W


All macaques
Male:
Mean: 7.34
SD: 1.39
N: 329
Female:
Mean: 5.32
SD: 0.72
N: 277
M. assamensis
Male:
Mean: 7.54
SD: 0.70
N: 12
Female:
Mean: 5.83
SD: 0.33
N: 6
M. cyclopis
Male:
Mean: 6.94
SD: 0.57
N: 7
Female:
Mean: 5.34
SD: 0.26
N: 9
M. fascicularis
Male:
Mean: 6.17
SD: 0.56
N: 46
Female:
Mean: 4.79
SD: 0.47
N: 37
M. fuscata
Male:
Mean: 6.86
SD: 0.80
N: 22
Female:
Mean: 5.71
SD: 0.36
N: 18
M. maura
Male:
Mean: 7.81
SD: 0.81
N: 30
Female:
Mean: 5.68
SD: 0.32
N: 16
M. mulatta
Male:
Mean: 6.44
SD: 0.55
N: 27
Female:
Mean: 5.01
SD: 0.58
N: 36
M. nemestrina
Male:
Mean: 9.98
SD: 1.10
N: 37
Female:
Mean: 6.58
SD: 0.60
N: 20
Frequency N
LP3OL
Female
Male
Female
Male

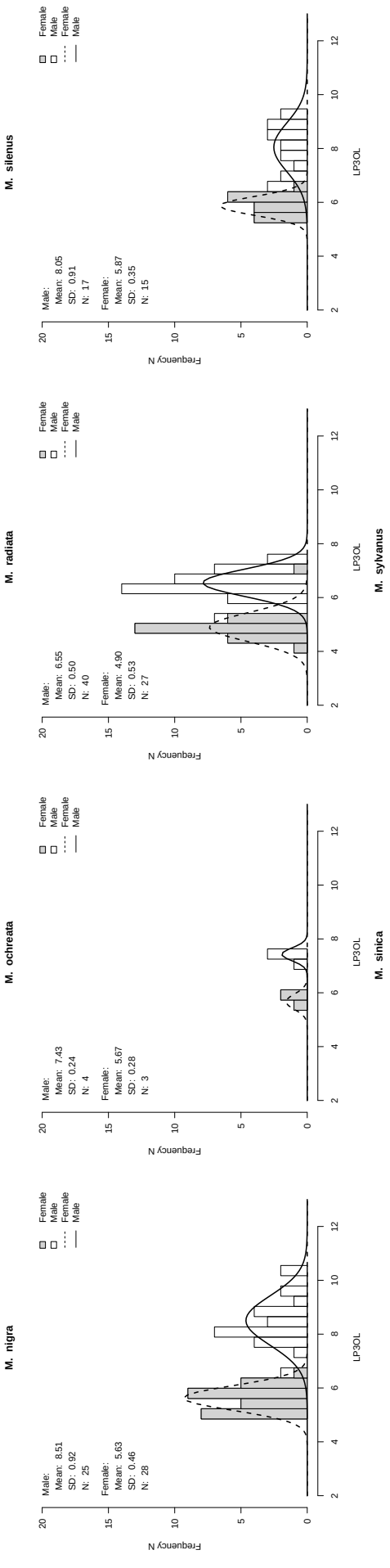


Fig. C.17 LP3OL

All macaques
Male:
Mean: 12.68
SD: 2.34
N: 301
Female:
Mean: 8.39
SD: 1.31
N: 266
M. assamensis
Male:
Mean: 13.87
SD: 1.18
N: 12
Female:
Mean: 9.88
SD: 0.77
N: 6
M. cyclopis
Male:
Mean: 11.78
SD: 1.15
N: 7
Female:
Mean: 8.14
SD: 0.57
N: 9
M. fascicularis
Male:
Mean: 10.71
SD: 1.23
N: 45
Female:
Mean: 7.29
SD: 0.94
N: 38
M. fuscata
Male:
Mean: 11.33
SD: 1.10
N: 21
Female:
Mean: 8.34
SD: 0.72
N: 18
M. maura
Male:
Mean: 13.29
SD: 1.47
N: 23
Female:
Mean: 9.31
SD: 0.76
N: 14
M. mulatta
Male:
Mean: 11.56
SD: 1.27
N: 23
Female:
Mean: 7.70
SD: 1.01
N: 36
M. nemestrina
Male:
Mean: 17.04
SD: 1.29
N: 33
Female:
Mean: 9.91
SD: 1.18
N: 20
Frequency N
LP3TL
Female
Male
Female
Male

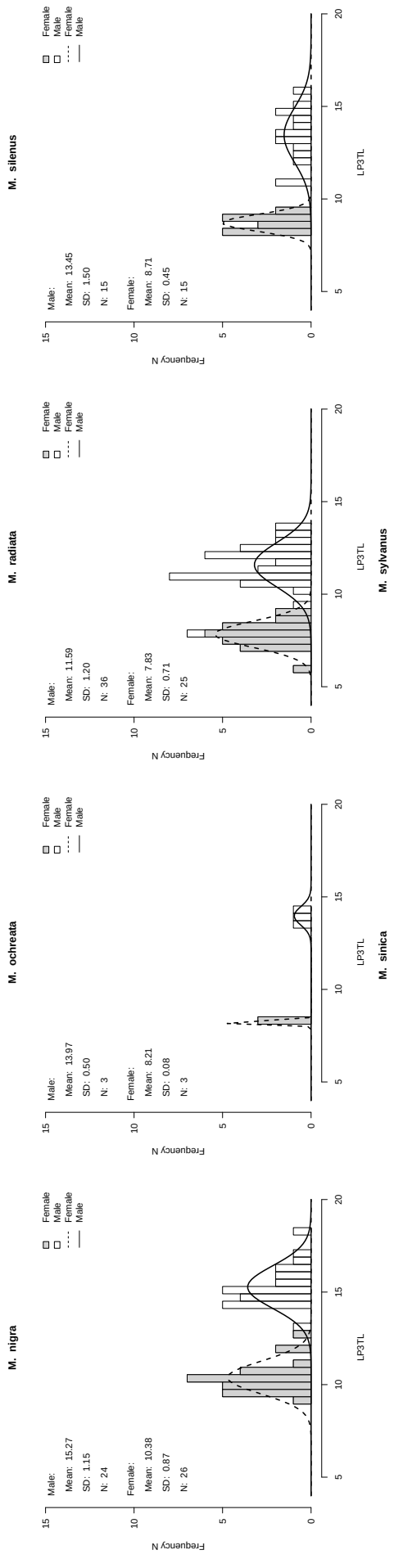


Fig. C.18 LP3TL

All macaques
Male:
Mean: 4.59
SD: 0.70
N: 340
Female:
Mean: 3.85
SD: 0.52
N: 279
M. assamensis
Male:
Mean: 4.78
SD: 0.22
N: 12
Female:
Mean: 4.43
SD: 0.10
N: 6
M. cyclopis
Male:
Mean: 4.37
SD: 0.20
N: 7
Female:
Mean: 3.98
SD: 0.26
N: 10
M. fascicularis
Male:
Mean: 3.92
SD: 0.31
N: 48
Female:
Mean: 3.51
SD: 0.33
N: 39
M. fuscata
Male:
Mean: 4.87
SD: 0.54
N: 22
Female:
Mean: 4.51
SD: 0.32
N: 17
M. maura
Male:
Mean: 4.91
SD: 0.38
N: 30
Female:
Mean: 4.16
SD: 0.41
N: 17
M. mulatta
Male:
Mean: 4.28
SD: 0.39
N: 29
Female:
Mean: 3.67
SD: 0.35
N: 34
M. nemestrina
Male:
Mean: 5.53
SD: 0.37
N: 37
Female:
Mean: 4.32
SD: 0.37
N: 22
Frequency N
LP3W
Female
Male
Female
Male

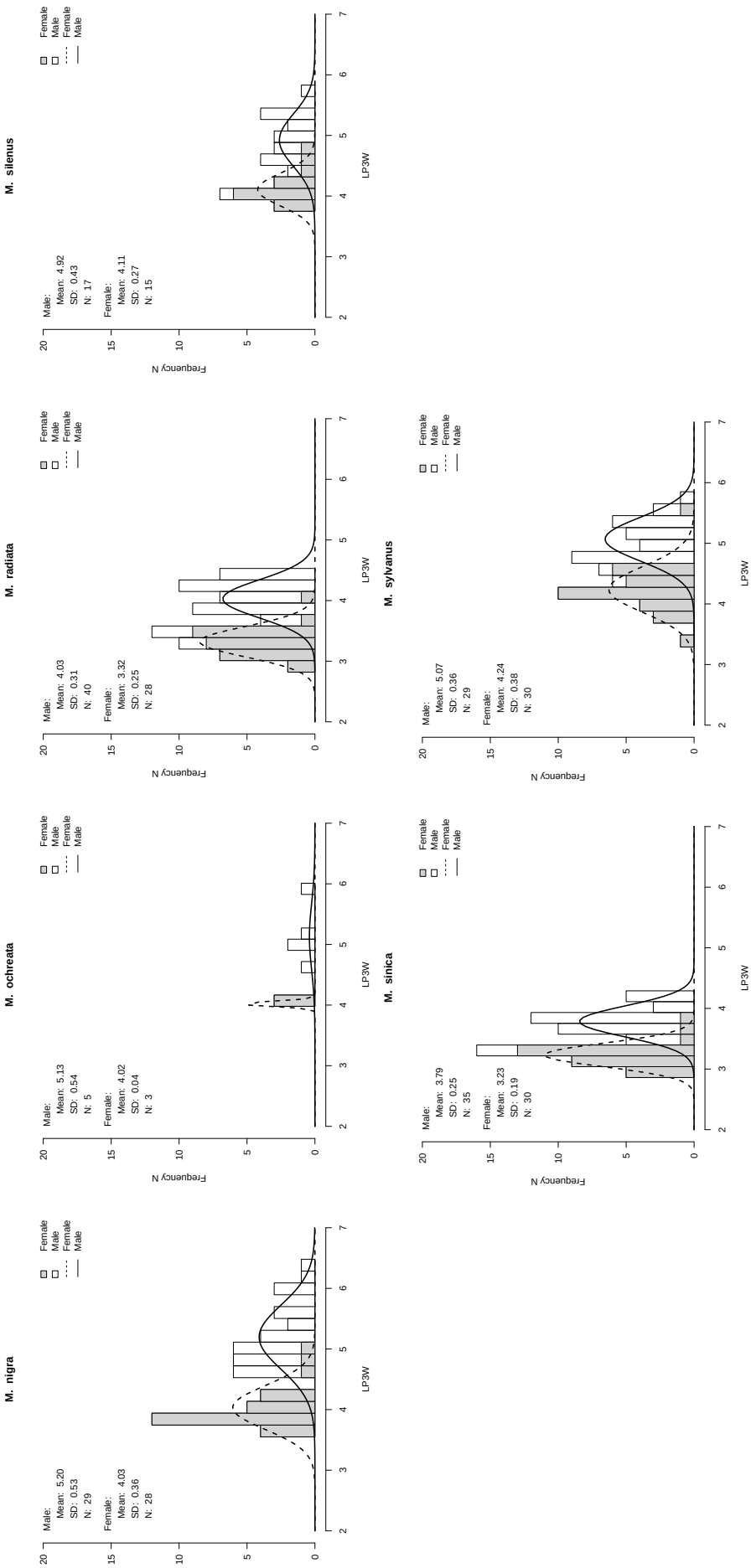

M. nigra
Male:
Mean: 5.20
SD: 0.53
N: 29
Female:
Mean: 4.03
SD: 0.36
N: 28
M. ochreata
Male:
Mean: 5.13
SD: 0.54
N: 5
Female:
Mean: 4.02
SD: 0.04
N: 3
M. radiata
Male:
Mean: 4.03
SD: 0.31
N: 40
Female:
Mean: 3.32
SD: 0.25
N: 28
M. silenus
Male:
Mean: 4.92
SD: 0.43
N: 17
Female:
Mean: 4.11
SD: 0.27
N: 15
M. sinica
Male:
Mean: 3.79
SD: 0.25
N: 35
Female:
Mean: 3.23
SD: 0.19
N: 30
M. sylvanus
Male:
Mean: 5.07
SD: 0.36
N: 29
Female:
Mean: 4.24
SD: 0.38
N: 30
Female
Male
Female
Male
Frequency N
LP3W

Fig. C.19 LP3W

All macaques
Male:
Mean: 5.73
SD: 0.74
N: 338
Female:
Mean: 5.41
SD: 0.60
N: 284
M. assamensis
Male:
Mean: 5.87
SD: 0.51
N: 11
Female:
Mean: 5.97
SD: 0.14
N: 6
M. cyclopis
Male:
Mean: 5.59
SD: 0.34
N: 7
Female:
Mean: 5.38
SD: 0.23
N: 11
M. fascicularis
Male:
Mean: 4.96
SD: 0.38
N: 47
Female:
Mean: 4.87
SD: 0.40
N: 40
M. fuscata
Male:
Mean: 6.11
SD: 0.45
N: 22
Female:
Mean: 5.80
SD: 0.30
N: 19
M. maura
Male:
Mean: 6.08
SD: 0.25
N: 28
Female:
Mean: 5.86
SD: 0.25
N: 16
M. mulatta
Male:
Mean: 5.29
SD: 0.35
N: 29
Female:
Mean: 5.14
SD: 0.40
N: 37
M. nemestrina
Male:
Mean: 6.96
SD: 0.51
N: 36
Female:
Mean: 6.31
SD: 0.39
N: 22
Frequency N
LP4L
Female
Male
Female
Male

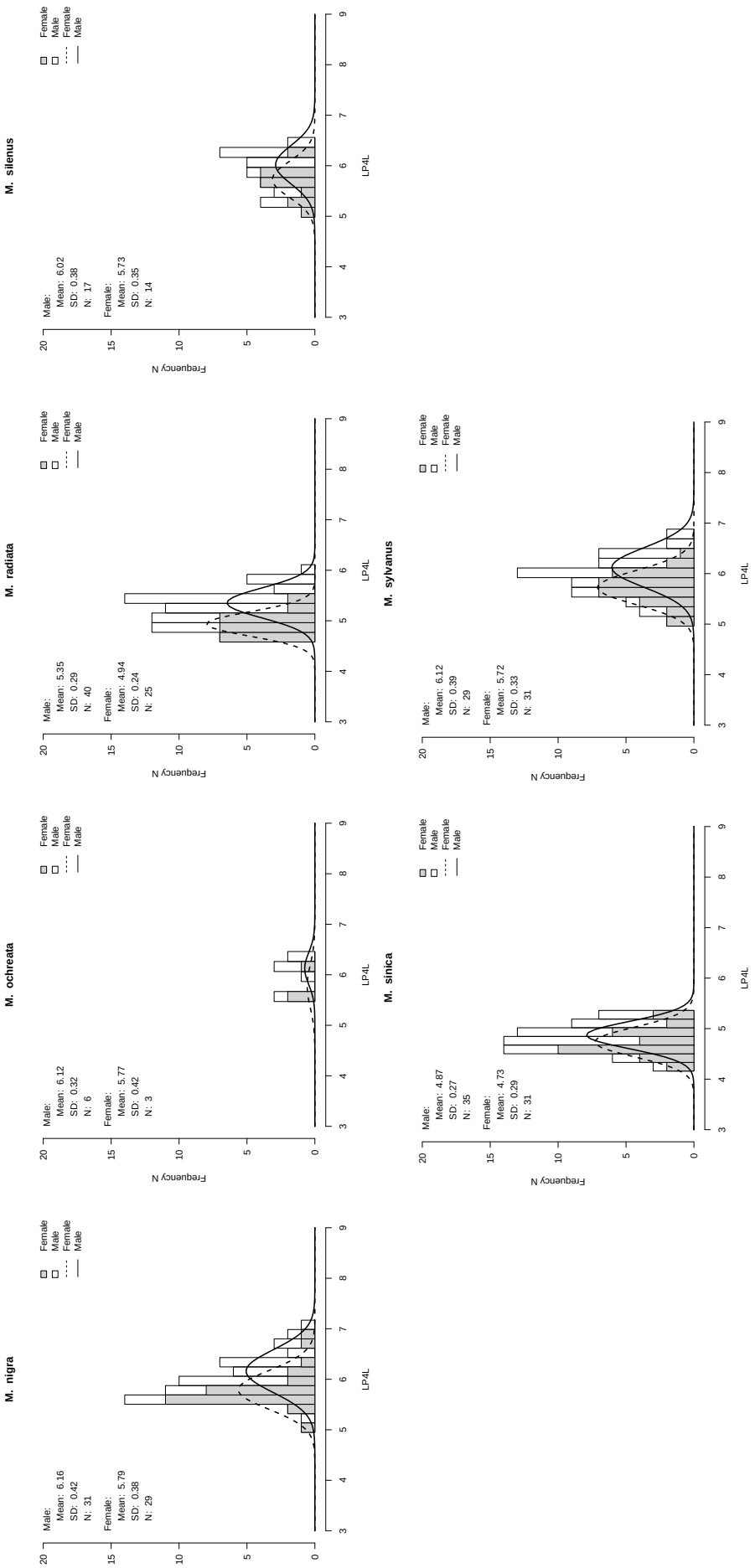
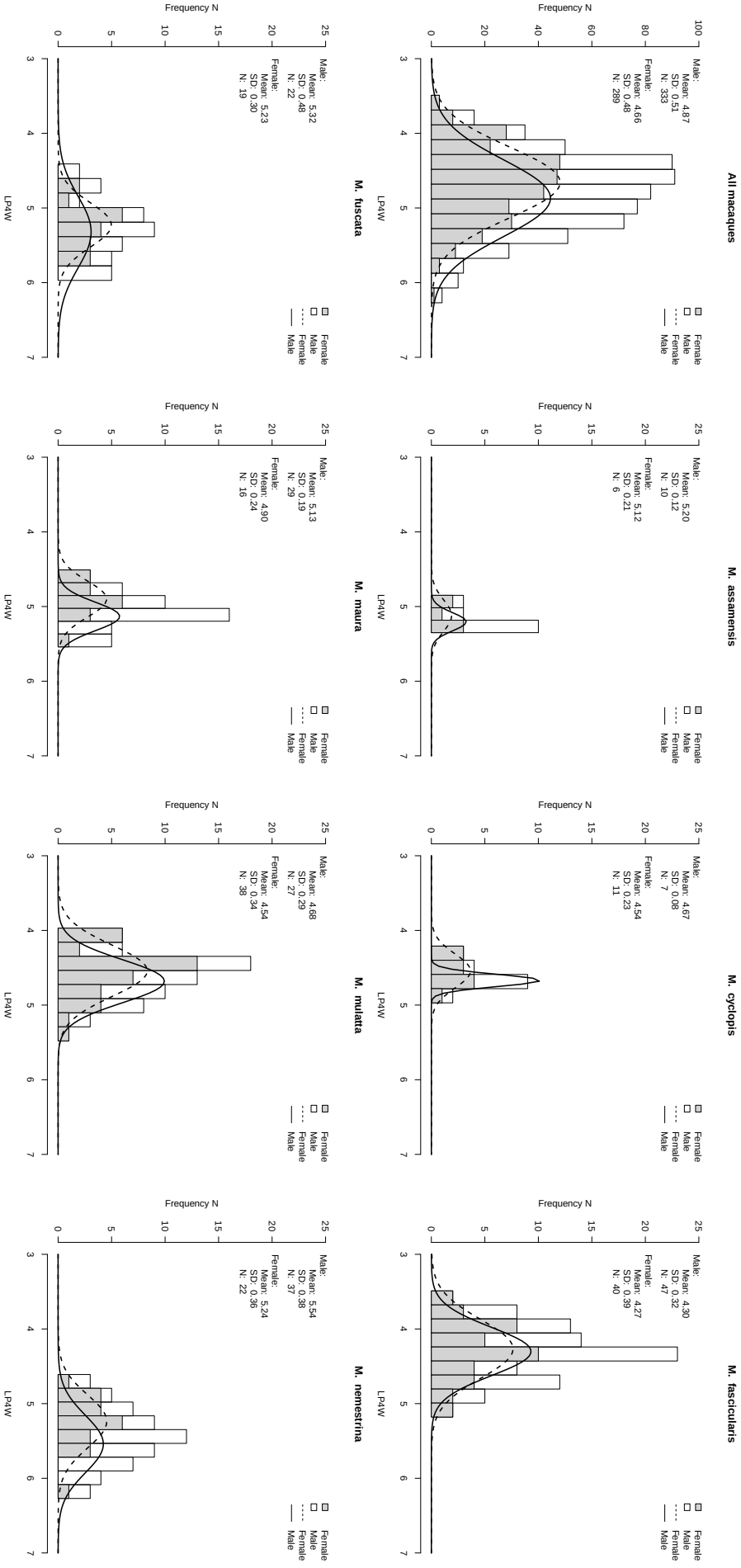

M. silenus
Male:
Mean: 6.02
SD: 0.38
N: 17
Female:
Mean: 5.73
SD: 0.35
N: 14
M. radiata
Male:
Mean: 5.35
SD: 0.29
N: 40
Female:
Mean: 4.94
SD: 0.24
N: 25
M. sylvanus
Male:
Mean: 6.12
SD: 0.39
N: 29
Female:
Mean: 5.72
SD: 0.33
N: 31
M. ochreata
Male:
Mean: 6.12
SD: 0.32
N: 6
Female:
Mean: 5.77
SD: 0.42
N: 3
M. sinica
Male:
Mean: 4.87
SD: 0.27
N: 35
Female:
Mean: 4.73
SD: 0.29
N: 31
M. nigra
Male:
Mean: 6.16
SD: 0.42
N: 31
Female:
Mean: 5.79
SD: 0.38
N: 29
Female
Male
Female
Male
Frequency N
LP4L

Fig. C.20 LP4L


All macaques
Male:
Mean: 4.87
SD: 0.51
N: 333
Female:
Mean: 4.66
SD: 0.48
N: 289
M. assamensis
Male:
Mean: 5.20
SD: 0.12
N: 10
Female:
Mean: 5.12
SD: 0.21
N: 6
M. cyclopis
Male:
Mean: 4.67
SD: 0.08
N: 7
Female:
Mean: 4.54
SD: 0.23
N: 11
M. fascicularis
Male:
Mean: 4.30
SD: 0.32
N: 47
Female:
Mean: 4.27
SD: 0.39
N: 40
M. fuscata
Male:
Mean: 5.32
SD: 0.48
N: 22
Female:
Mean: 5.23
SD: 0.30
N: 19
M. maura
Male:
Mean: 5.13
SD: 0.19
N: 29
Female:
Mean: 4.90
SD: 0.24
N: 16
M. mulatta
Male:
Mean: 4.68
SD: 0.29
N: 27
Female:
Mean: 4.54
SD: 0.34
N: 38
M. nemestrina
Male:
Mean: 5.54
SD: 0.38
N: 37
Female:
Mean: 5.24
SD: 0.36
N: 22
Frequency N
LP4W
Female
Male
Female
Male

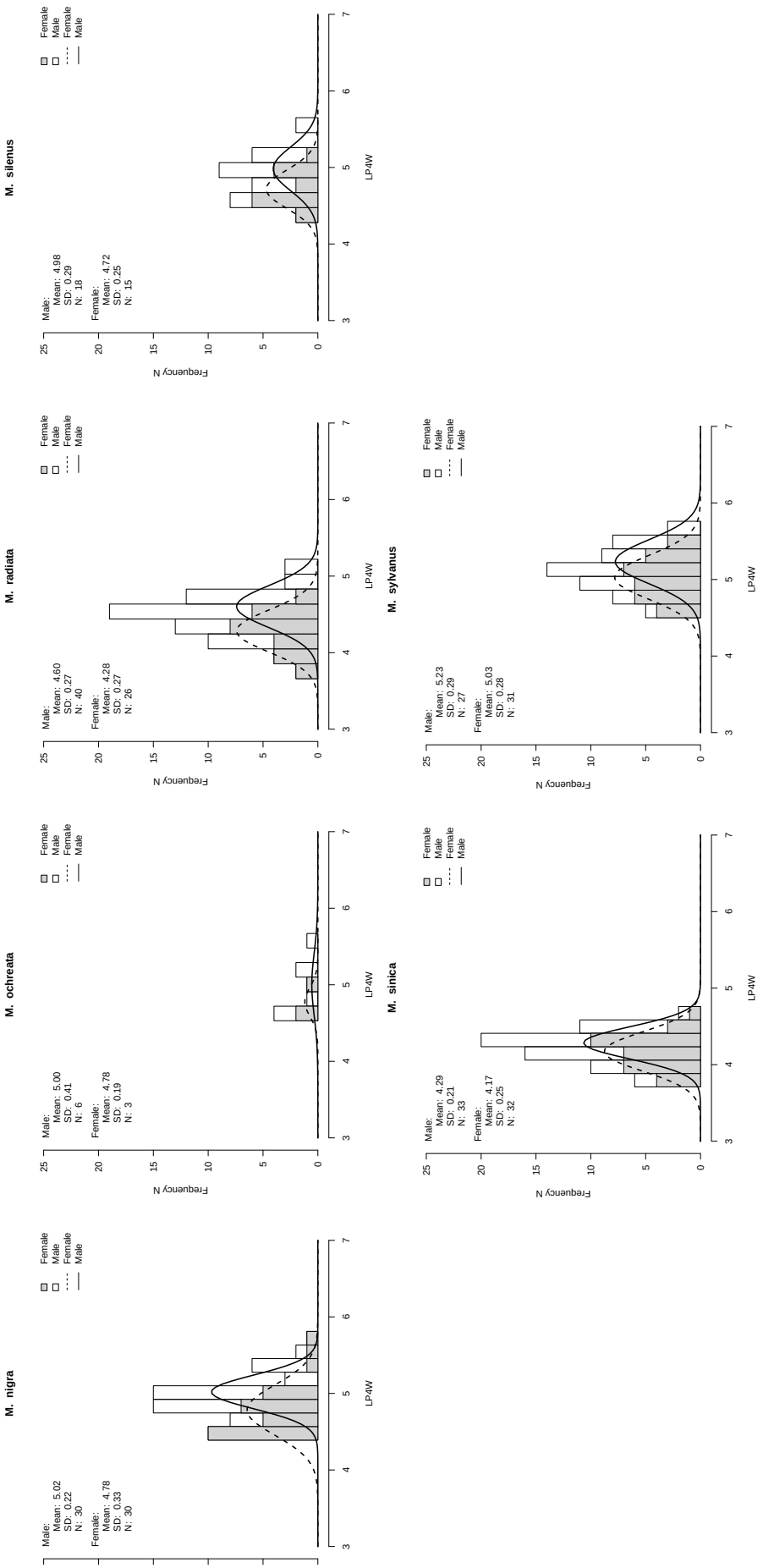
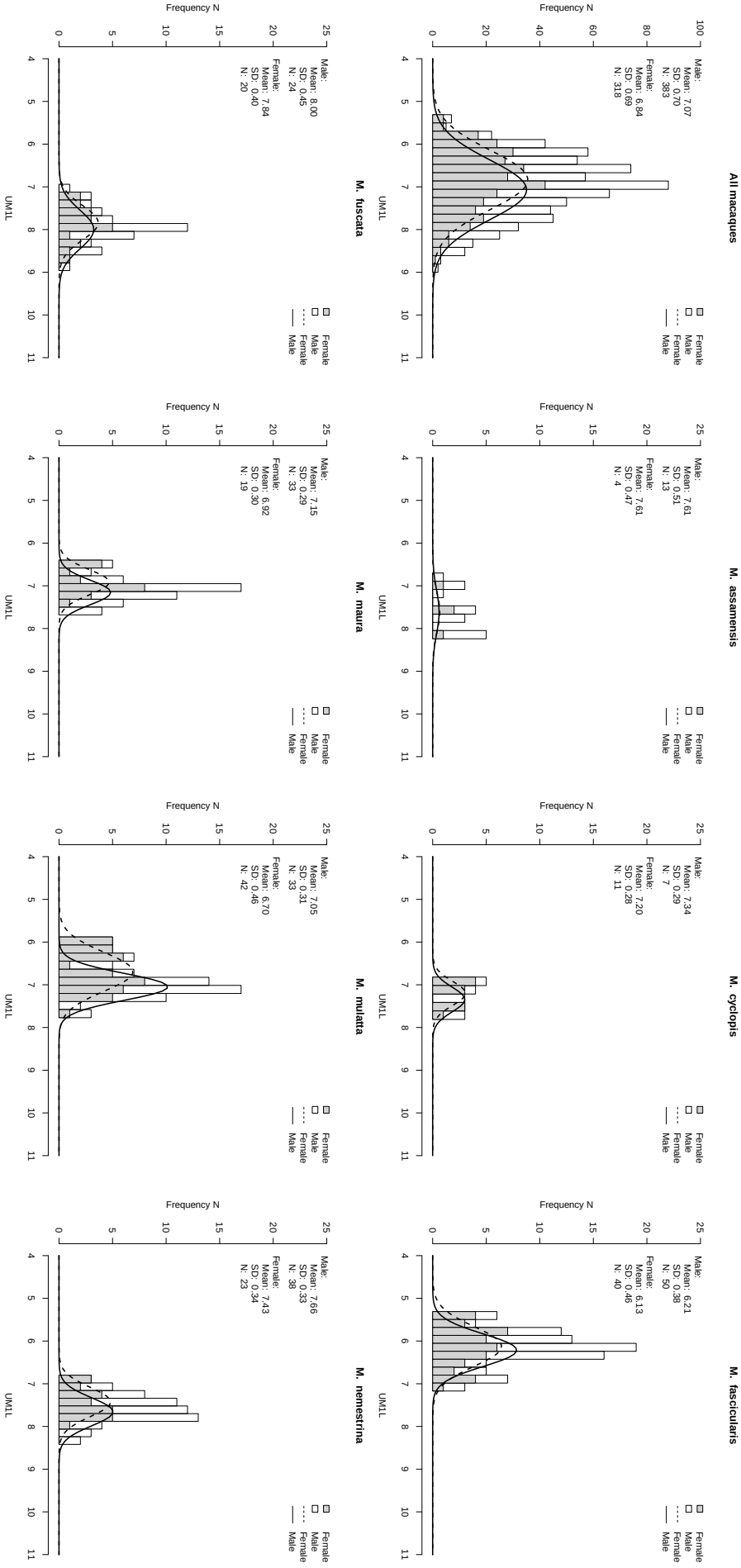

M. nigra
Male:
Mean: 5.02
SD: 0.22
N: 30
Female:
Mean: 4.78
SD: 0.33
N: 30
M. ochreata
Male:
Mean: 5.00
SD: 0.41
N: 6
Female:
Mean: 4.78
SD: 0.19
N: 3
M. radiata
Male:
Mean: 4.60
SD: 0.27
N: 40
Female:
Mean: 4.28
SD: 0.27
N: 26
M. silenus
Male:
Mean: 4.98
SD: 0.29
N: 18
Female:
Mean: 4.72
SD: 0.25
N: 15
M. sinica
Male:
Mean: 4.29
SD: 0.21
N: 33
Female:
Mean: 4.17
SD: 0.25
N: 32
M. sylvanus
Male:
Mean: 5.23
SD: 0.29
N: 27
Female:
Mean: 5.03
SD: 0.28
N: 31
Female
Male
Female
Male
Frequency N
LP4W

Fig. C.21 LP4W


All macaques
Male: Mean: 7.07 SD: 0.70 N: 383
Female: Mean: 6.84 SD: 0.69 N: 318
M. assamensis
Male: Mean: 7.61 SD: 0.51 N: 13
Female: Mean: 7.61 SD: 0.47 N: 4
M. cyclopis
Male: Mean: 7.34 SD: 0.29 N: 7
Female: Mean: 7.20 SD: 0.28 N: 11
M. fascicularis
Male: Mean: 6.21 SD: 0.38 N: 50
Female: Mean: 6.13 SD: 0.46 N: 40
M. fuscata
Male: Mean: 8.00 SD: 0.45 N: 24
Female: Mean: 7.84 SD: 0.40 N: 20
M. maura
Male: Mean: 7.15 SD: 0.29 N: 33
Female: Mean: 6.92 SD: 0.30 N: 19
M. mulatta
Male: Mean: 7.05 SD: 0.31 N: 33
Female: Mean: 6.70 SD: 0.46 N: 42
M. nemestrina
Male: Mean: 7.66 SD: 0.33 N: 38
Female: Mean: 7.43 SD: 0.34 N: 23
Frequency N
UM1L
Female
Male
Female
Male

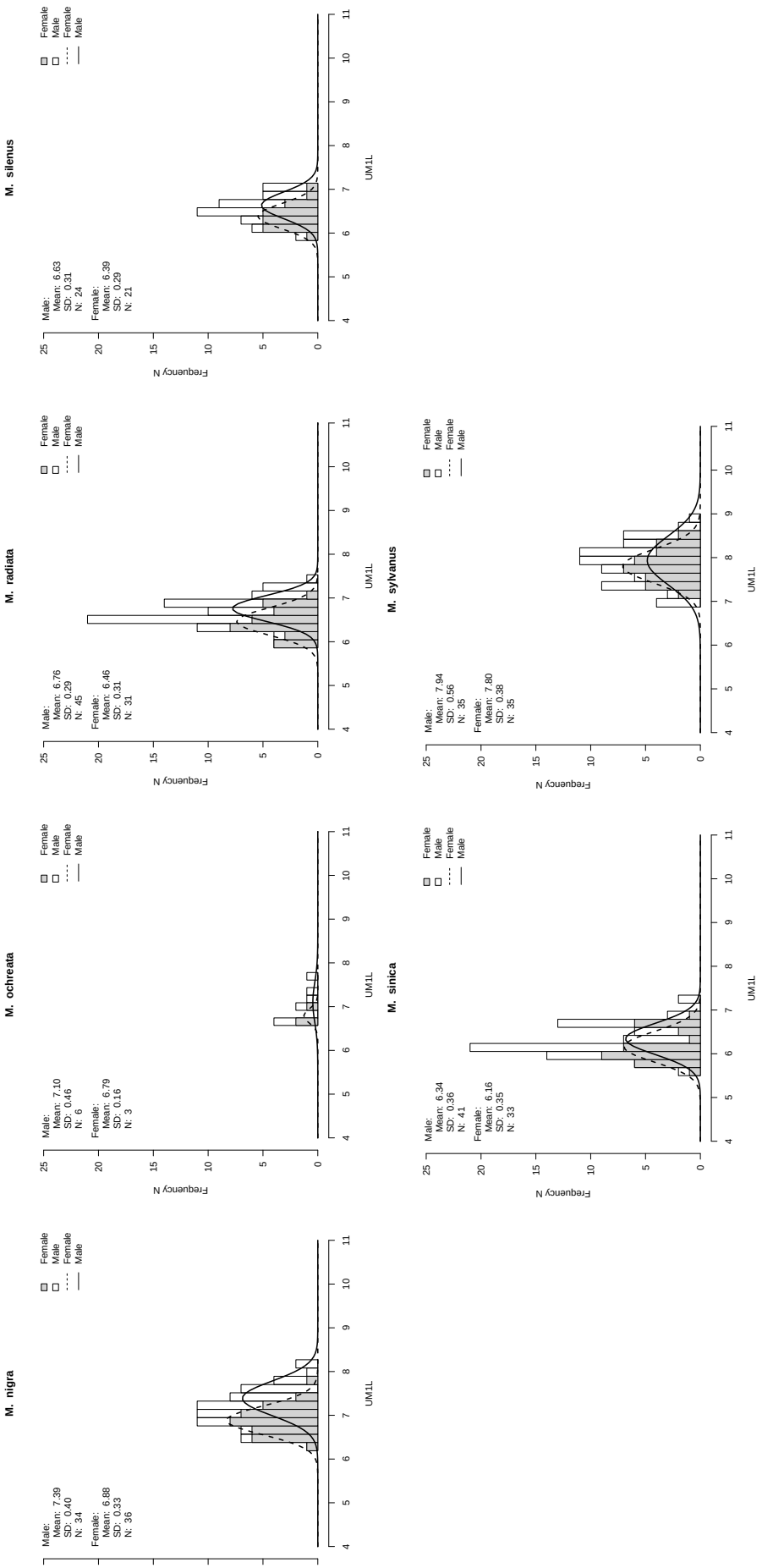

M. silenus
Male:
Mean: 6.63
SD: 0.31
N: 24
Female:
Mean: 6.39
SD: 0.29
N: 21
M. radiata
Male:
Mean: 6.76
SD: 0.29
N: 45
Female:
Mean: 6.46
SD: 0.31
N: 31
M. sylvanus
Male:
Mean: 7.94
SD: 0.56
N: 35
Female:
Mean: 7.80
SD: 0.38
N: 35
M. ochreata
Male:
Mean: 7.10
SD: 0.46
N: 6
Female:
Mean: 6.79
SD: 0.16
N: 3
M. sinica
Male:
Mean: 6.34
SD: 0.36
N: 41
Female:
Mean: 6.16
SD: 0.35
N: 33
M. nigra
Male:
Mean: 7.39
SD: 0.40
N: 34
Female:
Mean: 6.88
SD: 0.33
N: 36
Female
Male
Female
Male
Frequency N
UM1L

Fig. C.22 UM1L

All macaques
Male:
Mean: 6.81
SD: 0.65
N: 384
Female:
Mean: 6.58
SD: 0.59
N: 319
M. assamensis
Male:
Mean: 7.15
SD: 0.28
N: 13
Female:
Mean: 6.90
SD: 0.22
N: 4
M. cyclopis
Male:
Mean: 6.84
SD: 0.21
N: 7
Female:
Mean: 6.53
SD: 0.36
N: 11
M. fascicularis
Male:
Mean: 6.04
SD: 0.37
N: 51
Female:
Mean: 5.98
SD: 0.43
N: 40
M. fuscata
Male:
Mean: 7.84
SD: 0.48
N: 24
Female:
Mean: 7.59
SD: 0.39
N: 20
M. maura
Male:
Mean: 6.99
SD: 0.32
N: 34
Female:
Mean: 6.84
SD: 0.23
N: 19
M. mulatta
Male:
Mean: 6.80
SD: 0.37
N: 33
Female:
Mean: 6.51
SD: 0.42
N: 43
M. nemestrina
Male:
Mean: 7.46
SD: 0.38
N: 38
Female:
Mean: 7.07
SD: 0.39
N: 23
Frequency N
UM1AW
Female
Male
Female
Male

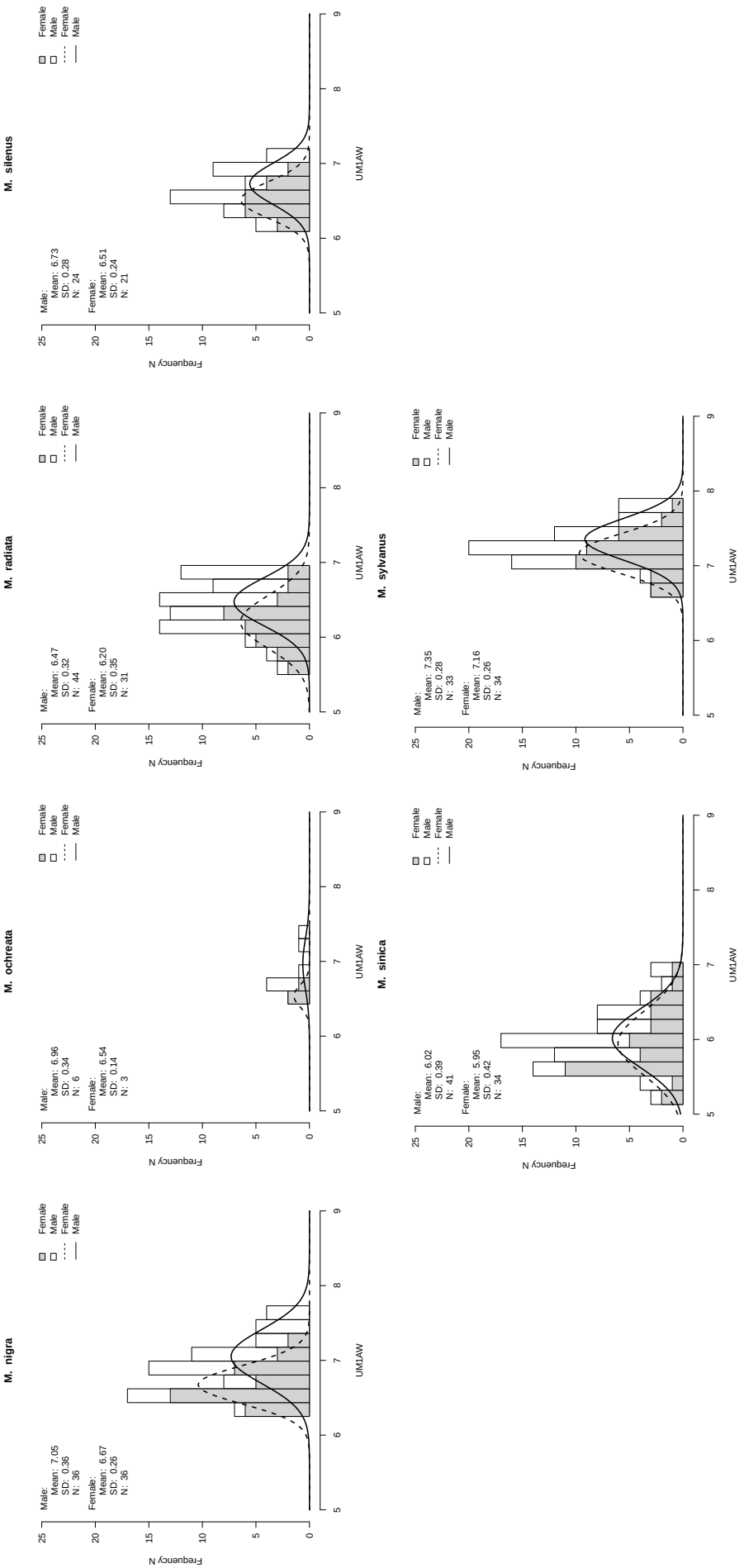
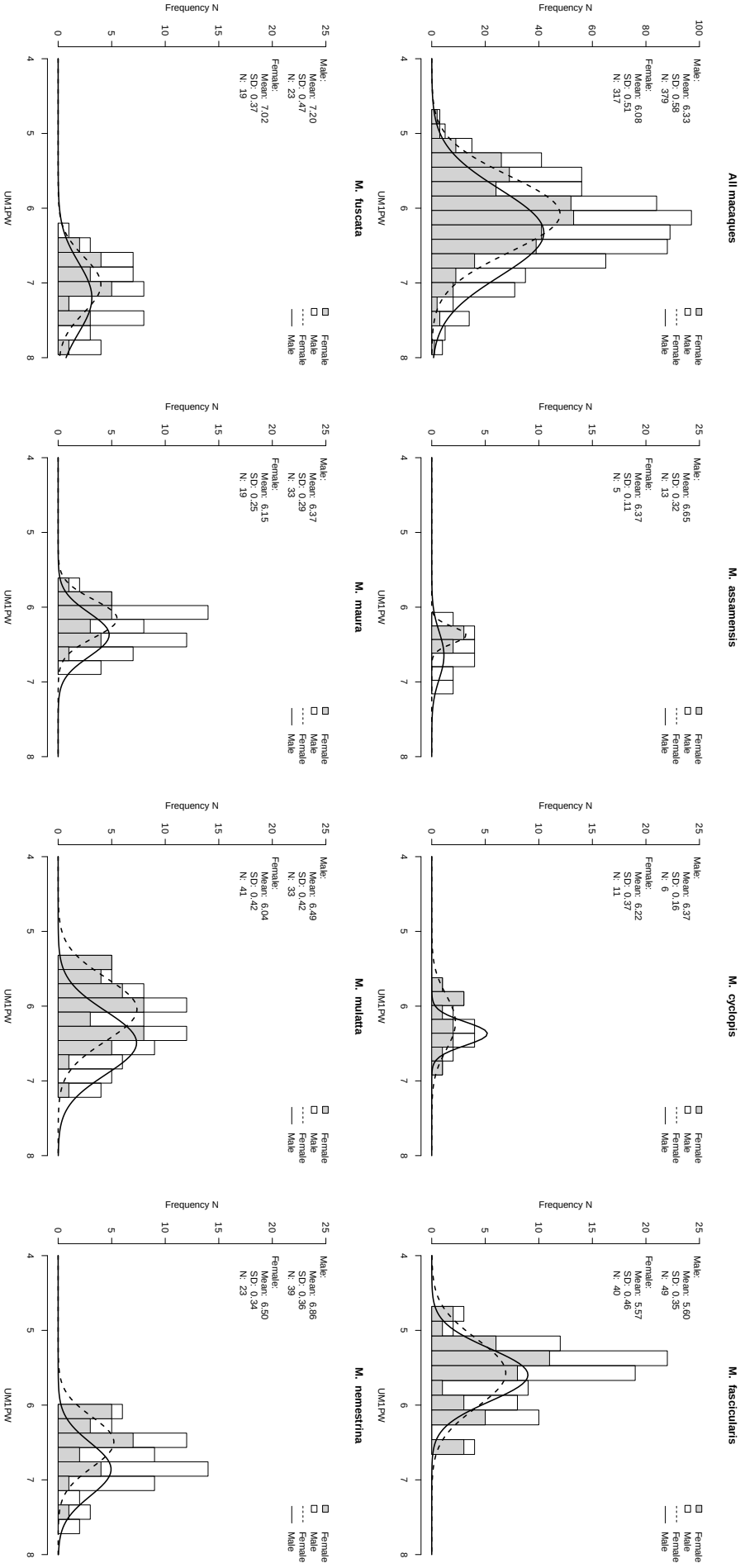


Fig. C.23 UM1AW


All macaques
Male:
Mean: 6.33
SD: 0.58
N: 379
Female:
Mean: 6.08
SD: 0.51
N: 317
M. assamensis
Male:
Mean: 6.65
SD: 0.32
N: 13
Female:
Mean: 6.37
SD: 0.11
N: 5
M. cyclopis
Male:
Mean: 6.37
SD: 0.16
N: 6
Female:
Mean: 6.22
SD: 0.37
N: 11
M. fascicularis
Male:
Mean: 5.60
SD: 0.35
N: 49
Female:
Mean: 5.57
SD: 0.46
N: 40
M. fuscata
Male:
Mean: 7.20
SD: 0.47
N: 23
Female:
Mean: 7.02
SD: 0.37
N: 19
M. maura
Male:
Mean: 6.37
SD: 0.29
N: 33
Female:
Mean: 6.15
SD: 0.25
N: 19
M. mulatta
Male:
Mean: 6.49
SD: 0.42
N: 33
Female:
Mean: 6.04
SD: 0.42
N: 41
M. nemestrina
Male:
Mean: 6.86
SD: 0.36
N: 39
Female:
Mean: 6.50
SD: 0.34
N: 23
Frequency N
UM1PW
Female
Male
Female
Male

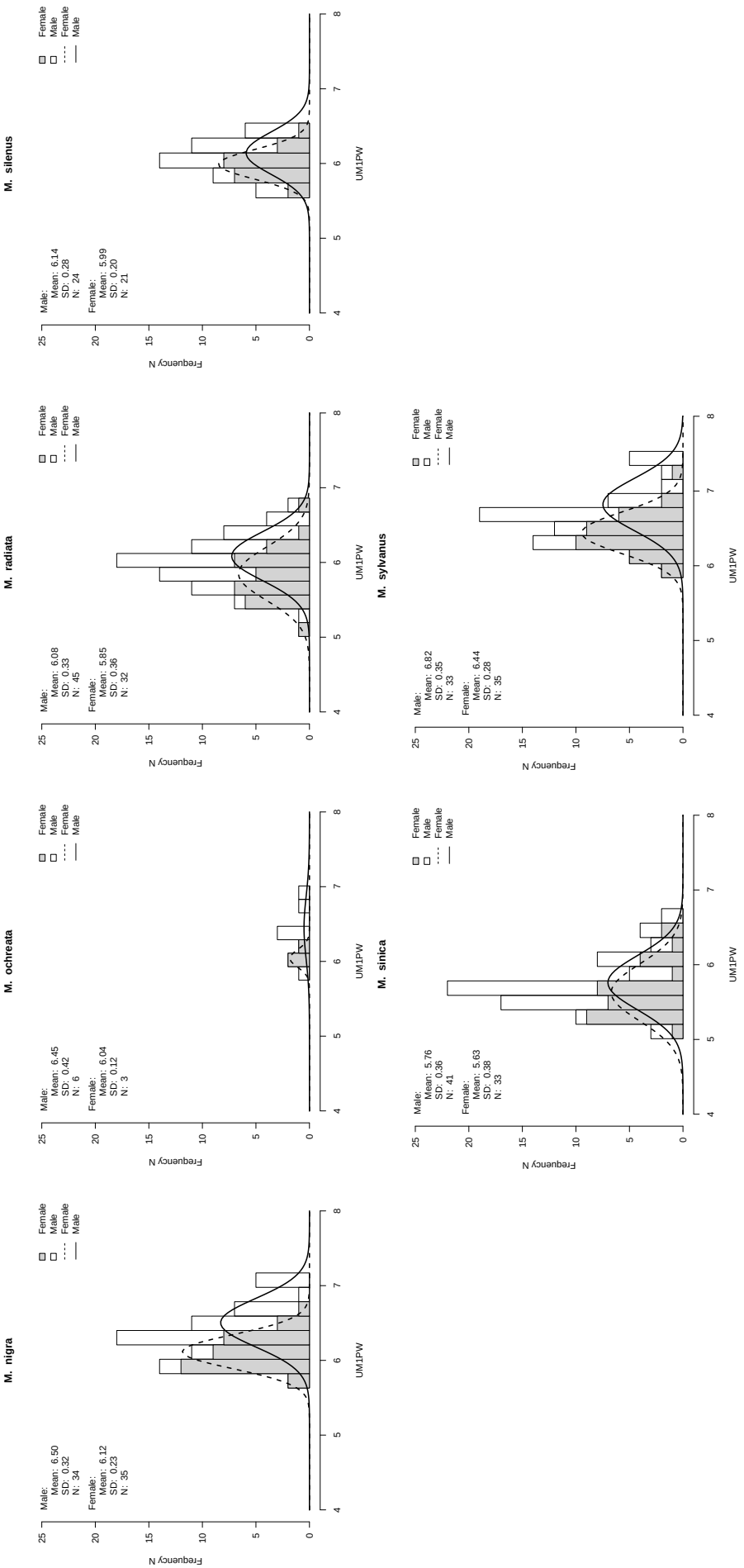


Fig. C.24 UM1PW

All macaques
Male:
Mean: 8.14
SD: 0.92
N: 368
Female:
Mean: 7.83
SD: 0.85
N: 306
M. assamensis
Male:
Mean: 8.84
SD: 0.44
N: 13
Female:
Mean: 8.80
SD: 0.12
N: 5
M. cyclopis
Male:
Mean: 8.08
SD: 0.44
N: 7
Female:
Mean: 7.87
SD: 0.33
N: 11
M. fascicularis
Male:
Mean: 7.04
SD: 0.45
N: 50
Female:
Mean: 7.00
SD: 0.58
N: 38
M. fuscata
Male:
Mean: 9.27
SD: 0.57
N: 23
Female:
Mean: 9.00
SD: 0.46
N: 20
M. maura
Male:
Mean: 8.20
SD: 0.48
N: 30
Female:
Mean: 7.92
SD: 0.45
N: 17
M. mulatta
Male:
Mean: 8.17
SD: 0.49
N: 32
Female:
Mean: 7.66
SD: 0.54
N: 41
M. nemestrina
Male:
Mean: 8.84
SD: 0.38
N: 37
Female:
Mean: 8.47
SD: 0.42
N: 22
Frequency N
UM2L
Female
Male
Female
Male

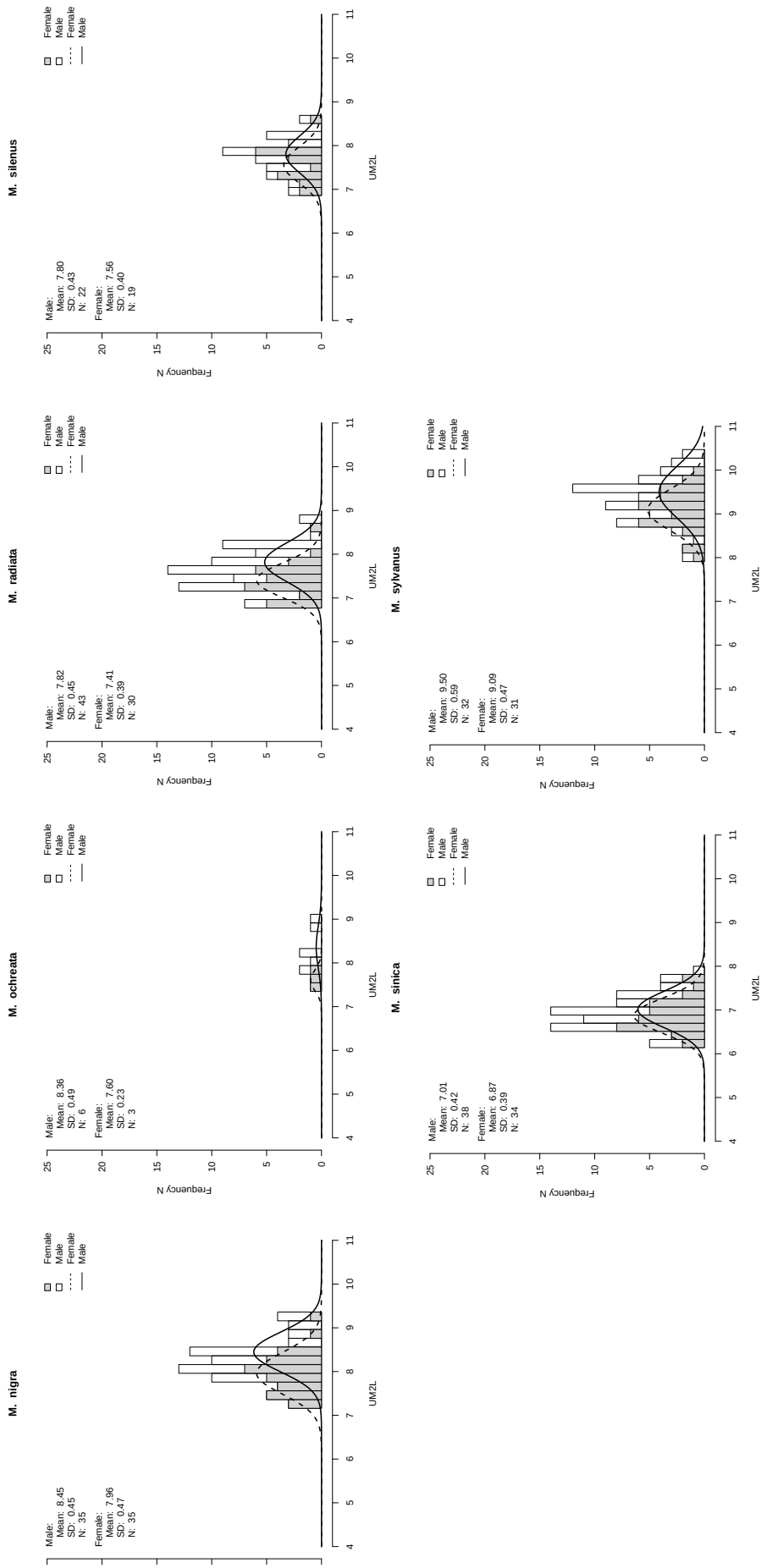

M. silenus
Male:
Mean: 7.80
SD: 0.43
N: 22
Female:
Mean: 7.56
SD: 0.40
N: 19
M. radiata
Male:
Mean: 7.82
SD: 0.45
N: 43
Female:
Mean: 7.41
SD: 0.39
N: 30
M. sylvanus
Male:
Mean: 9.50
SD: 0.59
N: 32
Female:
Mean: 9.09
SD: 0.47
N: 31
M. ochreata
Male:
Mean: 8.36
SD: 0.49
N: 6
Female:
Mean: 7.60
SD: 0.23
N: 3
M. sinica
Male:
Mean: 7.01
SD: 0.42
N: 38
Female:
Mean: 6.87
SD: 0.39
N: 34
M. nigra
Male:
Mean: 8.45
SD: 0.45
N: 35
Female:
Mean: 7.96
SD: 0.47
N: 35
Female
Male
Female
Male
Frequency N
UM2L

Fig. C.25 UM2L

All macaques
Male:
Mean: 7.91
SD: 0.84
N: 362
Female:
Mean: 7.56
SD: 0.80
N: 300
M. assamensis
Male:
Mean: 8.18
SD: 0.30
N: 13
Female:
Mean: 8.00
SD: 0.32
N: 5
M. cyclopis
Male:
Mean: 8.00
SD: 0.32
N: 7
Female:
Mean: 7.56
SD: 0.46
N: 11
M. fascicularis
Male:
Mean: 6.91
SD: 0.48
N: 50
Female:
Mean: 6.73
SD: 0.50
N: 39
M. fuscata
Male:
Mean: 9.17
SD: 0.58
N: 23
Female:
Mean: 8.95
SD: 0.43
N: 20
M. maura
Male:
Mean: 8.00
SD: 0.42
N: 30
Female:
Mean: 7.77
SD: 0.37
N: 17
M. mulatta
Male:
Mean: 7.97
SD: 0.49
N: 31
Female:
Mean: 7.47
SD: 0.57
N: 41
M. nemestrina
Male:
Mean: 8.58
SD: 0.41
N: 37
Female:
Mean: 8.12
SD: 0.52
N: 21
Frequency N
UM2AW
Female
Male
Female
Male

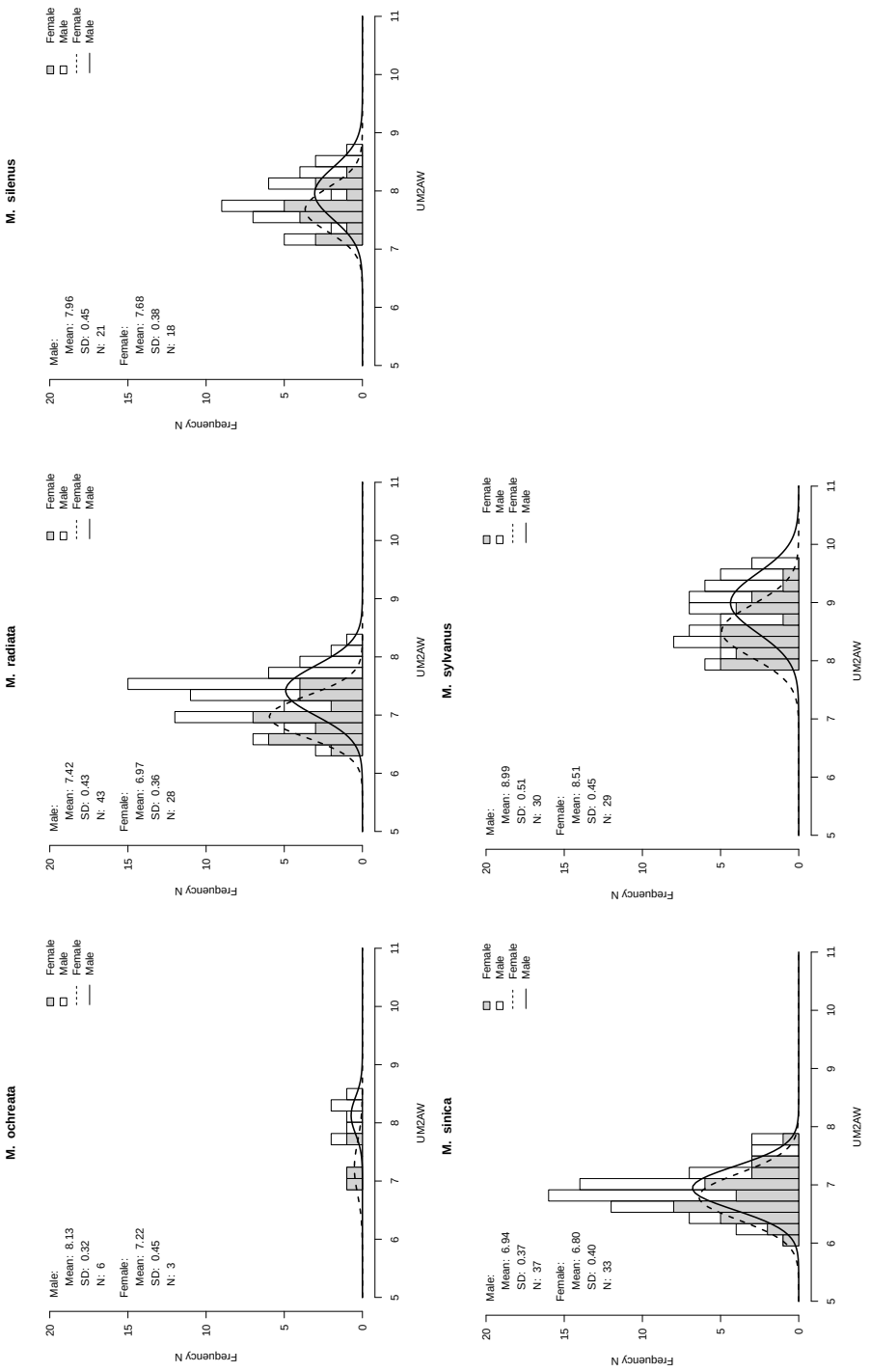
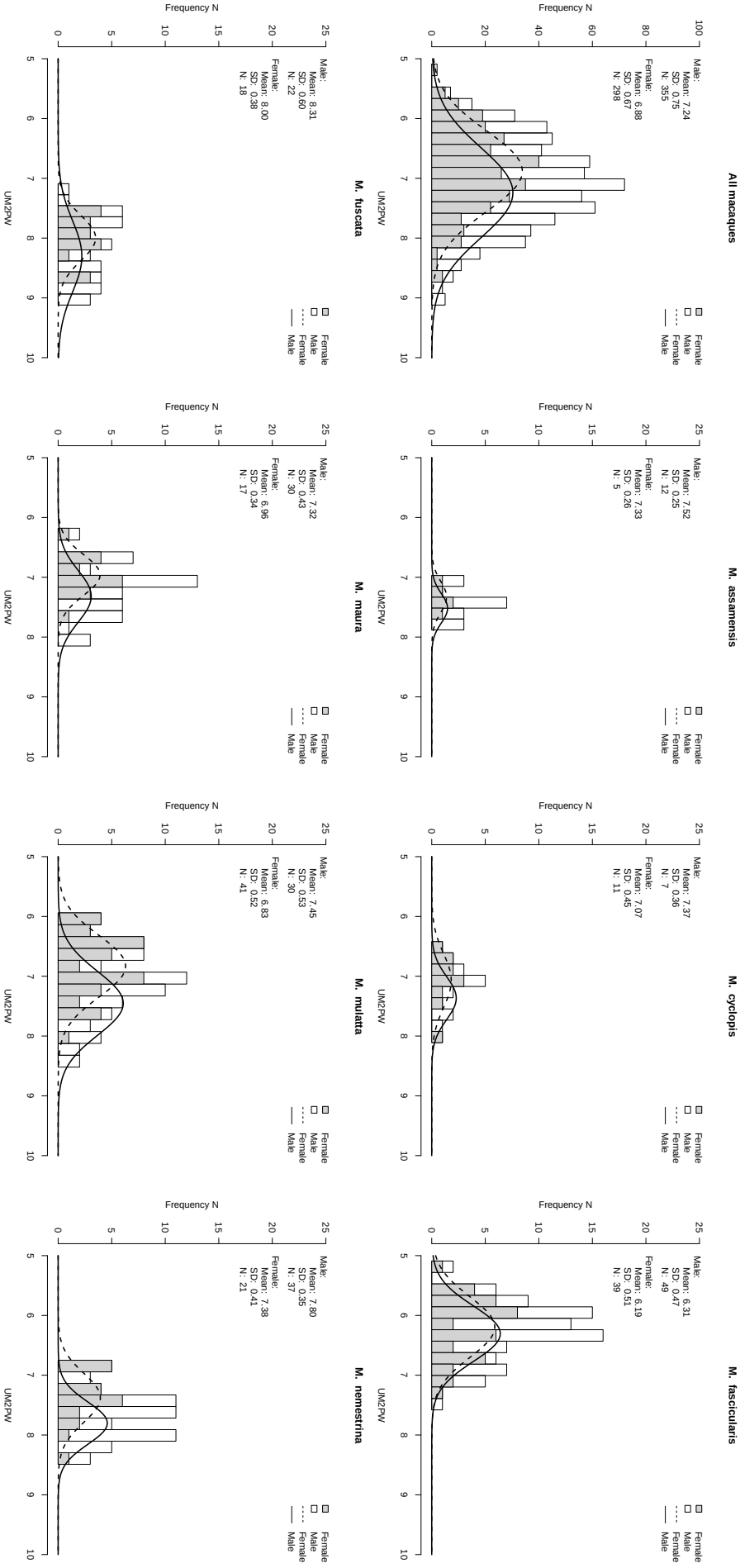


Fig. C.26 UM2AW


All macaques
Male:
Mean: 7.24
SD: 0.75
N: 355
Female:
Mean: 6.88
SD: 0.67
N: 298
M. assamensis
Male:
Mean: 7.52
SD: 0.25
N: 12
Female:
Mean: 7.33
SD: 0.26
N: 5
M. cyclopis
Male:
Mean: 7.37
SD: 0.36
N: 7
Female:
Mean: 7.07
SD: 0.45
N: 11
M. fascicularis
Male:
Mean: 6.31
SD: 0.47
N: 49
Female:
Mean: 6.19
SD: 0.51
N: 39
M. fuscata
Male:
Mean: 8.31
SD: 0.60
N: 22
Female:
Mean: 8.00
SD: 0.38
N: 18
M. maura
Male:
Mean: 7.32
SD: 0.43
N: 30
Female:
Mean: 6.96
SD: 0.34
N: 17
M. mulatta
Male:
Mean: 7.45
SD: 0.53
N: 30
Female:
Mean: 6.83
SD: 0.52
N: 41
M. nemestrina
Male:
Mean: 7.60
SD: 0.35
N: 37
Female:
Mean: 7.38
SD: 0.41
N: 21
Frequency N
UM2PW
Female
Male
Female
Male

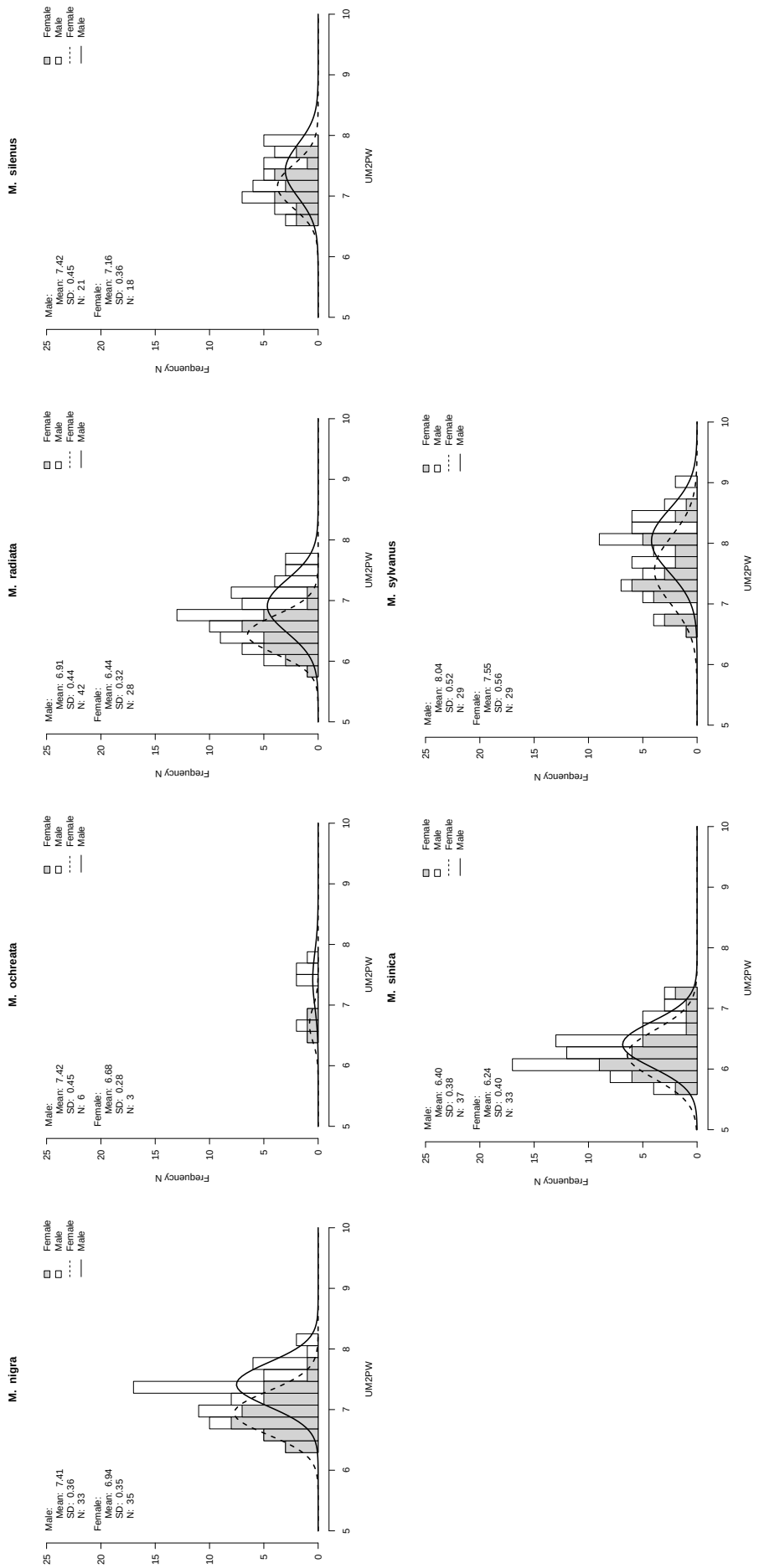
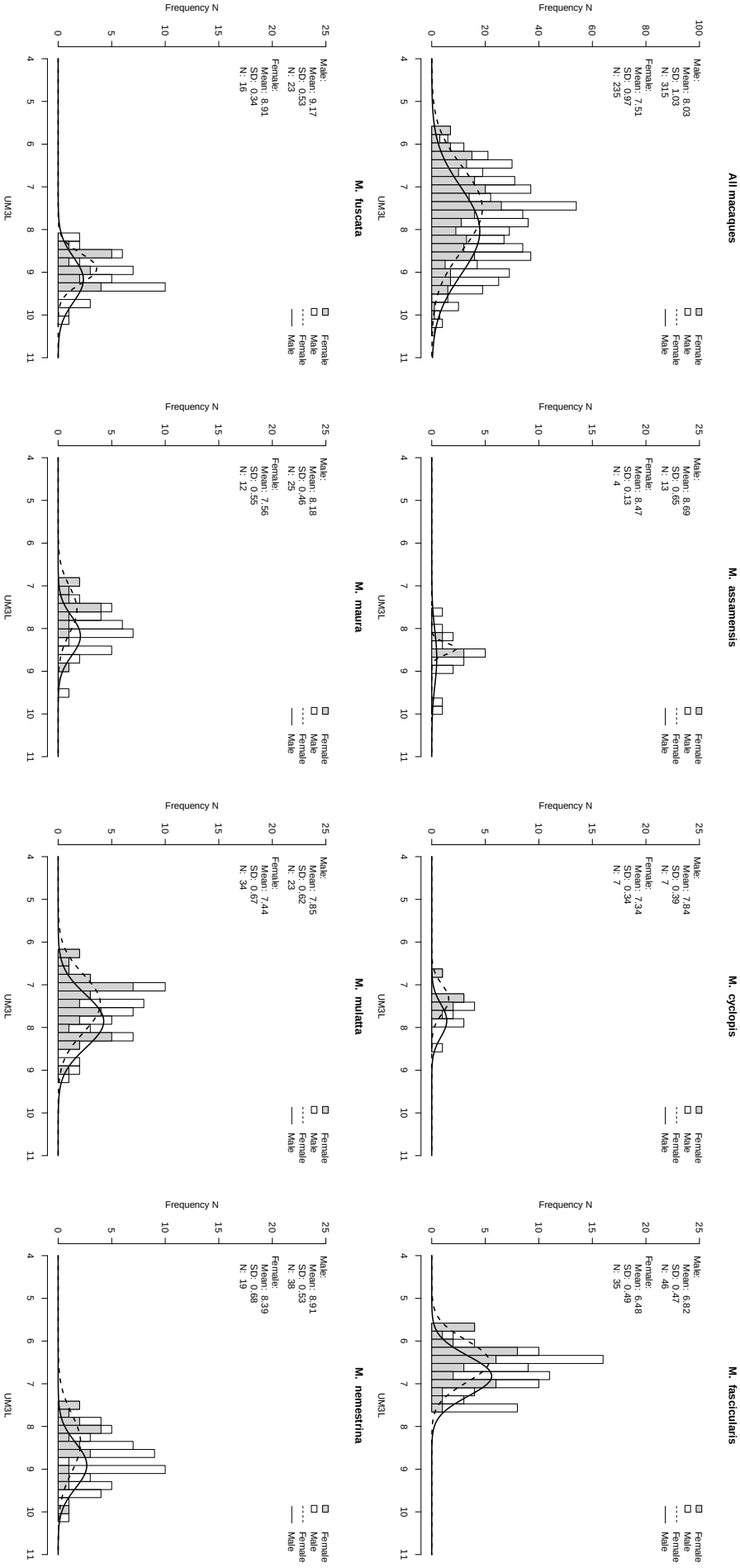


Fig. C.27 UM2PW


All macaques
Male:
Mean: 8.03
SD: 1.03
N: 315
Female:
Mean: 7.51
SD: 0.97
N: 235
M. assamensis
Male:
Mean: 8.69
SD: 0.65
N: 13
Female:
Mean: 8.47
SD: 0.13
N: 4
M. cyclopis
Male:
Mean: 7.84
SD: 0.39
N: 7
Female:
Mean: 7.34
SD: 0.34
N: 7
M. fascicularis
Male:
Mean: 6.82
SD: 0.47
N: 46
Female:
Mean: 6.48
SD: 0.49
N: 35
M. fuscata
Male:
Mean: 9.17
SD: 0.53
N: 23
Female:
Mean: 8.91
SD: 0.34
N: 16
M. maura
Male:
Mean: 8.18
SD: 0.46
N: 25
Female:
Mean: 7.56
SD: 0.55
N: 12
M. mulatta
Male:
Mean: 7.85
SD: 0.62
N: 23
Female:
Mean: 7.44
SD: 0.67
N: 34
M. nemestrina
Male:
Mean: 8.91
SD: 0.53
N: 38
Female:
Mean: 8.39
SD: 0.68
N: 19
Frequency N
UM3L
Female
Male
Female
Male

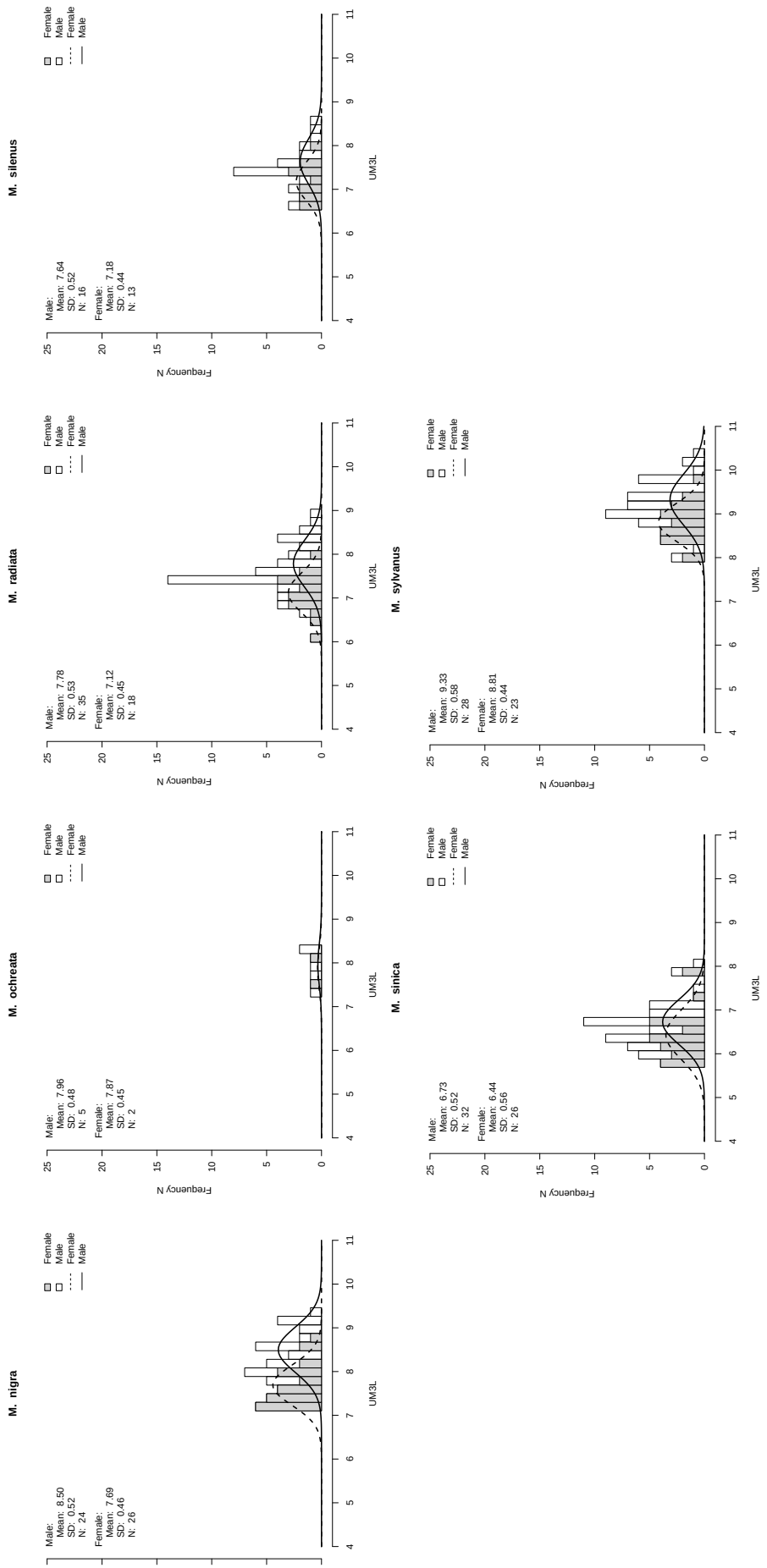

M. nigra
Male:
Mean: 8.50
SD: 0.52
N: 24
Female:
Mean: 7.69
SD: 0.46
N: 26
M. ochreata
Male:
Mean: 7.96
SD: 0.48
N: 5
Female:
Mean: 7.87
SD: 0.45
N: 2
M. radiata
Male:
Mean: 7.78
SD: 0.53
N: 35
Female:
Mean: 7.12
SD: 0.45
N: 18
M. silenus
Male:
Mean: 7.64
SD: 0.52
N: 16
Female:
Mean: 7.18
SD: 0.44
N: 13
M. sinica
Male:
Mean: 6.73
SD: 0.52
N: 32
Female:
Mean: 6.44
SD: 0.56
N: 26
M. sylvanus
Male:
Mean: 9.33
SD: 0.58
N: 28
Female:
Mean: 8.81
SD: 0.44
N: 23
Female
Male
Female
Male
Frequency N
UM3L

Fig. C.28 UM3L

All macaques
Male:
Mean: 7.86
SD: 0.96
N: 300
Female:
Mean: 7.34
SD: 0.91
N: 225
M. assamensis
Male:
Mean: 8.02
SD: 0.37
N: 13
Female:
Mean: 7.89
SD: 0.19
N: 4
M. cyclopis
Male:
Mean: 7.84
SD: 0.38
N: 7
Female:
Mean: 7.44
SD: 0.40
N: 7
M. fascicularis
Male:
Mean: 6.61
SD: 0.46
N: 44
Female:
Mean: 6.41
SD: 0.53
N: 34
M. fuscata
Male:
Mean: 9.12
SD: 0.62
N: 23
Female:
Mean: 8.74
SD: 0.49
N: 15
M. maura
Male:
Mean: 7.87
SD: 0.31
N: 22
Female:
Mean: 7.40
SD: 0.46
N: 12
M. mulatta
Male:
Mean: 7.94
SD: 0.55
N: 20
Female:
Mean: 7.31
SD: 0.73
N: 32
M. nemestrina
Male:
Mean: 8.67
SD: 0.45
N: 35
Female:
Mean: 8.16
SD: 0.68
N: 19
Frequency N
UM3AW
Female
Male
Female
Male

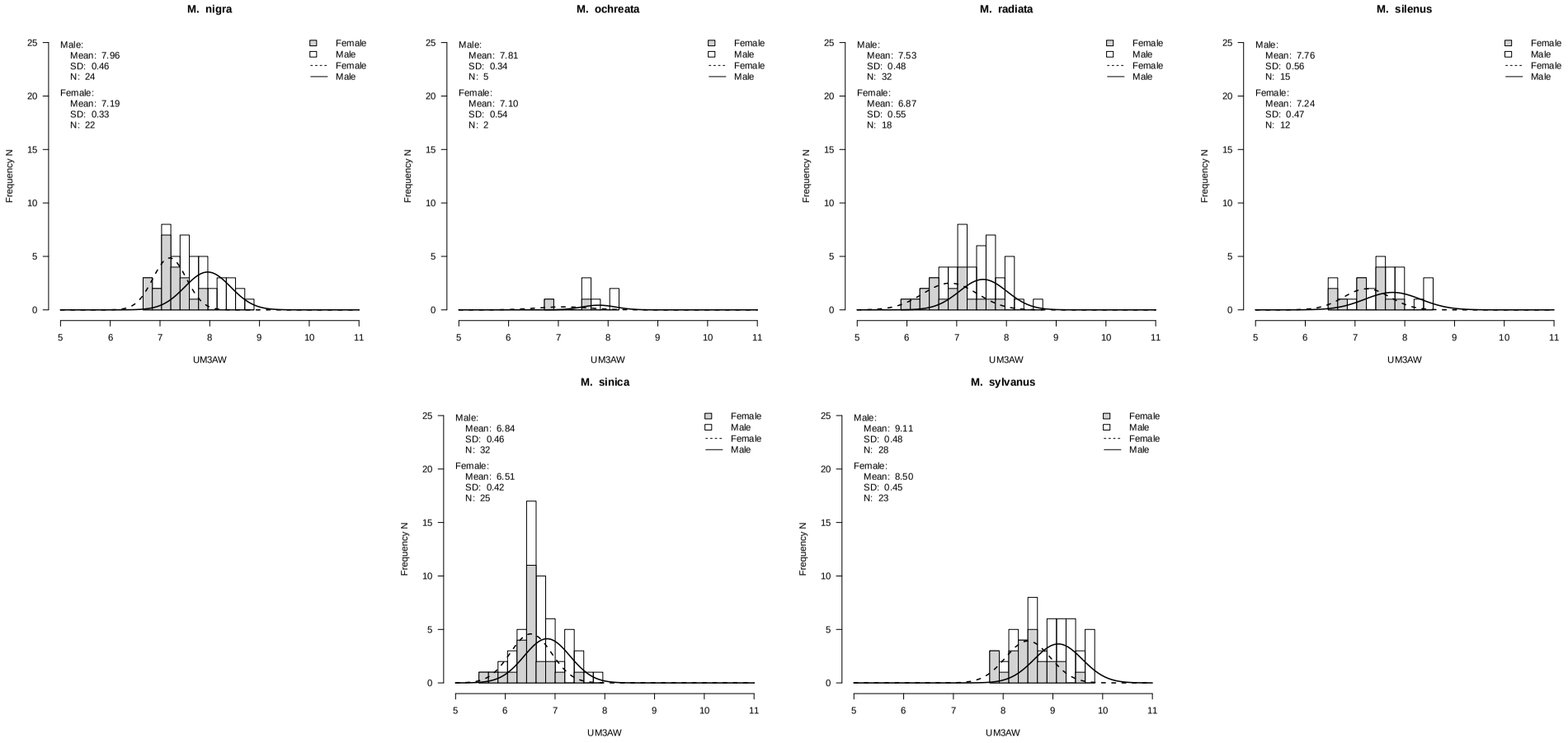
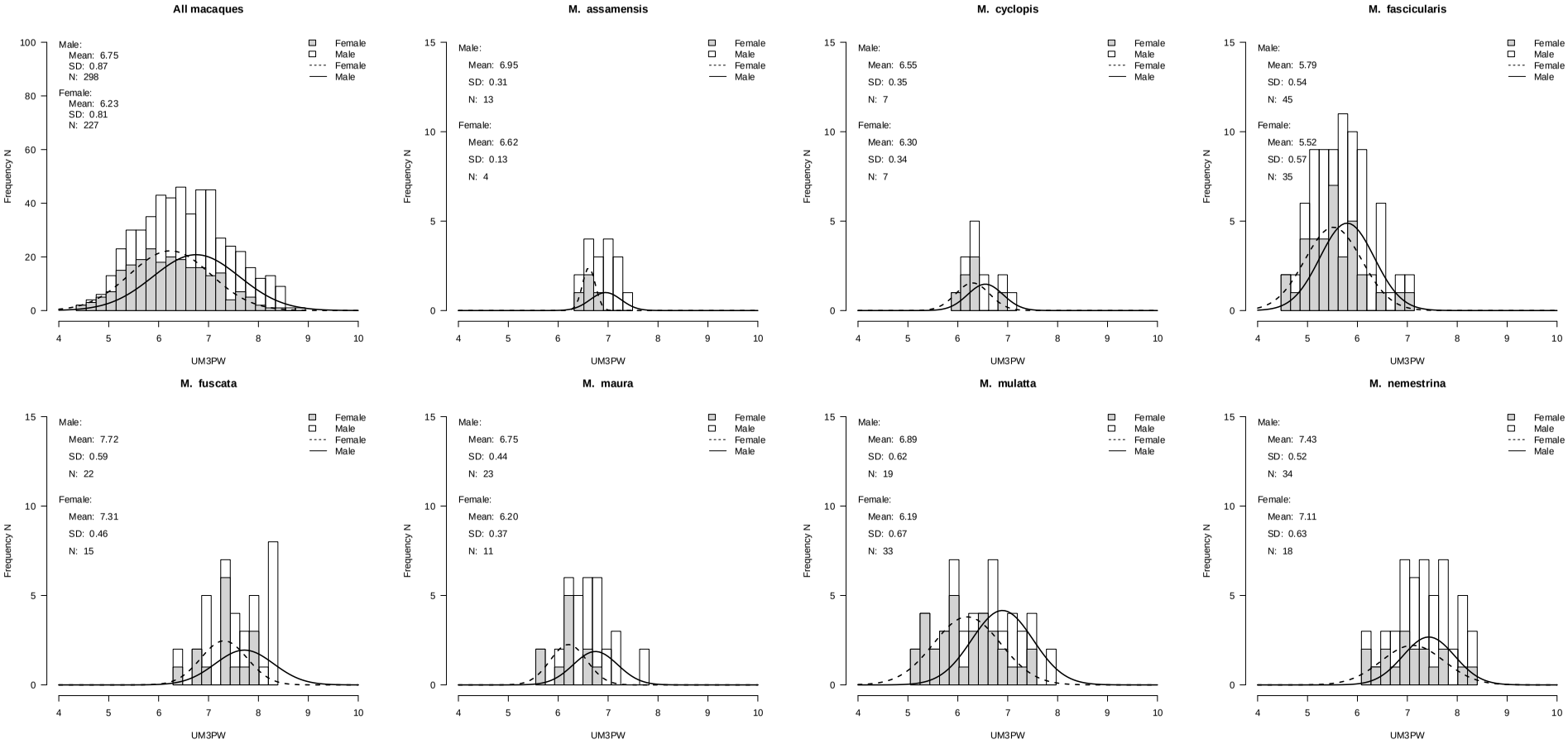


Fig. C.29 UM3AW


All macaques
Male:
Mean: 6.75
SD: 0.87
N: 298
Female:
Mean: 6.23
SD: 0.81
N: 227
M. assamensis
Male:
Mean: 6.95
SD: 0.31
N: 13
Female:
Mean: 6.62
SD: 0.13
N: 4
M. cyclopis
Male:
Mean: 6.55
SD: 0.35
N: 7
Female:
Mean: 6.30
SD: 0.34
N: 7
M. fascicularis
Male:
Mean: 5.79
SD: 0.54
N: 45
Female:
Mean: 5.52
SD: 0.57
N: 35
M. fuscata
Male:
Mean: 7.72
SD: 0.59
N: 22
Female:
Mean: 7.31
SD: 0.46
N: 15
M. maura
Male:
Mean: 6.75
SD: 0.44
N: 23
Female:
Mean: 6.20
SD: 0.37
N: 11
M. mulatta
Male:
Mean: 6.89
SD: 0.62
N: 19
Female:
Mean: 6.19
SD: 0.67
N: 33
M. nemestrina
Male:
Mean: 7.43
SD: 0.52
N: 34
Female:
Mean: 7.11
SD: 0.63
N: 18
Female
Male
Female
Male
Frequency N
UM3PW

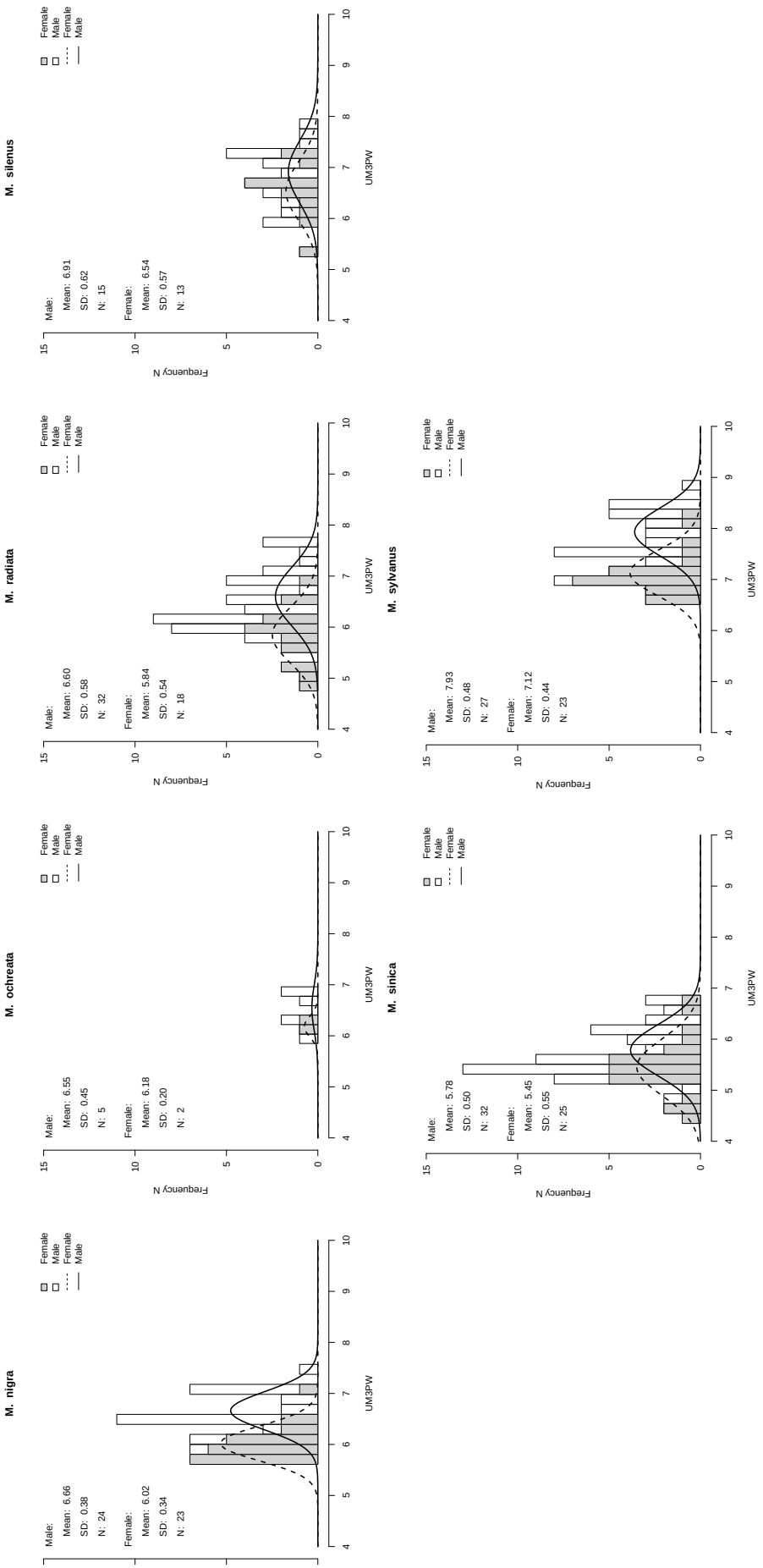
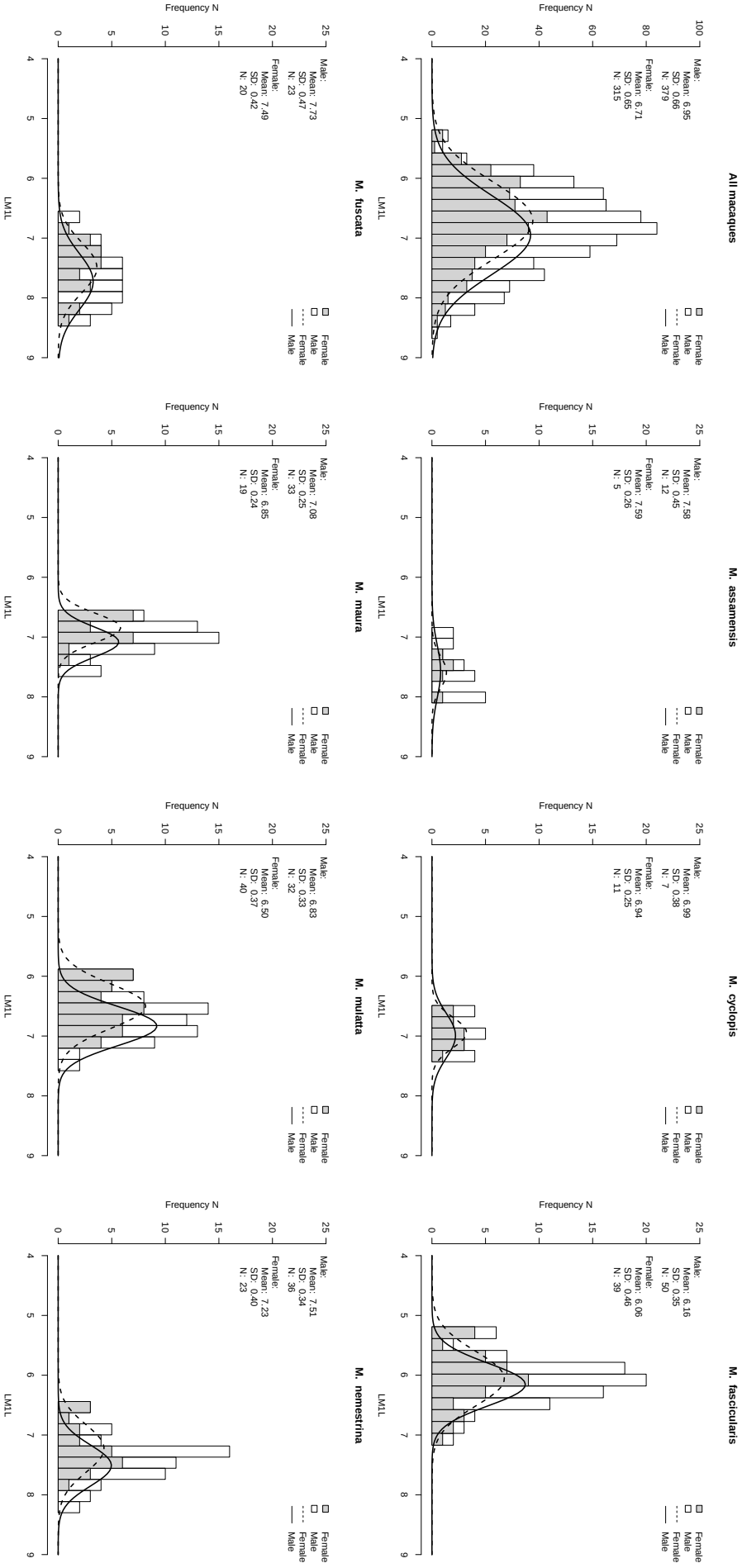


Fig. C.30 UM3PW


All macaques
Male: Mean: 6.95 SD: 0.66 N: 379
Female: Mean: 6.71 SD: 0.65 N: 315
M. assamensis
Male: Mean: 7.58 SD: 0.45 N: 12
Female: Mean: 7.59 SD: 0.26 N: 5
M. cyclopis
Male: Mean: 6.99 SD: 0.38 N: 7
Female: Mean: 6.94 SD: 0.25 N: 11
M. fascicularis
Male: Mean: 6.16 SD: 0.35 N: 50
Female: Mean: 6.06 SD: 0.46 N: 39
M. fuscata
Male: Mean: 7.73 SD: 0.47 N: 23
Female: Mean: 7.49 SD: 0.42 N: 20
M. maura
Male: Mean: 7.08 SD: 0.25 N: 33
Female: Mean: 6.85 SD: 0.24 N: 19
M. mulatta
Male: Mean: 6.83 SD: 0.33 N: 32
Female: Mean: 6.50 SD: 0.37 N: 40
M. nemestrina
Male: Mean: 7.51 SD: 0.34 N: 36
Female: Mean: 7.23 SD: 0.40 N: 23
Frequency N
LM1L
Female
Male
Female
Male

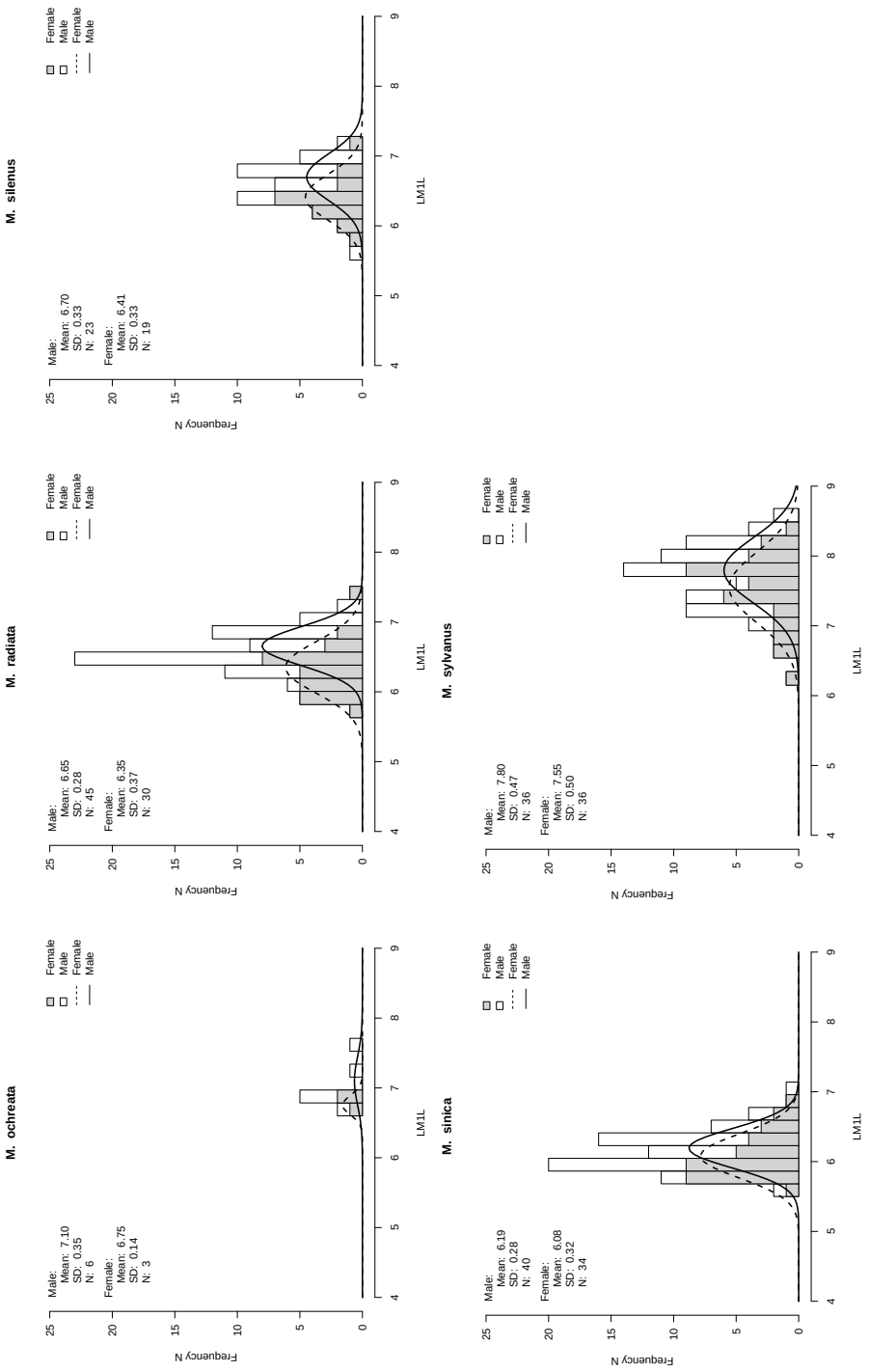

M. silenus
Male:
Mean: 6.70
SD: 0.33
N: 23
Female:
Mean: 6.41
SD: 0.33
N: 19
M. radiata
Male:
Mean: 6.65
SD: 0.28
N: 45
Female:
Mean: 6.35
SD: 0.37
N: 30
M. sylvanus
Male:
Mean: 7.80
SD: 0.47
N: 36
Female:
Mean: 7.55
SD: 0.50
N: 36
M. ochreata
Male:
Mean: 7.10
SD: 0.35
N: 6
Female:
Mean: 6.75
SD: 0.14
N: 3
M. sinica
Male:
Mean: 6.19
SD: 0.28
N: 40
Female:
Mean: 6.08
SD: 0.32
N: 34
M. nigra
Male:
Mean: 7.25
SD: 0.36
N: 36
Female:
Mean: 6.82
SD: 0.37
N: 36
Female
Male
Female
Male
Frequency N
LM1L

Fig. C.31 LM1L

All macaques
Male:
Mean: 5.57
SD: 0.55
N: 380
Female:
Mean: 5.38
SD: 0.52
N: 312
M. assamensis
Male:
Mean: 5.94
SD: 0.28
N: 12
Female:
Mean: 5.89
SD: 0.18
N: 5
M. cyclopis
Male:
Mean: 5.62
SD: 0.28
N: 7
Female:
Mean: 5.39
SD: 0.30
N: 11
M. fascicularis
Male:
Mean: 4.91
SD: 0.32
N: 51
Female:
Mean: 4.89
SD: 0.35
N: 39
M. fuscata
Male:
Mean: 6.16
SD: 0.46
N: 23
Female:
Mean: 6.13
SD: 0.37
N: 20
M. maura
Male:
Mean: 5.71
SD: 0.23
N: 33
Female:
Mean: 5.55
SD: 0.25
N: 19
M. mulatta
Male:
Mean: 5.59
SD: 0.33
N: 33
Female:
Mean: 5.32
SD: 0.35
N: 39
M. nemestrina
Male:
Mean: 6.04
SD: 0.35
N: 37
Female:
Mean: 5.76
SD: 0.36
N: 23
Frequency N
LM1AW
Female
Male
Female
Male

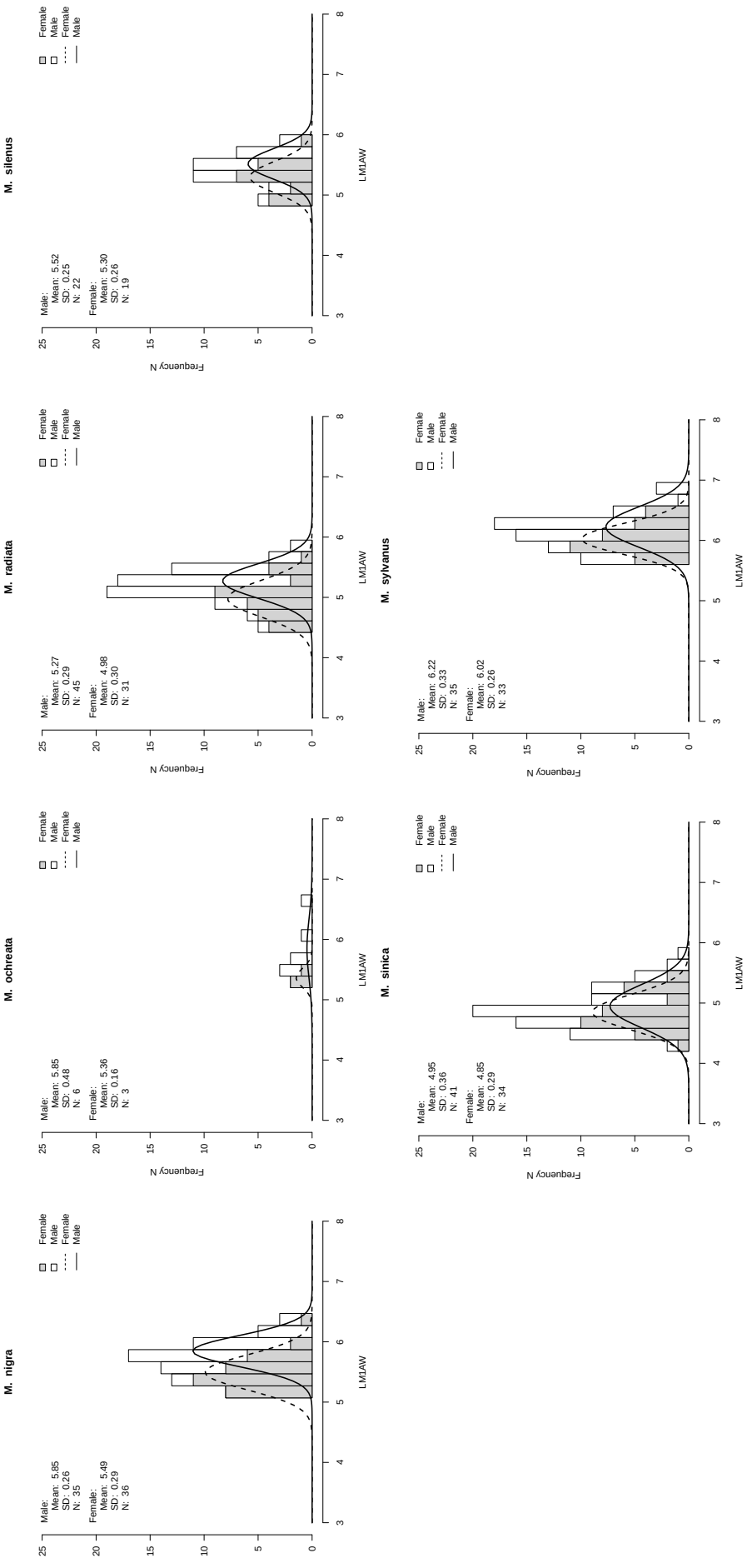
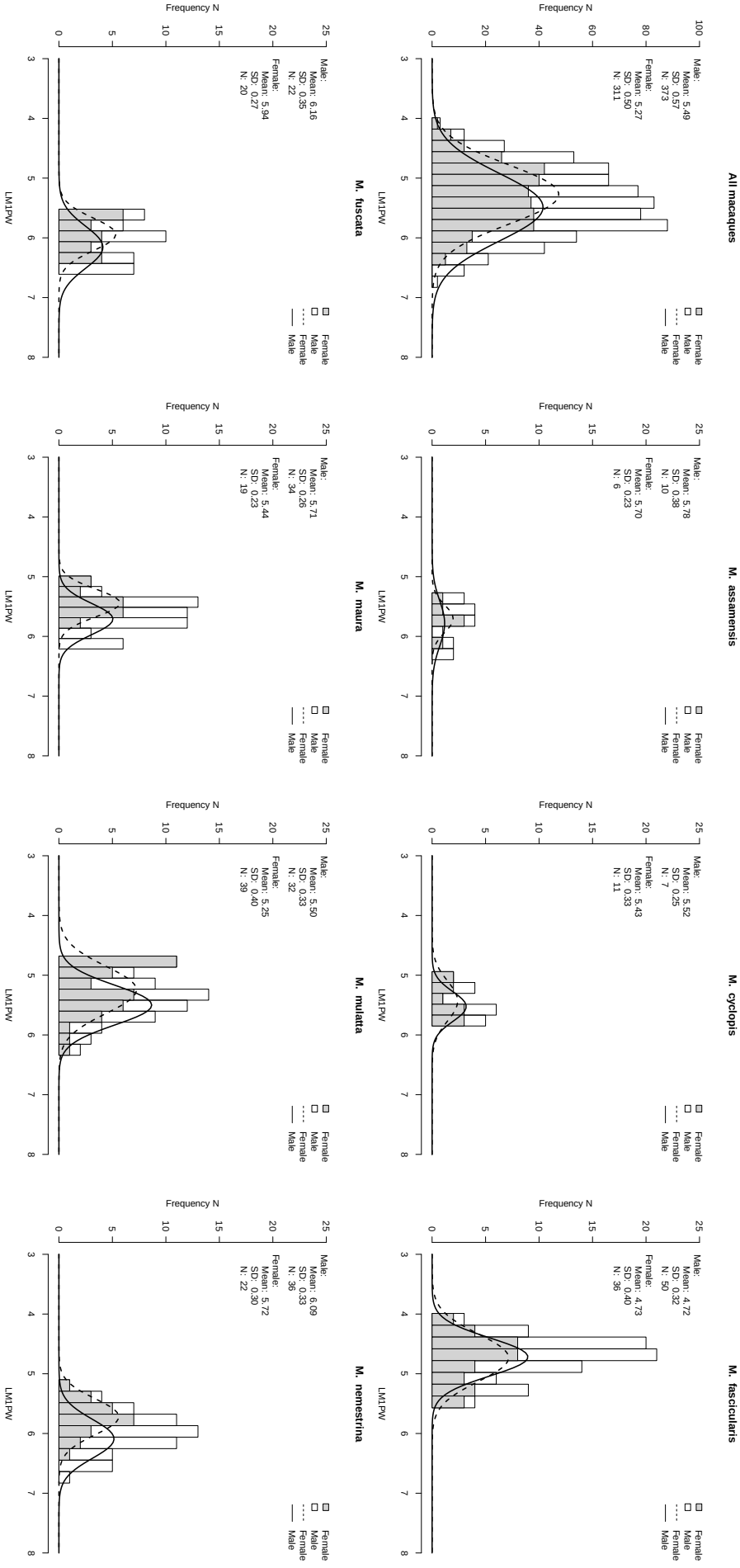


Fig. C.32 LM1AW


All macaques
Male:
Mean: 5.49
SD: 0.57
N: 373
Female:
Mean: 5.27
SD: 0.50
N: 311
M. assamensis
Male:
Mean: 5.78
SD: 0.38
N: 10
Female:
Mean: 5.70
SD: 0.23
N: 6
M. cyclopis
Male:
Mean: 5.52
SD: 0.25
N: 7
Female:
Mean: 5.43
SD: 0.33
N: 11
M. fascicularis
Male:
Mean: 4.72
SD: 0.32
N: 50
Female:
Mean: 4.73
SD: 0.40
N: 36
M. fuscata
Male:
Mean: 6.16
SD: 0.35
N: 22
Female:
Mean: 5.94
SD: 0.27
N: 20
M. maura
Male:
Mean: 5.71
SD: 0.26
N: 34
Female:
Mean: 5.44
SD: 0.23
N: 19
M. mulatta
Male:
Mean: 5.50
SD: 0.33
N: 32
Female:
Mean: 5.25
SD: 0.40
N: 39
M. nemestrina
Male:
Mean: 6.09
SD: 0.33
N: 36
Female:
Mean: 5.72
SD: 0.30
N: 22
Frequency N
LM1PW
Female
Male
Female
Male

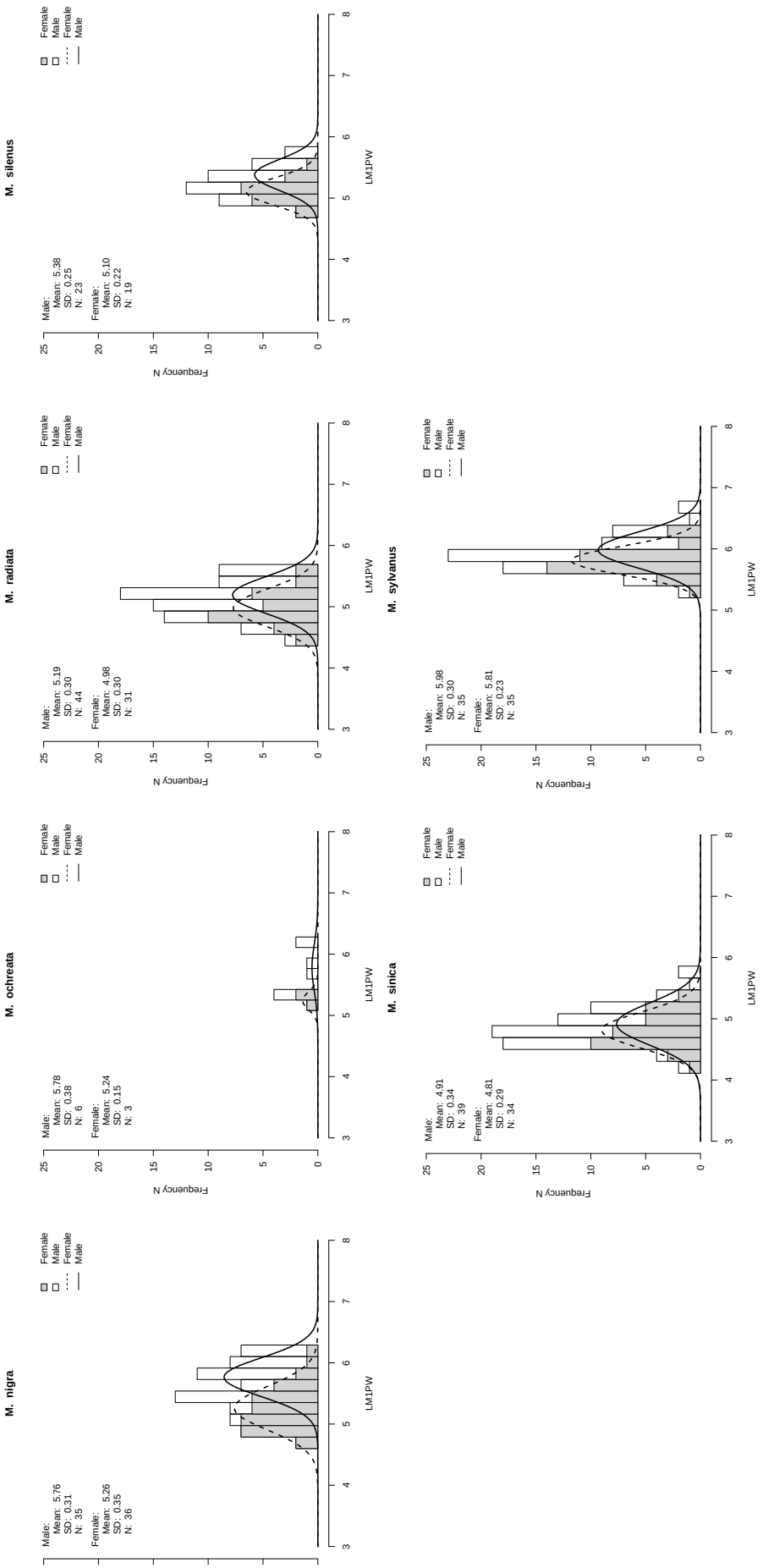


Fig. C.33 LM1PW

All macaques
Male:
Mean: 8.06
SD: 0.87
N: 367
Female:
Mean: 7.73
SD: 0.83
N: 307
M. assamensis
Male:
Mean: 8.78
SD: 0.44
N: 12
Female:
Mean: 8.72
SD: 0.33
N: 6
M. cyclopis
Male:
Mean: 8.21
SD: 0.48
N: 7
Female:
Mean: 7.94
SD: 0.35
N: 11
M. fascicularis
Male:
Mean: 7.07
SD: 0.39
N: 49
Female:
Mean: 6.91
SD: 0.59
N: 40
M. fuscata
Male:
Mean: 9.09
SD: 0.48
N: 22
Female:
Mean: 8.83
SD: 0.44
N: 20
M. maura
Male:
Mean: 8.10
SD: 0.41
N: 32
Female:
Mean: 7.79
SD: 0.48
N: 17
M. mulatta
Male:
Mean: 8.01
SD: 0.43
N: 32
Female:
Mean: 7.60
SD: 0.53
N: 40
M. nemestrina
Male:
Mean: 8.71
SD: 0.43
N: 36
Female:
Mean: 8.34
SD: 0.34
N: 22
Frequency N
LM2L
Female
Male
Female
Male

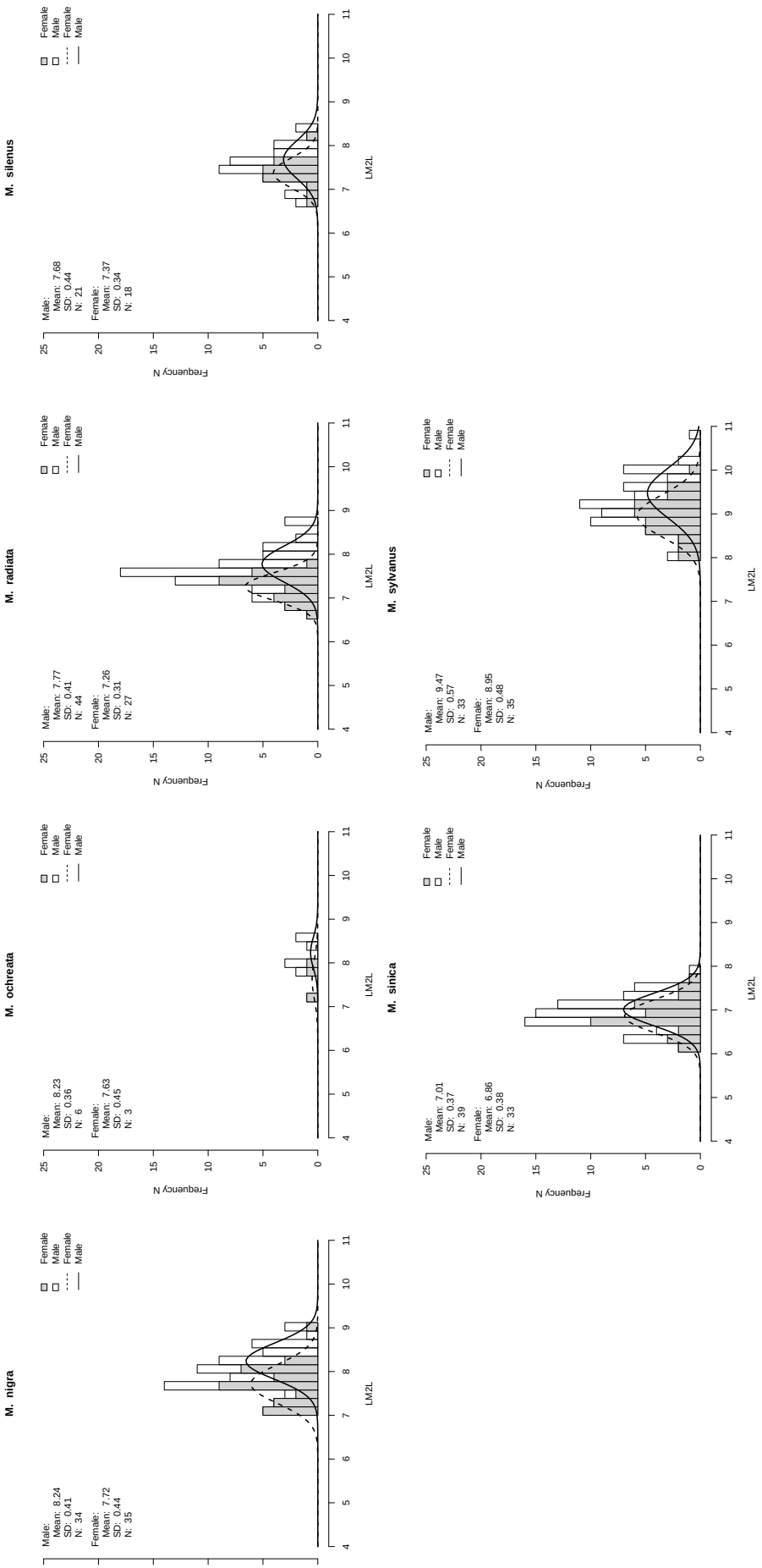
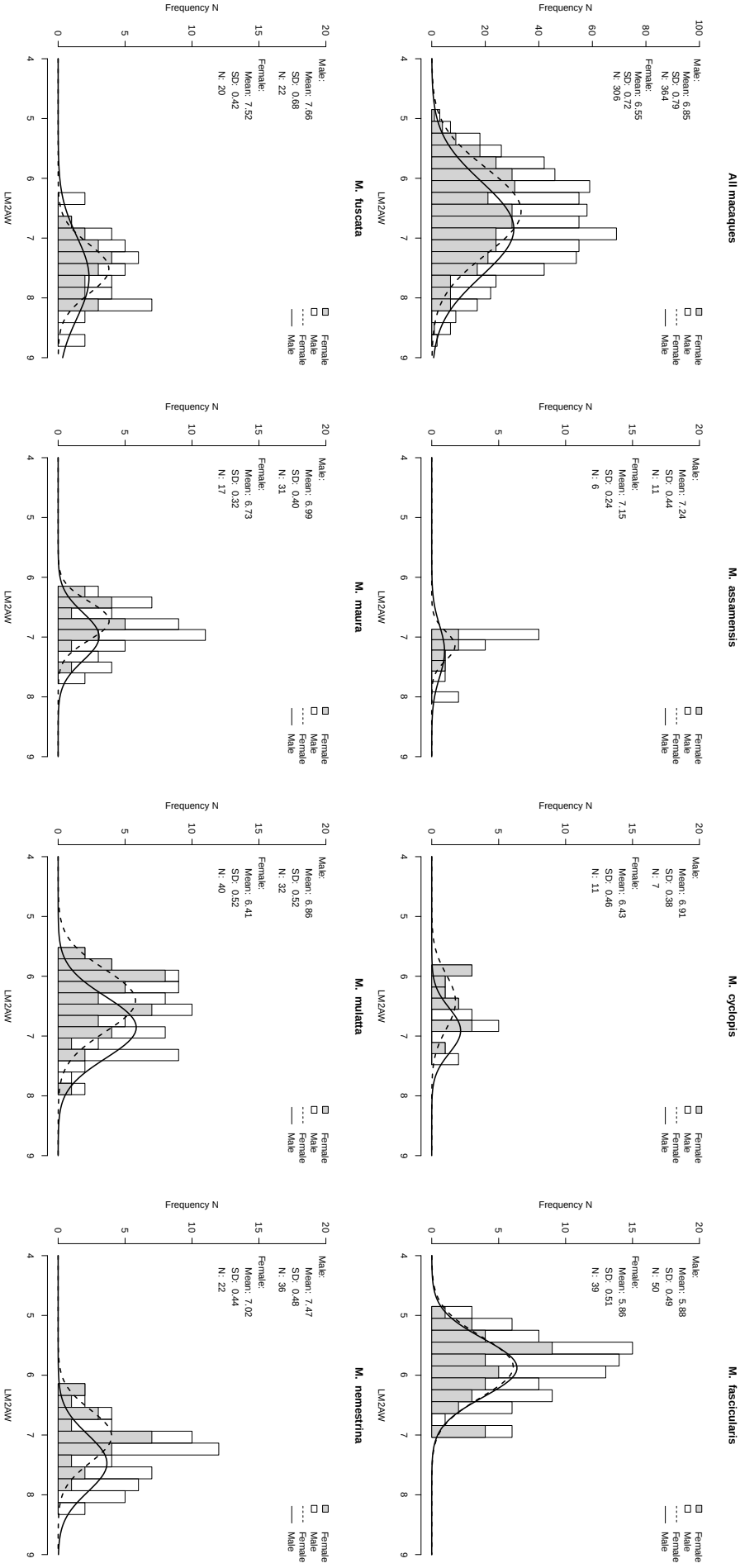

M. silenus
Male:
Mean: 7.68
SD: 0.44
N: 21
Female:
Mean: 7.37
SD: 0.34
N: 18
M. radiata
Male:
Mean: 7.77
SD: 0.41
N: 44
Female:
Mean: 7.26
SD: 0.31
N: 27
M. sylvanus
Male:
Mean: 9.47
SD: 0.57
N: 33
Female:
Mean: 8.95
SD: 0.48
N: 35
M. ochreata
Male:
Mean: 8.23
SD: 0.36
N: 6
Female:
Mean: 7.63
SD: 0.45
N: 3
M. sinica
Male:
Mean: 7.01
SD: 0.37
N: 39
Female:
Mean: 6.86
SD: 0.38
N: 33
M. nigra
Male:
Mean: 8.24
SD: 0.41
N: 34
Female:
Mean: 7.72
SD: 0.44
N: 35
Female
Male
Female
Male
Frequency N
LM2L

Fig. C.34 LM2L


All macaques
Male:
Mean: 6.85
SD: 0.79
N: 364
Female:
Mean: 6.55
SD: 0.72
N: 306
M. assamensis
Male:
Mean: 7.24
SD: 0.44
N: 11
Female:
Mean: 7.15
SD: 0.24
N: 6
M. cyclopis
Male:
Mean: 6.91
SD: 0.38
N: 7
Female:
Mean: 6.43
SD: 0.46
N: 11
M. fascicularis
Male:
Mean: 5.88
SD: 0.49
N: 50
Female:
Mean: 5.86
SD: 0.51
N: 39
M. fuscata
Male:
Mean: 7.66
SD: 0.68
N: 22
Female:
Mean: 7.52
SD: 0.42
N: 20
M. maura
Male:
Mean: 6.99
SD: 0.40
N: 31
Female:
Mean: 6.73
SD: 0.32
N: 17
M. mulatta
Male:
Mean: 6.86
SD: 0.52
N: 32
Female:
Mean: 6.41
SD: 0.52
N: 40
M. nemestrina
Male:
Mean: 7.47
SD: 0.48
N: 36
Female:
Mean: 7.02
SD: 0.44
N: 22
Frequency N
LM2AW
Female
Male
Female
Male

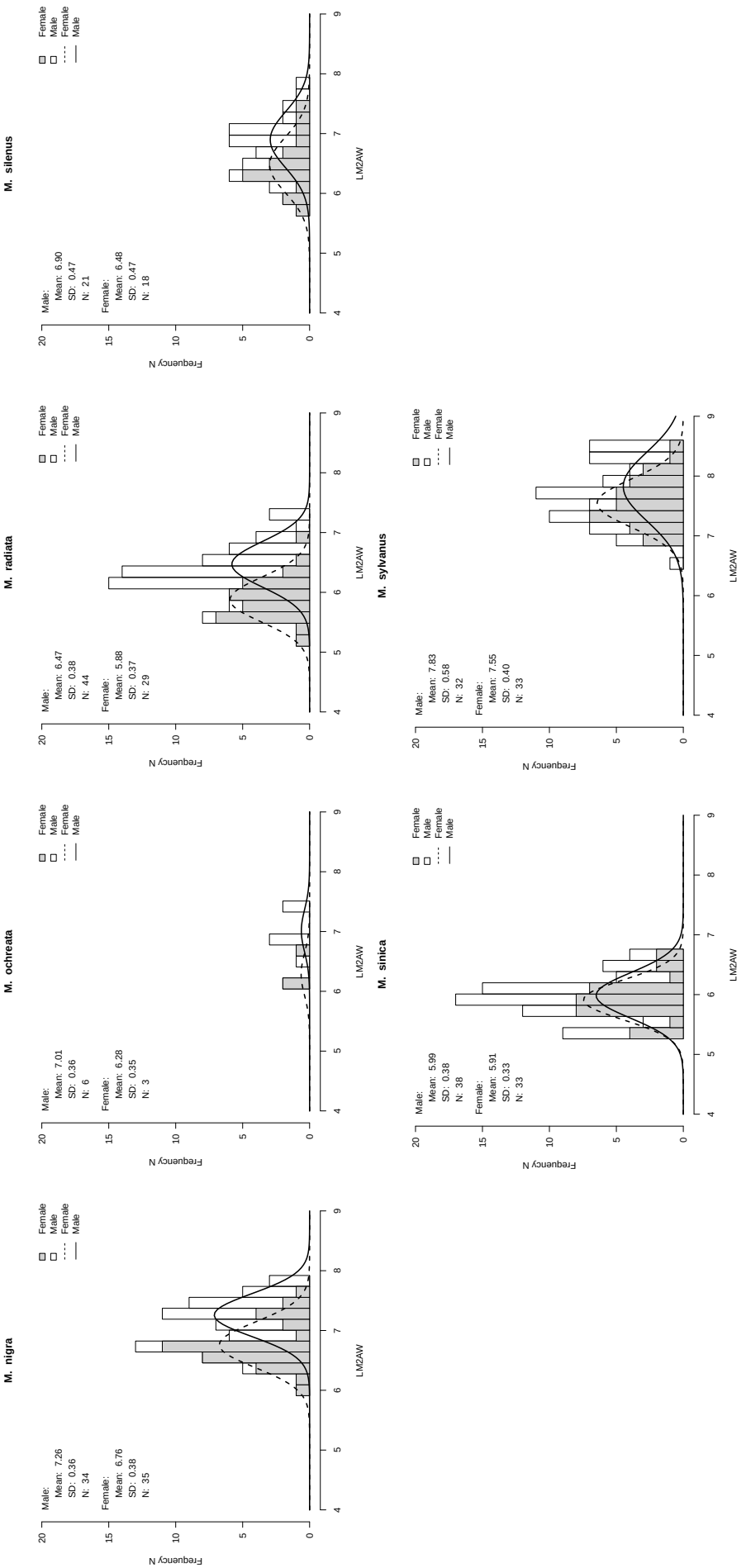


Fig. C.35 LM2AW

All macaques
Male:
Mean: 6.40
SD: 0.72
N: 359
Female:
Mean: 6.13
SD: 0.64
N: 297
M. assamensis
Male:
Mean: 6.81
SD: 0.39
N: 10
Female:
Mean: 6.90
SD: 0.24
N: 6
M. cyclopis
Male:
Mean: 6.44
SD: 0.36
N: 7
Female:
Mean: 6.11
SD: 0.38
N: 11
M. fascicularis
Male:
Mean: 5.45
SD: 0.42
N: 50
Female:
Mean: 5.47
SD: 0.48
N: 38
M. fuscata
Male:
Mean: 7.27
SD: 0.54
N: 21
Female:
Mean: 7.10
SD: 0.33
N: 20
M. maura
Male:
Mean: 6.59
SD: 0.34
N: 31
Female:
Mean: 6.38
SD: 0.25
N: 16
M. mulatta
Male:
Mean: 6.49
SD: 0.49
N: 32
Female:
Mean: 6.03
SD: 0.48
N: 37
M. nemestrina
Male:
Mean: 7.02
SD: 0.47
N: 37
Female:
Mean: 6.67
SD: 0.48
N: 22
Frequency N
LM2PW
Female
Male
Female
Male

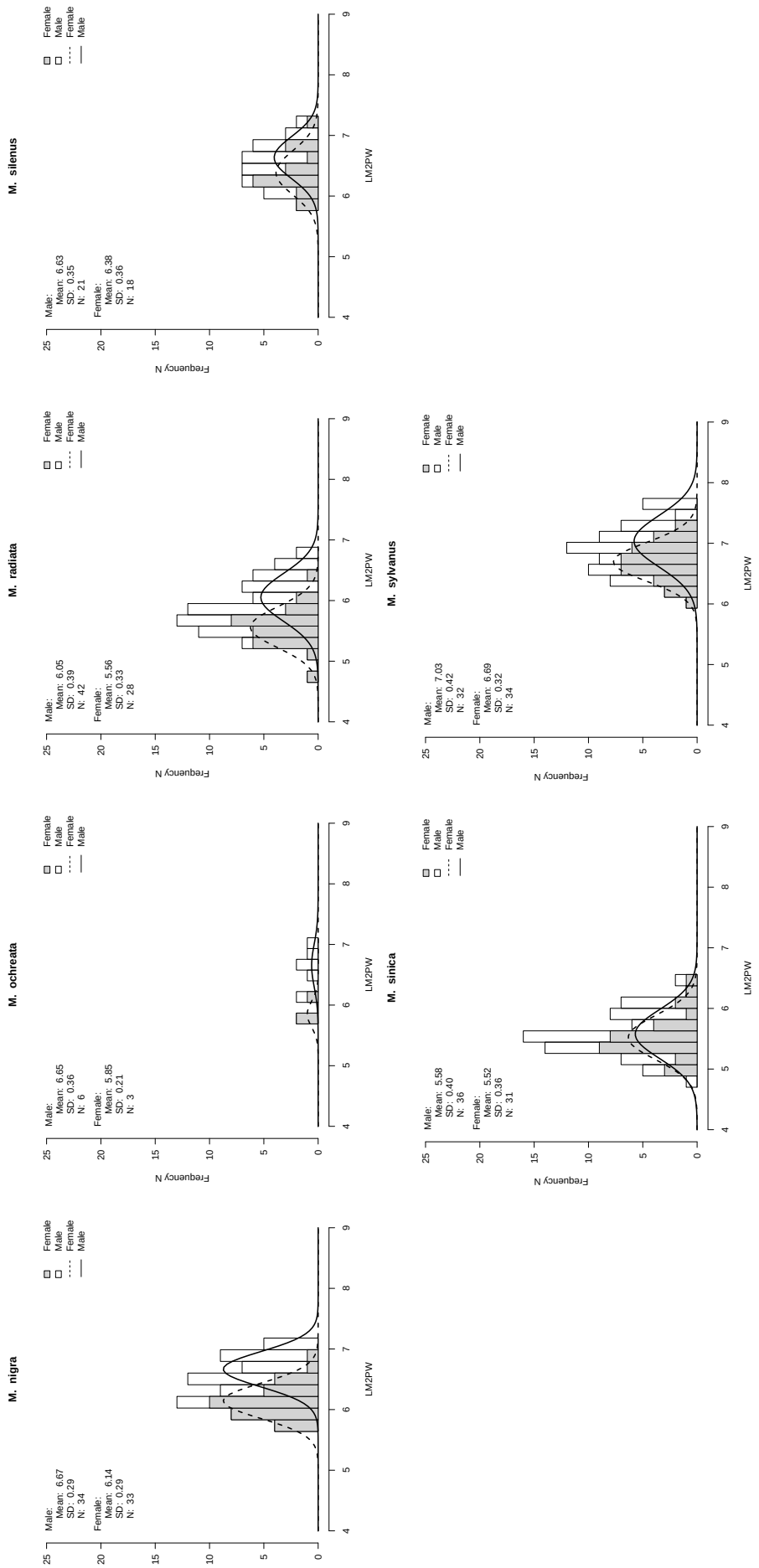
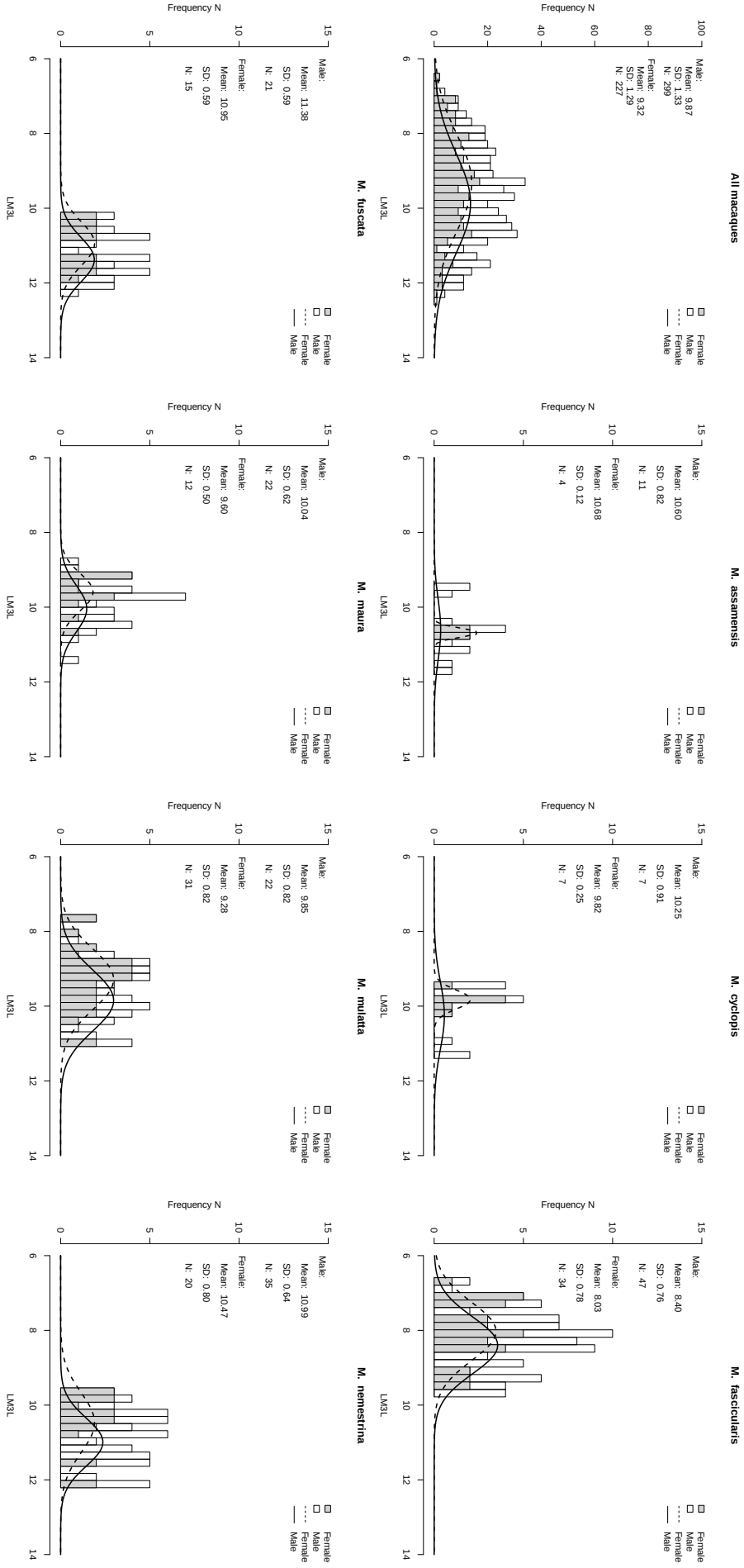


Fig. C.36 LM2PW


All macaques
Male:
Mean: 9.87
SD: 1.33
N: 299
Female:
Mean: 9.32
SD: 1.29
N: 227
M. assamensis
Male:
Mean: 10.60
SD: 0.82
N: 11
Female:
Mean: 10.68
SD: 0.12
N: 4
M. cyclopis
Male:
Mean: 10.25
SD: 0.91
N: 7
Female:
Mean: 9.82
SD: 0.25
N: 7
M. fascicularis
Male:
Mean: 8.40
SD: 0.76
N: 47
Female:
Mean: 8.03
SD: 0.78
N: 34
M. fuscata
Male:
Mean: 11.38
SD: 0.59
N: 21
Female:
Mean: 10.95
SD: 0.59
N: 15
M. maura
Male:
Mean: 10.04
SD: 0.62
N: 22
Female:
Mean: 9.60
SD: 0.50
N: 12
M. mulatta
Male:
Mean: 9.85
SD: 0.82
N: 22
Female:
Mean: 9.28
SD: 0.82
N: 31
M. nemestrina
Male:
Mean: 10.99
SD: 0.64
N: 35
Female:
Mean: 10.47
SD: 0.80
N: 20
Frequency N
LM3L
Female
Male
Female
Male

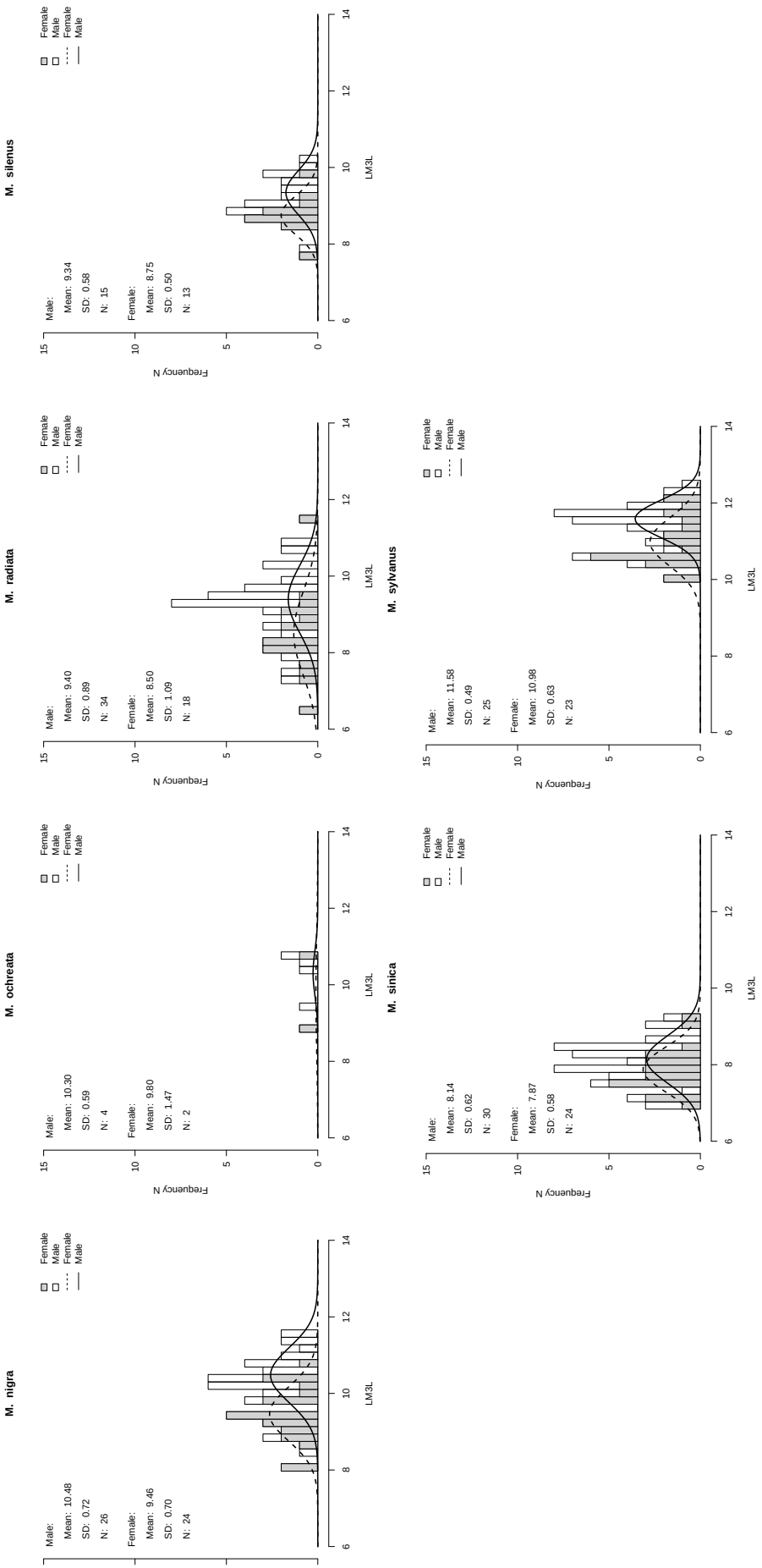
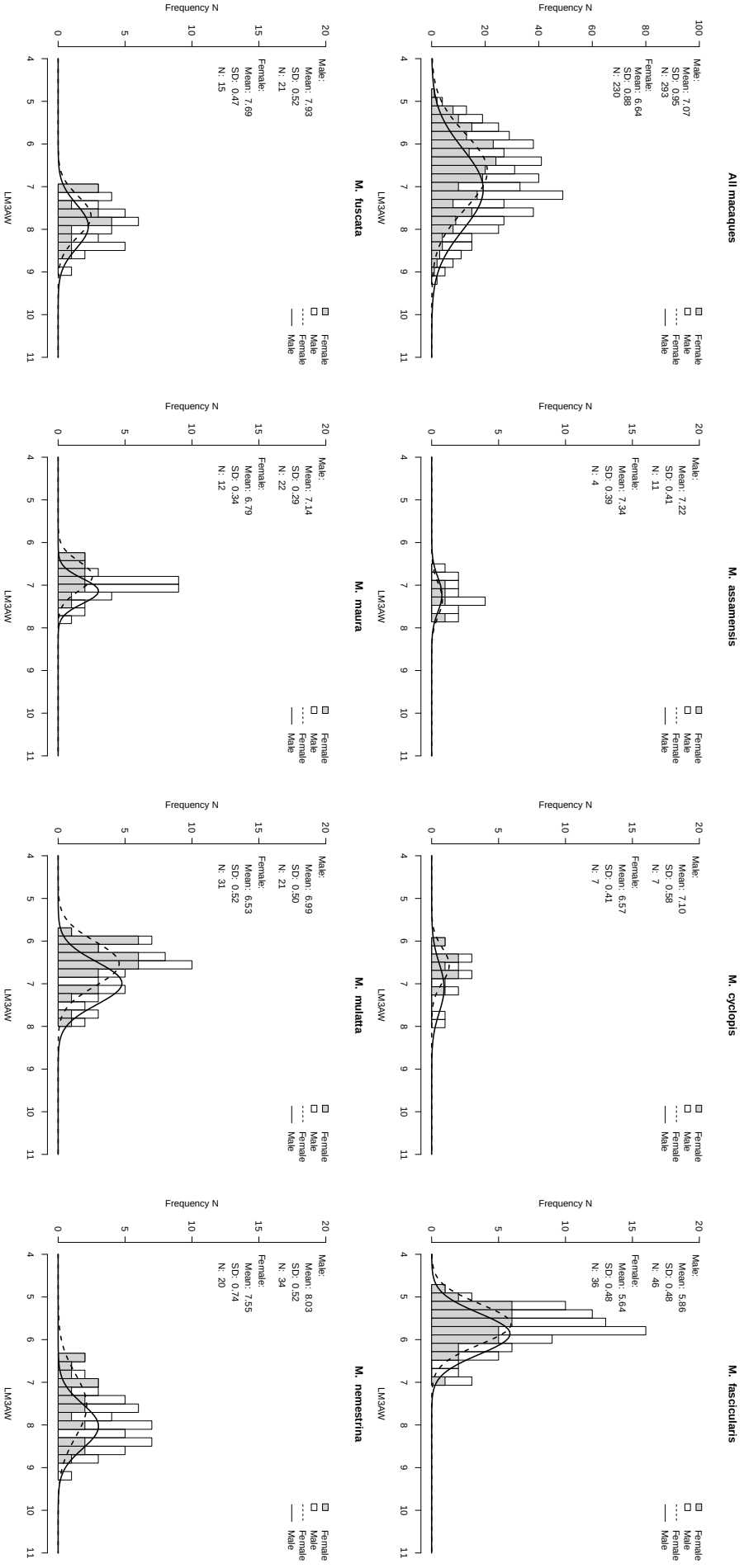

M. nigra
Male:
Mean: 10.48
SD: 0.72
N: 26
Female:
Mean: 9.46
SD: 0.70
N: 24
M. ochreata
Male:
Mean: 10.30
SD: 0.59
N: 4
Female:
Mean: 9.80
SD: 1.47
N: 2
M. radiata
Male:
Mean: 9.40
SD: 0.89
N: 34
Female:
Mean: 8.50
SD: 1.09
N: 18
M. silenus
Male:
Mean: 9.34
SD: 0.58
N: 15
Female:
Mean: 8.75
SD: 0.50
N: 13
M. sinica
Male:
Mean: 8.14
SD: 0.62
N: 30
Female:
Mean: 7.87
SD: 0.58
N: 24
M. sylvanus
Male:
Mean: 11.58
SD: 0.49
N: 25
Female:
Mean: 10.98
SD: 0.63
N: 23
Female
Male
Female
Male
Frequency N
LM3L

Fig. C.37 LM3L


All macaques
Male:
Mean: 7.07
SD: 0.95
N: 293
Female:
Mean: 6.64
SD: 0.88
N: 230
M. assamensis
Male:
Mean: 7.22
SD: 0.41
N: 11
Female:
Mean: 7.34
SD: 0.39
N: 4
M. cyclopis
Male:
Mean: 7.10
SD: 0.58
N: 7
Female:
Mean: 6.57
SD: 0.41
N: 7
M. fascicularis
Male:
Mean: 5.86
SD: 0.48
N: 46
Female:
Mean: 5.64
SD: 0.48
N: 36
M. fuscata
Male:
Mean: 7.93
SD: 0.52
N: 21
Female:
Mean: 7.69
SD: 0.47
N: 15
M. maura
Male:
Mean: 7.14
SD: 0.29
N: 22
Female:
Mean: 6.79
SD: 0.34
N: 12
M. mulatta
Male:
Mean: 6.99
SD: 0.50
N: 21
Female:
Mean: 6.53
SD: 0.52
N: 31
M. nemestrina
Male:
Mean: 8.03
SD: 0.52
N: 34
Female:
Mean: 7.55
SD: 0.74
N: 20
Frequency N
LM3AW
Female
Male
Female
Male

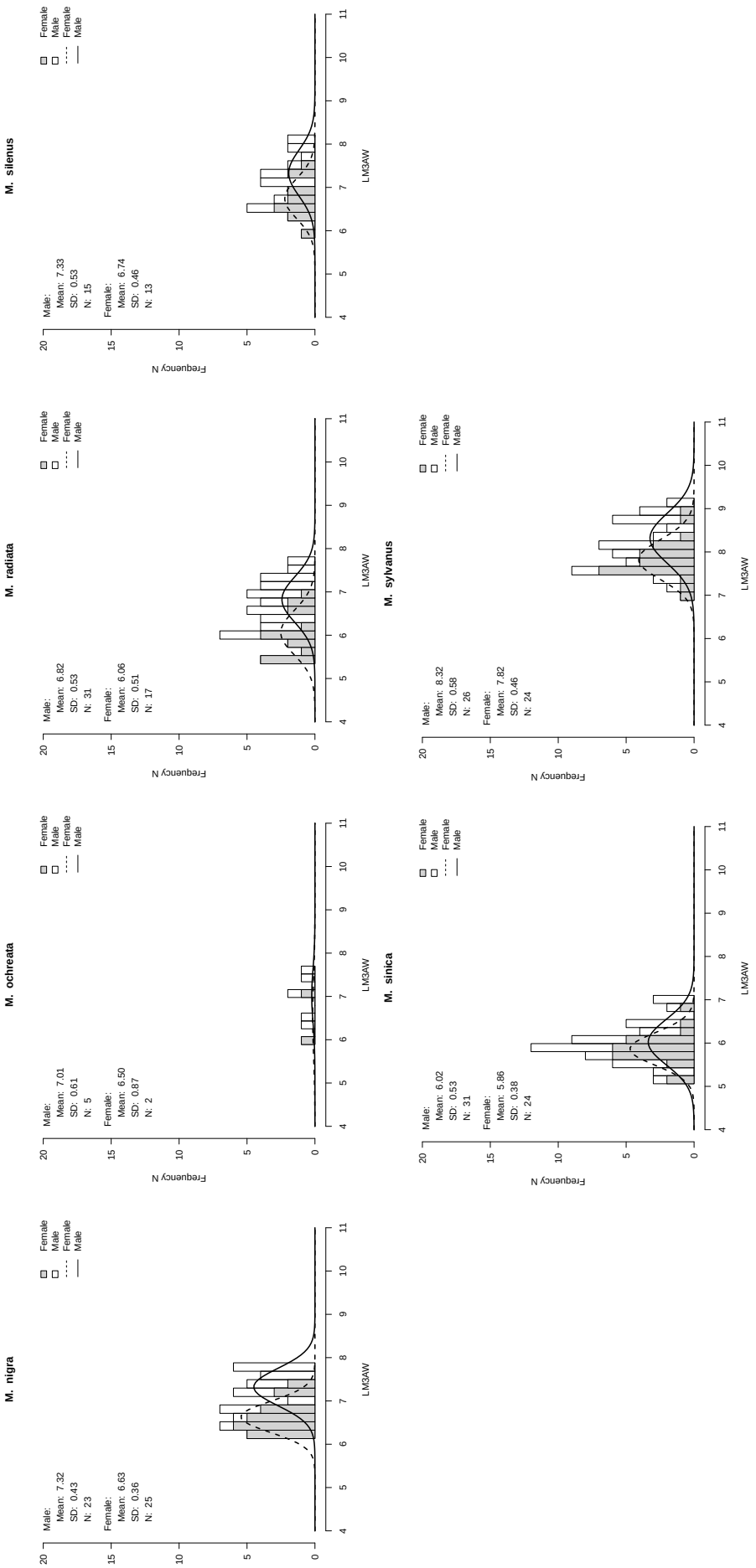


Fig. C.38 LM3AW

All macaques
Male:
Mean: 6.29
SD: 0.83
N: 292
Female:
Mean: 5.91
SD: 0.76
N: 227
M. assamensis
Male:
Mean: 6.60
SD: 0.35
N: 11
Female:
Mean: 6.59
SD: 0.24
N: 4
M. cyclopis
Male:
Mean: 6.27
SD: 0.54
N: 7
Female:
Mean: 5.89
SD: 0.35
N: 7
M. fascicularis
Male:
Mean: 5.21
SD: 0.43
N: 46
Female:
Mean: 5.05
SD: 0.42
N: 34
M. fuscata
Male:
Mean: 7.06
SD: 0.55
N: 21
Female:
Mean: 6.87
SD: 0.44
N: 14
M. maura
Male:
Mean: 6.49
SD: 0.33
N: 23
Female:
Mean: 6.09
SD: 0.39
N: 12
M. mulatta
Male:
Mean: 6.43
SD: 0.58
N: 21
Female:
Mean: 5.98
SD: 0.58
N: 32
M. nemestrina
Male:
Mean: 7.11
SD: 0.46
N: 34
Female:
Mean: 6.79
SD: 0.58
N: 19
Frequency N
LM3PW
Female
Male
Female
Male

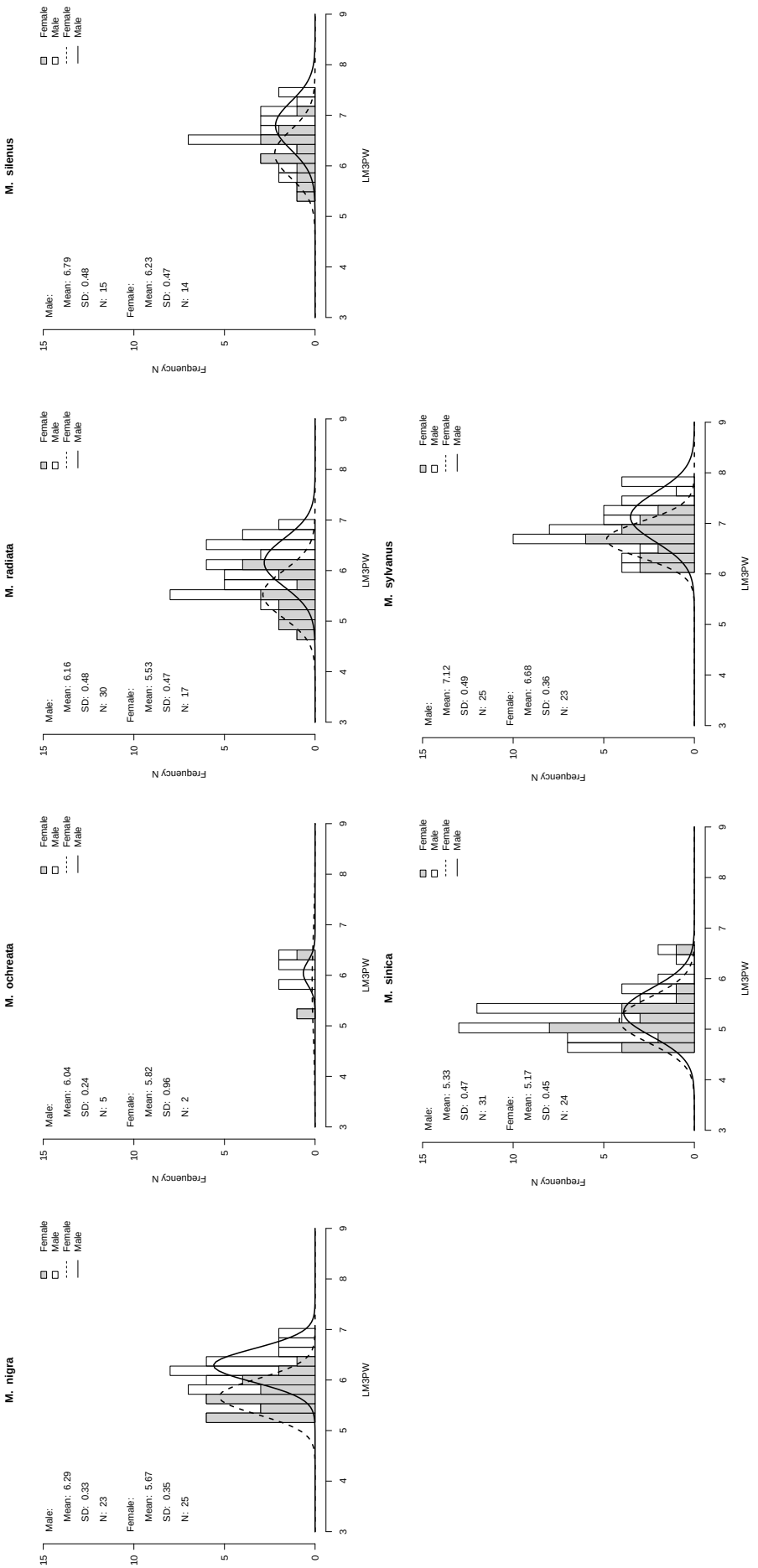


Fig. C.39 LM3PW

Appendix D

Variability: Supporting Information

Table D.1 PCA results of 59 craniodental variables within and between species. Tooth heights were excluded from the analysis (except those of the C/P_3 complex).

Variables					
	Within-species			Between-species	
PC	Eigenvalue	% variance		Eigenvalue	% variance
1	0.138	70.66		0.092	76.32
2	0.018	9.15		0.022	17.80
3	0.006	3.30		0.003	2.59
4	0.004	2.06		0.001	0.89
5	0.003	1.33		0.001	0.71
6	0.002	1.14		0.001	0.47
7	0.002	0.99		0.000	0.35
8	0.002	0.85		0.000	0.29
9	0.002	0.78		0.000	0.26
10	0.001	0.70		0.000	0.16
...	...	...	...	...	...
Total	0.195	100		0.121	100

'...' indicates that additional PCs were extracted, but because they explain negligible amounts of variance they are not displayed here.

	I1MD	I1LL	I2MD	I2LL	CMD	CBL	P3L	P3W	P4L	P4W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW
I1MD	1	0.622	0.452	0.656	0.691	0.597	0.663	0.543	0.713	0.564	0.544	0.570	0.471	0.560	0.574	0.540	0.574	0.580	0.553
I1LL		1	0.489	0.795	0.557	0.563	0.602	0.657	0.643	0.650	0.500	0.624	0.552	0.532	0.611	0.596	0.536	0.577	0.606
I2MD			1	0.622	0.356	0.407	0.605	0.586	0.603	0.597	0.544	0.626	0.519	0.504	0.598	0.537	0.490	0.586	0.517
I2LL				1	0.642	0.620	0.746	0.796	0.748	0.778	0.667	0.773	0.671	0.688	0.773	0.733	0.667	0.764	0.710
CMD					1	0.684	0.682	0.602	0.686	0.562	0.570	0.596	0.492	0.568	0.573	0.539	0.603	0.626	0.586
CBL						1	0.560	0.540	0.627	0.548	0.487	0.507	0.464	0.532	0.542	0.513	0.579	0.581	0.556
P3L							1	0.821	0.895	0.803	0.799	0.800	0.692	0.820	0.814	0.776	0.771	0.813	0.736
P3W								1	0.802	0.926	0.789	0.885	0.783	0.823	0.894	0.873	0.789	0.887	0.831
P4L									1	0.825	0.816	0.792	0.701	0.852	0.834	0.798	0.806	0.820	0.758
P4W										1	0.807	0.880	0.778	0.838	0.926	0.894	0.793	0.903	0.831
M1L											1	0.864	0.806	0.905	0.831	0.801	0.840	0.843	0.759
M1AW												1	0.850	0.852	0.937	0.887	0.808	0.912	0.824
M1PW													1	0.772	0.817	0.830	0.706	0.805	0.770
M2L														1	0.908	0.892	0.891	0.895	0.825
M2AW															1	0.947	0.845	0.959	0.876
M2PW																1	0.826	0.922	0.906
M3L																	1	0.899	0.859
M3AW																		1	0.930
M3PW																			1

N = 172

- 0.8 ≤ Pearson's r ≤ 1 (very strong)
- 0.6 ≤ Pearson's r < 0.8 (strong)
- 0.4 ≤ Pearson's r < 0.6 (moderate)
- 0.2 ≤ Pearson's r < 0.4 (moderate to weak)
- 0 < Pearson's r < 0.2 (weak to negligible)

(a) The male maxilla.

	I1MD	I1LL	I2MD	I2LL	CMD	CBL	P3L	P3W	P4L	P4W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW
I1MD	1	0.707	0.442	0.570	0.689	0.385	0.629	0.454	0.552	0.438	0.420	0.400	0.329	0.438	0.432	0.429	0.416	0.408	0.460
I1LL		1	0.572	0.730	0.594	0.413	0.619	0.569	0.581	0.573	0.444	0.512	0.477	0.492	0.540	0.542	0.473	0.504	0.559
I2MD			1	0.723	0.574	0.348	0.641	0.614	0.552	0.593	0.542	0.592	0.576	0.562	0.620	0.588	0.565	0.578	0.571
I2LL				1	0.646	0.548	0.736	0.752	0.666	0.742	0.675	0.706	0.710	0.697	0.750	0.726	0.691	0.738	0.719
CMD					1	0.583	0.805	0.626	0.751	0.597	0.621	0.609	0.541	0.645	0.621	0.613	0.641	0.594	0.598
CBL						1	0.466	0.475	0.500	0.498	0.508	0.519	0.522	0.527	0.523	0.528	0.551	0.542	0.523
P3L							1	0.824	0.875	0.805	0.768	0.776	0.714	0.793	0.794	0.785	0.769	0.762	0.758
P3W								1	0.786	0.897	0.773	0.824	0.806	0.812	0.854	0.842	0.804	0.838	0.826
P4L									1	0.847	0.819	0.810	0.735	0.862	0.835	0.806	0.817	0.807	0.773
P4W										1	0.814	0.864	0.830	0.868	0.914	0.885	0.840	0.894	0.860
M1L											1	0.881	0.851	0.930	0.868	0.841	0.876	0.868	0.787
M1AW												1	0.942	0.884	0.942	0.901	0.874	0.913	0.841
M1PW													1	0.839	0.906	0.915	0.824	0.879	0.839
M2L														1	0.920	0.889	0.914	0.903	0.839
M2AW															1	0.951	0.889	0.958	0.896
M2PW																1	0.848	0.919	0.908
M3L																	1	0.921	0.878
M3AW																		1	0.928
M3PW																			1

N = 171

- 0.8 ≤ Pearson's r ≤ 1 (very strong)
- 0.6 ≤ Pearson's r < 0.8 (strong)
- 0.4 ≤ Pearson's r < 0.6 (moderate)
- 0.2 ≤ Pearson's *r* < 0.4 (moderate to weak)
- 0 < Pearson's r < 0.2 (weak to negligible)

(b) The female maxilla.

Fig. D.1 Correlation matrix of tooth lengths and widths in the maxilla.

	I1MD	I1LL	I2MD	I2LL	CMD	CBL	P3OL	P3TL	P3W	P4L	P4W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW
I1MD	1	0.630	0.669	0.601	0.627	0.530	0.561	0.528	0.533	0.555	0.451	0.484	0.424	0.406	0.340	0.390	0.363	0.328	0.423	0.368
	I1LL	1	0.459	0.786	0.646	0.686	0.636	0.660	0.645	0.627	0.539	0.481	0.520	0.531	0.421	0.505	0.478	0.454	0.492	0.447
		I2MD	1	0.538	0.601	0.534	0.568	0.556	0.587	0.625	0.570	0.588	0.548	0.575	0.503	0.509	0.544	0.473	0.576	0.569
			I2LL	1	0.568	0.572	0.565	0.552	0.551	0.549	0.482	0.521	0.534	0.569	0.534	0.558	0.566	0.544	0.574	0.527
				CMD	1	0.870	0.849	0.819	0.804	0.800	0.721	0.622	0.626	0.674	0.580	0.649	0.644	0.581	0.704	0.650
					CBL	1	0.809	0.859	0.754	0.750	0.674	0.576	0.595	0.645	0.531	0.612	0.611	0.567	0.666	0.642
						P3OL	1	0.902	0.798	0.850	0.657	0.622	0.576	0.610	0.552	0.586	0.547	0.542	0.610	0.522
							P3TL	1	0.790	0.794	0.656	0.569	0.576	0.622	0.506	0.590	0.558	0.544	0.618	0.552
								P3W	1	0.852	0.873	0.739	0.786	0.786	0.740	0.798	0.772	0.727	0.798	0.721
									P4L	1	0.815	0.736	0.730	0.741	0.754	0.765	0.757	0.742	0.774	0.725
										P4W	1	0.746	0.845	0.822	0.806	0.879	0.864	0.768	0.855	0.821
N = 192											**M1L**	1	0.858	0.854	0.883	0.815	0.805	0.840	0.814	0.773
												M1AW	1	0.937	0.849	0.919	0.894	0.839	0.886	0.832
													M1PW	1	0.813	0.853	0.896	0.831	0.840	0.836
														M2L	1	0.899	0.867	0.888	0.875	0.821
															M2AW	1	0.928	0.852	0.929	0.850
																M2PW	1	0.862	0.907	0.925
																	M3L	1	0.870	0.837
																		M3AW	1	0.928
																			M3PW	1

0.8 ≤ Pearson's r ≤ 1 (very strong)
0.6 ≤ Pearson's r < 0.8 (strong)
0.4 ≤ Pearson's r < 0.6 (moderate)
0.2 ≤ Pearson's r < 0.4 (moderate to weak)
0 < Pearson's r < 0.2 (weak to negligible)

(a) The male mandible.

	I1MD	I1LL	I2MD	I2LL	CMD	CBL	P3OL	P3TL	P3W	P4L	P4W	M1L	M1AW	M1PW	M2L	M2AW	M2PW	M3L	M3AW	M3PW
I1MD	1	0.638	0.764	0.688	0.679	0.516	0.640	0.485	0.426	0.610	0.522	0.429	0.390	0.379	0.390	0.423	0.452	0.377	0.436	0.425
I1LL		1	0.480	0.812	0.611	0.630	0.643	0.560	0.468	0.636	0.507	0.395	0.405	0.398	0.409	0.483	0.503	0.454	0.483	0.444
I2MD			1	0.631	0.629	0.449	0.683	0.480	0.517	0.656	0.579	0.539	0.476	0.446	0.515	0.500	0.552	0.478	0.542	0.553
I2LL				1	0.757	0.747	0.796	0.702	0.630	0.766	0.686	0.581	0.594	0.578	0.578	0.647	0.670	0.583	0.659	0.627
CMD					1	0.681	0.731	0.701	0.530	0.694	0.616	0.464	0.470	0.452	0.423	0.525	0.532	0.481	0.550	0.528
CBL						1	0.676	0.688	0.556	0.682	0.577	0.548	0.499	0.508	0.539	0.551	0.564	0.531	0.558	0.524
P3OL							1	0.694	0.671	0.850	0.758	0.659	0.669	0.679	0.650	0.674	0.726	0.705	0.724	0.714
P3TL								1	0.650	0.735	0.631	0.558	0.556	0.548	0.531	0.587	0.584	0.544	0.567	0.525
P3W									1	0.801	0.848	0.779	0.819	0.783	0.764	0.809	0.805	0.769	0.793	0.753
P4L										1	0.872	0.771	0.768	0.752	0.792	0.792	0.809	0.794	0.795	0.757
P4W											1	0.824	0.875	0.851	0.844	0.893	0.885	0.836	0.889	0.843
M1L												1	0.881	0.874	0.925	0.867	0.844	0.860	0.855	0.813
M1AW													1	0.949	0.870	0.911	0.888	0.867	0.888	0.837
M1PW														1	0.861	0.886	0.905	0.855	0.866	0.857
M2L															1	0.906	0.878	0.890	0.875	0.827
M2AW																1	0.942	0.883	0.940	0.859
M2PW																	1	0.874	0.913	0.913
M3L																		1	0.913	0.884
M3AW																			1	0.927
M3PW																				1

N = 158

- 0.8 ≤ Pearson's r ≤ 1 (very strong)
- 0.6 ≤ Pearson's r < 0.8 (strong)
- 0.4 ≤ Pearson's r < 0.6 (moderate)
- 0.2 ≤ Pearson's r < 0.4 (moderate to weak)
- 0 < Pearson's r < 0.2 (weak to negligible)

(b) The female mandible.

Fig. D.2 Correlation matrix of tooth lengths and widths in the mandible.

Table D.2 A comparison of the magnitude of dental correlations of each dental variable to the remaining variables in the maxilla of males and females (across species), by tooth measurement, tooth, and tooth class.

	Sex					
	Males			Females		
	Measurement	Tooth	Class	Measurement	Tooth	Class
I1MD	0.343	0.351	0.377	0.239	0.274	0.341
I1LL	0.359			0.309		
I2MD	0.292	0.403		0.330	0.409	
I2LL	0.513			0.487		
CMD	0.354	0.330	0.330	0.401	0.326	0.326
CBL	0.307			0.251		
P3L	0.562	0.583	**0.592**	0.556	0.563	0.574
P3W	0.605			0.569		
P4L	0.587	0.600		0.565	0.586	
P4W	0.613			0.606		
M1L	0.554	0.557	0.590	0.570	0.584	**0.606**
M1AW	0.620			0.614		
M1PW	0.498			0.570		
M2L	0.597	**0.618**		0.614	**0.629**	
M2AW	0.647			**0.650**		
M2PW	0.611			0.622		
M3L	0.561	0.594		0.594	0.604	
M3AW	**0.650**			0.629		
M3PW	0.573			0.588		

Values are averages of r squared (r^2) representing correlational magnitudes (Marroig and Cheverud, 2001). Derived from correlation coefficients in Figure D.1. Values in bold represent the strongest correlations.

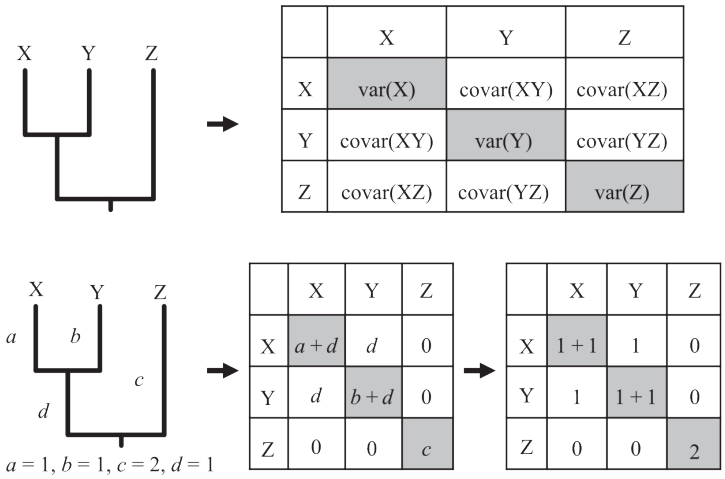
Table D.3 A comparison of the magnitude of dental correlations of each dental variable to the remaining variables in the mandible of males and females (across species), by tooth measurement, tooth, and tooth class.

	Sex					
	Males			Females		
	Measurement	Tooth	Class	Measurement	Tooth	Class
I1MD	0.246	0.286		0.273	0.284	
I1LL	0.326		0.301	0.296		0.334
I2MD	0.313	0.317		0.311	0.383	
I2LL	0.320			0.455		
CMD	0.480	0.461	0.461	0.349	0.346	0.346
CBL	0.443			0.343		
P3OL	0.438			0.496		
P3TL	0.430	0.475		0.361	0.451	
P3W	0.556		0.511	0.497		0.516
P4L	0.545	**0.547**		0.574	**0.581**	
P4W	0.549			0.587		
M1L	0.509			0.532		
M1AW	0.551	0.537		0.550	0.539	
M1PW	0.551			0.536		
M2L	0.512			0.537		
M2AW	0.562	0.543	**0.538**	0.580	0.568	**0.554**
M2PW	0.557			**0.588**		
M3L	0.503			0.543		
M3AW	**0.577**	0.533		0.585	0.556	
M3PW	0.519			0.540		

Values are averages of r squared representing correlational magnitudes (Marroig and Cheverud, 2001). Derived from correlation coefficients in Figure D.2. Values in bold represent the strongest correlations.

Appendix E

Size and Allometry: Supporting Information



	X	Y	Z
X	var(X)	covar(XY)	covar(XZ)
Y	covar(XY)	var(Y)	covar(YZ)
Z	covar(XZ)	covar(YZ)	var(Z)

	X	Y	Z
X	$a+d$	d	0
Y	d	$b+d$	0
Z	0	0	c

	X	Y	Z
X	$1+1$	1	0
Y	1	$1+1$	0
Z	0	0	2

Fig. E.1 An illustration from Kamilar and Cooper (2013) explaining how a phylogeny can be transformed into a phylogenetic variance-covariance (V-CV) matrix. Covariances represent the amount of shared evolutionary history denoted by the internal branch lengths connecting any pair of taxa since the last common ancestor (the root). There will necessarily be a covariance of 0 for at least one pair of taxa (here 'Z' with either 'X' or 'Y'), namely any pair that goes back to the deepest split, i.e., immediately following the last common ancestor. Variances in a phylogenetic V-CV matrix are denoted by the branch length from the last common ancestor to all (the root) to each tip (terminal taxa). In an ultrametric tree of extant species the variances of all taxa are identical.

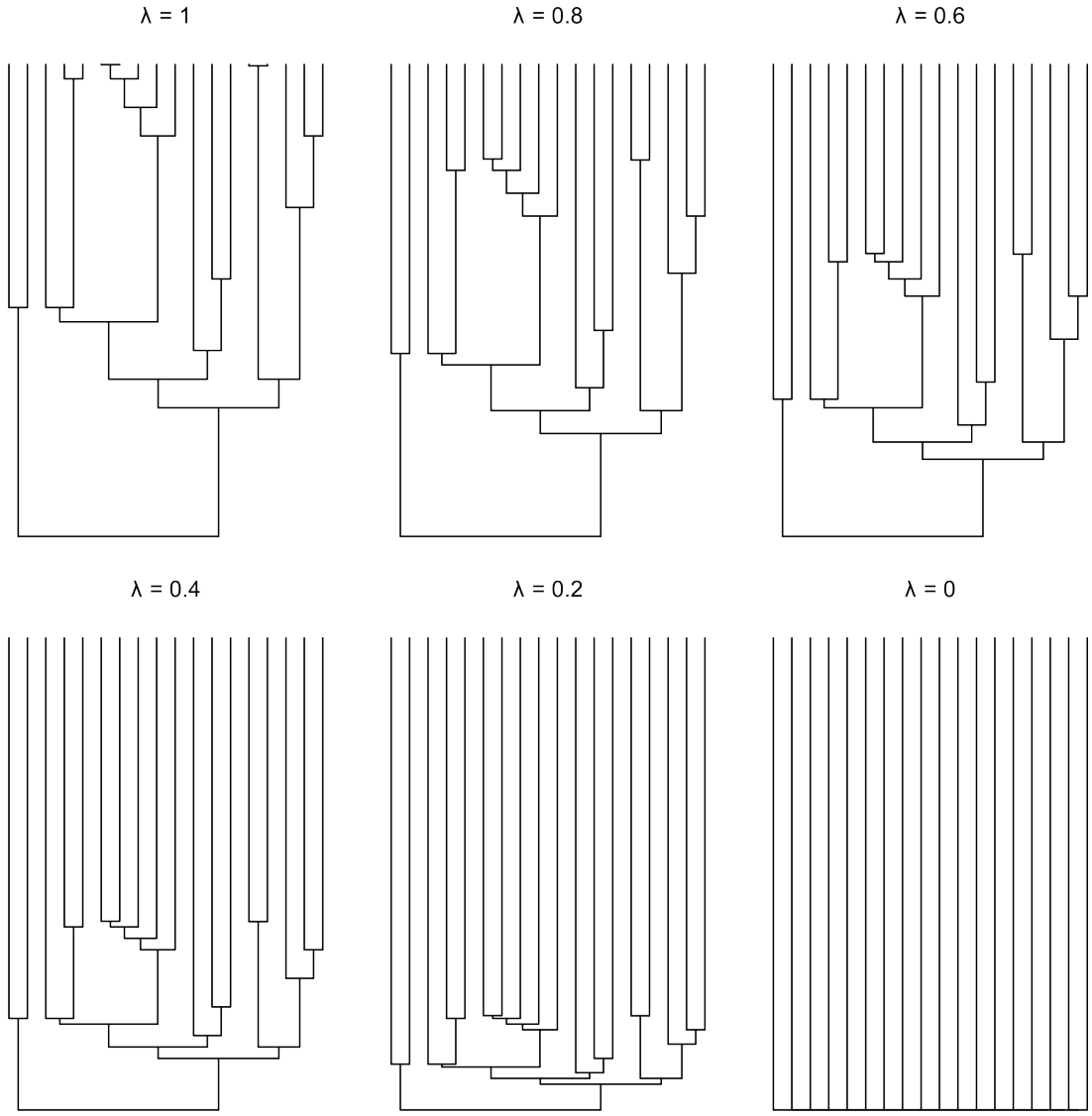


Fig. E.2 An illustration of how phylogenies are transformed depending on the magnitude of Pagel's λ from Symonds and Blomberg (2014b). In a phylogenetic generalised least squares (PGLS) regression, λ is first assessed by comparing the variance-covariance (V-CV) matrix based on the data against the phylogenetic V-CV matrix constructed from an independent phylogeny. Depending on the strength of congruence, a value between high ($\lambda = 1$) and low phylogenetic signal ($\lambda = 0$) is obtained. Subsequently, the V-CV matrix used in the error term of the regression is scaled to this value of λ. This figure illustrates how different values of Pagel's λ transform the branch lengths. It is the internal branches that reflect non-independent evolutionary history, and thus $\lambda = 0$ creates a star phylogeny where all species have had independent evolutionary trajectories since the split from the last common ancestor. $\lambda = 1$ keeps the phylogeny intact. Any intermediate value results in a down-scaling of the internal branches, reducing the amount of shared evolutionary history between taxa that is consequently corrected for.

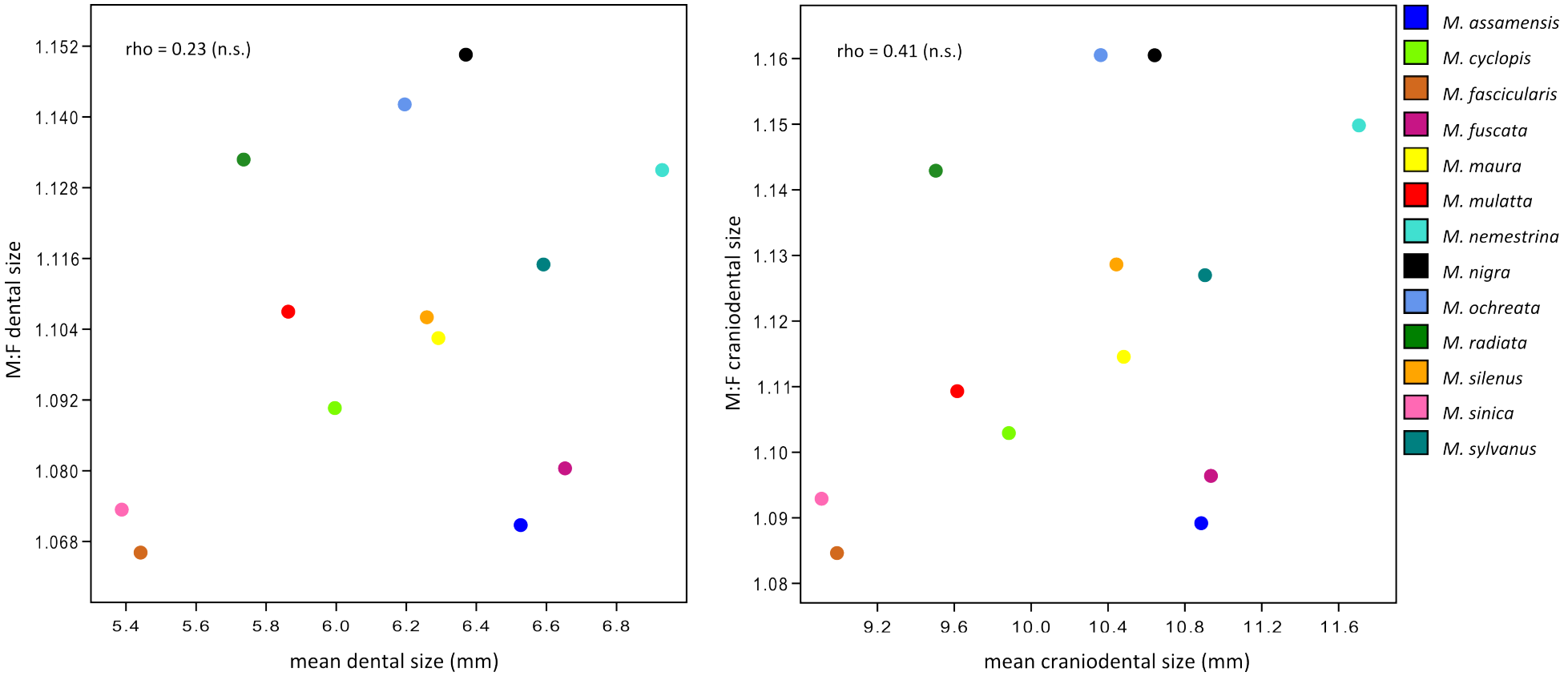


Fig. E.3 Scatterplots of sexual size dimorphism (SSD), measured as M:F ratios, in dental and craniodental size with overall size. Dental and craniodental size are represented by their geometric means (see Section 5.2). No relationship between SSD and size is discernable, and Spearman's rank correlations are nog significant (dental: $\rho = 0.23$, $p = 0.459$; craniodental: $\rho = 0.41$, $p = 0.162$).

Table E.1 Phenotypic correlations of 56 craniodental measurements to allometric size (PC 1)[a], within and between species. Correlations in *italics* indicate a lower correlation for tooth length than for the breadth(s) of the same tooth. Correlations in **boldface** indicate a higher correlation for tooth length than for the breadth(s) of the same tooth.

Measurement[b]	Within species	Between species
Uecm-ecm	0.409	0.769
PALWID	0.350	0.711
UIAW	0.412	0.726
UBCB	0.397	0.689
UpcRow	0.408	0.748
pr-alv	0.412	0.777
ba-pr	0.414	0.776
CALV	0.358	0.736
MUZL	0.329	0.747
Lecm-ecm	0.411	0.755
LIAW	0.374	0.591
LBCB	0.389	0.653
LpcRow	0.430	0.787
CONM1	0.376	0.788
mand height	0.349	0.726
mand breadth	0.427	0.654
go-go	0.317	0.672
UI1MD	*0.377*	*0.551*
UI1LL	0.469	0.557
UI2MD	*0.275*	*0.580*
UI2LL	0.469	0.615
UCMD	*0.410*	**0.622**
UCBL	0.457	0.546
UP3L	*0.368*	**0.695**
UP3W	0.421	0.656
UP4L	*0.396*	**0.750**
UP4W	0.435	0.663

Continued on next page

– continued

Measurement[b]	Within species	Between species
UM1L	*0.363*	0.660
UM1AW	0.409	0.689
UM1PW	0.436	0.612
UM2L	*0.405*	**0.691**
UM2AW	0.439	0.672
UM2PW	0.473	0.636
UM3L	*0.379*	**0.710**
UM3AW	0.452	0.656
UM3PW	0.457	0.630
LI1MD	*0.373*	*0.481*
LI1LL	0.418	0.528
LI2MD	*0.321*	*0.517*
LI2LL	0.423	0.683
LCMD	*0.426*	**0.680**
LCBL	0.451	0.653
LP3OL	*0.368*	*0.681*
LP3TL	*0.389*	*0.647*
LP3W	0.374	0.753
LP4L	*0.386*	**0.767**
LP4W	0.445	0.729
LM1L	*0.358*	**0.693**
LM1AW	0.417	0.677
LM1PW	0.428	0.658
LM2L	*0.390*	0.681
LM2AW	0.465	0.667
LM2PW	0.458	0.688
LM3L	*0.402*	0.687
LM3AW	0.459	0.695
LM3PW	0.447	0.676

[a] Derived in a PCA on the variance-covariance matrices of log-transformed data.

[b] Variable abbreviations are explained in Tables B.13 and B.14 in Appendix B.

Appendix F

Ecogeography: Supporting Information

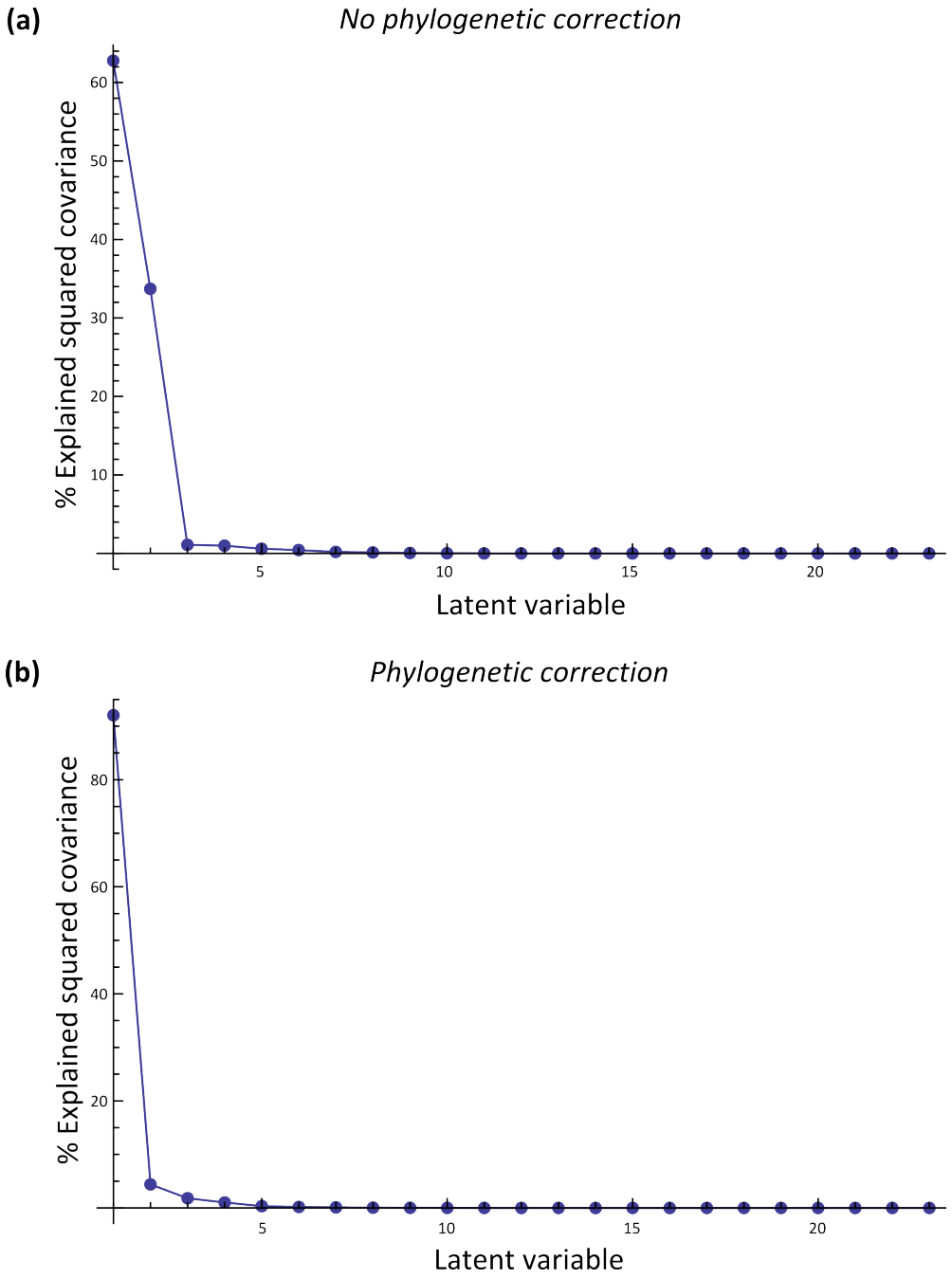


Fig. F.1 Scree plots of a) 2B-PLS without phylogenetic correction, and b) phylogenetic 2B-PLS. Latent variable 2 is diminished after accounting for phylogeny.

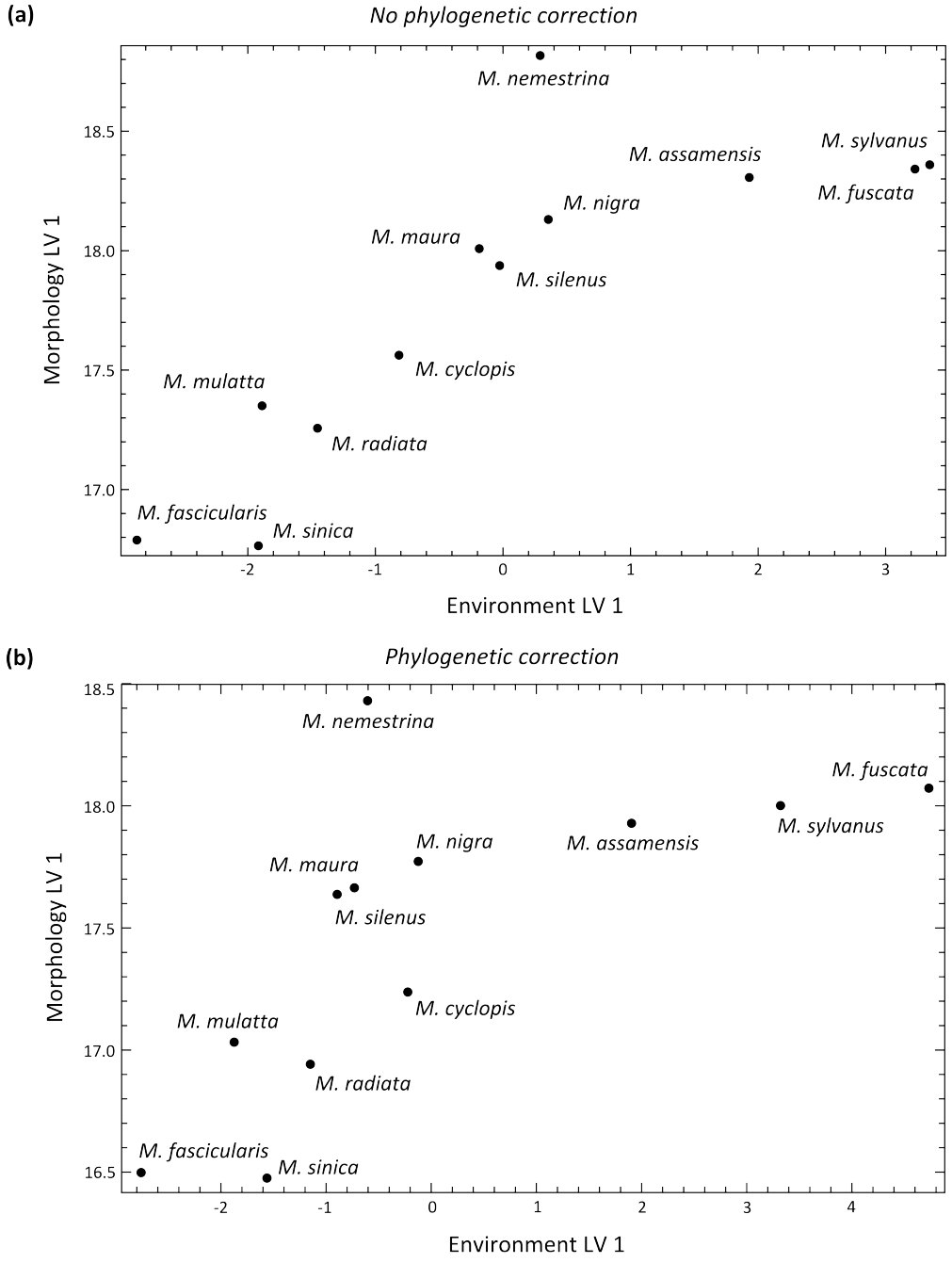


Fig. F.2 Scatter plots of partial least squares (PLS) scores on latent variable (LV) 1 for a) 2B-PLS without accounting for phylogeny, and b) phylogenetic 2B-PLS. In both cases, the covariance pattern between blocks shows a gradient in overall size: PLS scores vary from small-bodied species (e.g., *M. sinica* and *M. fascicularis*) to larger-bodied species (e.g., *M. sylvanus* and *M. fuscata*). See Table B.1 (in Appendix B) for species' body masses.

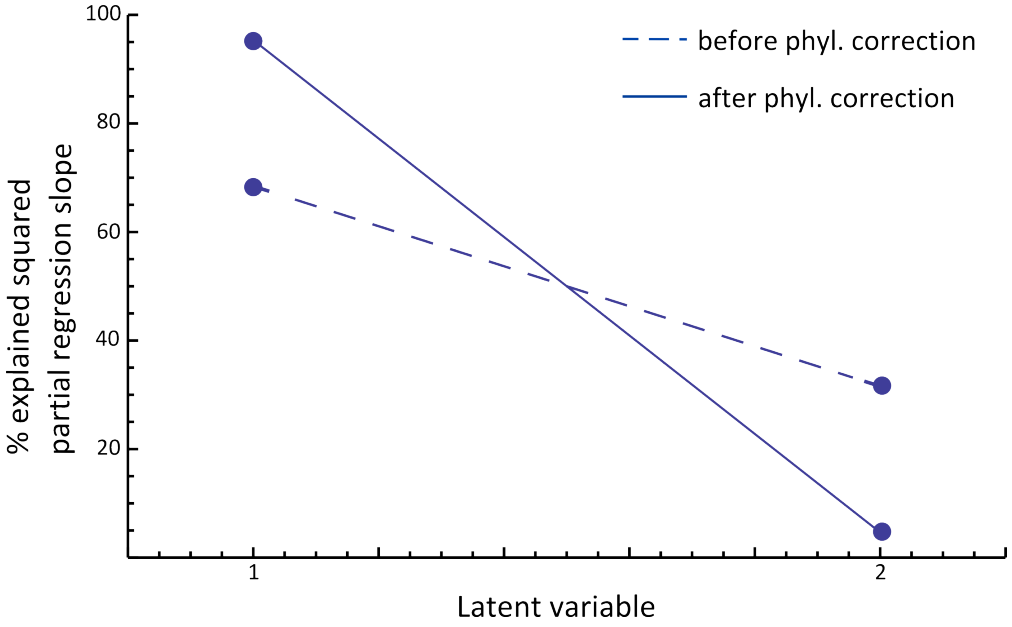


Fig. F.3 Scree plot of the reduced rank regression before and after phylogenetic correction. Prior to phylogenetic correction, the reduced rank regression extracted two distinct latent variables (i.e., spatial gradients) that successively explain the maximum amount of phenotypic variation between macaques. Following phylogenetic correction, the first latent variable (LV 1) alone can explain nearly 100% of the phenotypic variation between macaques that is spatially structured.

Appendix G

Phylogeny: Supporting Information

Table G.1 Blomberg's K, raw p-values, and adjusted p-values for the absolute size of all dental dimensions across all macaques (N = 13). Dimensions in boldface have K-values significantly higher than 0 based on both the raw and adjusted p-values. Dimensions in italics have K-values significantly higher than 0 based on the raw p-values only.[a]

Tooth dimension	K-statistic	raw p-value[b]	adjusted p-value
LCMD	**1.076**	**0.001**	**0.040**
LP3OL	**1.123**	**0.002**	**0.040**
UI1MD	*1.210*	*0.005*	*0.067*
LI1MD	1.034	0.013	0.104
LP3TL	1.054	0.013	0.104
LI2LL	0.928	0.029	0.193
LP4L	0.927	0.042	0.240
LI2MD	0.837	0.051	0.255
UCBL	0.826	0.07	0.287
LCBL	0.840	0.073	0.287
UCMD	0.800	0.079	0.287
LP3W	0.859	0.09	0.300
LI1LL	0.743	0.125	0.385
UI1LL	0.693	0.183	0.503
UP4L	0.738	0.189	0.503
LM3AW	0.793	0.201	0.503
LP4W	0.669	0.265	0.553
UP3L	0.655	0.271	0.553

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Table G.1 – *continued*

Tooth dimension	K-statistic	raw p-value[b]	adjusted p-value
UP4W	0.714	0.273	0.553
UP3W	0.673	0.307	0.553
LM1AW	0.709	0.313	0.553
LM1PW	0.667	0.313	0.553
LM2AW	0.723	0.321	0.553
LM3L	0.673	0.356	0.553
CALV	0.635	0.367	0.553
LM3PW	0.652	0.371	0.553
LM2L	0.710	0.379	0.553
LM1L	0.638	0.413	0.553
UM2L	0.670	0.423	0.553
UM1L	0.634	0.425	0.553
UI2LL	0.555	0.442	0.553
UM3PW	0.645	0.455	0.553
LM2PW	0.591	0.457	0.553
UM3AW	0.634	0.474	0.553
UM2PW	0.590	0.484	0.553
UM2AW	0.617	0.504	0.560
UM1PW	0.556	0.535	0.571
UM3L	0.605	0.542	0.571
UM1AW	0.544	0.57	0.585
UI2MD	0.460	0.676	0.676

[a] Statistical significance based on $\alpha = 0.05$. [b] One-tailed.

Table G.2 Blomberg's K, raw p-values, and adjusted p-values for the absolute size of all dental dimensions in the *silenus* lineage ($N = 5$). Only when the raw p-values are considered do some dimensions have K-values significantly higher than 0. [a]

Tooth dimension	K-statistic	raw p-value[b]	adjusted p-value
LI1MD	*1.527*	*0.006*	*0.126*
UP3W	*1.253*	*0.010*	*0.126*
LI2LL	*1.277*	*0.013*	*0.126*
UM2PW	*1.252*	*0.018*	*0.126*
UI1MD	*1.461*	*0.019*	*0.126*
UI2MD	*1.397*	*0.022*	*0.126*
UI2LL	*1.200*	*0.022*	*0.126*
UI1LL	*1.306*	*0.036*	*0.180*
UM3PW	*1.283*	*0.045*	*0.197*
LI2MD	1.520	0.050	0.197
LM2PW	1.154	0.058	0.197
LM3AW	1.111	0.059	0.197
LM3PW	1.225	0.074	0.217
UP4W	1.115	0.076	0.217
UP3L	1.094	0.084	0.224
LP3OL	1.085	0.093	0.233
UM2AW	1.000	0.248	0.556
LP4L	0.997	0.257	0.556
UM3AW	0.981	0.264	0.556
LP4W	0.950	0.310	0.590
UP4L	0.941	0.340	0.590
LI1LL	0.958	0.353	0.590
LP3W	0.927	0.354	0.590
LP3TL	0.902	0.354	0.590
LCBL	0.934	0.396	0.632
LM2AW	0.866	0.411	0.632
LCMD	0.906	0.483	0.716

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Table G.2 – *continued*

Tooth dimension	K-statistic	raw p-value[b]	adjusted p-value
CALV	0.844	0.523	0.731
UM1PW	0.864	0.568	0.731
UM2L	0.851	0.587	0.731
UCMD	0.834	0.595	0.731
LM1PW	0.855	0.616	0.731
UM1AW	0.861	0.626	0.731
LM2L	0.848	0.626	0.731
UM3L	0.844	0.640	0.731
UM1L	0.834	0.690	0.740
LM1AW	0.838	0.693	0.740
LM1L	0.837	0.703	0.740
LM3L	0.835	0.732	0.749
UCBL	0.793	0.749	0.749

[a] Statistical significance based on $\alpha = 0.05$. [b] One-tailed.

Table G.3 Blomberg's K, raw p-values, and adjusted p-values for the absolute size of all dental dimensions in the *sinica-fascicularis* lineage ($N = 7$). No dimensions have K-values significantly higher than 0 based on either the raw or the adjusted p-values.[a]

Tooth dimension	K-statistic	raw p-value[b]	adjusted p-value
LCBL	1.051	0.081	0.436
LP3TL	1.031	0.100	0.436
LM1PW	0.828	0.188	0.436
LCMD	0.887	0.192	0.436
UCBL	0.872	0.195	0.436
LM3L	0.787	0.198	0.436
UP3W	0.813	0.204	0.436
CALV	0.806	0.207	0.436
LP3W	0.752	0.209	0.436
UCMD	0.890	0.217	0.436

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Table G.3 – *continued*

Tooth dimension	K-statistic	raw p-value[b]	adjusted p-value
LM1AW	0.812	0.221	0.436
UM1L	0.759	0.224	0.436
LM2AW	0.777	0.239	0.436
UP4W	0.791	0.243	0.436
UP3L	0.719	0.253	0.436
UM2PW	0.784	0.258	0.436
UM1PW	0.786	0.264	0.436
LM2PW	0.774	0.267	0.436
LM1L	0.742	0.271	0.436
LP4L	0.713	0.271	0.436
LM3PW	0.773	0.276	0.436
LM3AW	0.767	0.279	0.436
UM2L	0.746	0.279	0.436
LI2LL	0.849	0.286	0.436
LP3OL	0.767	0.293	0.436
LM2L	0.757	0.299	0.436
UP4L	0.730	0.302	0.436
LP4W	0.707	0.306	0.436
UM1AW	0.723	0.320	0.436
UM3AW	0.731	0.340	0.436
UM2AW	0.756	0.354	0.436
UI1LL	0.672	0.362	0.436
LI1LL	0.689	0.363	0.436
UM3L	0.685	0.371	0.436
UI2LL	0.646	0.409	0.467
UM3PW	0.694	0.426	0.473
LI2MD	0.562	0.602	0.650
UI2MD	0.531	0.669	0.704
UI1MD	0.435	0.915	0.938

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Table G.3 – *continued*

Tooth dimension	*K*-statistic	raw *p*-value[b]	adjusted *p*-value
LI1MD	0.428	0.979	0.979

[a] Statistical significance based on $\alpha = 0.05$. [b] One-tailed.

Table G.4 Blomberg's *K*, raw *p*-values, and adjusted *p*-values for the relative size of all dental dimensions across all macaques ($N = 13$). Dimensions in boldface have *K*-values significantly higher than 0 based on both the raw and adjusted *p*-values. Dimensions in italics have *K*-values significantly higher than 0 based on the raw *p*-values only.[a]

Tooth dimension	*K*-statistic	raw *p*-value[b]	adjusted *p*-value
LCMD	**1.700**	**0.001**	**0.016**
LP3OL	**1.371**	**0.002**	**0.016**
LP3W	**1.362**	**0.003**	**0.020**
LP4L	**1.310**	**0.002**	**0.016**
UCMD	**1.279**	**0.001**	**0.016**
UI1MD	**1.159**	**0.002**	**0.016**
LP3TL	*1.073*	*0.013*	*0.063*
LI2LL	*1.062*	*0.012*	*0.063*
UP4L	*0.944*	*0.025*	*0.081*
LI1MD	*0.920*	*0.025*	*0.081*
LI2MD	*0.900*	*0.019*	*0.074*
LCBL	*0.898*	*0.017*	*0.074*
UP3L	*0.889*	*0.046*	*0.138*
LM3L	0.874	0.067	0.163
LM2L	0.874	0.175	0.310
LM3AW	0.870	0.107	0.228
UCBL	0.838	0.057	0.148
UP3W	0.821	0.050	0.139
UP4W	0.783	0.111	0.228
UI1LL	0.755	0.105	0.228
UM2L	0.723	0.337	0.453
LM3PW	0.719	0.147	0.287

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Table G.4 – *continued*

Tooth dimension	*K*-statistic	raw *p*-value[b]	adjusted *p*-value
UM3PW	0.712	0.164	0.305
LM1AW	0.698	0.194	0.323
LM2AW	0.695	0.302	0.423
UM3AW	0.694	0.236	0.368
UM2PW	0.656	0.278	0.417
UI2LL	0.654	0.371	0.482
LI1LL	0.652	0.199	0.323
UM1L	0.647	0.304	0.423
UM2AW	0.598	0.471	0.557
UM1PW	0.587	0.469	0.557
LM1PW	0.577	0.425	0.535
LM1L	0.556	0.578	0.637
UM3L	0.543	0.614	0.637
LM2PW	0.524	0.597	0.637
LP4W	0.520	0.533	0.611
UM1AW	0.508	0.621	0.637
UI2MD	0.463	0.785	0.785

[a] Statistical significance based on $\alpha = 0.05$. [b] One-tailed.

Table G.5 Blomberg's *K*, raw *p*-values, and adjusted *p*-values for the relative size of all dental dimensions across the *silenus* lineage ($N = 5$). Dimensions in italics have *K*-values significantly higher than 0 based on the raw *p*-values only.[a]

Tooth dimension	*K*-statistic	raw *p*-value[b]	adjusted *p*-value
UI2MD	*1.579*	*0.008*	*0.234*
LI1MD	*1.514*	*0.048*	*0.238*
UI1MD	*1.476*	*0.040*	*0.238*
LI2MD	1.454	0.055	0.238
UI1LL	*1.438*	*0.012*	*0.234*
UM3PW	*1.399*	*0.038*	*0.238*

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Table G.5 – *continued*

Tooth dimension	K-statistic	raw p-value[b]	adjusted p-value
UP3W	1.313	0.100	0.372
UI2LL	*1.298*	*0.034*	*0.238*
LI2LL	1.258	0.105	0.372
LP3OL	*1.230*	*0.031*	*0.238*
UP3L	1.188	0.145	0.400
UP4W	1.174	0.054	0.238
LM3PW	1.106	0.239	0.500
UM2PW	1.093	0.192	0.440
LP4L	1.087	0.182	0.440
LM3AW	1.070	0.154	0.400
LCMD	1.063	0.149	0.400
LCBL	1.015	0.138	0.400
LM2PW	1.012	0.254	0.500
UM3AW	0.995	0.264	0.500
UM2AW	0.976	0.269	0.500
UP4L	0.943	0.501	0.688
LI1LL	0.903	0.340	0.603
LP3W	0.892	0.373	0.609
LP4W	0.883	0.555	0.688
LP3TL	0.859	0.503	0.688
UCMD	0.857	0.375	0.609
UM2L	0.835	0.528	0.688
UM1PW	0.827	0.462	0.688
LM3L	0.824	0.573	0.688
UCBL	0.819	0.617	0.688
LM2L	0.817	0.512	0.688
LM1PW	0.816	0.699	0.717
LM2AW	0.815	0.791	0.791
LM1L	0.814	0.594	0.688

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Table G.5 – *continued*

Tooth dimension	K-statistic	raw p-value[b]	adjusted p-value
UM3L	0.812	0.682	0.717
UM1L	0.812	0.605	0.688
UM1AW	0.812	0.570	0.688
LM1AW	0.806	0.661	0.716

[a] Statistical significance based on $\alpha = 0.05$. [b] One-tailed.

Table G.6 Blomberg's K, raw p-values, and adjusted p-values for the relative size of all dental dimensions across the *sinica-fascicularis* lineage ($N = 7$). Dimensions in italics have K-values significantly higher than 0 based on the raw p-values only.[a]

Tooth dimension	K-statistic	raw p-value[b]	adjusted p-value
LCMD	*1.623*	*0.030*	*0.286*
LM3L	*1.303*	*0.033*	*0.286*
LCBL	*1.288*	*0.012*	*0.286*
UP3W	*1.137*	*0.036*	*0.286*
LP3TL	*1.131*	*0.040*	*0.286*
LP3W	1.123	0.055	0.286
LM1AW	1.069	0.074	0.286
UM2PW	1.055	0.067	0.286
UP4W	1.047	0.071	0.286
UCMD	1.043	0.088	0.286
LM3AW	1.030	0.072	0.286
UCBL	1.001	0.088	0.286
LM3PW	0.992	0.131	0.349
UM3AW	0.977	0.099	0.297
LM1PW	0.961	0.136	0.349
UM2AW	0.914	0.228	0.449
LI2LL	0.904	0.143	0.349
UM1PW	0.900	0.268	0.469
LM2AW	0.890	0.260	0.469
UM3PW	0.882	0.184	0.422
UM1AW	0.844	0.334	0.469
LM2PW	0.816	0.361	0.469
UM1L	0.813	0.228	0.449
LP3OL	0.754	0.230	0.449
LM2L	0.752	0.323	0.469
LP4L	0.740	0.329	0.469
UM2L	0.715	0.356	0.469

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Table G.6 – *continued*

Tooth dimension	K-statistic	raw p-value[b]	adjusted p-value
LI1LL	0.711	0.319	0.469
UP3L	0.711	0.351	0.469
UI1MD	0.703	0.322	0.469
LI2MD	0.648	0.463	0.573
UI1LL	0.638	0.503	0.577
UM3L	0.623	0.536	0.597
LI1MD	0.612	0.470	0.573
LM1L	0.576	0.503	0.577
LP4W	0.538	0.719	0.779
UP4L	0.466	0.842	0.888
UI2MD	0.461	0.881	0.888
UI2LL	0.444	0.888	0.888

[a] Statistical significance based on $\alpha = 0.05$. [b] One-tailed.