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ALLOMETRY OF TRUNK AND LIMBS IN NEW WORLD PRIMATES

City University of New York

Ph.D. 1982

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ALLOMETRY OF TRUNK AND LIMBS IN
NEW WORLD PRIMATES

by

DARIA DYKYJ

A dissertation submitted to the Graduate Faculty in
Anthropology in partial fulfillment of the require-
ments for the degree of Doctor of Philosophy, The
City University of New York.

1982

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The manuscript has been read and accepted for the Graduate Faculty in Anthropology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

October 7, 1982
date

Wanda J. Krzyz
Chairman of Examining Committee

Oct. 7, 1982
date

Jore Klumic
Executive Officer

Professor Eric Delson

Professor Leslie F. Marcus

Examining Committee

The City University of New York

Abstract

ALLOMETRY OF TRUNK AND LIMBS IN NEW WORLD PRIMATES

by

Daria Dykyj

Adviser: Professor Warren G. Kinzey

This study investigates the relationship between body size and relative limb length in fifteen genera of New World primates. Previous evidence from the Infraorders Strepsirhini and Catarrhini has suggested that increase in body size was often associated with relative forelimb elongation even in very differently adapted groups; Cartmill has proposed an adaptive basis for this effect. The present study determines if and how relative forelimb elongation occurs in the third extant primate Infraorder, the Platyrrhini.

Allometric analysis was performed on skeletal elements of the trunk (thoracic, lumbar and pelvic regions) and limbs (length and width of humerus, radius, femur, tibia, third metacarpal and third metatarsal) in fifteen

platyrrhine genera and six platyrrhine species. Three modes of allometric analysis were employed: the multivariate major axis method, the bivariate reduced major axis method, and the bivariate least squares method.

These analyses show that increase in body size among Platyrrhines is accompanied by a slightly greater rate of increase in forelimb length than in hindlimb length. This difference occurs throughout the Platyrrhini, in most functional and taxonomic subgroups, and within species. Particularly short hindlimbs in Alouatta and Lagothrix, and particularly long forelimbs in Ateles represent specializations in body proportions which act to separate further the forelimb and hindlimb slopes at the large bodied end of the platyrrhine size range. The most outstanding allometric feature identified is negative allometry of lumbar length in larger Platyrrhines; this serves to elongate both sets of limbs relative to the trunk and to facilitate climbing and suspensory adaptation at larger body sizes.

Intraspecific patterns differ from the intergeneric pattern and from each other, although four of the six species studied share a high incidence of negative allometry. This pattern is interpreted in terms of intraspecific maintenance of similar form and function within a wider range of body size than would be permitted by isometry.

Intergeneric platyrrhine allometry reveals greater conformity to geometric than to elastic similarity models although most allometric coefficients differ from those expected by either model. When shaft lengths scale non-isometrically with body size, their widths do not scale correspondingly, but rather inversely, with their lengths.

ACKNOWLEDGEMENTS

I wish to thank Dr. Sydney Anderson of the American Museum of Natural History and Dr. Richard W. Thorington, Jr. of the National Museum of Natural History for permission to examine skeletal collections in their care. I owe particular thanks to Dr. G. E. Erikson for allowing me to examine his collection of platyrrhine skeletons at Brown University.

My thanks are also due to the members of my dissertation committee, Dr. Warren G. Kinzey, Dr. Leslie A. Marcus and Dr. Eric Delson for their comments on each edition of the manuscript, in particular to Dr. Marcus for advising me on aspects of the quantitative analysis. I am especially indebted to Dr. William L. Jungers as the external reader, whose considerable experience in primate post-cranial allometry gave his constructive criticism of the manuscript special importance.

I thank my friend and former fellow student, Dr. Alfred L. Rosenberger for his encouragement and for allowing me to use data from his dissertation. In the latter stages of this work I have been fortunate in having the support of Dr. William Hodge, Director of Basic Sciences at the New York College of Podiatric Medicine, who made it possible for me to combine my duties to the College with preparation of the manuscript.

The expert help of Mrs. Cynthia Roach in preparing the final copy is deserving of both praise and thanks, and the help of Mr. Larry Powell in working out a computer tangle is much appreciated.

For the moral support which became a very necessary spur toward completion of this work, however, I thank my family, especially my mother for her boundless patience and faith. But it is to my husband, Walter T. French, and to his profound belief in the pursuit of knowledge, that I owe the will to have seen this work to its conclusion.

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I. INTRODUCTION

One of the most obvious morphological differences among animals is that of relative body proportions. Among primates, the group in which this aspect of morphology has been most extensively studied, such differences are highly varied and readily discernible. Differences in body proportions were among the characters discussed in the early and extensive review of the primates by Mivart (1867). Since then, and owing a debt to Mollison's (1911) early and classic analysis of body proportions in primates, interest in this aspect of primate morphology has remained high.

Among the many contributing investigators have been Keith (1903), Schultz (1930, 1937, 1938, 1953, 1973), Krieg (1930), Davenport (1935), Priemel (1937), Lumber (1939), Washburn (1942), Boné (1953), Gabis (1960), Erikson (1963), Knussman (1967), Maurer (1970-1971), Lessertisseur (1970), Lessertisseur and Jouffroy (1973, 1975), Ashton et al. (1975), Jouffroy and Lessertisseur (1978), McHenry (1978), Wood (1979b), Jungers (1979, 1982), Shea (1980), and Oxnard et al. (1981), to name but a few.

In most of these studies, especially the earlier ones, the Hominoidea were the focus of comparisons with a taxonomically broad spectrum of other primates. The result of this work was a characterization of the entire order as a comparative field for questions concerning human evolution. These works have produced an extensive set of descriptions of primate body form, one which continues to provide a basis for the formation of hypotheses in current research.

i Primate Limb Length, Locomotion and Body Size

The most salient dimensional characteristic of primate body form to emerge from these studies was relative limb length, expressed by the intermembral index as the ratio of forelimb length to hindlimb length. The range of this ratio for primates suggests a taxonomic, functional, and size axis (Figs. I.1, I.2) with (a) larger, long-armed hominoid primates at one end, (b) monkeys, having variably longer hindlimbs than forelimbs, centrally, and (c) most small and strepsirrhine primates at the long-legged extreme. As it is reasonable to suppose that relative limb length is functionally significant (Gregory 1912; Evans 1942; Gray 1944; Howell 1944; Rashevsky 1947; Hildebrand 1968; Daag 1973; Ward and Sussman 1979), it is not surprising to find this sequence reflective of known primate locomotor patterns.

Primates with very long hindlimbs, such as Tarsius, Galago, and the indriids (but with the exception of Homo, a terrestrial biped) are known for habitual vertical clinging and leaping (Hall-Craggs 1965; Napier and Walker 1967; Jouffroy and Gasc 1974; Walker 1974; Niemitz 1977); those with exceptionally long forelimbs, such as most hominoids, are known for brachiation and other forelimb suspensory and support activities (Carpenter and Durham 1968; McKinnon 1971; Andrews and Groves 1976; Fleagle 1977b). Thus, toward the extreme ends of this range in primates, the intermembral index clearly reflects functional dominance of forelimbs or hindlimbs.

To a lesser extent, primates with only moderately longer forelimbs or hindlimbs also demonstrate this in their positional behavior: frequent leaping in relatively long-legged langurs and other colobine monkeys¹ (Ripley 1967, 1977a, 1977b; Wells and Wood 1975; Mittermeier and Fleagle 1976; Fleagle 1977a, 1977b, 1978a; Morbeck 1977; Rose 1978), suspensory behavior in the relatively long-armed Ateles and Brachyteles (Cant 1977; Mittermeier and Fleagle 1976; Mittermeier 1978; Fleagle and Mittermeier 1980). But the positional behavior of these primates

¹The positional versatility of these and other primates brings to mind Ripley's (1967, 1977a, 1977b) caution against rigid application of locomotor typologies. For this reason locomotion is viewed here as a range of behavior rather than as a strictly segregated set of patterns.

also includes locomotor modes such as quadrupedal walking which are more generally shared with other primates in the middle range of relative limb length (Rose 1973, 1974).

The primates which show the least exclusivity or dominance in either limb set have indices between 90 and 100, indicating only slightly longer hindlimbs. They include the habitually pronograde quadrupedal monkeys such as Papio and Theropithecus (Rose 1973), the unique Lorisinae, known for their slow quadrupedal walking and climbing (Walker 1969; Charles-Dominique 1971; Dykyj 1980), and Alouatta (Mendel 1976) which in addition to pronograde quadrupedalism engages in suspensory behavior using both sets of limbs as well as the tail.

The range of the intermembral index suggests the additional but more problematic gradient of body size. That is, relatively longer hindlimbs are generally to be found among the smaller primates (Indri, Propithecus, and Homo are exceptions), while relatively longer forelimbs are found at the large-bodied end of the range. The association is indistinct when all of the primates are considered together (Figs. I.1 and I.2) but becomes more definite when they are subdivided into smaller taxonomic units (Fig. I.3).

The apparent, if only general, correspondence between body size and limb proportions has been studied in

catarrhine primates by Biegert and Maurer (1972). They compared limb length with trunk length and concluded that, in this group, forelimb length scaled at a higher rate than body size (skeletal trunk length) and hindlimb length, resulting in higher intermembral indices in larger than in smaller Catarrhines. They noted that this scaling was not uniform, however, and varied particularly in hominoids, producing the extreme limb lengths observed in certain hominoid genera.

The thesis of these authors with respect to hominoids was that the limb proportions of the African apes, Pan and Gorilla, represent the least departure from the characteristic scaling of limb length to body size in the Catarrhini as a group. For the remaining hominoids they hypothesized that selection has acted to increase the length of one or both sets of limbs at an even greater rate than that for other Catarrhines, thus focusing on alteration of proportions rather than on body size. They specified an exceptional increase in limb length relative to body size for the forelimbs of Pongo, for the hindlimbs of Homo, and for both sets (but with the forelimb rate still exceeding the hindlimb rate) in Hylobates.

These findings of Biegert and Maurer were subsequently tested with multivariate analysis by Corruccini (1978). This analysis showed that while the scaling of limb length

to body size varied within the catarrhine sample, on the whole forelimb length did increase at a greater rate relative to body size than did hindlimb length. In the opinion of Corruccini, however, it would be unwarranted to draw any significant evolutionary or functional conclusion from this finding in view of the high degree of variability in the scaling of limb lengths in the group in general, and among the Hominoidea in particular.

A more recent analysis of limb length and body size in Catarrhines has been conducted by Jungers (1982). Jungers found, as Corruccini had also noted, that reduction of lumbar length in larger Catarrhines, especially the hominoids, is responsible for the high coefficients of scaling for forelimbs observed by Biegert and Maurer. His scaling of limb length against body mass also revealed, however, that the effect of relative increase in forelimb length was created by a reduction of hindlimb length relative to body mass, and that this holds for the Catarrhines as a group, as well as among the hylobatids and the pongids.

While Biegert and Maurer did not argue an invariant conformity of points to a slope, they did, for the most part, take a classic broad view of morphological differences. This approach, however, has had the disadvantage of losing information specific to the individuals or

groups contributing to the sample. Jungers stresses the point that within a taxonomically broad comparison of limb length scaling there may exist considerable adaptive and functional differences that are overlooked, thereby reducing the relevance and interest of any patterns which may be found.

Despite their reservations, Corruccini and Jungers are in agreement with Biegert and Maurer as regards the most broadly applicable finding of their three separate and methodologically different studies: there is an absolute and relative increase in forelimb length to hindlimb length with body size increase in Catarrhines. Nevertheless, and following Jungers, the significance of this generalization, which submerges a good deal of adaptive diversity, is not yet clear.

One of the difficulties for discovering the evolutionary and functional relationship between form and size has been the common assumption that a particular relation must be repeated on different taxonomic levels (Gray 1946; Bertalanffy and Pirozynski 1952; Leutenegger 1977; Larson 1978). That this is very often not the case is exemplified by the well known difference between intra-specific scaling of brain size to body size (Bertalanffy and Pirozynski 1952; Stephen 1972; Gould 1975a; Lande 1979; Steudel, in press). The corresponding problem in

limb length scaling is that slopes for forelimb length relative to body size in lower taxa do not necessarily replicate those for higher taxa. As each of the groups represented in a taxonomically broad comparison has its own uniquely adaptive limb length to body size relationship, critics such as Jungers (1979, 1982) ask what meaning their combined effect could have, beyond the purely circumstantial. If we pursue a more than circumstantial significance for the catarrhine phenomenon of relatively greater increase in forelimb length with body size increase, we face the question of why the two (limb length and body size) should be related at all. Presumably natural selection may act as, if not more, effectively on limb length directly as through a modification of body size, if this is indeed an intervening variable.

However, Catarrhini are not the only group to exhibit relative forelimb length increase with body size increase. Jungers demonstrated a similar effect among certain living (1979) and subfossil (1977, 1978, 1980) lemuriforms. In the living lemurs, and especially in the indriids, the characteristic body form shows considerably shorter forelimbs than hindlimbs, resulting in some of the lowest intermembral indices in the primate range; it is also in this group that the hindlimbs provide the greatest power and propulsion in locomotion among primates (Walker 1974).

Yet Jungers (1979) found that within each of the groups of lemuriforms he investigated forelimb length increased relative to hindlimb length with body size increase. Moreover, he found (1980) the same pattern occurring among certain subfossil lemuriform primates such as Daubentonia robustus and Palaeopropithecus, despite differences in intermembral ratios and probable modes of locomotion.

Jungers' most extensive study was of the subfossil lemuroid Megaladapis (Jungers 1976, 1978), the largest and most robust of the subfossil forms, whose probable positional behavior has been compared to that of the Australian marsupial Phascolarctos. Jungers found that in Megaladapis relative elongation of the forelimbs with body size increase occurred as a result of radical decrease in hindlimb length. He explained that the net shift toward longer forelimbs, raising the intermembral ratio, improved the ability to maintain the body, at its larger size, on vertical supports. The reduction in hindlimb length enabled the body's center of gravity to remain close to the support and to be more efficiently controlled by the feet.

Jungers based his functional interpretation on Cartmill's (1974) analysis of claw function and body size in arboreal locomotion. Cartmill argued that for small animals on vertical and sloping supports, claws are more efficient than grasping extremities. In large arboreal

animals, he maintained, neither claws nor grasping hands and feet would be sufficient in themselves to effectively overcome the gravitational force coming into play on such supports. Therefore, he suggested, in large climbing primates grasping extremities are augmented by the greater stability and control provided by having relatively longer forelimbs and shorter hindlimbs.

Relatively shorter hindlimbs bring the body's center of gravity closer to the support. This acts to minimize gravitational moments about the point of foot contact on the support and to reduce the tendency of the caudal end of the body to rotate away from the support. Elongation of forelimbs in a larger body permits the hands to reach around a major portion of the support while allowing the trunk of the body to lean away from it. In this position, body weight descends partially against the support, thus reducing some of the frictional force necessary in the feet to resist sliding.

Cartmill's model is one of three recently proposed to account for external forces on the body of a climbing mammal. In a biomechanical review of these three analyses, Bock and Winkler (1978) concluded that Cartmill's model applies more accurately than those of Badoux (1974) and Niemitz (1977). This review was primarily concerned, as was Cartmill's analysis, with the external forces acting

at the points of hand and foot contact with the support. But the approval given by Bock and Winkler to this aspect of Cartmill's model lends credence to his related suggestion that relative elongation of forelimbs and reduction of hindlimbs would aid in the resolution of such forces.

Thus, regardless of the actual limb proportions described by the intermembral indices of certain diverse primate groups (Catarrhini, Hylobatidae, Pongidae, Indriidae, Lemuridae, and a number of subfossil lemuriforms), the forelimb is frequently effectively lengthened with an increase in body size. The precise relationship between limb length and body size, however, varies greatly from one group to another. Cartmill has offered a possible solution to Jungers' paradoxical finding that primates with widely different adaptations show similar changes in body form with body size increase: that relative forelimb elongation may be a general and biomechanically necessary adaptive response in arboreal primates of increasing size, augmenting their more specialized adaptations to particular locomotor modes.

ii The Platyrrhini

In his comparative sample Corrucini (1978) included members of the Neotropical Platyrrhini. While limb proportions in this group have received some attention

(Priemel 1937; Lumer and Schultz 1947; Erikson 1963, 1969; Jungers and Fleagle 1980), there has been no focused analysis comparable to those on the scaling of limb lengths in Catarrhines and Strepsirrhines. In his predominantly catarrhine analysis, Corruccini concluded that the scaling of limb lengths among Platyrrhines was essentially similar to that in Catarrhines. Indeed, various parallels have been drawn between members of these two major anthropoid groups, especially between the largest, suspensory atelines and certain hominoids (Lumer and Schultz 1947; Carpenter and Durham 1968; Fleagle 1976; Stern 1976).

The classic work of this kind was that of Erikson (1963, 1969), who compared limb and trunk proportions and locomotion in a number of platyrrhine primates with those of adaptively similar catarrhine and strepsirrhine primates. The locomotor typology utilized by Erikson (also by Krieg 1930; Priemel 1937; Thorington 1972, among others) was established by Mollison (1911); it divides the Platyrrhini into three types: small "springers", such as Saguinus; intermediate-sized "climbers", such as Cebus; and large "brachiators", such as Ateles.

More recent comparisons of New and Old World primates have drawn attention to similarities between the locomotor behavior of platyrrhine "springers" -- e.g., Cebuella

(Kinzey et al. 1975; Moynihan 1976); Saguinus (Thorington 1968; Izawa 1975); and Callicebus (Kinzey 1977) -- and of certain "vertical clinging and leaping" Strepsirhines. The locomotion of the squirrel monkey and of the tamarin have also received comparative mention in reference to that of the smallest of the catarrhine monkeys, Miopithecus talapoin (Gautier-Hion 1971). And the frequent suspensory positional modes of the Ateline genera have attracted interest from workers seeking adaptive parallels with those of Old World hominoids (Erikson 1963; Stern 1976).

Among the relatively few extensive studies of platyrrhine locomotion per se (but see Carpenter and Durham 1968; Mendel 1976; Mittermeier and Fleagle 1976; Cant 1977; Mittermeier 1978; Garber 1979), recent observations by Fleagle and Mittermeier (1980) of sympatric primates in Surinam are of particular interest. These observations supported the typological correlation between locomotor mode and body size, as well as a predictable correspondence between these variables and relative limb proportions: among the primates studied, longer hindlimbs are associated with "springing" and small bodies, while relatively longer forelimbs are associated with climbing, forelimb suspension, and large bodies.

When measured against that of the Catarrhines, however, the size range of platyrrhine primates is not as broad, nor locomotor differences as distinct, as among the Old World genera. There are fewer taxa in the Neotropical group and their classification is currently in considerable debate.

The Platyrrhini, or Ceboidea, have two traditional familial divisions, Callitrichidae and Cebidae (Simpson 1945; Hill 1957, 1960, 1962; Napier and Napier 1967). The Callitrichidae represent an organization of morphology and positional behavior that is frequently regarded as generalized, while the Cebidae are comparatively derived in both respects. The Callitrichidae consist of four closely related genera, Cebuella, Callithrix, Saguinus, and Leontopithecus, as well as the more problematic genus Callimico. This family includes the majority of Erikson's (1963) "springers", characterized by small size, a body form comprising a long spine, long hindlimbs, and short forelimbs (Thorington 1972, Hershkovitz 1977), and springing and rapid branch running as frequent modes of locomotion.

There is general consensus as to the membership of two cebid sub-families. The first of these is the Atelinae, including Alouatta, Lagothrix, Ateles, and Brachyteles. These animals are the largest in body size

and have fully prehensile tails which contribute considerably to suspensory locomotor and postural activities. The other undisputed cebid sub-family is the Pitheciinae, including Pithecia, Chiropotes, and Cacajao; these primates are less well known behaviorally. Both Pithecia and Chiropotes are known for versatile and acrobatic locomotion (Moynihan 1976). Pithecia is outstanding in having very long hindlimbs, comparable to those of the Catarrhines Colobus and Presbytis; like them, it is now known to be a frequent leaper (Mittermeier and Fleagle 1980).

The relations of the remaining genera have presented a long-standing problem for taxonomists. These genera include one primate of intermediate size, Cebus; and three of small size: Saimiri, Aotus, and Callicebus. Cebus, the representative genus of the "climbing" type of locomotion in Erikson's (1963) study, has often been taxonomically grouped with Saimiri (Hill 1960; Simpson 1945; Rosenberger 1979). In size and body proportions, however, Cebus is similar to the pitheciine Cacajao, and most closely approaches a "generalized" form of arboreal quadrupedalism in the New World, as does Macaca in the Old (see Erikson 1963).

Aotus and Callicebus are extremely similar to each other in size and body proportions but, like Cebus and

Saimiri, are taxonomically separated (Hill 1960; Cronin and Sarich 1975; HersHKovitz 1977) as often as they are grouped (Simpson 1945; Rosenberger 1979; Ford 1980b). They are curious in being more like callitrichids than like other Cebids in body size, proportions, and locomotion.

Saimiri is similarly small in size but shares with Cebus limbs of more equal length. Certain limb and trunk proportions of Saimiri -- particularly the intermembral index -- are, suprisingly, more similar to these of Cebuella, the smallest of all monkeys, than to those of any other Platyrrhines. This is interesting in view of the placement of Saimiri, along with Cebus, with the Callitrichidae (this new grouping then being renamed "Cebidae" in contrast to "Atelidae") in Rosenberger's recent (1979) taxonomic revision of Platyrrhini. It is also interesting in view of his suggestion that Cebuella may be a dwarf form. Furthermore, Cebuella and Saimiri (along with Leontopithecus and the Pitheciinae) were described as "erratic" in Erikson's (1969) comparison of ranges of locomotor adaptation in New and Old World primates.

At present, and setting aside the still open question of platyrrhine monophyly (Ciochon and Chiarelli, 1980), three taxonomic schemes for Platyrrhini are available.

These have all been based on recent morphological re-analyses. In these revisions three generic groupings remain unchanged: Atelinae, Pitheciinae, and Callitrichinae/dae), accounting for twelve of the sixteen genera. Hershkovitz has further separated Aotinae (Aotus and Callicebus) and Cebinae (Cebus and Saimiri). He retained the standard Callitrichid-Cebid division, but counted Callimiconidae (Callimico) as a third, coordinate, grouping at the familial level.

Rosenberger (1979) and Ford (1980b) have introduced more extensive rearrangements, on the basis of cranial and postcranial characters, respectively. In Rosenberger's classification Cebus and Saimiri have been grouped with the callitrichids, while Aotus and Callicebus are grouped with the Pitheciinae. Cebuella is included in Callithrix as a dwarf. Ford (1980b) also proposed two main groups, one of which includes all four of the problematic genera: Cebus, Saimiri, Aotus, and Callicebus. The second, more derived, group includes the remaining genera. Ford argued that the callitrichines, in particular, are derived and dwarfed (Peters 1978; Ford 1980a, b), a contention supported by Leutenegger (1980) and others.

In summary, the relative taxonomic status of most platyrrhine genera has remained unchanged since Simpson's (1945) standardization of mammalian systematics; it is

his scheme that represents the traditional or common classification. The most radical departures from this scheme have been in the recent revisions of Rosenberger (1979) and Ford (1980b); these have differed primarily in the placement of Aotus, Callicebus, Saimiri and Cebus. In each case the result is a restructuring of the Callitrichidae-Cebidae grouping. Whether either of these classifications is better supported by the data to be presented below remains to be seen; for analysis and discussion the traditional division of Callitrichidae and Cebidae will be used.

iii Methods of Allometry

The possible relevance of body size to body form has been implicitly and explicitly suggested throughout the history of the study of primate body proportions. Mollison (1911) and Boné (1953), for example, devised quantitative methods for dealing with the effects of size difference on their ratio data. More broadly, the importance of scaling to function and morphology was known to Galileo (see Gould 1966; Schmidt-Nielsen 1975), was illustrated by D'Arcy Thompson (1917), and has been a major theme in the works of Rensch (1951, 1954, 1960) and others (Bertalanffy 1938, 1950; Stahl 1962, 1963). The principal quantitative devices employed in the study of propor-

tions have been ratios, such as the intermembral index, whose use has chiefly been descriptive. Their employment as variables in quantitative analysis, however, has raised criticism (Hayami and Matsukuma 1970; Blackith and Reyment 1971; Atchley et al. 1976; Atchley 1978; Atchley and Anderson 1978; Albrecht 1978).

For questions of scaling regression analysis is a more appropriate tool than simple comparison of ratios. The most biologically relevant form of the regression equation is $y = a x^b$, established by Huxley (1932) as the standard method of size and shape analysis. The equation states that the value of variable 'y' is determined by the value of variable 'x' (usually representing some measure of body size) where the intercept is 'a' and 'x' is raised to the power 'b'. The use of ratios for describing differences in shape among animals of different size, implies a linear relationship among the variables. But the wide applicability of the regression equation to size-shape data has shown that non-linearity is the rule in biological systems. Ratios retain their utility as descriptive tools for comparing static proportions, but for predicting changes in shape in relation to size the regression equation is necessary and has become the principal method of bivariate allometry: the study of change in shape with change in size. (Gould 1966).

For many years after Huxley's (1932) exposition, and following his lead, bivariate allometry was further developed and applied largely with reference to growth data (Schultz 1933; Robb 1935a, b, 1937; von Bertalanffy 1938; Lumer 1939; Lumer and Schultz 1941, 1947; Clark and Medawar 1945). Problems in interspecific and "size" (Gould 1966) allometry were also treated (Robb 1936; Lumer 1940; Newell 1949; von Bertalanffy and Pirozynsky), but less frequently until Gould's (1966) review of allometry and his reappraisal of its importance to problems both of growth and of evolution. The increase of interest in size allometry which has since developed may be related to theoretical and methodological developments in evolutionary biology in the last three decades.

Among the theoretical developments is the emergence of body size as a character of interest. The rise of evolutionary ecology and its concern with the distribution and diversity of organisms has introduced questions about the ecological and selective importance of body size differences among animals (Hutchinson 1959; Hutchinson and MacArthur 1959; Foster 1964; Grant 1965; Ashmole 1968; McNab 1971; Van Valen 1973; Niles 1973; Wilson 1975; Downhower 1976; Heaney 1978; Dhondt et al. 1979; Kaplan and Salthe 1979; Searcy 1979; Tennis et al. 1979). These questions have led to others concerned with evolutionary processes on the broad scale (Stanley 1973;

Løvtrup et al. 1974; Hallam 1975, 1978; Boucot 1976; Hayami 1978) as well as those concerning the importance of body size to primate evolution and adaptation (Milton and May 1976; Clutton-Brock and Harvey 1977; Clutton-Brock et al. 1977; Godfrey 1977; Albrecht 1978b; Fleagle 1978b; Grand 1978; Marshall and Corruccini 1978; Fleagle and Mittermeier 1980; Temerin et al. 1980).

Concurrent with these developments has been the diversification of sophisticated quantitative methods within the last two decades, along with the refinement of the computer. The analysis of large sets of data has thus been made possible by complex multivariate methods virtually impossible to perform manually (see Olson and Miller 1958 for a precursor of such methods). While the bivariate regression model is still used for simpler allometric problems, there are new, multivariate methods of size and shape analysis which can now be applied to more complex problems (Jolicoeur 1963b; Blackith and REyment 1971; Oxnard 1973; Rightmire 1976; Watson and Broadhurst 1976; Bookstein 1977; Corruccini and Henderson 1978; Lande 1979; Corruccini 1981; Humphries et al. 1981).

Yet a third development stimulating recent interest in size allometry has been the growing study of the dependence of physiological and biomechanical functions on body size or mass. Body size is generally used as a convenient

standard of comparison for dimensional variables and is examined as a source of dimensional variability. In works addressing questions of systematics, allometry is frequently used to attempt to distinguish those characters derived as effects of body size increase or decrease in evolution, and thus not taxonomically reliable, from those uniquely and directly acted upon by natural selection (Gould's "criterion of subtraction" 1975a, b; Corruccini 1975a, 1976; Corruccini and Henderson 1978).

An alternative approach considers body size itself as a character subject to selection, and is interested in precisely those characters which are size-dependent, for they reveal the mechanical and physiological constraints on the evolution of form and function (Stahl 1962, 1963; Alexander 1971; Gould 1975b; McMahon 1975b; Schmidt-Nielsen 1975; McMahon and Kronauer 1976; Pedley et al. 1977; Sweet 1980).

Well before the appearance of allometry as a field of interest in morphology, D'Arcy Thompson established the groundwork for this approach in his On Growth and Form (1917). Later, Rashevsky (1947), Kleiber (1947), Pearson (1948), Hill (1950), and others helped to discover morphological, physiological, and energetic correlates of body size differences in various biological systems and in a wide variety of animal groups (Brown and Lasiewski 1972;

Gold 1973; Dawson 1976; Schmidt-Nielsen 1977; Alexander and Jayes 1978; Prange et al. 1979; Linstedt and Calder 1981). Allometric research on these subjects has also flourished in recent years and has just begun to provide models relevant for application to problems of locomotion (Taylor et al. 1970; Schmidt-Nielsen 1972; Taylor et al. 1972; Calow and Alexander 1973; Heglund et al. 1974; Alexander and Goldspink 1977; Pedley 1977; Emerson 1978; Zug 1978).

iii Allometry and Similarity Models

When a body increases in mass its other dimensions must increase proportionately so as to maintain similar function at the new size. There are a number of similarity models which can be used to predict the scaling of parts of a body required by an increase in its size, each based on some underlying mechanical function or principle. The expected rate of increase, however, is dependent upon the particular model employed and upon the functions selected as critical (Stahl 1963; McMahon 1975c; Blum 1977). The most generally applicable model for biological systems is that of geometric similarity (Gould 1966, 1971a; Alexander 1971; McMahon 1973, 1975b; Schmidt-Nielsen 1975). This model is based on the geometric relations among linear measurements, surface area, and volume, viz.:

length (any linear dimension) is proportional to mass to the $1/3$ power, area to mass to the $2/3$ power, and length to area to the $1/2$ power. When such relations obtain, the scaling of the dimensions considered is said to be isometric (McMahon 1977; Gould 1971). When the allometric, or regression, coefficient is higher than that expected on the hypothesis of geometric similarity, the condition is known as positive allometry, and negative allometry when the coefficient is lower. A body in which limb segment lengths scale isometrically with each other maintains the same limb proportions, or intermembral ratio, at a larger size. If one set of limbs, but not the other, scales with positive, or negative, allometry, there is a change in limb proportions when body size changes. A disproportionate change in scaling may be associated with significant alteration in locomotor behavior or other functions related to relative and absolute limb lengths over even a small size change (Stahl and Gummerson 1967).

An alternative allometric model of increasing interest is that of elastic similarity, proposed by McMahon (1973, 1975b, c, 1977). This scaling system is based on the criterion of elasticity, by which external diameters, or bone shaft widths, must scale so as to maintain similarity of elastic deflection under buckling and bending loads. This functional similarity is maintained when

diameters scale as length to the $3/2$ power, so that, following from this primary relations: length is proportional to mass to the $1/4$ power and diameter to mass to the $3/8$ power. With reference to limbs then, shaft diameter (McMahon 1973, 1975a), or width, must increase at a greater rate than shaft length in order to maintain similar elasticity, or, more functionally, resistance to bending.

The potential advantage of this model over that of geometric similarity is that it provides a biomechanical basis for the explanation of differences in form and of the evolution of such differences. Bending is the most critical stress for bone (Pauwels 1948, 1968; Currey 1970; Kummer 1972; McMahon 1973; Preuschoft and Weinmann 1973) and thus seems justifiably the focal problem for the scaling of support elements with increasing mass. Support for this model may be found in Kleiber (1947), Rashevsky (1947), Pearson (1948), Heglund et al. (1974), McMahon (1975a), McMahon and Kronauer (1976), Alexander (1977) Alexander et al. (1977), Howell and Pylka (1977), Maloiy et al. (1979); but there is some evidence arguing against its universality even in skeletal support systems (Gould 1967; Dodson 1975a; Prange 1977; Prange et al. 1979). Recently, Alexander, Jayes et al. (1979) have shown that among the mammalian groups they studied the only one in which lengths scaled in accordance with

the elastic similarity model (length proportional to mass^{1/4}) was the Bovidae although the scaling of shaft diameters in different groups offered greater support.

The fact that bones of larger animals are relatively thicker than those of smaller ones is so well known that it is an expected departure from the rules of geometric similarity (Hill 1950; Schultz 1953; Jolicoeur 1963a; Gould 1966; Sprent 1972; Schmidt-Nielsen 1975). That diameter is proportional to length to the 3/2 power can, in fact, also be explained by geometric similarity. As a one-dimensional (that is linear) measure, diameter or width should scale isometrically with length (i.e., as L^1). However, in order to maintain the strength of bone (which scales proportionately to cross-sectional area of the shaft) under increasing mass, cross-sectional area of bone must frequently scale as mass (or length³). Width or diameter of the shaft, as area^{1/2}, must then scale as length^{3/2}. Under geometric similarity this is a very common exception, while under elastic similarity it is the rule. Since both models can explain this relation, it cannot represent, as it did in McMahon (1975a), a test of one of them. The dependent functions, such as the scaling of length to mass^{1/4} (elastic similarity) vs. mass^{1/3} (geometric similarity), are better suited for such a test. It is on the basis of the scaling of length to mass, in fact, that

Alexander, Jayes et al. (1979) have shown that McMahon's model does not apply to most mammalian groups which they sampled.

v Extreme Shaft Widths in Primates

Contrary to both similarity models, Preuschoft and Weinmann (1973) have argued that relative limb segment thickness may decrease rather than increase with increasing body size. Moreover, there is evidence in primates of limbs with extremely thin shafts, as in Hylobatids, Pongo, Ateles, Limmopithecus, Tarsius, and Propithecus (Schultz 1953; Preuschoft and Weinmann 1973), or extremely thick shafts as in Megaladapis (Schultz 1953; Jungers 1976) in relation to their lengths. In all these examples the limb bone segments are also unusually long (and thin) or unusually short (and thick) in relation to the trunk.

The length, slenderness, and straightness of the forelimb shafts in hylobatids and Ateles have often been explained as adaptations to suspensory locomotion and to the tensile stresses acting on those limbs. Howell and Pylka (1977) have found similarly long and thin hindlimb elements in some bats and apply the same reasoning to their data. Their argument was that the tensile and bending stresses acting during suspensory locomotion are of lesser moment than the compressive and bending stresses acting during

pronograde positional activities, and do not require the additional bone strength that greater bone width would provide (see Fleagle 1977).

While this may be so for the magnitude of bending moments, it is unlikely to be true of tensile as against compressive forces, for in suspensory activities (and particularly in brachiation), the entire weight of the body must often be borne by only one or two limbs; while at the same time the strength of bone is known to be only half as resistant to tensile as to compressive force (Alexander 1968:436). Whatever may be the reduction in bending moments applicable to each limb during forelimb suspension, the fact that the load distributed over four limbs during pronograde activities must here be carried by one or two suggests that in this case an explanation of shaft diameter in terms of behavioral function alone is inadequate.

Such an explanation is even less applicable for other, less well advertised instances of shaft slenderness; viz., those of Tarsius and Propithecus (Schultz 1953). Here, the long bones in question are those of the hindlimbs, which, as in the forelimbs of the primates discussed above, are of exceptional length. The positional repertoires of these two forms, specializing in arboreal saltation, are at the opposite end of the positional spectrum

from those discussed above. The combined action of powerful bending and compressive forces during saltation is likely to result in vastly greater stresses than those imposed on the hindlimbs of walking and running quadrupeds (Alexander 1975a). Here, too, the long, slender bones bear all the body weight during jumping and leaping. These difficulties in interpreting shaft slenderness are compounded by the case of Hylobates, whose hindlimbs are also very long and slender, but whose locomotor pattern rarely, if ever, includes either saltation or hindlimb suspension.

Thus, again, an explanation of shaft slenderness in terms of behavior alone is inadequate. An alternative explanation, first suggested by Schultz (1953), is that this slenderness is a function of special selection for the length of a limb or of a limb segment; when selection acts to elongate individual segments of the skeleton, their diameters increase at a lower rate to length than when it acts to increase body size. Under body size increase load increases more rapidly than length (weight and mass are proportional to length³ by geometric similarity and to length⁴ by elastic similarity) so that a disproportionate increment in diameter relative to length would be required to maintain resistance to bending. But as the weight of all other body structures is unaffected under length increase of limb a segment, overall load increases only slightly, probably well within the capacity of the

bones for resisting bending moments, and little or no adjustment in shaft diameter is required. (A long, slender tube may fail by buckling, but Wainwright et al. (1976:259) pointed out that, in general, the long bones of vertebrates have an effective safety factor of about 5.).

A corollary to this hypothesis is suggested by additional observations made by Schultz (1953) on Alouatta. This genus shares a fully prehensile tail with Atelines and also engages in suspensory behavior, limited however, to postural modes relying heavily on the tail (Mendel 1976; Mittermeier and Fleagle 1976). Limb lengths, almost equal in the fore and hind sets, are notably shorter relative to vertebral length than they are in Atelines. But the most significant difference is that the shaft diameters of the hindlimbs are very thick. Though this shaft thickness is not as marked as shaft slenderness in some Atelines, what is arresting is the reversal in the configuration: limb bones which are comparatively short and thick, rather than long and slender.

If a selective increment in limb segment length independent of body size allows for relatively thinner shafts, what should happen to the relationship between shaft length and thickness under a selective reduction in length? If body size remains otherwise unchanged, a bone reduced in length must nevertheless continue to bear an overall load

which is relatively unchanged; it cannot suffer too great a decrement in its resistance to bending, and it will not, therefore, scale down in diameter as it would if limb reduction were accompanied by reduction in body size.

While the evidence for bone length reduction in primates is scanty, there is at least one relevant case: that of Megaladapis, which impressed Schultz (1953) as having notably short and thick limbs. This observation has recently been confirmed by Jungers (1976, 1978) who has also shown the biomechanical and allometric effects of hindlimb reduction in this fossil primate. Moreover, what little is known of allometric size reduction and dwarfing in other mammalian groups indicates an increase in relative robusticity when contrasted with structures scaling with body size increase (Gould 1975).

An analysis of these special cases of exceptionally thin and exceptionally thick limb bones in primates depends upon the determination of the general pattern of positive and negative length allometry, which is the topic of this research.

vi Summary and Hypotheses to be Tested

The foregoing introduction has presented several aspects of a long-standing problem in morphology, that of the functional relationship between relative limb length and body size. An apparent increase in forelimb length relative to hindlimb length with increase in body size has been reported for different groups of catarrhine and strepsirhine primates. Cartmill (1974) has suggested that it may be a widely applicable adaptation of arboreal animals to biomechanical problems resulting from increasing mass, an explanation which has been applied to a specific case by Jungers (1976). I present an analysis of limb length allometry in the third major group of extant primates, the Platyrrhini, with particular attention to the applicability of Cartmill's functional interpretation and to allometric comparability of New and Old World primate groups. The following hypotheses will be tested:

1. That there is a general increase in forelimb length relative to hindlimb length in association with body size increase throughout the Platyrrhini.
2. That relative forelimb length increases in association with body size increase within different taxonomic (with reference to certain current taxonomic schemes) and functional (with reference to differences in locomotor behavior ranging from springing, branch running and walking, to climbing and suspensory modes)

subgroups of Platyrrhini.

3. That the allometry of shaft lengths and widths conforms more closely to the model of geometry similarity, than to the model of elastic similarity.
4. That exceptionally positive or negative allometry of limb segment lengths to body weight is accompanied by exceptionally negative or positive allometry of the respective shaft widths.

II MATERIALS AND METHODS

i Composition of Data

Measurements of limb and vertebral segments were taken from 333 adult skeletons of Platyrrhine primates. The data were collected at the American Museum of Natural History, New York (172 individuals), at the National Museum of Natural History, Washington D.C. (59 individuals), and from the collection of Dr. G. E. Erikson, Brown University, Providence (102 individuals). Table II.1 identifies these skeletons by genus, species, and sex. (For the geographical origins of the skeletons, where available, see Appendix I. For the full data for each skeleton, see Appendix II.).

Maturity of individuals was judged by epiphyseal fusion of limb bones. There were faintly visible suture lines in some cases, but in all cases where suture lines were visible and skulls for the same skeletons available, the dentition showed complete eruption of permanent teeth. In five individuals vertebral epiphyses had not yet fully fused even though fusion was complete in the limb bones;

these specimens were retained and an estimate was made of the vertebral body length of the unfused vertebrae.

Of the total sample, 37 individuals (11%) were known to have died in captivity. As their skeletons showed no visible differences from wild-caught specimens, and as they were fairly evenly distributed throughout the sample (with the partial exceptions of Ateles, 5 individuals, and Cebuella, 5 individuals), they were retained. While the condition of most of the skeletons was excellent, 34 individuals (10%) showed evidence of healed fractures or of some degree of osteoarthritis. Limb bones of the right side were measured when all were available. When the right side was incomplete or contained fractured or arthritic bone the left side was measured instead. Specimens were not measured when the effects of fracture or disease showed probable impairment of function, even if only on one side.

Since the research design called for approximately 40 measurements to be taken on each complete skeleton (depending upon the number of vertebrae in the skeleton), the likelihood of missing data due to unavailable or broken bones was high. Thus, 39% of the sample is incomplete and was necessarily excluded from intraspecific analyses. Analysis of the data using means of variables, however, enabled all the data to be used in intergeneric analyses.

ii Description of Data

Measurements were taken with Helios dial calipers and recorded to the nearest 0.01cm. Lengths of limb bones in the largest genera (Alouatta, Lagothrix, Ateles) were taken on an osteometric board with a metal rule and recorded to the nearest 0.10cm.

Before measuring vertebral body length, the numbers of thoracic and lumbar vertebrae were recorded, using both the standard (rib-bearing and non-bearing) definitions of these vertebrae and the facet-type definitions proposed by Washburn and Buettner-Janusch (1952). Skeletal trunk length was determined as recommended by Biegert and Maurer (1972). The required measurements included:

- a) ventral lengths of all thoracic and lumbar vertebrae;
- b) partial length of sacrum, from lumbo-sacral articulation to caudal tip of ventral sacro-iliac margin; and
- c) ilio-ischial length from caudal margin of sacro-iliac joint to caudal extent of ischial tuberosity.

These measurements were combined into the following variables:

<u>variable</u>	<u>definition</u>
STL	skeletal trunk length (a + b + c above)
ThR	thoracic vertebral length, using the rib-bearing definition (e.g. Schultz 1938; Schultz and Straus 1945)
ThF	thoracic vertebral length, using the facet type definition (Washburn and Buettner-Janusch 1952)
LuR	lumbar vertebral length (rib-bearing definition)
LuF	lumbar vertebral length (facet type definition)
Pel	pelvic length (b + c above)
ThP	thoraco-pelvic length (ThF + Pel above)

The following measurements were taken of limb bone lengths:

<u>variable</u>	<u>definition</u>
HL	length of humerus, from head to capitulum
RL	length of radius, from superior margin of radial head to tip of styloid process
McL	length of third metacarpal, greatest length between head and base
FL	length of femur, from head to medial condyle

TL	length of tibia, from intercondylar eminence to tip of medial malleolus
MtL	length of third metatarsal, greatest length between head and base

External diameters of long bones were measured at mid-bone, as suture closure made estimation of mid-shaft too uncertain. Mid-bone was determined by halving the measured length of the bone, and the following diameters were recorded:

<u>variable</u>	<u>definition</u>
HN	minimum diameter of humerus
HX	maximum diameter of humerus
HD	mean (minimum + maximum/2) diameter of humerus
RN	minimum diameter of radius
RX	maximum diameter of radius
RD	mean (minimum + maximum/2) diameter of radius
McN	minimum diameter of third metacarpal
McX	maximum diameter of third metacarpal
McD	mean (minimum + maximum/2) diameter of third metacarpal
FN	minimum diameter of femur
FX	maximum diameter of femur

FD	mean (minimum + maximum/2) diameter of femur
TN	minimum diameter of tibia
TX	maximum diameter of tibia
TD	mean (minimum + maximum/2) diameter of tibia
MtN	minimum diameter of third metatarsal
MtX	maximum diameter of third metatarsal
MtD	mean (minimum + maximum/2) diameter of third metatarsal

Finally, weight (WT) was recorded whenever available for the skeletons measured but only three genera were well represented with such data: Alouatta, Saimiri, and Cebus. Fortunately, other data for these three genera were also abundant, with sample sizes sufficiently large to permit intrageneric analyses to be performed. The remaining genera, however, were supplied with mean weights taken from corresponding genera in Rosenberger (1979:574).

iii Notes on Selection of Variables

a) body weight

The preferred measure of body size in allometry is weight. Even though weight, or mass, may not be a perfect expression of an animal's "size" (Gould 1975a), it is nevertheless the closest approximation to the animal's physical entirety that can be measured. While a wide

variety of characters has been used to represent body size (Pilbeam and Gould 1974; Kay 1975; McHenry 1976; Mobb and Wood 1977; Wood 1979a), the alternative measure most often used is body length. Unlike weight, body length is measured in many ways: suprasternal notch to symphysis (Schultz 1938), sitting height (Boné 1953); skeletal trunk length (Biegert and Maurer 1972); axis to sacral length (Dodson 1975a), etc.; therefore, different estimates of body length are not readily comparable.

An additional disadvantage in using body length as a measure of size is that body length (trunk or vertebral length) is composed of vertebral segments in sections which tend to scale differently from each other. Both Corruccini (1978) and Jungers (1982) discovered this in their analyses of catarrhine allometry. Jungers found that while Biegert and Maurer's (1972) skeletal trunk length variable scaled consistently with body mass among Strepsirhines (1979), it did not do so in Catarrhines due to lumbar reduction in hominoids. Since a reduced lumbar region is also known in atelines (Keith 1903; Schultz and Straus 1945), an alternate trunk length variable, ThP or thoraco-pelvic length, was created to eliminate the effect of this reduction. Figure III.1. shows that ThP scaled against body weight describes an unbroken slope, thus better corresponding to the notion of a body size length variable (see more discussion of the thoraco-pelvic variable in chapter III).

But weight data are, finally, indispensable if both the allometry of vertebral sections and of limb segments is to be studied. That is, how well body length approximates our notion of "body size" depends upon its scaling to body weight. Without it, as in Hildebrand's (1952) analysis of canid limb proportions, comparability of results is limited and there is little basis for interpretation of results.

Weight data for use in broad comparative studies may be collected from the literature (e.g., Kay 1975) for specific taxa of interest. It is not always possible, however, to obtain comparable weight data in this way. Some workers prefer to take weights of eviscerated wild-shot specimens (e.g., Alexander et al. 1977) while in other cases weights for mature and immature individuals may be combined (see in Hershkovitz 1977).

A listing of weights for platyrrhine primates, taken from various sources, is given by Napier and Napier (1967); another, taken from wild-shot specimens at the Field Museum of Natural History, Chicago, is given by Rosenberger (1979). Mean weights by genus from each of the two lists were compared in the present study by a log-transformed matched-pair t test (Senter 1969). This test (Table II.2) determined the magnitude of the difference between the two sets of means, (but excluded those for Cebuella and Cacajao,

for which data were unavailable in one or both lists). The magnitude of this difference ($t = 2.05$; $p > 0.05$) was judged not significant. The two sets of means are very similar by the measure of the correlation coefficient ($r = 0.9880$) and either may thus with reasonable confidence be taken to approximate actual mean body weights in these genera. Rosenberger's means were selected to represent body weight for the twelve genera for which my own data do not provide sufficient information.¹ Rosenberger's figures are preferable to those of Napier and Napier because they are all based on mature wild-shot animals; they are preferable to an average of the two because of the possibility that some of the same animals may have been included in both samples.

b) definition of vertebrae

Thoracic and lumbar vertebrae are usually distinguished by whether or not they bear ribs. In measuring them for the purpose of obtaining a vertebral column length, the distinction is of no importance. It may be important, however, when thoracic and lumbar regional lengths are themselves variables. Washburn and Buettner-Janusch (1952) proposed the criterion of facet type for defining both

¹Allometric comparability between weight data available with the skeletons in this study and mean weights derived from Rosenberger (1979) is given in Table II.3.

kinds of vertebrae. They pointed out that intervertebral facets of the last two or three thoracic vertebrae are of the lumbar type and thus functionally allied with the lumbar series, an observation made earlier by Slijper (1946), and discussed with reference to New World monkeys by Erikson (1963) and Thorington (1972). Because both ways of drawing the distinction between thoracic and lumbar vertebrae reflect functionally significant dichotomies, both definitions were used.

c) external diameter as a parameter of bone strength

As the questions concerning bone shafts in this study are of a general rather than of specific nature (as contrasted with e.g., experimental bone strength studies), the measure of diameter used here will be the mean of the minimum and maximum diameters. This standardizes the measurement for comparative purposes, particularly in the absence of the necessary information on differential stress concentrations in the long bones of different species. Minimum and maximum diameters can in most cases be taken to represent the least and the greatest resistance to local stresses at a particular cross-sectional level in the shaft.

It is well known that cortical thickness (Pauwels 1948, 1968; Amtmann 1971; Kummer 1972; Lovejoy et al. 1976; Riesenfeld 1976; Brandt and Siegel 1978; Jungers

and Minns 1979; Pickerell et al. 1979) and mineral (and cortical) density (Saville and Smith 1966; Wright and Hayes 1977; Morey and Baylink 1978; Burr 1980), both essential to bone strength, are ontogenetically responsive to environmental conditions and to variable stress patterns, and alter considerably with age (Evans 1977; Garn and Shaw 1976; Montoye et al. 1976; Ortner 1977; Martin and Atkinson 1977). Preuschoft and Weinmann (1972) are among many who have emphasized the importance of cortical thickness to the strength of bone shafts.

Cortical thickness can be increase by endosteal (internal diameter) or periosteal (external diameter) deposition (Hoyte and Enlow 1966; Enlow 1977), or by both. When it is increased by endosteal deposition it is possible, argued Preuschoft and Weinmann, to have relatively more slender limb bones with increasing body weight. The conclusion is contrary to the postulate, central to the elastic similarity model, that robusticity necessarily increases with weight, and to the common assumption that outer bone width represents bone strength.

Despite this possible qualification, however, there is ample justification for continuing to use external diameter as a measure of relative bone strength, particularly for interspecific problems. Virtually all of the research on parameters of bone strength has been done on

the intraspecific and individual levels. This is necessarily so, for only at these levels can causal relations be studied with experimental precision. But in a comparative study such as that presented here, it is the generic group rather than the individual or species that is of primary interest. This means that any variable is necessarily an approximation of a range of individual variation in morphology and in its associated functions. It is therefore better to standardize the location of the measurement on the bone even though individual precision will be lost. Indeed, there exists evidence of interspecific comparability in spite of intraspecific variability. Burr (1978, 1979) showed that, while intraspecific patterns of mineral density along bone shafts are highly variable in Saguinus, Saimiri, and Macaca, interspecific differences among these genera are not significant. Burr et al. (1981) discovered similarities in local stress patterns and in cross-sectional geometry in primates as different as Macaca and Homo. Interspecific similarity of bone density in mammals has been reported by Currey (1970) and Wainwright et al. (1976). Lovejoy et al. (1976) have shown that the cross-sectional shape of the human tibial cortex is highly variable, affecting local bone strength, but that the cross-sectional area remains fairly constant.

Furthermore, while considerable local bone remodeling occurs endosteally in response to local stresses

(Hoyte and Enlow 1966) it is nevertheless unlikely that the adaptation of bone shafts to substantial weight increase would occur largely by deposition of endosteal bone. It is a fundamental principle of mechanics that for the same cross-sectional area of material, a hollow cylinder (or tubular bone) with large diameter and thin wall is more resistant to bending and torsional stress than one with a lesser diameter and thicker wall. According to beam theory, this is because the farther from the center of the cross-section or from the centroidal (neutral) axis (at which the stress is zero) the mass is distributed, the greater is the second moment of the area I (or of the moment of inertia) (Smith and Walmsley 1959; Pauwels 1968; Alexander 1968, 1975; Kummer 1972; Preuschoft and Weinmann 1972; Lovejoy et al. 1976; Wainwright et al. 1976; Currey 1970). The parameter I/R (where R is the radius from centroid to outer diameter) is equivalent to strength in resisting bending (Wainwright et al. 1976). Therefore, if greater strength is required in a bone shaft, and if it is energetically efficient (as is usually the case) to avoid adding more bone to the cortical area, it is more advantageous for the external diameter to increase rather than the internal diameter. . These considerations offer substantial support for the accepted practice (also followed by McMahon 1973) of using external diameter to represent bone strength.

iv Methods of Analysis

a) ratios

The following ratios were calculated from untransformed data. Each ratio is multiplied by 100 and rounded to the nearest integer.

$\frac{\text{ThR}}{\text{STL}}$	$\frac{\text{ThF}}{\text{STL}}$	} Ratios of vertebral lengths (by both rib and facet definitions) to skeletal trunk length;
$\frac{\text{LuR}}{\text{STL}}$	$\frac{\text{LuF}}{\text{STL}}$	
$\frac{\text{Pel}}{\text{STL}}$		
$\frac{\text{HL} + \text{RL}}{\text{STL}}$		Ratio of forelimb length to skeleton trunk length;
$\frac{\text{FL} + \text{TL}}{\text{STL}}$		Ratio of hindlimb length to skeletal trunk length;
$\frac{\text{HL} + \text{RL}}{\text{FL} + \text{TL}}$		Intermembral index.

b) descriptive statistics

Basic statistics and multivariate analysis of these data were performed at the CUNY computer facility using the Wylbur data editing system (CUNY Computer Center 1973) and the SAS data analysis system (Helwig and Council 1979).

Pearson product-moment correlation coefficients for each group were obtained by using the SAS PROC CORR procedure on log-transformed data. The output included the correlation coefficient and its significance probability

(assuming bivariate normality) for each pair of variables. The SAS PROC PLOT procedure was used to obtain plots on both untransformed and log-transformed data.

c) analysis of allometry

Years of research in allometry have shown that the relation between two variables is often best described by a logarithmic curve, particularly when the variables are measured in different scales (such as length and weight) and when the size range is broad. The allometric equation is now generally applied as a matter of course to log-transformed data, for which its form is $\log y = \log a + b \log x$, where 'x' and 'y' are variables, 'a' is a constant (representing the intercept) (Gould 1971), and 'b' is the allometric coefficient. Smith (1980) and Albrecht (1980) argued that, contrary to common understanding, transformation is not necessary for most variables. While it does no harm to an allometric analysis to do so, Smith maintained, most pairs of variables to which the equation is applied scale in a linear trend without transformation. All variables were nevertheless transformed in this study in order to maintain as much consistency as possible in the treatment of the data. Otherwise, at least the weight (WT) variable would have to have been transformed, judging by preliminary untransformed plots using this variable.

In either case the application of the allometry equation varies according to different methods of estimating term 'b' which, because real data describe a sample of biological variability, can only represent an approximation of the relation between (log) x and (log) y. The commonest method of deriving the allometric coefficient is the "least squares" method, usually computed as $r_{xy} s_y / s_x$, which determines the regression, or allometric, coefficient 'b' (Gould 1974; Emerson 1978; Larson 1978). The variable 'x' is assumed to be free of error, or other variability, and with all error variance attributed to the dependent 'y'. The likelihood that any biological variable may be free of such error is so slim that on this assumption the least squares method has been strongly criticized (Kermack and Haldane 1950; Jolicoeur 1963; Sprent 1972; Gould 1975b; Kuhry and Marcus 1977). Certain students of primate evolution, however, espouse the least squares method precisely because it assumes independence of the 'x' variable (Goldstein et al. 1978; Post et al. 1978; Smith 1981b; Jungers 1982). In their opinion an assumption of the independence of body size (as the 'x' variable) underlies all our investigations in allometry. Thus, the feature of this method which has been criticized on statistical grounds is made an advantage by biological criteria.

Other methods of estimating the value of the allometric coefficient frequently used include the reduced major axis method (Kermack and Haldane 1950; Cock 1966; Kidwell and Chase 1967; Gould 1974; Lande 1979; Wood 1979a), the major axis method (Haldand 1950; Reeve 1950; Gould 1975b), and the Bartlett three-group method (Kidwell and Chase 1967; Dodson 1976) while still other methods have been proposed recently (Kuhry and Marcus 1977; Mosimann and James 1980). None of the established methods, however, while avoiding the controversial assumption of the least squares method, has been able to escape criticism on other grounds (reviewed in Kuhry and Marcus 1977).

Differences among the results derived by different methods of estimating the allometric coefficient depend strongly on the degree of correlation between the variables tested. When using bivariate allometric techniques investigators frequently apply not just one, but two or three methods (usually least squares, reduced major axis, and major axis) as a way of compensating for the shortcomings of each method taken by itself (Pilbeam and Gould 1974; Gould 1975b, Cracraft 1976; Alexander, Jayes et al. 1979; Jungers 1979; Maloiy et al. 1979). Such comparisons have shown that the allometry coefficients generated by these methods are almost identical when the correlation coefficient is 0.95 and higher. Two methods in particular, least squares and reduced major axis, are in their simplest form

distinguished solely by the correlation coefficient ($b = r_{xy}s_y/s_x$, $b = s_y/s_x$, respectively). Smith (1980, 1981b) has argued that the correlation coefficient is too often interpreted as an indication of biological relationship when this is not necessarily the case. It is used here, however, in its statistical meaning only.

An allometric technique frequently used in the analysis of large data sets is a by-product of the multivariate Principal Components Analysis (PCA). This is one of the simplest, most robust, and most widely used multivariate methods for finding underlying relationships among variables characterizing a set of individuals (Kowalski 1972; Andrews and Williams 1973; Corruccini 1975b, 1976). From an analysis of the relations among the original variables, PCA derives a ranked set of latent variates (principal components): new variables weighted by corresponding elements of eigenvectors along each principal component axis. Beginning with the first principal component, each successive component isolated accounts for a progressively smaller proportion (eigenvalue) of the total variance in the data.

Elements of the first principal component (PC I) may share similar sign and value, suggesting a biological factor affecting all the variables (which, as an additional advantage of PCA over other multivariate methods, are identifiable with elements of the eigenvectors and princi-

pal components). As overall size is such a factor, when PC I satisfies these two conditions (or at least that of similar sign), it is often described as a "size" vector (Jolicoeur and Mosimann 1960; Gould 1967; Blackith and Reyment 1971). The elements within each of the second to the last eigenvectors are then unequal in sign. However, these remaining "shape" vectors are not necessarily free of the effects of size, even though this is a widespread interpretation.

Jolicoeur (1963a, b) showed that the directional cosines of the standardized first eigenvector represent the major axis solution of a generalized allometry equation. Hypotheses of isometry among the variables may be tested against a predicted equivalence of the directional cosines; alternatively, bivariate allometric coefficients may be determined from the ratio of the cosines of two selected variables. Kuhry and Marcus (1977) noted that the chief objection to the major axis technique, that of scale-dependence, is removed by a log-transformation of the data.

While the major axis bivariate solution is equivalent to that of its multivariate version, its bivariate computation for a large number of variables and samples is cumbersome in comparison to other bivariate methods. A disadvantage of using the multivariate major axis solution, however, is that significance statistics and confidence

intervals are not provided nor can they be readily computed.

Nevertheless, the analysis of allometric problems by PCA as outlined by Jolicoeur (1963a, b) has been extensive (Gould 1967, 1975b; Thorington 1972; Van Gerven 1972; Corruccini 1975a; Dodson 1975b, 1976; Cracraft 1976; Corruccini and Henderson 1978; Marshall and Corruccini 1978). Several investigators have introduced variations in the method (Ciochon and Corruccini 1975; Dodson 1975a, b, c; Kay 1975; Manaster 1979), and still others have applied other, related techniques, such as Factor Analysis (Gould 1974, 1975a).

The most recent criticism of PCA major axis allometry has been presented by Jungers and German (1978). Their chief criticism concerned the use of the first principal component or eigenvector to represent the body size character in the absence of such a character in the data. This criticism does not apply to the analyses in the present study, which include three alternative body size variables: weight, skeletal trunk length and thoraco-pelvic length. More pertinent is the problem, noted by Jolicoeur (1963b) but not widely discussed, that the value of bivariate allometric coefficients derived from PCA may vary for the same pairs of variables in different analyses, depending upon which other variables are included in each analysis. In the present study different combinations of variables were

used for PCA in order to compensate for gaps in the data; this did at first result in exactly the sort of discrepancies described by Jungers and German. The difficulty was alleviated by using means of variables rather than individual measurements for intergeneric analysis, thus also resolving the problem of missing data on that level of analysis. In the analysis of intraspecific data it was found that the greatest variation in results was effected by the inclusion of skeletal trunk length, and of the metacarpal and metatarsal variables. In intraspecific PCA, therefore, these variables were thereafter excluded.

Finally, Jungers and German pointed out that the PCA method of deriving allometric coefficients demands an equal distribution of values with positive and negative signs about isometry (1.00). Comparison with the results of bivariate allometric methods, however, shows that even when this condition is not met the differences are small, particularly when means of variables are used. In general, given the problems inherent in any and all of these methods, and the consequent failure of any of them to win universal acceptance, the most judicious use of allometric coefficients, however derived, is one which does not place too much weight on their absolute, as opposed to their relative values.

In the present work Principal Components Analysis, using a written SAS PROC MATRIX program on log-transformed data, was the major technique employed for intergeneric analyses. These analyses were supplemented with allometric coefficients derived by the bivariate methods of least squares and reduced major axis. The SAS PROC CORR program used on log-transformed data provided correlation coefficient with significance values, as well as standard deviations for the bivariate computations. These methods, however, did not provide significance values for allometric coefficients or confidence intervals for the slopes.

v Data Assembly

Table II. 1 shows that many skeletons in the sample were identifiable by species as well as by genus. With the exceptions of monospecific genera and of Alouatta, however, their number was not large enough for the genera to be effectively subdivided by species in analysis. Therefore, the principal analyses were necessarily of generic differences. Where a species sample was large and complete enough, it was analysed intraspecifically along with other species; the results of these intraspecific analyses are discussed in chapter V.

Analyses were conducted not only on the full sample but also on a variety of functionally and taxonomically coherent subsets:

<u>subset</u>	<u>description</u>
ALL	For the entire sample (<u>15</u> genera) analysis was performed on means of variables.
SMALL	Initial plots of observations and of means of variables indicated discontinuities in certain slopes, forming at least two size-groups. The SMALL group includes: <u>Cebuella</u> , <u>Callithrix</u> , <u>Callimico</u> , <u>Leontopithecus</u> , <u>Aotus</u> , <u>Callicebus</u> , <u>Saimiri</u> , and <u>Saguinus</u> .
LARGE	A second size-group, including <u>Pithecia</u> , <u>Cacajao</u> , <u>Chiropotes</u> , <u>Cebus</u> , <u>Lagothrix</u> , <u>Ateles</u> , and <u>Alouatta</u> .
NOATELS	The three ateline genera (<u>Alouatta</u> , <u>Lagothrix</u> , <u>Ateles</u>) were excluded from this sample to determine the degree to which the distinctive limb lengths in this subfamily may obscure or distort a more general pattern of platyrrhine allometry.
GGs	The family Cebidae (Simpson 1945) in traditional usage: <u>Aotus</u> , <u>Callicebus</u> , <u>Saimiri</u> and <u>Cebus</u> , the three pitheciine genera; and the three ateline genera.
ALR-C	'Cebidae' proposed by Rosenberger (1979): <u>Cebus</u> and <u>Saimiri</u> grouped with the traditional <u>Callitrichidae</u> (<u>Cebuella</u> , <u>Callithrix</u> ,

Callimico, Leontopithecus, Saguinus) (in the present study, however, traditional separation of Cabuela and Callithrix is maintained).

ALR-A

'Atelidae' proposed by Rosenberger (1979):

Aotus and Callicebus in addition to the three pitheciine and three ateline genera.

SMF

Derived platyrrhines, as defined by Ford (1980), including all Platyrrhines except Cebus, Saimiri, Aotus and Callicebus.

by species

Separate intraspecific analysis was performed on Alouatta senicula, A. caraya, A. palliata, Cebus apella, Aotus trivirigatus, and Saimiri sciureus.

III RESULTS: ALLOMETRY OF BODY SIZE

i Vertebral Number and Proportions of the Skeletal Trunk

Table III.1 lists the fifteen genera under study by order of increasing number of thoraco-lumbar vertebrae. This number varies between eighteen and twenty-two but the modal number in the group is nineteen. In eleven genera, combinations of thoracic and lumbar vertebrae change (whether by rib or facet definition) while the combined number of nineteen remains constant. The smallest modal number of vertebrae is found among the largest Platyrrhines, Ateles and Lagothrix, while two small Platyrrhines, Aotus and Saimiri, have the largest number.

Tables III.2 and III.3 present ratios of lengths of vertebral sections arranged in gradients which reflect change in the number of thoraco-lumbar vertebrae. Table III.2 shows that Aotus and Callicebus have relatively the longest lumbar regions. They also have the shortest functional (using the facet type definition) thoracic regions, even though Aotus has a comparatively large number of thoracic vertebrae. Since these two genera have almost equal body weight and skeletal trunk length, the length of

their vertebral bodies must differ. Thus, both the numbers and dimensions of vertebrae are subject to variation between genera and may affect the comparability of the vertebral or trunk length variable.

ii Allometry of the Skeletal Trunk

In figure III.1 skeletal trunk length and its main subdivisions (thoracic length, lumbar length, pelvic length and thoraco-pelvic length) are plotted against weight. The slopes of skeletal trunk length, thoracic length and pelvic length are visibly similar by their contrast to the slope of lumbar length and by differences in intercept among them (Table III.4). All the variables scale similarly, with a positive slope, among the smaller genera (Table III.5, SMALL). In the larger genera, however, the slope of the lumbar region is negative (Table III.5, LARGE). This discontinuity in lumbar slope makes the allometry of skeletal trunk length inconsistent with weight and flattens the curve.

In slope and intercept the thoracic and pelvic lengths are similar to each other throughout *Platyrrhini* (Table III.4) and, unlike skeletal trunk length, are unaffected by the reversal from positive lumbar allometry in small *Platyrrhines* to negative lumbar allometry in large *Platyrrhines*. This is true whether the facet or rib definitions of the

vertebrae are used. Table III.4 presents allometric coefficients, intercepts and correlation coefficients for all the skeletal trunk length variables scaled to weight. While the allometric coefficients of all three methods employed do not correspond precisely, it is clear that the pattern visually presented in figure III.1 is here numerically expressed by all three: a radical negative allometry of lumbar length in large Platyrrhines reduces their relative trunk length in comparison with small Platyrrhines, and lowers the slope of the skeletal trunk length in the whole group.

As the allometry of the lumbar region is so eccentric in comparison with other trunk regions, its effect on skeletal trunk length is to make this variable less reliable as a representative of "body size". Such eccentricity, or sudden change in slope, does not characterize thoracic and pelvic lengths. While the allometry of these two parts of the trunk is somewhat positive to weight, their slopes nevertheless are more alike and more consistent with weight throughout the group. Therefore, a new variable, thoraco-pelvic length (ThP) was created as a potential alternative to skeletal trunk length in representing body size. The new variable is the combined thoracic and pelvic length ($ThF + Pel$), those parts of the trunk length which are necessarily increased with body mass: (a) to accommodate essential thoracic organs in an overall increase in body

structure and function (i.e. heart, lungs), and (b) provide skeletal support and muscular attachment in the transmission of increased weight to the hindlimbs. The lengths of these regions of the trunk, therefore, may not be as freely subject to truncal positional adaptation as is the lumbar region. Thoraco-pelvic length will therefore be used for allometric analysis where body weight is unavailable, and comparatively with skeletal trunk length and weight where such data permit.

Table III.4 gives allometric coefficients for thoracic and lumbar lengths as defined by both rib-bearing and facet type definitions. The lumbar length coefficient is lower than that of thoracic length in both sets, but the coefficients for both facet-defined thoracic and lumbar regions are higher. These figures indicate that the functional (by facet) thoracic region scales positively to body weight, but when it is joined by the remaining rib-bearing (functionally lumbar) vertebrae its allometric coefficient drops; this is a result of the influence of reduced lumbar allometry. Thus, the facet type definition of thoracic and lumbar vertebrae better separates allometric fields associated with different functions in the thoraco-lumbar region. Therefore, the thoracic and lumbar lengths used in analysis henceforth will be those defined by facet type alone.

Figure III.1 shows that three genera, Aotus, Callicebus, and Saimiri, are found at the peak of the lumbar

curve. In this position it is difficult to determine which of the two slopes may more reasonably incorporate the lumbar lengths of these three genera. These primates are closer in size to other small Platyrrhines and fit adequately around the lumbar slope formed by them. Moreover, the long lumbar regions of these three primates do not suggest allometric commonality with larger primates even though that is the traditional taxonomic affiliation of these genera. Thus, relative length of parts of the trunk may be more reflective of body size thresholds (and body size related positional functions) than of taxonomic affinities. For these reasons the platyrrhine subsets SMALL and LARGE were formed in addition to the taxonomic subsets treated below.

Table III.5 shows that thoracic and pelvic lengths scale differently in each group and in neither case approximate isometry. Rather than scaling isometrically, most variables forming thoraco-pelvic lengths scale positively to weight. An interesting difference exists between the positive allometric coefficient for thoracic length in SMALL, and the relatively lower one for the same variable in LARGE. This suggests that functional thoracic length in small Platyrrhines may be scaling in adaptation to the relatively greater metabolic rate in small mammals, in comparison to that of larger bodied animals (Pearson 1948), as a result of their greater rate of heat loss. Thus,

while both thoracic and pelvic lengths scale far more evenly with body weight in the Platyrrhini than does lumbar length, expectations of isometry even in these variables are unwarranted. The most outstanding data in Table III.5 are the allometric coefficients of lumbar length in the two size groups: in the group SMALL, lumbar length has the highest of all the allometric coefficients, while in the group LARGE, it has the lowest.

Table III.6 compares allometric data of four taxonomic subgroups of Platyrrhini: the traditional Cebidae (Simpson 1945; Hershkovitz 1977), the derived Platyrrhines of Ford (1980), and the two revised families proposed by Rosenberger (1979), "Cebidae" and "Atelidae" (see page 56). Allometric coefficients in Ford's group (SMF) and in Rosenberger's "Cebidae" (ALR-C) are similar, differing chiefly in the exponents for lumbar length. Allometric exponents for the same variables in the group ALL (Table III.4) are equally similar to those of both these groups, but also differing from them in the exponent for lumbar length. In each of the three groups, Platyrrhines of small and large body size are mixed, blending the more extreme differences in the scaling of vertebral regions that was revealed by subdividing the sample into SMALL and LARGE subsets. In the traditional Cebidae (GGS) and in the "Atelidae" of Rosenberger (ALR-A), small and large Platyrrhines are also mixed but in each case the majority

of genera is large in size. Exponents for lumbar length are again low but there is also a reduction in that of thoracic length and skeletal trunk length.

iii Discussion

Earlier students of vertebral morphology have remarked on the relative uniformity of the number of precaudal vertebrae in primates. (Keith 1903; Priemel 1937; Schultz 1938; Schultz and Straus 1945). In contrast, the numbers of vertebrae within regions of the vertebral column were found to be quite variable both intraspecifically and interspecifically, especially in the thoracic and lumbar regions. Keith (1903) and later investigators perceived that differences in the relative lengths of the two regions evolved by the transformation of the last thoracic and first lumbar vertebrae: as the number of vertebrae in one section increases, that in the adjoining section decreases. Thus, in larger catarrhine and platyrrhine primates the number of lumbar vertebrae has been reduced in connection with upright positional modes, while the number of thoracic vertebrae has been increased (Krieg 1903; Priemel 1937; Schultz 1938, 1961; Washburn 1942; Erikson 1963; Rose 1975; Cartmill and Milton 1977).

The effect of such transformations on relative thoracolumbar functional lengths has here been demonstrated in

Platyrrhines in greater detail. While the modal thoracolumbar number of nineteen is maintained in most Platyrrhines, a reduction in the number of vertebrae devoted to lumbar function has a reductive effect on total trunk length. In this manner the slope of skeletal trunk length to weight drops off in association with relative lumbar reduction.

In Ateles and Lagothrix this trend in reduction has progressed as far as elimination of one lumbar vertebra from the entire series, reducing the thoracolumbar number to eighteen. In contrast, supernumerary vertebrae occur in certain small primates: Aotus and Saimiri. Thorington (1972) mentions a primitive number of ten thoracic and nine lumbar (by facet) vertebrae in Sciureus. If these numbers (or thirteen thoracic and six lumbar by the rib-bearing and non-rib-bearing criteria, respectively, Keith 1903; Schultz and Straus 1945) were also primitive for primates, then in Aotus one thoracic and two lumbar vertebrae have been added, while in Saimiri the additional vertebra is thoracic. The relatively longest lumbar regions, however, are found in Aotus and Callicebus. In Callicebus the modal number of vertebrae is nineteen but a thoracic vertebra has become a lumbar. This gives Callicebus relatively the shortest thoracic region (twelve rib-bearing, nine by facet type) among the Platyrrhines studied.

The differences in thoraco-lumbar composition in these three small primates are too subtle, however, to suggest corresponding positional differences. Each of them exhibits elongation of one or both parts of the thoraco-lumbar trunk. Callicebus and Aotus clearly have relatively the longest lumbar regions among Platyrrhines, suggesting the greatest truncal flexibility (Slijper 1946; Ankel 1972; Rose 1975), but these two genera have arrived at a very similar effect by two morphological alternatives. Flexibility of the trunk is necessary for springing movement and it is especially at the end of the thoracic, and beginning of the lumbar, series that most of this movement takes place (Thorington 1972). This is the location of all the vertebral modifications described for these three genera.

Allometric coefficients for variables of trunk length to body weight further demonstrate the fundamental difference in lumbar allometry from that of thoracic and pelvic allometry: the relative increase in thoracic and pelvic lengths to body weight is regular in Platyrrhini, while allometry of lumbar length changes from positive to negative in the middle of the platyrrhine body size range.

The greatest contrast in the allometry of thoracic and lumbar lengths within Platyrrhines is achieved by a division of the group according to small and large body

size. Saimiri, Aotus and Callicebus are grouped among other small-bodied Platyrrhines, thus separating the springing, branch running and walking primates from climbing and suspensory primates. This division reveals the extreme differences in lumbar scaling: it is the most positive trunk length variable in small, and the most negative trunk length variable in large, Platyrrhines. A less prominent allometric difference in the two groups is a shift toward more positive allometry in the pelvic region and more negative allometry in the thoracic region of large Platyrrhines; this shift has little effect, however, on combined thoraco-pelvic allometry. The result of these figures concerning change in body form with change in body size is that: (a) the trunk length relatively increases in all its parts in small, springing Platyrrhines; and (b) trunk length relatively decreases in large, climbing and suspensory Platyrrhines. The difference in these two allometric patterns suggests that a threshold of body size (or body mass) may exist in arboreal mammals above which it is less advantageous to support positional behavior patterns which depend upon a long, flexible trunk; and the converse: that the adaptive advantages of positional behavior patterns which rely upon short, inflexible trunks may be precluded by too small a body size.

Allometry of different taxonomic subdivisions of the fifteen genera does not provide a basis for favoring any

one of the current classifications of the Platyrrhini over another. Differing allometric coefficients generated for trunk length variables in the four taxonomic groups tested merely reflect differences in the combinations of genera from the two size-groups.

Allometry of parts of the trunk show little correspondence to either the geometric or elastic similarity models. Platyrrhine skeletal trunk length and thoracic (by facet) length in large Platyrrhines are the most nearly isometric of trunk length variables. The composite nature of the skeletal trunk length, however, especially the extreme divergence of the allometry of lumbar length from that of other trunk variables, suggests that the correspondence of skeletal trunk length to isometry may be superficial only.

Because of the eccentric allometry of lumbar length, thoraco-pelvic length was proposed as a more consistent expression of "body size" than skeletal trunk length; however, neither measure is ideal. By all three methods of allometry, skeletal trunk length in the group of fifteen platyrrhine genera is slightly negative and thoraco-pelvic length is slightly positive. Since all skeletal parts are subject to allometric and other morphological change in evolution, there is probably no universal skeletal feature from which "body size" may be extrapolated.

However, even if thoraco-pelvic length were widely isometric with weight, this would not reduce the value of skeletal trunk length in the study of functional body proportions. The measure of trunk length has been used in two senses: (a) as an alternative estimate of "body size" and, (b) as one of the set of links in the functional link system of the body. In its first sense the total trunk length is not essential, since it is merely representative of another quantity--"body size"--and depends on an assumption of uniform scaling with the preferable estimate of the physical entirety of an organism, body weight. Some part of the trunk length, such as thoraco-pelvic length, which scales more uniformly than does total trunk length, may therefore be a more appropriate body size estimate. In the second sense above, total trunk length is an essential quantity, as it represents a length of functional significance in relation to the lengths of other links in the lever system. This latter significance of the trunk length is that which is described by a ratio of limb length to trunk length.

Finally, the lumbar region in Platyrrhines can affect the skeletal trunk length in more than one way (numbers of vertebrae and differences in relative lengths of vertebral bodies) and cannot be depended upon as an element in a standard body size estimate. Biegert and Maurer (1972) recommended the use of a lumbar vertebra in skeletally

incomplete fossil assemblages for the estimation of skeletal trunk length. Investigation of the skeletal trunk in primates, however, has shown that selection of a lumbar vertebra would be the poorest choice for this purpose, as was also shown for Catarrhini by Jungers (1982).

IV RESULTS: INTERGENERIC LIMB ALLOMETRY

1 Platyrrhine Limb Proportions

Intermembral ratios given in Table IV.1 suggest relative forelimb increase with increase in body size. This effect is not as pronounced throughout the range of the fifteen genera as it is when the ateline group is compared with the rest. Ratios of non-ateline genera range between 71 and 88 with no consistent increase between the smaller and larger genera. Several callitrichids, as well as Aotus and Callicebus, show low values of the index indicating relatively long hindlimbs, or short forelimbs, along the body size gradient. But Cebuella, the smallest primate among them shows a comparatively high index at 82, and that for Leontopithecus, at 88, is the highest after the atelines. Among Platyrrhines of intermediate size, Pithecia has a particularly low intermembral index of 75, comparable to that of as many as half the smaller genera.

Forelimb and hindlimb lengths in relation to skeletal trunk length, however, show that both sets of limbs increase more regularly in length, with a somewhat greater

rate in forelimbs. These ratios also reflect the differences in regional lengths of the trunk as described in chapter III. For example, ratios of the forelimb and hindlimb lengths relative to skeletal trunk length in Aotus and Callicebus are among the lowest in the whole sample; in the latter genus they represent the absolutely lowest values (59 for forelimb and 79 for hindlimb). In comparison with Aotus, which has the same intermembral index, these values for Callicebus indicate a relatively longer trunk. Data given in chapter III indicate that Aotus possesses supernumerary vertebrae while Callicebus has incorporated a thoracic vertebra into its lumbar series. Thus, the trunk is elongated in both leading to relative shortening of the limbs in comparison to other Platyrrhines. Otherwise, in body proportions these two primates are very similar to the smaller callitrichids Callithrix and Saguinus, while a similar likeness may be observed between Saimiri and Cebuella. In the latter pair, however, the limbs are more equal in length and longer in relation to the trunk.

Among primates of intermediate size, Chiropotes, Cacajao and Cebus share similar ratios of limb lengths relative to trunk length. The intermembral limb length in these primates is within the range of those of several small Platyrrhines, such as Cebuella, Leontopithecus, and Saimiri. But an important difference between the small

and intermediate primates in these data is that the limbs are clearly longer in relation to the trunk in pitheciines and in Cebus than they are in the smaller Platyrrhines. The low intermembral index of Pithecia is reflected in comparatively short forelimbs and long hindlimbs to trunk length. Of the intermediate primates, the proportions of Pithecia make it most suited for the frequent leaping observed in this genus by Fleagle and Mittermeier (1980).

The three larger genera, Alouatta, Lagothrix and Ateles are distinguished by having almost equally long forelimbs and hindlimbs; their intermembral indices range between 97 and 106. Greater differences among them may be discerned, however, in the length of limbs relative to trunk length. While Alouatta and Lagothrix share very similar intermembral indices, the limbs of the former are considerably shorter relative to trunk length. In Lagothrix the length of limbs to trunk length as well as to each other is almost equal. Ateles is outstanding in having both much longer forelimbs and hindlimbs than the trunk length. The largest ateline, Brachyteles, for which data were unavailable for this study is also, however, known to have forelimbs longer than the trunk length (Erikson 1963; Napier and Napier 1967).

ii Allometry of Limb and Limb Segment Lengths

Plots of mean forelimb (Fig. IV.1) and hindlimb (Fig. IV.2) segment lengths to mean body weight show uniform increase of all lengths with body size. Inspection of the figures suggests similar scaling of the two more proximal shaft lengths in each set of limbs. From visual inspection alone, the greatest difference in allometry within each limb set concerns that of metacarpal and metatarsal lengths, which are separated from other shafts in their respective limbs by much lower intercepts, reflecting the much shorter lengths of these bones to those of the proximal segments. Relative uniformity to all segment length slopes to weight indicates that the generic variation more apparent in ratios of limb length to skeletal trunk length (Table IV.1) has masked a more direct allometry of limb length to body weight.

Table IV.2 gives allometric coefficients for limb segment lengths to weight and to thoraco-pelvic length, and shows that the exponents of the forelimb segments are greater than those of the hindlimb segments. The allometry of proximal and distal limb segments differs only slightly; the radius is slightly positive to humerus while the tibia is slightly negative to femur. Greater increase in overall forelimb than hindlimb lengths is continued in the hand and foot elements: third metacarpal length scales at a greater rate than third metatarsal length. These lengths

scale negatively to the more proximal segments in their respective limbs, however, indicating relative reduction in the lengths of these bones as limb lengths increase.

Slopes of forelimb (sum of the lengths of humerus and radius) and hindlimb (sum of the lengths of femur and tibia) lengths to weight (Fig. IV.3) and to thoraco-pelvic length (Fig. IV.4) illustrate the slightly greater increase of forelimb length, than of hindlimb length, to body size. Allometry coefficients of forelimb and hindlimb lengths to all these body size variables, body weight, skeletal trunk length and thoraco-pelvic length, are given in Table IV.3A. The coefficients for limb lengths to skeletal trunk length are strongly positive because of relative reduction in the skeletal trunk length of larger primates. In relation to thoraco-pelvic length and to weight, however, the positive allometry of both sets of limbs is much reduced.

Figures IV.3 and IV.4 show that the slopes of limb lengths are fairly uniform throughout the Platyrrhines with the exception of atelines. In this sub-family there is a sharp decrease in hindlimb length in Alouatta and Lagothrix, and a sharp increase in forelimb length in Ateles. Because of these two deviations the Atelinae was removed from the sample and allometry coefficients were determined for the remaining genera together, as the group NOATELS. The results show (Table IV.3B) an expected slight

increase in allometry of hindlimb length and slight decrease in forelimb allometry. With ateline forelimb and hindlimb deviations removed from the platyrrhine sample, it may be seen (Fig. IV.5) that slopes for these limbs in the remaining genera are more parallel; indeed, the relative increment in forelimb exponents is so small that the limb lengths are virtually isometric with each other.

A division of the platyrrhine genera into LARGE and SMALL subgroups, (suggested by the marked differences in trunk length allometry discovered between these groups in chapter III) reveals that the slight positive allometry observed in the group NOATELS occurs among the larger Platyrrhines only. Table IV.4 reveals a considerable difference in the group LARGE between positive allometry of forelimb segments and negative allometry of hindlimb segments. Previous analysis of the group NOATELS (which excluded the three ateline genera), and its comparison with the group ALL (including all fifteen genera), indicated that these exponents are strongly influenced by the limb lengths of atelines. Thus, the difference between forelimb and hindlimb exponents of Cebus together with the pitheciine genera cannot be as great as those of LARGE.

Table IV.5 shows that, in contrast to the large Platyrrhines, the allometry of hindlimb segment lengths in small Platyrrhines is slightly positive to that of the

forelimb segment lengths. As in the group NOATELS, however, the difference is so slight, particularly between the exponents of limb lengths to body weight, that again, the limb lengths are virtually isometric with each other. These slight differences between hindlimb and forelimb length allometry in SMALL and NOATELS suggest that a gradual shift occurs toward increase in the rate of scaling of the forelimb relative to hindlimb with body size increase.

Slopes and allometric coefficients for forelimb and hindlimb lengths are little changed when generated for different taxonomic subgroups (Tables IV.6 and IV.7). The standard taxonomic separation of Callitrichidae and Cebidae is pictured in figure IV.5. It shows a near equivalence of slopes in Callitrichidae (allometric data for this group were not computed due to its small number of genera). The forelimb slope in Cebidae is very like that of Callitrichidae, but the two groups differ in their slopes for hindlimb length, indicating relative hindlimb reduction in Cebidae. This is also evident in Rosenberger's (1979) division of Platyrrhini: the slopes (Fig. IV.7) and allometric coefficients for his "Atelidae" are very similar to those of the traditional Cebidae. Moreover, the slopes for his "Cebidae" are also visibly similar to those of the traditional Callitrichidae. Thus, in Rosenberger's revision, the exclusion of Cebus and Saimiri

from Cebidae, and their inclusion among Callitrichidae, makes relatively little difference to the limb allometry of both the traditional and revised groups.

Excluding Ford's (1980) primitive Platyrrhines (Aotus, Callicebus, Saimiri and Cebus) from the fifteen genera leaves a "derived" (Fig. IV.8) group; the forelimb and hindlimb slopes in this case are visibly similar to those of the group ALL (Fig. IV.3). Comparison of the allometric coefficients for forelimb and hindlimb allometry in all the taxonomic subgroups indicates the same pattern: positive allometry of forelimb length to both weight (Table IV.6) and to thoraco-pelvic length (Table IV.7). This difference between forelimb and hindlimb allometry is least in "Cebidae" (ALR-C), while the basis for a greater degree of difference in the other three groups is that each of them includes the Atelinae.

iii Allometry of Shaft Widths

The allometry of shaft diameters scaled to body weight presents a similarity of slope among segments in each limb (Figs. IV.9 and IV.10) that is similar to that of shaft lengths (Figs. IV.1 and IV.2). Table IV.8 shows that all shaft diameters scale similarly to body weight, with exponents ranging from 0.34 to 0.40. For the four principal segments of the limbs, the exponents are either 0.36 or

0.37, or very close to the value of 0.375 given by the elastic similarity model. Allometric coefficients for the diameters of metacarpal segment are higher (0.39 and 0.40), while those for the diameter of the metatarsal segment are lower (0.34 to 0.36). These figures indicate that the allometry of shaft widths to body weight does not directly correspond to the allometry of shaft lengths (Table IV.2), whose range of allometric coefficients is relatively broader.

Allometry of shaft widths to their respective lengths, however, presents a very different pattern. Allometric coefficients for shaft diameters to their lengths (Table IV.8) reveal a wider range (0.84 to 1.26), with greater differences among the various limb segments. The lowest allometric coefficients for diameter are found in the radius and humerus (0.84 to 0.86) while the highest belongs to metatarsal III. Comparison with shaft length allometry in Table IV.2 shows that the radius and humerus lengths have the highest exponents, especially those scaled to thoraco-pelvic length, while those for the length of metatarsal III are lowest. Indeed, this inverse allometry between shaft lengths and their widths is seen in the remaining segments as well: those segment lengths scaling more positively have more negatively scaling widths, while those lengths scaling more negatively, have more positively

scaling widths. This is illustrated in figures IV.11 (forelimb segment diameters) and IV.12 (hindlimb segment diameters). In each, the slope for the metacarpal and metatarsal diameters is higher than that for the other segments of the limb. Figure IV.12 shows a discontinuity in the common slope for diameters of femur and tibia which corresponds to the division of the Platyrrhines into large and small groups. In the group SMALL the two limb lengths scaled very similarly (Table IV.5) to each other, but in the group LARGE (Table IV.4) the forelimb segment exponents were very positive (0.46 and 0.54 scaled to weight, 1.18 and 1.36 scaled to thoraco-pelvic length) and the hindlimb segment exponents very negative (0.27 and 0.27 scaled to weight, 0.69 and 0.68 scaled to thoraco-pelvic length). Comparison of Table IV.9 with Table IV.4 demonstrates the inverse relationship in the scaling of shaft widths to their shaft lengths conclusively: in the group LARGE, the allometric coefficients for the forelimb segment diameters scaled to their lengths are 0.77 and 0.70, while for the hindlimb segments they are 1.51 and 1.38.

On the possibility that allometry of minimum and maximum diameters might be more informative than their mean for each shaft, allometry coefficients for these variables were derived and are given in Table IV.10.

Again, there is more variation in the scaling of these diameters to their shaft lengths than there is to weight. In each case the greatest relative allometric difference occurs between minimum and maximum diameters of the radius, in which it is the minimum diameter that has the higher coefficient than the maximum. Otherwise, no regularity in the allometry of these two variables is revealed such as to suggest that either would be a better width dimension than the mean of both.

iv Discussion

Limb and trunk proportions of platyrrhine primates describe an unevenly graded series of genera in which limbs become relatively longer to trunk and the forelimb relatively longer to hindlimb with increasing body size. Analysis of body size variables in chapter III revealed that lumbar reduction in large Platyrrhines, especially Atelinae, negatively affects the allometry of skeletal trunk length to body weight. As a result, limb length scaled to skeletal trunk length shows distinct positive allometry in both sets of limbs and this is reflected in limb to trunk length ratios. However, when scaled to thoraco-pelvic length and to body weight, allometry coefficients for limb lengths are much lower, with those for forelimbs slightly positive

and for hindlimbs slightly negative.

The allometric difference between forelimbs and hindlimbs in Platyrrhini is further affected by ateline deviations from the two slopes. Alouatta and Lagothrix have relatively shorter hindlimbs than most other Platyrrhines, while Ateles has relatively much longer forelimbs. Allometry coefficients for the Platyrrhines from which the three ateline genera have been excluded (NOATELS) show a relative equalization of allometry between forelimbs and hindlimbs, although a slight positive forelimb allometry persists. When the Platyrrhines are subdivided into SMALL and LARGE groups, it is clear that among small Platyrrhines it is the hindlimbs, rather than forelimbs, which scale at a slightly greater rate to body size. Unlike the very distinctive difference in the allometry of lumbar length between LARGE and SMALL subgroups (compare Fig. III.1 with Figs. IV.3 and IV.4), however, the ateline limb lengths serve to substantially increase an essentially slight difference between larger and smaller Platyrrhines.

Thus there are three factors behind platyrrhine limb allometry which together help to account for the body forms described by ratios. The first is a very slight difference between the scaling of forelimbs and hindlimbs. In small Platyrrhines the femoral length scales at a greater

rate than the other shafts but the allometry of radial length gains as body size increases.

The second factor is the acutely shorter hindlimb length of Alouatta and Lagothrix on the one hand, and the acutely longer forelimb length of Ateles on the other. Thus, in the atelines, forelimbs are effectively longer than those of other Platyrrhines although this has been achieved by two different alternatives: (a) reduction in hindlimb length and (b) increase in forelimb length. The forelimb slope for Platyrrhines is thus raised by the forelimb length of Ateles, while the hindlimb slope is lowered by the hindlimb lengths of Alouatta and Lagothrix.

Superimposed upon this pattern is lumbar length increase in small Platyrrhines and decrease in large ones. The decrease is more distinctive and more acute, as shown in chapter III, and results in relative elongation of both sets of limbs in the larger Platyrrhines. When scaled against the skeletal trunk length, therefore, not only the allometry coefficient for the forelimb is very high, but also that for the hindlimb (though still comparatively lower than that for the forelimb).

The atelines do not represent the only deviations from the forelimb and hindlimb slopes to body size (Figs. IV.3 and IV.4), but theirs are more influential in occurring at the large end of the body size range. In comparison

to other Platyrrhines on the limb length to body weight slopes, for example, forelimbs are relatively long in Cebuella, Leontopithecus, Aotus and Cacajao, they are relatively short in Saguinus and Cebus. The hindlimbs of Callimico and Aotus are relatively long, while those of Callithrix and Leontopithecus are relatively short. Thus, by deviating from these slopes, each genus reveals the adaptive differences in its limb lengths from those of other genera. The close distribution of points about the slopes, however, suggests that such deviations are small adjustments on a common allometric pattern.

Differences in platyrrhine length allometry corresponding to locomotor function are indistinct. The limb lengths of atelines clearly segregate this group from among other Platyrrhines, thus separating those primates known for suspensory behavior. Division of the remaining Platyrrhines is made difficult by the very small degree of allometric difference remaining between that group known for climbing (Pitheciinae, Cebus and, more problematically, Saimiri), and that known for branch running, walking and springing. Nevertheless, the data do show that increase in forelimb length relative to body size and to hindlimb length is more properly and progressively associated with climbing and suspensory behaviors.

Subdivision of the Platyrrhini by taxonomic groups, however, again reveals very little. Those genera of

particular taxonomic interest, Callicebus, Saimiri, and Cebus, although with the possible exception of Aotus, fit neatly into the platyrrhine slopes. This is a very different situation from that of Catarrhini (Biegert and Maurer 1972; Corruccini 1978; Jungers 1982) in which different taxonomic subgroups reveal very different patterns of allometry in association with considerably different adaptations. In Platyrrhini the Atelinae have been regarded as most adaptively distinct and this is reflected also in their contribution to platyrrhine allometry.

The allometry of shaft diameter in Platyrrhines is less variable when scaled to weight than when scaled to shaft length. Most exponents of mean shaft diameter scaled to weight fall within a narrow margin (0.36 - 0.37) of that predicted by the elastic similarity model (0.375). However, shaft diameters scaled to shaft lengths fall within a margin of isometry rather than that exponent expected by the elastic similarity model (1.50). Furthermore, the exponents of shaft lengths to thoraco-pelvic length also fall within a range of isometry (0.84 - 1.08), while their exponents to weight are greater than the expected values by either similarity model (geometric similarity 0.33, elastic similarity 0.24). Thus, the elastic similarity model is supported only by the allometry of mean shaft diameters to body weight. In the allometry of shaft widths

to shaft lengths and of shaft lengths to thoraco-pelvic length, allometric coefficients approach isometry. The allometry of shaft lengths to body weight, however, shows no relationship with either model.

The observation of Schultz (1953) that in some primates shafts are long and thin while in others they are short and thick has been supported here by allometric data. Positive allometry of segment length corresponds to negative allometry of segment widths, and negative allometry of segment lengths corresponds to positive allometry in segment widths. As Schultz hypothesized, however, this relationship was not expected to obtain between shaft width and body weight. Indeed, in relation to body size, allometric coefficients for shaft widths are much more uniform. These data lend credence to his explanation: that when selection acts to increase or decrease the length of a bone directly (without acting on overall body size), then the width of the bone remains adapted to the unchanged weight rather than to the changing length of the bone. Thus, as Gould (1967) reported for Pelycosaurus, shaft width is adaptive to weight.

V RESULTS: INTRASPECIFIC ALLOMETRY

1 Trunk and Limb Proportions

Table V.1 gives ratios of trunk and limb length variables to skeletal trunk length in six species: Aotus trivirigatus, Saimiri sciureus, Cebus apella, Alouatta caraya, A. senicula and A. palliata. Data for A. trivirigatus and S. sciureus, both members of monospecific genera, have appeared elsewhere (Tables III.1, III.2 and IV.1) and of the remaining four, those of particular interest are the three species of Alouatta. These data show that A. senicula and A. palliata have very long lumbar regions in comparison with A. caraya, in which the three trunk regions are of virtually equal length. Difference in lumbar length among these species is reflected in ratios of limb length to trunk length, showing that both A. senicula and especially A. palliata have relatively shorter limbs than A. caraya. Taking these data together, the greatest difference among the three exists between A. caraya and A. palliata: both have forelimbs and hindlimbs of approximately equal length but in A. palliata both sets of limbs are comparatively short.

ii Trunk and Limb Allometry

Table V.2 gives coefficients of allometry and correlation for trunk length and weight variables in the six species. It is immediately apparent that differences in allometric coefficients derived by the three methods are greater than those presented in the previous chapters, in which means of variables were used. Correlation coefficients are far lower and have a great effect on allometric coefficients generated by least squares in comparison with the other two methods. Also unlike the preceding intergeneric analyses, missing data disallows the use of the same specimens, and the same number of specimens, for all three methods of analysis. The results in this chapter are, therefore, presented very tentatively and discussed in general outline only.

Since it cannot be known how skeletal trunk length or thoraco-pelvic length body weight in four of the six species, neither of these variables can be distinguished as being a better expression of overall size than the other. Lumbar reduction has been shown (chapter III) to occur in larger platyrrhine genera but this is not necessarily the case among adults of different size within a species. It is equally possible that all three parts of the trunk in any species may scale isometrically with weight, in which case skeletal trunk length would be an

excellent body size variable. Toward gaining some idea of the allometry of different parts of the trunk, lumbar and pelvic lengths were scaled to thoracic length.

Table V.2 shows that, with the exception of A. senicula, lumbar length scales to thoracic length at a greater rate than does pelvic length, contrary to inter-generic allometry for these variables. In A. trivirigatus the allometric difference between the two lengths is the greatest, indicating that the already long lumbar region of this species among Platyrrhines is at least maintained, if not increased, with intraspecific size (or thoracic length) increase. In S. sciureus and in C. apella allometric coefficients to thoracic length are low, indicating a posterior trunk length reduction with thoracic increase. This is supported in both species by the allometry of the skeletal trunk length which decreases relatively with weight increase. To a lesser extent, reduction in posterior trunk length also occurs in the species of Alouatta. Thus, while most of these species do undergo lumbar length reduction with size increase (assuming that thoracic length scales approximately with overall size), as occurs inter-generically, this is usually accompanied by an even greater relative reduction in pelvic length.

Tables V.3 and V.4 give the results of allometric analysis of limb lengths for the six species. While the

allometry coefficients derived by the three methods vary greatly in some cases, nevertheless the relative order or ranking of the coefficients is the same by all three. This, then, is the only reliable feature of allometric analysis when using a highly variable sample.

In the two smallest species, A. trivirigatus and S. sciureus, forelimb and hindlimb lengths scale virtually isometrically with each other. Among the various allometric coefficients for these two species (Table V.3) there is evidence of slight positive allometry of forelimb length to hindlimb length. This difference is more apparent in C. apella, particularly in the allometric coefficients of limb lengths to thoraco-pelvic and skeletal trunk lengths. While the allometric coefficients of A. trivirigatus are either close to isometry or scale positively to body size, those of S. sciureus and C. apella are all negative to all three measures of body size. Negative allometry of limb lengths also characterizes the species of Alouatta. Among the three, however, there is one, A. palliata, in which the hindlimb length scales positively to the forelimb length. This species is also outstanding, however, in lacking significant correlation between forelimb length and thoraco-pelvic length.

Tables IV.5 through IV.10 give allometric coefficients of limb segment lengths and widths in detail for each of

the six species. These data demonstrate the now familiar allometric pattern wherein negative allometry of shaft lengths occurs with positive allometry of shaft widths. Strongly negative allometry of shaft lengths to thoracopelvic and to skeletal trunk lengths is ubiquitous in all but A. trivirgatus and these coefficients are matched by extremely high allometric coefficients of shaft widths.

iii Discussion and Summary

Analysis of six platyrrhine species was made difficult by the fragmentation of originally sizeable generic samples for Cebus and Alouatta. Given the paucity of museum collections for many species and subspecies, and the lack of agreement on allometric methodology, allometry on such a fine level of analysis is unrewarding. Contrary to intuitive reasoning, this is a case in which the narrower the focus, the lesser the precision of analysis.

The powerful effect of many sources of variability on small samples of narrow taxonomic focus is much reduced in taxonomically broader analyses. These sources include, for example, subspecific and geographic differences. Appendix I gives subspecies and locality designations for the skeletons measured and shows that each species sample is of multiple geographic origin and subspecific composition.

Another source of variation intraspecifically is sex, which was known for most skeletons. Initial division of species by sex, however, further reduced sample size, thus counteracting the possible reduction of variability by the division. Evidence in the literature on sexual dimorphism has suggested that a common pattern of sexual dimorphism exists not only among primates (Schultz 1938, 1956; Trotter 1975; Vilensky 1979; Wood 1976) but also in other mammals (Ondrias 1960). This is, essentially, that allometric rates are the same for both sexes of a species and that those perceptible differences in form are chiefly due to differences in the ultimate sizes achieved in each. Preliminary intergeneric analysis of the platyrrhine data by sex supported this generalization. One of the most emphatic conclusions made by Schultz (1973; Lumer and Schultz 1947) concerning relative limb length is that, far from being sexually dimorphic, the intermembral ratio is the least variable intraspecifically. For these reasons, analysis of allometry by sex was not pursued.

In addition to those sources of intraspecific variability already mentioned are individual differences, including the effects of disease, captivity, etc. Indeed, Schultz (1926, 1930, 1937, 1947, 1956, 1973) remarked on the "extraordinarily high" intraspecific and intrageneric variability in primates. Low correlation coefficients

may be taken as evidence of intraspecific sample variability (see Smith 1981a) as many variables are poorly correlated intraspecifically in contrast to the high correlations for the same variables in intergeneric analysis. Given this degree of internal variability,, the results obtained from analysis by different methods can only be very different as well. This is particularly true of major axis and reduced major axis methods as opposed to least squares.

Consequently, the allometric analysis of the six platyrrhine species can only be discussed in relative terms. While there were large differences in the values of allometric coefficients obtained by these three methods, the relative values of the coefficients to each other were preserved by each. On this basis a summary of the analyses follows for each species.

Aotus trivirgatus (Tables V.2, V.3 and V.5)

Proximal shafts scale positively to distal shafts, with the highest allometric coefficients in the humerus; larger individuals have slightly longer humeri, thus longer forelimbs. The limb lengths scale approximately with the positive (to thorax and pelvis) allometry of lumbar length, thus maintaining similar limb to trunk proportions in larger individuals.

Saimiri sciureus (Tables V.2, V.3 and V.6)

All trunk regions (to thoracic length and to weight) and all shaft lengths indicate very negative allometry. Both limb sets are relatively reduced with increasing body size. This is accompanied by greatly increased robusticity of shafts to their lengths. The result is diminution of all lengths without, however, change in intermembral proportions.

Cebus apella (Tables V.2, V.3 and V.7)

Allometry of both lumbar and pelvic lengths is negative to thoracic length though not so much as in S. sciureus. Forelimb lengths scale positively to hindlimb lengths, more so in the radius than in the humerus, but all segments scale negatively to body size, and increase in robusticity. The result is a shorter trunk and slightly longer forelimbs than hindlimbs in larger individuals of the species. As in A. trivirgatus, the limb lengths are more isometric with skeletal trunk length than with thoracopelvic length.

Alouatta caraya (Tables V.2, V.4 and V.8)

This species has a relatively shorter lumbar region than that of A. senicula or A. palliata (Table V.1). Yet the lumbar region of the species is allometrically more positive and, if anything, increases slightly in larger individuals. Allometry of forelimb length is

positive to hindlimb length, although all segment lengths scale negatively to body size.

Alouatta senicula (Tables V.2, V.4 and V.9)

In this species forelimb segments also scale positively to hindlimb segments, but much more so than in A. caraya. Hindlimb segments scale negatively in length but positively in diameter. Larger individuals of this species have relatively longer forelimbs, more robust hindlimbs, and shorter lumbar length.

Alouatta palliata (Tables V.2, V.4 and V.10)

Contrasting with both A. caraya and A. senicula, the allometry of forelimb segments in this species, the largest of the three, is negative to the hindlimb segments. Thus, larger individuals of this species have relatively shorter and more robust forelimbs than hindlimbs, with trunk length also somewhat reduced.

Stahl and Gummerson (1965) and others have pointed out that a small shift in the allometric coefficient can result in a change in form over a large size range. In some of the species presented here the possibility exists of considerable change in intermembral proportions over a given size range. One of these would be A. senicula with its distinct potential for forelimb elongation. However, intraspecific ranges of body size are not sufficient for the expression of such a potential difference even in

primates such as Alouatta and Cebus, two of the most sexually dimorphic Platyrrhines. Indeed, the negative length allometry to body size so common in these species may be a means of preventing excessive variation in proportions within the intraspecific body size range.

VI DISCUSSION AND CONCLUSIONS

This study investigates the relationship between body size and relative limb length in fifteen genera of New World primates. Evidence from Strepsirhini (Jungers 1979) and Catarrhini (Biegert and Maurer 1972; Corruccini 1978; Jungers 1982) has suggested that increase in body size is often associated with relative forelimb elongation even in very differently adapted groups. Cartmill (1974) has proposed an adaptive basis for this effect, and the present study determines if, and how, this may occur in the third extant primate infraorder, the Platyrrhini. Also of interest is how well platyrrhine functional and taxonomic subgroups may be allometrically distinguished from each other. Furthermore, the data provide an opportunity to test the biomechanically based model of elastic similarity (McMahon 1973). Allometric analysis was performed chiefly by means of a widely used multivariate method, Principal Components Analysis (of which the standardized first principal component provides the major axis solution of a generalized allometry equation), with additional analysis by two bivariate allometric methods:

reduced major axis and least squares. The results were given in three parts: allometry of body size, inter-generic limb allometry, and intraspecific allometry.

1 Estimation of Body Size

Since body weight, the preferred body size variable for allometry, was not available with most skeletons in this study, mean weights from an outside source (Rosenberger 1979) were used with means of variables for intergeneric analysis. This analysis initially included also skeletal trunk length (STL, sensu Biegert and Maurer 1972) and the comparison of these two body size estimates showed that skeletal trunk length is a compound variable and that its thoracic, lumbar and pelvic parts do not scale consistently with estimated mean generic body weights. While thoracic and pelvic lengths scale with a linear, though slightly positive, slope to weight, lumbar length scales positively to weight in small Platyrrhines but negatively in large Platyrrhines. This finding supports well-known observations (Krieg 1903; Schultz 1938, 1961; Schultz and Straus 1945; Erikson 1963; Rose 1975) on the trunk in primates: orthograde posture and locomotion are associated with lumbar reduction

The use of skeletal trunk length as a standard measure of body size thus invalidates the assumption of

allometric continuity. Jungers (1982) has shown that Biegert and Maurer's (1972) positive limb length allometry in Catarrhines can be attributed to their use of skeletal trunk length. In this group, as in Platyrrhines, lumbar length was negatively allometric. In Platyrrhines, this also occurs in larger genera: Atelinae, Cebus and perhaps less so in Pitheciinae. In Catarrhines, negative allometry of the lumbar region was found in hominoids and in the larger cercopithecoid monkeys. Further complicating Biegert and Maurer's results, according to both Corruccini (1978) and Jungers (1982), is their use of limb length to skeletal trunk length ratios as scaled to skeletal trunk length, violating the independence of the variables compared. Instead of using the skeletal trunk length, Corruccini relied upon the set of directional cosines of the standardized first Principal Component as a body size vector (Jolicoeur 1963b). This method has been criticized also (Jungers and German 1978), and the alternative used by Jungers (1982) was body mass, which permitted, as it did in the present platyrrhine study, an allometric analysis of the skeletal trunk prior to analysis of limb length allometry.

Therefore, the skeletal trunk length cannot be considered a body size estimate universally equivalent to body weight. In Platyrrhines the combined thoracic and pelvic lengths, which are not as adaptively variable as is

the lumbar region, are more appropriate for this purpose. These two truncal regions are likely to be indicative of overall body size, as: (a) the thoracic length, especially as defined by facet type, is indicative of the size of the thoracic cavity, which houses the cardio-respiratory organs, and (b) increase in pelvic length is indicative of increase in weight transferred to the hindlimbs. The thoraco-pelvic length was introduced as a potential alternative to overall body size estimation by skeletal trunk length, especially in the size allometry of groups having variable lumbar adaptation. But even this measure of body size is not universally applicable: Jungers (1982) showed variable and negative allometry of both thoracic (by rib-bearing definition) and sacral trunk lengths in hominoids, while the allometry of thoraco-pelvic length in Platyrrhines is not isometric with, but slightly positive to, body weight.

11 Limb Length Allometry

The allometry of limb segment lengths scaled to all three body size variables (body weight, skeletal trunk length and thoraco-pelvic length) reveals that limb segments within each limb scale similarly to each other throughout the Platyrrhini. The humerus and radius share very similar allometric coefficients within the forelimb,

as do the femur and tibia in the hindlimb. The forelimb exponents, however, are higher than those of the hindlimb, expressing positive allometry of forelimb length to hindlimb length in *Platyrrhini*.

In the forelimb, the radius scales slightly positively to the humerus, while in the hindlimb the femur scales positively to the tibia. Metacarpal and metatarsal lengths scale negatively to the more proximal shafts in their respective limbs, with the metacarpal length scaling more positively to the metatarsal.

Allometric analysis of subgroups of the *Platyrrhini* show, however, that relative elongation of the limbs, and of forelimbs in particular, is brought about in three ways:

1. Separation of the three ateline genera from the total of fifteen reveals only a slight relative forelimb elongation in the remaining twelve genera. Furthermore, in a group of only small *Platyrrhines*, the forelimb length scales slightly negatively to the hindlimb length. Allometry of shaft diameters suggest that between *Platyrrhines* of small and intermediate body size, relative forelimb elongation is produced by a relative reduction of hindlimb length in the larger genera.

2. This slight difference between forelimb and hindlimb slopes among most *Platyrrhines* is emphasized, however,

by Atelinae at the large end of the body size range. The relatively short hindlimbs of Alouatta and Lagothrix serve to depress the hindlimb slope, while the relatively long forelimbs of Ateles serve to elevate the forelimb slope.

3. The negative allometry of lumbar length in large Platyrrhines, most perceptibly in Atelinae, serves to elongate both sets of limbs.

Thus, as body size increases in Platyrrhines, both sets of limbs become elongated, with only slightly greater relative increase in forelimb length. The greatest relative difference in limb lengths is achieved by specializations in the lengths of the hindlimbs and forelimbs among the Atelinae, and strongly influences the allometric coefficients generated for these limbs in the Platyrrhini.

Biegert and Maurer (1972), Corruccini (1978) and Jungers (1982), all using different methods, have shown greater relative increase in forelimb length than hindlimb length with body size increase in Catarrhines. Biegert and Maurer argued that the limb proportions of certain hominoids may be attributed to body size increase on a common catarrhine allometric pattern (greater forelimb than hindlimb length increase with body size increase). Corruccini and, more recently and extensively, Jungers argued that allometric patterns in the Hominoidea are

sufficiently diverse and different from those of other Catarrhines that their body form cannot be explained by mere size allometry. Rather, they argued, hominoid body proportions result from different adaptations to a variety of different behaviors.

It is important to recognize that Biegert and Maurer did not separate their catarrhine sample into subgroups as done by both Corruccini and Jungers. Both these authors separated the Hominoidea in different ways (Corruccini: Chimpanzee, Gorilla, Man; Jungers: Pongidae, African pongids, Hylobates, et al.), thus reducing the taxonomic focus, and compared them to broader taxonomic divisions of primates (Corruccini: Cercopithecoidea, Ceboidea, Prosimii; Jungers: Catarrhini, Cercopithecoidea). In both cases internal group allometry in hominoids was quite different from that of the common catarrhine slopes.

Jungers found that in different hominoid subgroups most limb and trunk lengths scale negatively to body mass: in larger members of these groups the limbs are relatively shorter to body size than required by geometric similarity. This allometry exists in direct contradiction to the course that evolution must have taken in producing in each hominoid the extreme limb lengths that intermembral and limb to trunk length ratios describe. Equally importantly, however, and despite the negative allometry of limb length to mass, the forelimb in each case scales more positively

than does hindlimb length. Thus, whatever the relative reduction of limb lengths to body mass in these primates, allometry still produces a relatively longer forelimb than hindlimb length with body size increase.

Among the Cercopithecoidea, both authors found allometric exponents for limb lengths to be near isometry (to "body size" as well as to each other), with forelimb length slightly positive and hindlimb length slightly negative. Moreover, in all cases of hindlimb allometry they found that the tibia scales more negatively than other segment lengths and (in all but some hominoids, Jungers 1982) the radius more positively. These same allometric features are found in Platyrrhines.

Corruccini (1978) noted that Platyrrhines (Ceboidea) have more in common with cercopithecoids than with Catarrhines or with hominoids. Other similarities between the two groups of monkeys include the difficulty (as Corruccini mentioned for cercopithecoids) in distinguishing taxonomic subgroups by allometric data, and the fact that lumbar reduction is not universal (noted by Jungers for cecopithecoids) in the group but occurs in its large members.

It is evident, then, as both these authors asserted, that allometric patterns in hominoids and cercopithecoids are very different and that among different groups there

are major differences in limb proportions. Yet whatever the actual values of allometric coefficients on different taxonomic levels, relative forelimb lengths within these groups increase with body size in one way or another.

Biegert and Maurer (1972) did not deny the evolution of specialized adaptations and related proportions in the hominoids. Rather, they proposed a common foundation of greater relative forelimb than hindlimb length increase with body size, to which different hominoids have evolved exceptions. Results of the present platyrrhine investigation also suggest a dual-level mechanism of arboreal positional adaptation. Relative to both body size and to hindlimb length, the forelimb length in Platyrrhines increases at a gradual rate. Without the reduction in lumbar length in large Platyrrhines (increasing limb length to total trunk length) and the emphasis of platyrrhine limb length slopes created by Ateline specializations, this effect would be unremarkable. It is nevertheless discernible in several different combinations of genera. Locomotor specializations, insofar as they are expressed by limb proportions, are in contrast, expressed by more distinct deviations from these slopes.

Considering the diversity of adaptations represented by all Catarrhines and Platyrrhines, such results appear to be too general to be meaningful. It is common practice to view and to seek differences between differently

adapted primates in terms of specialization, hence there is no problem in focusing on the long forelimbs of atelines or of hominoids. Such a selective focus, however, obscures possible underlying adaptations shared more generally, such as gradual allometric forelimb increase. Cartmill (1974) has presented a possible explanation for such a widely occurring allometric phenomenon. He argued that increasing body size in arboreal primates produce potential mechanical inefficiency in maintaining and moving a body on a vertical support. To overcome this effect, the forelimbs must increase disproportionately to the hindlimbs.

According to his analysis of external forces acting on a body on a vertical support (supported by Bock and Winkler 1977), the feet exert a frictional force against the support which tends to rotate the caudal end of the body away from the support. The amount of force necessary to resist gravity (frictional force exerted at foot contact with support) disproportionately increases with increasing mass. Elongation of forelimbs permits a wider grasp around the support while permitting the trunk to lean away from the support. In this position the cranio-caudal weight transfer is directed in part against the support, relieving some of the force necessary at foot contact and resisting backward rotation of the trunk.

In other words, increasing body size imposes a common mechanical problem on arboreal primates to which a common solution is applied apart from, or in addition to, those adaptations specific to different arboreal niches. As this problem is so fundamental to arboreal primates, it is not relevant to insist on distinguishing adaptive types within this category as arguments against it. The best support of this model, and of viewing such a general level of adaptation, is that many very differently adapted primates show relative forelimb increase within their groups (within most combinations of Platyrrhines, Catarrhines, and many Strepsirhines). It is, instead, more useful to view forelimb elongation on this level as size-dependent fine-tuning within any arboreal positional adaptation, whether or not it may be considered specialized.

Some degree of forelimb elongation, therefore, is not directly related to any particular locomotor or positional adaptation but, rather, more generally to the arboreal habitat. When lumbar length reduction is additionally considered, a set of factors in the evolution of body form in primates may be suggested. Scurrying and springing locomotion is more efficient for small animals than for large (Brown et al. 1973) and necessitates a relatively long trunk and hindlimbs. Body size increase reduces the efficiency of this form of locomotion and, in

the arboreal context, leads to greater climbing locomotion.¹ Climbing is facilitated by longer limbs to trunk and by equalization of relative limb length; hence, relative increase in forelimb length and relative reduction in trunk length. This may be the important shift in the evolution of body form between smaller, more "primitive" primates and medium-sized "monkey-like" primates.

The most important change in Platyrrhines was reduction in vertebral length as a method of elongating both sets of limbs for better climbing ability and producing a more compact trunk. In addition to this, limb length was somewhat evened out by modest forelimb length increase associated with body size increase. To the extent that differentiation in limb length can be distinguished beyond this pattern, it may be viewed as adaptation to more specific locomotor behaviors. Some elongation of the forelimbs may apply as a prior condition in the evolution of adaptations to more specialized locomotor niches at larger body sizes.

¹The great exceptions to this generalization are the indriids which, rather than abandoning leaping, have maintained isometry of lumbar length and have further adapted (extreme elongation of hindlimbs) to a particular form of vertical clinging and leaping. Substrate composition in Malagasy dry forests, however, is better suited to supporting such large leaping primates, perhaps encouraging such adaptation, than most other forest types in which primates are found. Even in this locomotor niche, as Jungers (1982) showed, however, forelimbs tend to increase relative to body size within the group.

iii Ateline-Hominoid Parallels

The data presented here show that the Atelinae have comparatively longer forelimbs beyond the increment in forelimb length to body size exhibited by other Platyrrhines. The limb proportions evolved in the three genera studied here show that forelimb and hindlimb length in Alouatta and Lagothrix is very similar, with Lagothrix having a relatively shorter trunk. The forelimbs in Ateles are actually longer than the hindlimbs but the even greater difference between the spider monkey and Alouatta and Lagothrix is that both sets of limbs are considerably longer relative to trunk length.

Such features of ateline bodyform, and especially the frequent use of suspensory positional modes, have long been the bases for ateline-hominoid comparisons (Erikson 1963; Tuttle 1975; Stern 1976; Stern et al 1980). These comparisons have sought to discover morphological similarities in the presumed adaptation of these primates to forelimb suspension. (Oxnard 1963, 1967; Ashton and Oxnard 1964; Lewis 1974; Corruccini 1975c; Corruccini et al. 1975; Jenkins 1977; Rosenberger 1979; Stern et al. 1980). Recent interest in comparing atelines and hominoids has recognized the locomotor differences actually encompassed by these primates while still seeking adaptive and morphological correspondences.

Alouatta, for example, has been presented as a likely adaptive precursor type to Pongo (Stern 1971, 1976). Stern noted that Pongo is a large and slow acrobatic climber. Its very long forelimbs are required in climbing for the massive body sizes it attains. Stern maintained that Alouatta, a considerably smaller primate than Pongo, occupies a locomotor niche among Platyrrhines similar to that of Pongo among hominoids. Alouatta has also been likened to African ponids, whose forelimbs among the non-human hominoids are relatively shortest. The relevant features of this comparison also include large size and relatively robust build but comparatively low incidence of forelimb suspensory locomotion, in contrast to Pongo.

More comparable to hominoids, in particular to Hylobates (rather than the larger Symphalangus), is Ateles. In both primates both sets of limbs are very long and suspensory behavior is frequent. In Ateles the forelimbs are also used more extensively for suspensory behavior than they are in other atelines. Ateles does not, however, possess the extreme limb lengths of the gibbon nor its very great difference between forelimb and hindlimb lengths. The degree of limb lengthening to body size in Ateles has enabled suspensory locomotor behavior, but the almost equal length of the limbs as well as the presence of a fully prehensile tail, necessarily results in much more equal participation of both sets of limbs and tail in suspensory functions.

While seeking adaptive correspondences between the larger Platyrrhines and the hominoids is intuitively attractive, it is unlikely that any can be precisely delineated (Tuttle 1975). For example, despite certain hindlimb muscular similarity between Alouatta and Pongo (Stern 1971, 1976), the fact that both sets of limbs in Alouatta are quite short is undoubtedly functionally relevant to the fact that the locomotion of this primate is most frequently quadrupedal and pronograde. Moreover, suspensory modes in all three primates are uniquely dependent upon prehensile tail function. Indeed, suspensory behavior in Alouatta is performed largely by the hindlimbs and tail.

Given these differences between platyrrhine and catarrhine primates disposed to suspensory behavior, the real basis for seeking parallels has depended on three commonalities. Within their respective groups (Catarrhini and Platyrrhini) the hominoids and atelines have in common (a) suspensory behavior of some kind and in some degree, (b) relatively longer forelimbs to hindlimbs than other members of their group, and (c) the largest body sizes in their respective groups.

That the forelimbs do participate in suspensory locomotion has often masked the fact that in the hominoid case it is a function virtually exclusive to forelimbs, while

in atelines it is virtually equally shared with three other "limbs". In the same way hominoid-oriented emphasis on the intermembral ratio has ignored the equally important functional relationship between suspensory behavior and limb length relative to trunk².

With increase in body mass, the larger the trunk the longer must the limbs be in order to propel it in suspensory locomotion. Pongo attains quite a large trunk size and body weight, but even its very long forelimbs do not permit active brachiation but rather a versatile kind of climbing which includes suspensory posture and movement ("anti-prongrade", Stern 1971, 1976; "transferring", Tuttle 1975; "quadrumanous climbing", Fleagle 1977c). African pongids are not primarily known for forelimb suspensory locomotion at all although, and significantly, the smaller and younger members do so more readily. These primates have evolved large trunk sizes, large body mass, and only somewhat longer forelimbs than hindlimbs, all of which are more efficiently put to use in knuckle-

²Cartmill and Milton (1977) have further complicated the search for similarity with hominoid suspensory adaptation by introducing the slow-climbing locomotion of the Lorisinae as a model for hominoid precursor adaptation. These small primates have nearly equal limb lengths (IMI 88-92, Napier and Napier 1967) and very long, flexible trunks. It is this author's belief that the unique lack of floating phase in their locomotion results in an also unique utilization of the trunk and limbs (Dykyj, 1980).

walking. Hylobatids, having smaller body mass and exceptionally long limbs to trunk length have thus reduced their proportion of non-locomotor, or non-propulsive, mass more than any other primates. These features greatly reduce energy requirements for locomotion and facilitate speed and agility.

The functional ateline-hominoid comparison best works for Ateles and Hylobates, with the important difference in five-limb vs two-limb suspension between them (in consideration of which, the cartwheel-like suspensory locomotion of the spider monkey gives it its name). The greatest difference in proportions among the three atelines is in the lengths of limbs relative to the trunk rather than in the intermembral ratios. With a larger trunk, the limbs have more work to do to achieve the same locomotor agility. Suspensory behavior is known to be comparatively less frequent in Lagothrix than in Ateles. In Alouatta, with relatively the longest trunk in atelines, it is associated primarily with feeding posture rather than with locomotion, and is greatly dependent upon the tail (Mendel 1976).

Whether further body size increase in the atelines could lead to greater morphological and behavioral similarity to the hominoids (or, whether or not in their present body size, form and locomotor behavior the atelines

may be considered a hypothetically prior adaptive complex to that of the hominoids) cannot yet be judged. To answer this question, more extensive intrageneric and intra-specific data is required as well as better understanding of the differences between inter- and intraspecific allometry.

The sample sizes for Ateles and Lagothrix were too small to examine internally. Therefore, all that can be known about them at present is how their mean limb and trunk lengths compare with those of other primates and how these affect platyrrhine allometry. What effect increase in body size in either of these genera (or their species) would have on their limb lengths and resulting proportions cannot be judged from their current form or their position on platyrrhine slopes.

Only the Alouatta sample among atelines permitted an intraspecific allometric analysis. This tentatively showed (in relation to all three estimates of body size) that the three species are dissimilar in limb length allometry. Intraspecific patterns of allometry in Alouatta must lead to eventual differences in body proportions if body size were to increase substantially. In two of the three species studied, A. caraya and A. senicula, forelimb length would increase relatively and absolutely. In A. senicula this increase would be more acute as the allometry

of forelimb segments is very positive, while in A. caraya the increase would be less marked with the same size increase and due, rather, to a somewhat negative allometry of the hindlimb segments.

The indications for A. palliata, however, are that with body size increase, the forelimbs would decrease in length relative to hindlimbs. In this case, and contrary to limb allometry in Platyrrhines and in other primate groups, larger size would not be accompanied by forelimb increase. If this is an accurate estimate of the limb allometry in this species, then it is a very interesting subject for further study, both allometric and behavioral. Interesting also is the fact that A. palliata, the largest of these three species, also has the relatively longest trunk, or relatively shortest limbs, among them.

iv Functional and Taxonomic Considerations

Analysis of the means of variables for the remaining (non-ateline) genera indicates relatively little digression from the slopes. Certain genera show unusual elongation (for their size) (Aotus, Cacajao) or shortening (Saguinus) of both limb sets. In other genera one set of limbs may depart from a slope more than another set (long hindlimbs in Callimico and Pithecia; long forelimbs in Ateles and Leontopithecus). These deviations represent a more

distinctive (or specialized) degree of adaptation in these particular primates than in those whose limb lengths conform more closely to the slopes. They suggest that comparative behavioral study of these primates might be particularly revealing of adaptive differences.

Other than in the case of negative lumbar allometry, however, these deviations do not combine to reflect any familiar subgroupings of Platyrrhines. In fact, the body size gradient itself, by whatever body size estimate, lines up functional groups already familiar to us. In agreement with Erikson (1963) the small size end of this range includes the "springers": the Callitrichidae as well as Aotus, Callicebus and Saimiri (a "climber" in Erikson 1963, but a more frequent "leaper" in Fleagle and Mittermeier 1980). Among these small primates with long trunks, three are distinguished in having specialized trunk lengths by addition, or other numerical variation, of vertebrae to a presumed primitive (Schultz 1938, 1961; Schultz and Straus 1945; Erikson 1963; Thorington 1972; Ankel 1972) thoraco-lumbar combination: Aotus, Saimiri, and Callicebus. The effect of these changes, particularly in Aotus and Callicebus, has been to increase the functional lumbar length. While locomotor observations are incomplete for most Platyrrhines, evidence suggests that the use of this potentially greater lumbar flexibility is not equivalent

in these genera. Aotus has been observed to engage in much leaping and springing but Callicebus, having very similar body mass and relative limb and trunk lengths, has been observed to use these modes comparatively little (Pat Wright, personal communication). Thus, the morphological potential for springing movement exists in Callicebus but is engaged less. The same may be true of other primates, in which case it is even more interesting to determine the selective basis for such morphological, and presumed functional, similarities.

This group is followed along the size gradient by Pitheciinae, Cebus and Atelinae which are allometrically distinguished from the smaller group by their relative trunk length reduction. The limbs are consequently relatively longer than in the smaller primates, a condition which may be related to the greater incidence of climbing in these larger primates. Also characteristic in this group is more equal limb length which, as with lumbar reduction, is more pronounced in atelines. The pitheciines and Cebus together do not diverge greatly from allometric slopes for limb lengths although their values for hindlimb lengths (to weight and to thoraco-pelvic length) suggest some degree of the relative shortening that is more pronounced in Alouatta and Lagothrix.

Thus, the difference in lumbar allometry between small and large Platyrrhines is the most functionally

significant result of analysis. The allometry of limb length does not illuminate adaptations of the individual genera (each as a group of similarly adapted species) except insofar as certain primates diverge from the slopes. These are primates sufficiently different in their range and use of locomotor modes that they have evolved greater differences in proportions from other Platyrrhines. The slopes for limb lengths themselves show only small departures from isometry with body size (weight or thoraco-pelvic length). The differences effected in proportions in this way, and by virtue of the change in lumbar scaling in most Platyrrhines, are sufficient to account for a wide range of behavior.

If no functional or locomotor group uniformly departs from the platyrrhine slopes for limb and trunk lengths to size, neither does any taxonomic group. Slopes generated for length variables showed minor variations, none of which provided a basis for supporting any of the currently completing platyrrhine classifications over another.

The division of Platyrrhines by lumbar allometry is clearly not a taxonomic one since no other evidence suggests an alliance of Aotus, Saimiri and Callicebus together with Callitrichidae but without the inclusion of Cebus. With the effect of this allometric character removed, by using weight or thoraco-pelvic length for body size, allometry is conservative throughout the group.

Within subgroups, the differences in proportions among the small number of participating genera have greater effect on slopes; for example, the slopes for "Cebidae" (combining the Callitrichidae with Saimiri and Cebus, Rosenberger 1979) differ from Callitrichidae alone only for lumbar length. This effect is produced primarily by Cebus, whose shortened lumbar length depresses the slope for the entire group. With Saimiri and Cebus withheld from the traditional Cebidae (forming Rosenberger's "Atelidae"), there is again little allometric difference. In this case the absence of these two genera is little felt as Cebus is similar in position along the slopes to Pitheciinae while Saimiri is similar to Aotus and Callicebus. Because of the central position of these four primates on the scale of body size, and their overall conformity to the slopes, their segregation from the other genera to form a primitive platyrrhine group (Ford 1980b) also produces little variation in the resulting slopes.

Allometry of Platyrrhine limb and trunk lengths, therefore, does not readily sort out taxonomic subgroups. Only in lumbar length is there a "natural" subdivision and this is functionally, rather than taxonomically, significant. Of all the variables, lumbar length is most allometrically interesting in Platyrrhines. And of all the platyrrhines studied here, those most complex in this character are Aotus, Callicebus and Saimiri. These data

do not support Ford's (1980) relegation of these three genera, in addition to Cebus, to a primitive status among Platyrrhines.

While dwarfing figures in two of the current platyrrhine classifications (Cebuella in Rosenberger 1979, and the callitrichid group in Ford 1980a, b), the data from this study show no sign that this has occurred. None of the findings here suggest allometric effects of size reduction, either as having occurred within a genus or a group of genera. Experimental work on various mammals indicates that the possible allometric effects of dwarfism are manifold (Boettieger and Osborn 1938; Hersh 1941; Ferm and Kilham 1965; Cock 1966; Gould 1975b; Johnson 1978), and evolutionary dwarfism is itself difficult to recognize in all but a few cases (Marshall and Corruccini 1978; Gould 1975b). Thus, the data do not provide evidence in support of Ford's (1980) hypothesized dwarfing of the callitrichid primates, and for two reasons. The first is that the comparative allometry of dwarfism is entirely unknown even though lineage reduction in size is believed by some (Hayami, 1978; Marshall and Corruccini 1978) to occur, at least theoretically, as often as size increase. Secondly, allometric evidence given here shows that it is particularly in the callitrichids that a primitive or generalized vertebral structure and allometry is maintained, arguing conservatism at least in body form, of

this group.

v Intraspecific Allometry

Intraspecific analysis of adults of six species showed that on this level of allometry variables are often poorly correlated and more variable than those of higher taxa. High intraspecific variability in primates is well known (Schultz 1926, 1973; Gould 1975b; Larson 1978; Wood 1979a) confounding intuitive reasoning that a finer taxonomic focus leads to better expression of biological meaning than does a broader focus. Thus, the species is the smallest reproductively isolated taxonomic unit, but on this level individual variation as well as variation due the geographic, ecological, demographic and other factors has far greater effect on the data than it does in higher taxonomic levels (Wood 1979a).

More importantly, however, intraspecific and interspecific slopes rarely correspond to each other (Gray 1946; Bertalanffy and Pirozynski 1952; Gould 1966, 1971, 1975b, 1977; Larson 1978; Steudel, in press). In the present study, intraspecific allometry was variable and did not conform to the intergeneric slopes. In four of the species, however (Aotus trivirgatus, Cebus apella, Alouatta caraya and Alouatta senicula), the allometric exponents for the forelimb were greater than those for the hindlimb, while in two (Saimiri sciureus and Alouatta palliata) those of the

hindlimb were greater.

Thus, in four of the six species, larger adults possess relatively longer forelimbs than hindlimbs. While the effect of relative forelimb elongation repeats that found intergenerically, the allometric exponents for limb segments are dissimilar, indicating independent deviation of similar results. Most dissimilar between the two levels of comparison is the intraspecific predominance of negative allometry. In the four species lacking weights, lumbar (by facet type definition) and pelvic sections of the trunk were scaled to thoracic (by facet type definition) length and in all but two cases (positive lumbar to thoracic length in Aotus trivirgatus and Alouatta caraya) the allometric coefficients were negative. The morphological result of this is that among adults within the species, increase in thoracic length is accompanied by relative reduction in the lumbar and pelvic parts of the trunk.

Extreme in the incidence of intraspecific negative allometry are Saimiri sciureus and Cebus apella. With the exception of shaft diameters scaled positively to their lengths, all other trunk and limb variables scale negatively in these species, most so in S. sciureus. Thus, in large adults of these species all limb segments are relatively shorter and thicker, in addition to shorter trunk segments, than those of smaller adults. Or, conversely, larger adults of these two species, are proportionately

more massive than smaller adults. A similar interpretation was made by Jungers and Fleagle (1980) from a longitudinal study of two species of Cebus. They showed that C. apella gains mass at a greater rate than does C. albifrons, resulting in adults of heavier build. The allometry of limb segment lengths to weight was negative in both species, however, with those of C. apella more so than C. albifrons.

Within-group negative allometry has often been reported (Leutenegger 1973, 1976; Gould 1975a, b; Larson 1978; Jungers 1979, 1981 and others) in apparent contradiction to evidence of ratios. For example, in his extensive study of intraspecific allometry of selected primates including Homo sapiens, Boné (1953) concluded that segmental reduction typically occurs with body size increase, especially in New World monkeys (in his sample: Saimiri sciureus, Cebus capucinus and Ateles geoffroyi). Negative limb length allometry was also found in Hominoidea and its subgroups by Jungers (1982).

Such differences between intraspecific and interspecific allometry need not be viewed with great surprise, nor that intraspecific, or within-group, allometry is usually lower (Larson 1978). A species must remain adapted to its niche by maintaining the combination of traits which have evolved for the purpose, such as a particular set of body proportions. All species, however, range in body size

in greater or lesser degree due to such factors as sexual dimorphism, local food size, etc. Under such conditions, positive allometry within a species may disturb the most beneficial proportions of important segments of the body. Under positive allometry lengths would differ more widely than body mass, and in order to maintain the same body form throughout the species, variation in body size would be insupportable. Instead, body size is given a broad latitude in some species or groups (as among hominoids, Jungers 1982) and is expressed as negative allometry of body segments or, conversely, as positive allometry of body mass (Jungers and Fleagle 1980). Negative intraspecific (or intragroup) allometry permits relatively greater variation in body size without bringing about potentially hazardous changes in form. Larson (1978: 101) gave the same interpretation for low intraspecific scaling of organ weights in Macaca arctioides:

"low values for intraspecific slopes in organ-body weight relationships indicate that at a specified level of body weight, there is an optimal organ weight... which varies less than does body size itself".

Even so, most intraspecific analyses, small but distinct relative forelimb elongation accompanies weight increases in adjustment to increases of external forces acting on the arboreal body.

vi Allometry and Similarity Models

Geometric similarity requires that shaft diameters (widths) scale to shaft lengths^{1.00}, and that both scale to weight^{.33}. By the model of elastic similarity (McMahon 1973), shaft diameters should scale to shaft lengths^{1.5}, shaft diameters to weight^{.38} and shaft lengths to weight^{.24}.

The intergeneric allometric coefficients presented here for *Platyrrhini* conform to the model of elastic similarity in only one relation: that of shaft diameter to body weight. The range of exponents for most segments is narrow, and is in part due to differences in the results generated by different allometric methods. Thus, the range of allometric coefficients for all shaft diameters to body weight in *Platyrrhini* is 0.34 to 0.40 and includes coefficients derived by all three methods. The range of coefficients generated by one method alone is narrower: 0.36 to 0.40 by both major axis and reduced major axis, or 0.34 to 0.39 by least squares. In each case this range is distributed closer to the value of 0.38 (elastic similarity) than 0.33 (geometric similarity).

The ranges of allometric coefficients for shaft length to body weight in *Platyrrhini* are greater than those of shaft diameters, as well as being higher than required by either model (0.24 by elastic similarity, 0.33 by geometric similarity). Indeed, many of the allometric coefficients

for diameter to weight correspond to those of their shaft lengths scaled to weight. The intergeneric allometry of shaft diameters scaled to their lengths shows no approximation to the exponent of 1.5, as required by elastic similarity, but rather reveals a range about isometry. Where shaft lengths scale isometrically with either trunk length or thoraco-pelvic length, their diameters are also frequently isometric with trunk length or thoraco-pelvic length. Thus, the allometric coefficients most supportive of the elastic similarity model, shaft diameter to weight, may instead be correspondent to the positive allometry of most shaft lengths to weight.

In intraspecific allometry, many allometric coefficients of shaft diameters to shaft lengths are in the neighborhood of 1.50, as required by elastic similarity. However, the allometric coefficients of these same shaft lengths to body size variables are usually lower than those required by both models. The correspondence between the exponents for the diameters to shaft length with the required elastic similarity exponent, therefore, is circumstantial.

Unequivocal support for the elastic similarity model would require that shaft diameter scale to shaft length^{1.5} when shaft length scales to weight²⁴. Unequivocal support for the model of geometric similarity would be a demonstration of isometry between shaft diameter and shaft length

(diameter scaling to length¹) when shaft length scales to weight^{.33}. As is characteristic of models, however, their criteria are approximated, rather than precisely satisfied, in nature. In the present study of the Platyrrhini, allometry of shaft lengths, shaft widths and body weight demonstrates a closer conformity to the model of geometric similarity than to the model of elastic similarity.

McMahon's model depends upon a precise relationship between biomechanical parameters, such as resistance to bending in response to increase in weight or gravitational load, but which is obviously a more flexible one in arboreal and other mammals (see Maloiy and Alexander 1979). The allometry of segment lengths and diameters may well support such a model in groups whose locomotor adaptations approach the limits of flexibility, such as the ungulates. And while in such forms certain parameters of gait have also been shown to agree with the model, such as stride length and speed at the trot-gallop transition, these parameters would probably fail to do so in primates, whose locomotion is much more diversified.

The evolution of terrestrial quadrupedalism of ungulates has produced a limited set of well defined locomotor parameters (McMahon 1977b; Taylor 1977) and an equally well defined set of associated morphological specializations. But locomotor parameters of ungulate locomotion are

neither necessarily distinct nor relevant in a group like the primates. The arboreal habitat, to which primate locomotion is chiefly adapted, does not require and often does not permit stride regularly, full extension of limbs or great speed. Thus, the important locomotor parameter to the investigation of the model of elastic similarity, speed at trot-gallop transition, is not likely to be comparable in arboreal primates (Vilensky 1980). Since standard locomotor parameters are more difficult to isolate in primates, their relationship to allometric morphological parameters is also more difficult to gauge. The very generality of locomotor form and function in primates argues against any precise adherence to a similarity model. As Maloiy and Alexander (1979) suggest, the locomotor demands in many mammalian groups, as in primates, are probably well within the safe range of bone strength and can tolerate allometric variability (Currey 1977).

In Platyrrhines, shaft widths and lengths scale similarly with body weight. The allometry of shaft widths to shaft lengths diverges, however, from the allometry of shaft lengths to skeletal trunk length or to thoraco-pelvic length. Thus, the observations of Schultz (1953) on the inverse relationship of limb segment thickness and length are supported by platyrrhine allometry, but the effect is very general. On the intergeneric level, negative allometry of hindlimb elements in Alouatta, Lagothrix and other

large Platyrrhines is associated with positive allometry of the same shaft widths. Positive allometry in lengths of forelimb segments is associated with negative allometry of their widths. The slight positive allometry of shaft lengths in small Platyrrhines is matched by slight negative allometry in their widths. But the effect is most emphatically revealed in intraspecific allometry where very negative allometry of limb segment lengths to body size is accompanied by very positive allometry of their widths to their lengths. Schultz explained that when selection acts to elongate a limb bone without increasing overall body size, the width of that bone remains adapted to the relatively unchanged body mass or weight; thus the shaft becomes relatively thinner. Conversely, when a shaft length alone among other dimensions of the body is reduced by selection, it becomes relatively thicker because it still supports a relatively unchanged mass. The allometry of shaft lengths to body size, and in shaft widths to their lengths, therefore support both the observations and explanation of Schultz.

Intraspecific allometry of shaft widths expresses this effect less regularly, however, although it occurs in S. sciureus, C. apella, A. caraya and A. palliata: negative allometry of shaft lengths is accompanied by positive allometry of shaft widths. Again, intraspecific patterns are blurred by variability common on that level of analysis.

The intraspecific allometry of shaft widths, however, seems even more irregular than that of length variables.

There is no question that allometric patterns are more sharply defined on a broad scale of comparison. This is at least in part due to the greater ranges of body size on which to scale other dimensions. But such patterns emerge on the grand scale also because they may represent a broader tolerance of variation in some critical parameter (such as bone strength) that is only approached (and perceived) when the variability of small taxa is combined. Larson (1978;101) discovered greater intraspecific variation about isometry in organ weights of Macaca arctoides and concluded similarly that:

"(1) interspecific slopes represent those mechanical scaling criteria which insure maintenance of function over a wide range of body sizes; (2) intraspecific slopes reflect the variability permitted above and below this line at a given level of body size".

A shaft width hypothesis that is not supported by the platyrrhine data is that of Preuschoft and Weinmann (1973). These authors maintained that bone widths may decrease with increasing body size rather than increasing isometrically (as required by geometric similarity) or scaling positively to weight (as required by elastic similarity). The intergeneric evidence, as already stated, is toward isometry of shaft widths with shaft lengths and with weight. Intraspecifically, negative scaling

of diameter to body size (weight) occurs only in S. sciureus, together with negative scaling of virtually all lengths to body size. This is, however, hardly adequate supporting evidence. Preuschoft and Weinmann's (1972:249) own tabulation of selected catarrhine girth/weight ratios in support of their hypothesis, in fact, deny it. When their ratios for five primates are scaled against estimated body weights (Napier and Napier 1967), the ratio scales to weight^{.41}: positive rather than negative allometry. While the bases for reasoning that adaptation of internal diameter may increase bone strength without the aid of external diameter increase are well established, this does not seem to occur in most animals. It would be interesting to discover why a theoretical possibility fails to be realized; it is possible, for example, that generalizations from ontogenetic adaptation in bone strength are not entirely applicable to problems of evolutionary adaptation.

vii Ratios and Allometric Coefficients

In this work, the presentation of allometric data in each chapter is preceded by a review of relevant ratio data. It is clear that ratios and allometric coefficients do not correspond to each other (Jungers 1979) but both provide important information about body form.

Ratios of segment lengths are to be distinguished from allometric coefficients in that ratios are descriptive of the body structure of a group or individual at one time; they describe an existing mechanical system and are therefore functionally meaningful. To compare the forelimb length to hindlimb length is to suggest how much propulsive locomotor function might be shared by the limbs. Or, a comparison of the limb length to total trunk length indicates what proportion of the body mass is non-propulsive, thus requiring greater effort to transport; or, (cf. Grand 1972) how great an area around the trunk can be covered by the limbs. These sets of bodily dimensions have been favored by selection, in the evolution of their present functions, and the dimensions of their segments are the points on an allometric slope.

As different animals are also of different sizes, the comparative study of ratio data has suffered from the difficulties of separating differences in shape from the effects of difference in size. An allometry coefficient describes how much change in a dimension is incremented with change in size in a group of species, individual, etc. Like the correlation coefficient, (Smith 1980), however, it has not guaranteed biological significance.

For this reason a similarity model is important in allometry, as a point of comparison and as an explanatory foundation. The deviation of a slope from isometry

suggests that factors other than differences in body size among the individuals or taxa under study have acted to result in the position of the points on the slope. Such an explanation is also relevant for an individual point diverging from an isometric slope. But the allometric coefficient has no direct relationship to the individual points from which it is derived. Unlike the ratio, which describes a static condition, the allometric coefficient describes change within a set of such conditions.

Furthermore, allometry, as opposed to isometry, changes proportions and, to the extent that limb and trunk proportions represent mechanically significant lever length relationships, potentially alters their functions. Unless isometry obtains among length segments, selection for increase in body size ultimately involves changes in positional behavior. Thus, an allometric coefficient, unlike the ratio, may bear little relevance to present function but is indicative of potentially significant changes in function from the present condition.

vii Methods of Allometric Analysis

Three methods of allometry were used to determine allometric coefficients: major axis (using the multivariate Principal Components solution of Jolicoeur 1963b), reduced major axis, and least squares. The multivariate major axis, and least squares. The multivariate major axis method has

the advantage that many variables may be analyzed together. Where variables are more diverse than those analyzed here, other aspects of the analysis may be of equal interest. The most recent and extensive criticism of this method was by Jungers and German (1978) who specified several problems. The present study has avoided most of these, such as using the first component in place of a size variable: in this study three body size variables were used. Another criticism, that the coefficients derived differ with the composition of variables in the analysis, was virtually eliminated by the use of means of variables in intergeneric analysis.

While the use of the multivariate major axis solution was thus better supported for intergeneric analyses, reduction of sample size by missing data, as well as inherent intraspecific variability, strongly affected intraspecific multivariate analysis.

The bivariate methods, reduced major axis and least squares, are easily computed, but not efficiently for large data sets. While much has been written about the statistical parameters of these two methods, in computation they are distinguished by the correlation coefficient. A high coefficient produces very similar results among all three methods. Indeed, despite the theoretical differences underlying each of these methods, the use of highly correlated intergeneric means of variables virtually disposes

of differences among them in the results. By contrast, the intraspecific allometric coefficients derived by these methods varied considerably and were, therefore, treated very tentatively in discussion.

Similarity of allometric coefficients by different methods lends confidence in the results but many data cannot be analysed using means of variables. Since none of the methods is free of criticism and none can claim universal preference, the sometimes large differences in allometric coefficients detract from the utility of allometric analysis. This is serious consideration in any attempt to analyse data in relation to geometric similarity. Isometric values are specific but variation in admittedly imperfect methodology, in addition to the many uncontrolled sources of variability (such as in intraspecific analysis) in the data, lead to ambiguous results. Given these persistent problems in allometry, discussion can safely regard only the relative values of allometric coefficient, not the absolute.

ix Conclusions

1. The limb length and body size relationship in *Platyrrhines* is affected by three allometric factors:

- a. With increasing body size, forelimb lengths increase at a greater rate than hindlimb

lengths in Platyrrhines. This is demonstrated in different taxonomic subgroups of genera as well as intraspecifically. As body size increases from small Platyrrhines to those of intermediate body size, however, the relative increase in forelimb length is very small.

- b. Apart from this allometric discrepancy, different adaptations in body proportions of Alouatta, Lagothrix, and Ateles produce relatively even longer forelimbs in this largest-bodied subfamily, further separating the higher forelimb, and lower hindlimb slopes in Platyrrhines.
- c. The most outstanding allometric character in platyrrhine allometry is lumbar length, which scales positively in small (branch running, walking and springing primates) and negatively in large (climbing and suspensory) Platyrrhines with respect to body size. The effect of this is to elongate both sets of limbs to the trunk, with increasing body size, in large bodied Platyrrhines

2. Limb and trunk allometry has primarily functional, rather than taxonomic, significance in Platyrrhines. Allometry

in Platyrrhines is consistent and conservative in all length variables except lumbar length. However, the allometry of this variable does not clarify the taxonomic affinities of those primates of greatest interest in current classifications: Aotus, Callicebus, Saimiri and Cebus. The evidence of vertebral composition and allometry in these four primates, however, argues against a primitive status relative to other platyrrhines.

The allometry of lumbar length is positive in small, and negative in large, Platyrrhines. This sharply separates primates adapted to branch walking, running and springing from those adapted to climbing and suspensory positional modes.

3. The elastic similarity model is apparently not as mechanically relevant to primate allometry as it may be to other, terrestrially adapted, mammals. Allometry coefficients for both shaft lengths and diameters to body size more closely approximate exponents corresponding to geometric similarity than to those of elastic similarity.

4. Allometry of shaft lengths to body size and of shaft widths to their respective lengths demonstrates that when shaft lengths scale non-isometrically (positively or negatively to body weight), their widths do not increase or decrease correspondingly but rather scale inversely with their length (negatively or positively, respectively, to

their lengths). When shaft lengths are increased or decreased without alteration of overall body size, therefore, their shaft widths remain adapted to the load imposed on them by body mass.

TABLES

<u>sy</u>	<u>genus</u>	<u>N</u>	<u>M</u>	<u>F</u>	<u>species</u>	<u>N</u>	<u>M</u>	<u>F</u>
A	<u>Alouatta</u>	70	21	29	<u>senicula*</u>	34	7	16
					<u>caraya *</u>	23	14	8
					<u>palliata*</u>	12	2	2
					<u>belzebul</u>	1		1
B	<u>Aotus</u>	21	7	10	<u>trivirigatus*</u>	21	7	10
C	<u>Ateles</u>	18	5	5	<u>paniscus</u>	1	1	
					<u>belzebuth</u>	2	1	1
					<u>geoffroyi</u>	5		2
D	<u>Cacajao</u>	14	3	2	<u>rubicundus</u>	3	2	1
E	<u>Callicebus</u>	19	11	5	<u>moloch</u>	11	5	3
					<u>torquatus</u>	1		1
F	<u>Callimico</u>	4	2	2	<u>goeldi</u>	4	2	2
G	<u>Callithrix</u>	24	9	9	<u>jacchus</u>	6	1	
					<u>argentata</u>	2		
					<u>chrysoleuca</u>	1		1
H	<u>Cebuella</u>	18	11	5	<u>pygmaea</u>	18	11	5
I	<u>Cebus</u>	37	23	14	<u>apella*</u>	22	15	7
					<u>albifrons</u>	7	3	4
					<u>nigrivittatus</u>	8	5	3
J	<u>Chiropotes</u>	11	3	6				
K	<u>Lagothrix</u>	18	9	4	<u>lagotricha</u>	6	3	3
L	<u>Leontopithecus</u>	2		1	<u>rosalia</u>	1		1
M	<u>Pithecia</u>	13	4	4	<u>pithecia</u>	5	2	2
N	<u>Saguinus</u>	39	11	13	<u>fuscicollis</u>	1	1	
					<u>illigeri</u>	2		2
					<u>melanoleucas</u>	1	1	
					<u>midas</u>	2	1	1
					<u>mystax</u>	3	3	
					<u>geoffroyi</u>	5	1	
					<u>leucopus</u>	4		2
O	<u>Saimiri</u>	25	13	12	<u>sciureus*</u>	25	13	12
		<u>333</u>	<u>132</u>	<u>119</u>		<u>237</u>	<u>101</u>	<u>90</u>

Table II.1 List of genera and species used in this study; sy, symbol for genus used in plots; N, number of skeletons measured; M, males; F, females; *, used for species analysis.

<u>Rosenberger 1979</u>				<u>Napier and Napier 1967</u>		
<u>genus</u>	<u>species</u>	<u>N</u>	<u>$\bar{X}_g$</u>	<u>species</u>	<u>N</u>	<u>$\bar{X}_g$</u>
<u>Callimico</u>	<u>goeldi</u>	11	481	<u>goeldi</u>	11	472
<u>Callithrix</u>	<u>jacchus</u>	14	329	<u>sp.</u>	13	225
<u>Saguinus</u>	<u>midas</u>	12	588	<u>sp.</u>	15	348
<u>Leontopithecus</u>	<u>rosalia</u>	3	610	<u>rosalia</u>	2	517
<u>Callicebus</u>	<u>torquatus</u>	15	1139	<u>moloch</u>	1	681
<u>Aotus</u>	<u>trivirigatus</u>	14	746	<u>trivirigatus</u>	4	969
<u>Saimiri</u>	<u>sciureus</u>	10	795	<u>sciureus</u>	19	700
<u>Pithecia</u>	<u>sp.</u>	7	2487	<u>sp.</u>	11	1492
<u>Chiropotes</u>	<u>satanas</u>	19	2476	<u>sp.</u>	2	2950
<u>Cebus</u>	<u>capucinus</u>	13	3083	<u>sp.</u>	18	2235
<u>Alouatta</u>	<u>senicula</u>	14	6049	<u>sp.</u>	8	6556
<u>Lagothrix</u>	<u>lagotricha</u>	8	6875	<u>sp.</u>	14	6275
<u>Ateles</u>	<u>belzebuth</u>	15	8055	<u>sp.</u>	3	6002

Table II.2 Comparison of mean gram body weights ($\bar{X}_g$) for thirteen platyrrhine genera from two external sources (Rosenberger 1979; and Napier and Napier 1967); N, number of specimens for each mean weight. Log-transformed matched pair t test: $t = 2.05$, n.s. ($p > 0.05$); $r = 0.9738$, $p < 0.001$.

	I		II	
A. Major Axis	<u>x=WT (N=58)</u>		<u>x=WT (N=15)</u>	
	<u>r</u>	<u>b</u>	<u>r</u>	<u>b</u>
STL	0.9603	0.24	0.9599	0.31
ThF	0.9611	0.33	0.9888	0.37
Pe1	0.9784	0.39	0.9873	0.41
B. Least Squares				
	<u>r</u>	<u>b</u>	<u>r</u>	<u>b</u>
STL	0.9613	0.37 (N=57)	0.9599	0.30
ThF	0.9603	0.59 (N=59)	0.9888	0.37
Pe1	0.9777	0.53 (N=58)	0.9873	0.41

Table II.3 Allometry of selected variables using internal and external sources of body weight data; A, using the multivariate major axis method; B, using the bivariate least squares method; I, individual body weights from this study combining Alouatta, Cebus and Saimiri only; II, mean body weights from Rosenberger (1979) for twelve platyrrhine genera combined with mean weights of Alouatta, Cebus and Saimiri from this study.

<u>genus</u>	<u>a</u>	<u>b</u>	<u>c</u>	<u>d</u>	<u>e</u>	<u>f</u>
<u>Ateles</u>	8055	32.81	8	18	14/4	12/6
<u>Lagothrix</u>	6875	33.13	16	18	14/4	12/6
<u>Alouatta</u>	6709	33.98	53	19	14/5	12/7
<u>Cebus</u>	2764	27.25	22	19	14/5	11/8
<u>Cacajao</u>	2400	29.69	10	19	14/5	11/8
<u>Chiropotes</u>	2476	26.83	8	19	13/6	10/9
<u>Pithecia</u>	2487	26.16	9	19	13/6	10/9
<u>Callimico</u>	481	16.26	2	19	13/6	10/9
<u>Callithrix</u>	329	14.11	17	19	13/6	10/9
<u>Cebuella</u>	125	8.93	7	19	13/6	10/9
<u>Leontopithecus</u>	610	17.29	2	19	13/6	10/9
<u>Saguinus</u>	588	15.64	33	19	13/6	10/9
<u>Callicebus</u>	1140	24.18	17	19	12/7	9/10
<u>Saimiri</u>	927	19.97	22	20	13/7	11/9
<u>Aotus</u>	746	23.01	21	22	14/8	11/11

Table III.1 Number of thoracic and lumbar vertebrae of Platyrrhines in this study; a, mean gram body weight; b, mean skeletal trunk length; c, number of skeletons; d, modal number of thoraco-lumbar vertebrae; e, modal numbers of thoracic and lumbar vertebrae using rib-bearing definition; and f, using facet-type definition.

<u>genus</u>	<u>ThF/STL</u>	<u>LuF/STL</u>	<u>Pel/STL</u>	<u>ThF/LuF</u>
<u>Ateles</u>	35	27	40	12/6
<u>Lagothrix</u>	33	33	34	12/6
<u>Alouatta</u>	32	37	31	12/7
<u>Cebus</u>	30	41	29	11/8
<u>Cacajao</u>	30	42	27	11/8
<u>Chiropotes</u>	29	47	24	10/9
<u>Leontopithecus</u>	28	48	24	10/9
<u>Cebuella</u>	26	49	25	10/9
<u>Saguinus</u>	28	49	23	10/9
<u>Pithecia</u>	27	50	23	10/9
<u>Callithrix</u>	27	50	23	10/9
<u>Callimico</u>	27	50	23	10/9
<u>Saimiri</u>	27	50	23	11/9
<u>Aotus</u>	24	54	22	11/11
<u>Callicebus</u>	24	55	20	9/10

Table III.2 Ratios among parts of the skeletal trunk using facet-type definition of thoracic (ThF) and lumbar (LuF) vertebrae; STL, skeletal trunk length; Pel, pelvic length; ThF/LuF, ratio of modal numbers of thoracic and lumbar vertebrae; genera arranged in descending order of LuF.

<u>genus</u>	<u>ThR/STL</u>	<u>LuR/STL</u>	<u>ThR/LuR</u>
<u>Ateles</u>	42	20	14/4
<u>Lagothrix</u>	44	22	14/4
<u>Alouatta</u>	42	27	14/5
<u>Cebus</u>	41	30	14/5
<u>Cacajao</u>	39	34	14/5
<u>Chiropotes</u>	41	35	13/6
<u>Cebuella</u>	39	36	13/6
<u>Callimico</u>	39	37	13/6
<u>Pithecia</u>	40	37	13/6
<u>Callithrix</u>	39	38	13/6
<u>Leontopithecus</u>	36	40	12/7
<u>Saguinus</u>	38	40	12/7
<u>Saimiri</u>	36	41	13/7
<u>Aotus</u>	34	43	14/8
<u>Callicebus</u>	36	44	12/7

Table III.3 Ratios among thoracic (ThR), lumbar (LuR) and skeletal trunk (STL) lengths using rib-bearing definition of vertebrae; ThR/LuR, ratio of modal numbers of thoracic and lumbar vertebrae; genera arranged in descending order of LuR.

x=WT		MA		RMA		LSQ	
Y	r	b	a	b	a	b	a
STL	0.9599	0.31	0.37	0.31	0.37	0.30	0.40
ThF	0.9888	0.37	-0.36	0.37	-0.36	0.37	-0.36
ThR	0.9842	0.34	-0.13	0.34	-0.13	0.34	-0.13
LuF	0.6977*	0.19	0.40	0.18	0.43	0.18	0.43
LuR	0.5964*	0.17	0.34	0.16	0.37	0.16	-0.37
Pel	0.9873	0.42	-0.56	0.42	-0.55	0.41	-0.53
ThP	0.9906	0.39	-0.14	0.39	-0.14	0.39	-0.14

Table III.4 Allometry of mean trunk length variables to body weight using three methods of allometry: Major axis (MA), reduced major axis (RMA) and least squares, (LSQ); WT, weight; STL, skeletal trunk length; ThF, thoracic length (facet type definition); ThR, thoracic length (rib-bearing definition); LuF, lumbar length (facet type definition); LuR, lumbar length (rib-bearing definition); Pel, pelvic length; ThP, thoraco-pelvic length; r, correlation coefficient; a, log intercept; *, r = not significant ($p > 0.05$), all other $r = p < 0.001$.

LARGE

<u>y</u>	<u>r</u>	<u>MA</u>		<u>RMA</u>		<u>LSQ</u>	
		<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>
STL	0.9077	0.19	0.79	0.18	0.83	0.18	0.83
ThP	0.9470	0.39	-0.14	0.39	-0.14	0.37	-0.07
ThF	0.9378	0.31	-0.15	0.32	-0.19	0.30	-0.11
LuF	-0.6760*	0.18	0.42	0.17	0.45	0.17	0.45
Pel	0.9465	0.47	-0.75	0.47	-0.75	0.45	-0.66

x = WT

SMALL

<u>y</u>	<u>r</u>	<u>MA</u>		<u>RMA</u>		<u>LSQ</u>	
		<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>
STL	0.9641	0.45	0.00	0.46	-0.03	0.44	0.03
ThP	0.9749	0.41	-0.19	0.41	-0.19	0.40	-0.17
ThF	0.9806	0.42	-0.50	0.42	-0.50	0.41	-0.47
LuF	0.9447	0.51	-0.46	0.52	-0.48	0.49	-0.41
Pel	0.9613	0.40	-0.50	0.40	-0.05	0.38	-0.44

x = WT

Table III.5 Allometry of mean trunk length variables in LARGE and SMALL Platyrrhines, r, correlation coefficient; b, allometric coefficient; a, log intercept; WT, mean weight; STL, skeletal trunk length; ThP, thoracopelvic length; ThF, thoracic (by facet) length; LuF, lumbar (by facet) length; Pel, pelvic length; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; * $p > 0.05$, all other $r = p < 0.001$.

GGS				SMF		
<u>y</u>	<u>r</u>	<u>b</u>	<u>a</u>	<u>r</u>	<u>b</u>	<u>a</u>
STL	0.9086	0.20	0.73	0.8854	0.32	0.32
ThP	0.9684	0.39	-0.17	0.9609	0.39	-0.15
ThF	0.9505	0.32	-0.22	0.9372	0.37	-0.37
LuF	-0.4990*	0.25	0.19	0.4711*	0.25	0.18
Pel	0.9744	0.47	-0.77	0.9748	0.42	-0.56

ALR-A				ALR-C		
<u>y</u>	<u>r</u>	<u>b</u>	<u>a</u>	<u>r</u>	<u>b</u>	<u>a</u>
STL	0.9328	0.17	0.87	0.9474	0.31	0.36
ThP	0.9722	0.37	-0.07	0.9670	0.39	-0.15
ThF	0.9536	0.32	-0.19	0.9622	0.37	-0.37
LuF	-0.7858*	0.16	0.52	0.8797	0.14	0.51
Pel	0.9775	0.41	-0.52	0.9666	0.42	-0.56

x = WT

Table III.6 Allometry of mean trunk length variables in four taxonomic subgroups of Platyrrhini; GGS, traditional Cebidae of Simpson (1945); SMF, derived Platyrrhines of Ford (1980); ALR-A, "Atelidae" of Rosenberger (1979); ALR-C, "Cebidae" of Rosenberger (1979); STL, skeletal trunk length; ThP, thoraco-pelvic length; ThF, thoracic (by facet) length; LuF, lumbar (by facet) length; Pel, pelvic length; WT, mean body weight; r, correlation coefficient; b, allometric coefficient derived by the major axis method; a, log intercept; *, r = p > 0.05, all other r = p < 0.001.

	<u>genus</u>	<u>WT</u>	<u>IMI</u>	<u>FORE</u> <u>STL</u>	<u>HIND</u> <u>STL</u>
A	<u>Cebuella</u>	125	82	70	86
	<u>Callithrix</u>	329	75	62	82
	<u>Callimico</u>	481	71	64	90
	<u>Saguinus</u>	588	76	63	83
	<u>Leontopithecus</u>	610	88	72	82
	<u>Aotus</u>	746	75	63	84
	<u>Saimiri</u>	927	80	69	86
	<u>Callicebus</u>	1140	75	59	79
B	<u>Cacajao</u>	2400	83	80	96
	<u>Chiropotes</u>	2476	81	75	93
	<u>Pithecia</u>	2487	75	73	97
	<u>Cebus</u>	2764	82	77	95
C	<u>Alouatta</u>	6709	97	86	88
	<u>Lagothrix</u>	6875	99	96	97
	<u>Ateles</u>	8055	106	126	119

Table IV.1 . Ratios of Intermembral and Trunk Lengths in Platyrrhini; A, small body size; B, intermediate body size; C, large body size; WT, mean gram body weight; IMI, intermembral index; Fore/STL, ratio of forelimb length to skeletal trunk length; Hind/STL, ratio of hindlimb length to skeletal trunk length.

A.			MA		RMA		LSQ	
	<u>y</u>	<u>r</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>
HL		0.9790	0.43	-0.42	0.43	-0.36	0.42	-0.33
RL		0.9776	0.44	-0.42	0.44	-0.42	0.43	-0.46
McL		0.9737	0.36	-0.82	0.37	-0.85	0.36	-0.82
FL		0.9763	0.37	-0.15	0.39	-0.16	0.38	-0.13
TL		0.9781	0.35	-0.06	0.35	-0.06	0.34	-0.03
MtL		0.9468	0.29	-0.41	0.29	-0.41	0.28	-0.38

x = WT

B.								
HL		0.9884	1.08	-0.24	1.09	-0.26	1.08	-0.24
RL		0.9846	1.10	-0.31	1.11	-0.31	1.10	-0.31
McL		0.9322	0.91	-0.66	0.95	-0.70	0.89	-0.64
FL		0.9766	0.94	-0.02	1.00	-0.09	0.97	-0.06
TL		0.9657	0.83	-0.08	0.89	-0.02	0.86	-0.05
MtL		0.9933	0.73	-0.29	0.74	-0.30	0.74	-0.30

x = ThP

Table IV.2 Allometry of mean limb segment lengths scaled to (A) mean weight and to (B) mean thoraco-pelvic length; a, log intercept; b, allometric coefficient; r, correlation coefficient; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; HL, humerus length; RL, radius length; McL, metacarpal III length; FL, femur length; TL, tibia length; MtL, metatarsal III length; WT, body weight; ThP, thoraco-pelvic length; all $r = p < 0.001$.

A. ALL			MA		RMA		LSQ	
<u>y</u>	<u>x</u>	<u>r</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>
Fore	ThP	0.9880	1.08	0.05	1.10	0.03	1.09	0.04
Hind	ThP	0.9732	0.89	0.34	0.95	0.27	0.93	0.30
Fore	STL	0.9652	1.41	-0.68	1.38	-0.64	1.33	-0.57
Hind	STL	0.9777	1.15	-0.24	1.19	-0.30	1.16	-0.26
Fore	WT	0.9847	0.43	-0.13	0.43	-0.13	0.43	-0.13
Hind	WT	0.9762	0.37	0.14	0.37	0.14	0.37	0.14
B. NOATELS								
Fore	ThP	0.9924	1.05	0.08	1.05	0.08	1.04	0.09
Hind	ThP	0.9890	1.03	0.20	1.03	0.20	1.02	0.21
Fore	STL	0.9737	1.15	-0.36	1.16	-0.37	1.1	-0.33
Hind	STL	0.9860	1.13	-0.22	1.12	-0.22	1.10	-0.19
Fore	WT	0.9782	0.42	-0.10	0.42	-0.10	0.41	-0.08
Hind	WT	0.9789	0.41	0.03	0.41	0.03	0.40	0.06

Table IV.3 Allometry of mean forelimb and hindlimb lengths to three mean estimates of body size; A, for the group ALL (all fifteen genera); B, for the group NOATELS (all genera excluding atelines); a, log intercept; b, allometric coefficient; r, correlation coefficient; MA, major axis method; RMA, reduced major axis; LSQ, least squares method; Fore, forelimb length; Hind, hindlimb length; ThP; thoraco-pelvic length; STL, skeletal trunk length; WT, body weight; all $r = p < 0.001$.

<u>y</u>	<u>r</u>	<u>MA</u>		<u>RMA</u>		<u>LSQ</u>	
		<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>
HL	0.9249	0.46	-0.53	0.43	-0.42	0.40	-0.31
RL	0.9292	0.54	-0.85	0.49	-0.67	0.46	-0.56
FL	0.8758	0.27	0.21	0.24	0.32	0.21	0.43
TL	0.8412	0.27	0.17	0.24	0.28	0.20	0.43

x = WT

HL	0.9656	1.18	-0.36	1.15	-0.32	1.11	-0.27
RL	0.9571	1.36	-0.62	1.27	-0.51	1.22	-0.45
FL	0.9169	0.69	0.31	0.66	0.35	0.60	0.43
TL	0.8785	0.68	0.29	0.64	0.34	0.57	0.43

x = ThP

Table IV.4 Allometry of mean limb segment lengths in LARGE Platyrrhines; a, log intercept; b, allometric coefficient; r, correlation coefficient; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; HL, humerus length; RL, radius length; FL, femur length; TL, tibia length; WT, body weight; ThP, thoraco-pelvic length; all $r = p < 0.001$.

<u>y</u>	<u>r</u>	<u>MA</u>		<u>RMA</u>		<u>LSQ</u>	
		<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>
HL	0.9649	0.41	-0.36	0.40	-0.33	0.41	-0.36
RL	0.9407	0.43	-0.45	0.41	-0.40	9.38	-0.32
FL	0.9429	0.45	-0.38	0.43	-0.33	0.41	-0.27
TL	0.9603	0.43	-0.32	0.41	-0.27	0.40	-0.24

x = WT

HL	0.9879	1.00	-0.17	1.00	-0.17	0.98	-0.16
RL	0.9751	1.03	-0.23	1.02	-0.22	0.99	-0.19
FL	0.9831	1.09	-0.16	1.07	-0.14	1.05	-0.12
TL	0.9920	1.05	-0.12	1.03	-0.10	1.03	-0.10

x = ThP

Table IV.5 Allometry of mean limb segment lengths in SMALL Platyrrhines; a, log intercept; b, allometric coefficient; r, correlation coefficient; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; HL, humerus length; RL, radius length; FL, femur length; TL, tibia length; WT, body weight; Thp, thoraco-pelvic length; all $r = p < 0.001$.

<u>GGS</u>		<u>MA</u>		<u>RMA</u>		<u>LSQ</u>	
<u>y</u>	<u>r</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>
Fore	0.9606	0.44	-0.17	0.44	-0.17	-0.42	-0.10
Hind	0.9164	0.32	0.32	0.32	0.32	0.29	0.42
<u>SMF</u>							
Fore	0.9874	0.44	-0.45	0.43	-0.42	0.43	-0.42
Hind	0.9829	0.37	0.13	0.37	0.13	0.36	0.16
<u>ALR-C</u>							
Fore	0.9830	0.41	-0.09	0.40	-0.06	0.39	-0.03
Hind	0.9862	0.39	0.07	0.39	0.07	0.38	0.10
<u>ALR-A</u>							
Fore	0.9586	0.44	-.16	0.41	-0.06	0.40	-0.02
Hind	0.9417	0.28	0.46	0.27	0.49	0.25	0.56

x = WT

Table IV.6 Allometry of mean forelimb and hindlimb lengths in four taxonomic subgroups of Platyrrhini; GGS, traditional Cebidae of Simpson (1945); SMF, derived Platyrrhines of Ford (1980); ALR-C, "Cebidae" of Rosenberger (1979); ALR-A, "Atelidae" of Rosenberger (1979); Fore, forelimb length; Hind, hindlimb length; WT, mean body weight; a, log intercept; b, allometric coefficient; r, correlation coefficient; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; all $r = p < 0.001$.

<u>CGS</u>		<u>MA</u>		<u>RMA</u>		<u>LSQ</u>	
<u>y</u>	<u>r</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>
Fore	0.9723	1.16	-0.05	1.15	-0.03	1.12	0.00
Hind	0.9604	0.84	0.41	0.83	0.42	0.80	0.46
<u>SMF</u>							
Fore	0.9932	1.11	0.02	1.10	0.03	1.10	0.03
Hind	0.9880	0.94	0.28	0.94	0.28	0.93	0.29
<u>ALR-C</u>							
Fore	0.9890	0.99	0.13	0.99	0.13	0.98	0.13
Hind	0.9921	0.96	0.26	0.96	0.26	0.96	0.26
<u>ALR-A</u>							
Fore	0.9869	1.17	-0.05	1.16	-0.04	1.14	-0.12
Hind	0.9630	0.75	0.52	0.74	0.53	0.72	0.56

x = ThP

Table IV.7 Allometry of mean forelimb and hindlimb lengths scaled to thoraco-pelvic length in four taxonomic subgroups of Platyrrhini; GGS, traditional Cebidae of Simpson (1945); SMF, derived group of Ford (1980); ALR-C, "Cebidae" of Rosenberger (1979); ALR-A, "Atelidae" of Rosenberger (1979); Fore, forelimb length; Hind, hindlimb length; ThP, thoraco-pelvic length; a, log intercept; b, allometric coefficient; r, correlation coefficient; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; all $r = p < 0.001$.

<u>y</u>	<u>x</u>	<u>r</u>	<u>MA</u>		<u>RMA</u>		<u>LSQ</u>	
			<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>
HD	WT	0.9920	0.37	-1.42	0.36	-1.39	0.36	-1.39
RD	WT	0.9904	0.37	-1.61	0.37	-1.61	0.37	-1.61
McD	WT	0.9854	0.40	-1.96	0.40	-1.96	0.39	-1.93
FD	WT	0.9887	0.36	-1.35	0.36	-1.35	0.35	-1.32
TD	WT	0.9856	0.37	-1.44	0.36	-1.41	0.36	-1.41
MtD	WT	0.9692	0.36	-1.84	0.35	-1.74	0.34	-1.74
HD	HL	0.9902	0.85	-1.05	0.86	-1.06	0.85	-1.05
RD	RL	0.9837	0.84	-1.20	0.85	-1.21	0.84	-1.20
McD	McL	0.9234	1.11	-1.06	1.12	-1.07	1.04	-1.04
FD	FL	0.9833	0.93	-1.16	0.94	-1.16	0.92	-1.15
TD	TL	0.9885	1.06	-1.33	1.07	-1.34	1.06	-1.33
MtD	MtL	0.9798	1.26	-1.27	1.26	-1.27	1.24	-1.26

Table IV.8 Allometry of mean limb segment diameters in *Platyrrhini*; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; a, log intercept; b, allometric coefficient; r, correlation coefficient; HD, humerus diameter; RD, radius diameter; McD, metacarpal III diameter; FD, femur diameter; TD, tibia diameter; MtD, metatarsal III diameter; HL, humerus length; RL, radius length; McL, metacarpal III length; FL, femur length; TL, tibia length; MtL, metatarsal III length; WT, body weight; all $r = p < 0.001$.

<u>x=shaft length</u>				<u>x=WT</u>		
<u>SMALL</u>						
<u>y</u>	<u>r</u>	<u>b</u>	<u>a</u>	<u>r</u>	<u>b</u>	<u>a</u>
HD	0.94774	0.80	-1.02	0.9704	0.33	-1.31
RD	0.9487	0.74	-1.14	0.9601	0.32	-1.48
FD	0.9798	0.81	0.81	0.9630	0.37	-1.38
TD	0.9871	0.96	-1.25	0.9619	0.42	-1.58
<u>LARGE</u>						
HD	0.9437	0.77	-0.95	0.9712	0.36	-1.38
RD	0.9587	0.70	-1.04	0.9772	0.37	-1.61
FD	0.9531	1.51	-1.84	0.9573	0.41	-1.53
TD	0.9222	1.38	-1.70	0.9370	0.37	-1.45

Table IV.9 Allometry mean limb segment diameters in groups SMALL and LARGE; a, log intercept; b, allometric coefficient; r, correlation coefficient; HD, humerus diameter; RD, radius diameter; FD, femur diameter; TD, tibia diameter; WT, body weight; computed by major axis method; all $r = p < 0.001$.

<u>y</u>	<u>x</u>	<u>r</u>	<u>MA</u>		<u>RMA</u>		<u>LSQ</u>	
			<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>	<u>b</u>	<u>a</u>
HN	HL	0.9795	0.90	-1.08	0.86	-1.02	0.84	-1.01
HX	HL	0.9773	0.91	-1.03	0.85	-0.97	0.83	-0.95
RN	RL	0.9741	0.93	-1.27	0.90	-1.24	0.87	-1.21
RX	RL	0.9631	0.85	-1.11	0.81	-1.08	0.78	-1.05
FN	FL	0.9821	0.96	-1.16	0.92	-1.12	0.90	-1.10
FX	FL	0.9753	1.01	-1.16	0.94	-1.10	0.92	-1.07
TN	TL	0.9719	1.15	-1.45	1.06	-1.36	1.03	-1.33
TX	TL	0.9736	1.11	-1.26	1.06	-1.22	1.03	-1.19
HN	WT	0.9791	0.37	-1.38	0.37	-1.38	0.36	-1.35
HX	WT	0.9777	0.38	-1.37	0.36	-1.31	0.35	-1.28
RN	WT	0.9595	0.37	-1.60	0.39	-1.66	0.37	-1.60
RX	WT	0.9647	0.35	-1.45	0.35	-1.45	0.34	-1.42
FN	WT	0.9608	0.32	-1.20	0.36	-1.33	0.35	-1.30
FX	WT	0.9752	0.35	-1.25	0.36	-1.28	0.35	-1.25
TN	WT	0.9731	0.36	-1.44	0.37	-1.47	0.36	-1.44
TX	WT	0.9379	0.31	-1.14	0.37	-1.33	0.35	-1.27

Table IV.10 Allometry of mean minimum and maximum shaft diameters; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; a, log intercept; b, allometric coefficient; r, correlation coefficient; HN, RN, FN, TN, minimum diameters of humerus, radius, femur and tibia, respectively; HX, RX, FX, TX, maximum diameters of humerus, radius, femur, and tibia, respectively; HL, RL, FL, TL, lengths of humerus, radius, femur and tibia, respectively; all $r = p < 0.001$.

A

	<u>N</u>	<u>STL</u>	<u>Th/Lu</u>	<u>a</u>	<u>b</u>	<u>c</u>
A. <u>trivirigatus</u>	18-21	23.01	11/11	24	54	22
S. <u>sciureus</u>	22-24	19.97	11/9	27	50	23
C. <u>apella</u>	11.12	27.05	11/8	31	41	29
A. <u>caraya</u>	20-21	33.05	12/7	33	34	33
A. <u>senicula</u>	19-20	33.94	11.8	32	38	30
A. <u>palliata</u>	9.12	36.08	12/8	30	39	30

B

	<u>IMI</u>	<u>F/STL</u>	<u>H/STL</u>
A. <u>trivirigatus</u>	75	63	84
S. <u>sciureus</u>	80	69	86
C. <u>apella</u>	82	75	92
A. <u>caraya</u>	97	90	92
A. <u>senicula</u>	95	85	89
A. <u>palliata</u>	100	81	81

Table V.1 Ratios of the trunk and limbs in six platyrrhine species; A, ratios of parts of the skeletal trunk; B, ratios of limb lengths; N, number of skeletons; STL, skeletal trunk length; Th/Lu, modal numbers of thoracic (ThF) and lumbar (LuF) vertebrae; a, ratio ThF/STL; b, ratio LuF/STL; c, ratio Pel/STL; IMI, intermembral index; F/STL, ratio of forelimb length (HL+RL) to skeletal trunk length; H/STL, ratio of hindlimb length (FL+TL) to skeletal trunk length.

		MA					RMA	LSQ
y	x	N	r	b	N	r	b	b
A. <u>trivirigatus</u>								
LuF	ThF	15	0.6607	1.80	18	0.6341 ²	1.42	0.90
Pel	ThF	15	0.5530	0.93	18	0.5382 ³	0.86	0.46
S. <u>sciureus</u>								
LuF	ThF	19	0.4233	0.50	23	0.3701*	0.71	0.26
Pel	ThF	19	0.4715	0.26	22	0.4748 ³	0.40	0.19
STL	WT	19	0.6253	0.18	20	0.6729 ²	0.25	0.17
ThP	WT	13	0.6040	0.15	20	0.6864 ¹	0.27	0.19
C. <u>apella</u>								
LuF	ThF	10	-0.1847	0.77	11	-0.1930*	0.68	-0.13
Pel	ThF	10	0.4590	0.81	11	0.5216*	0.52	0.27
STL	WT	10	0.9669	0.23	10	0.9669 ¹	0.21	0.20
ThP	WT	10	0.7680	0.24	10	0.7680 ²	0.29	0.22
A. <u>caraya</u>								
LuF	ThF	18	0.3978	0.86	21	0.5041 ³	1.08	0.55
Pel	ThF	18	0.6258	0.83	20	0.6558 ²	0.84	0.55
A. <u>senicula</u>								
LuF	ThF	14	0.4729	0.29	20	0.4457 ³	0.54	0.24
Pel	ThF	14	0.9050	1.22	20	0.6569 ²	0.96	0.63
A. <u>palliata</u>								
LuF	ThF	8	0.3152	-1.81	12	0.5018*	0.84	0.42
Pel	ThF	8	0.0166	0.40	12	0.9329 ¹	0.82	0.77

Table V.2 Allometry of trunk length variables in six platyrrhine species; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; b, allometric coefficient; r, correlation coefficient; ThF, thoracic length; LuF, lumbar length; Pel, pelvic length; ThP, thoraco-pelvic length; STL, skeletal trunk length; WT, body weight; ¹, $r = p < 0.001$; ², $r = p < 0.01$; ³, $r = p < 0.05$; *, $r =$ not significant.

		MA				RMA		LSQ
y	x	N	r	b	N	r	b	b
<u>A. trivirigatus</u>								
Fore	ThP	15	0.8110	1.39	15	0.8109 ²	1.14	0.93
Hind	ThP	15	0.8668	1.35	18	0.8211 ¹	1.14	0.94
Fore	STL	15	0.9333	1.02	18	0.9279 ¹	1.07	0.99
Hind	STL	15	0.9320	1.00	18	0.9076 ¹	1.07	0.97
<u>S. sciureus</u>								
Fore	ThP	12	0.5161	0.62	17	0.6420*	0.55	0.35
Hind	ThP	12	0.5627	0.64	16	0.6202*	0.52	0.32
Fore	STL	12	0.5911	0.59	17	0.6683*	0.60	0.40
Hind	STL	12	0.6342	0.62	16	0.7042*	0.57	0.40
Fore	WT	12	0.7076	0.10	19	0.7269 ²	0.15	0.11
Hind	WT	12	0.6938	0.11	17	0.7152*	0.14	0.10
<u>C. apella</u>								
Fore	ThP	10	0.6405	0.82	11	0.6431*	0.75	0.48
Hind	ThP	10	0.6606	0.74	11	0.6639*	0.65	0.43
Fore	STL	10	0.8974	0.86	11	0.8981 ¹	1.04	0.93
Hind	STL	10	0.9228	0.78	11	0.9232 ¹	0.91	0.84
Fore	WT	10	0.8830	0.20	20	0.9268 ¹	0.21	0.20
Hind	WT	10	0.8646	0.18	20	0.8931 ¹	0.19	0.17

Table V.3 Allometry of forelimb and hindlimb lengths in A. trivirigatus, S. sciureus and C. apella; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; N, number of skeletons; b, allometric coefficient; r, correlation coefficient; Fore, forelimb length; Hind, hindlimb length; ThP, thoraco-pelvic length; STL, skeletal trunk length; WT, body weight; ¹, r = p < 0.001; ², r = p < 0.01; *, r = not significant (p > 0.05).

		<u>MA</u>				<u>RMA</u>		<u>LSQ</u>
<u>y</u>	<u>x</u>	<u>N</u>	<u>r</u>	<u>b</u>	<u>N</u>	<u>r</u>	<u>b</u>	<u>b</u>
<u>A. caraya</u>								
Fore	ThP	18	0.8321	0.85	18	0.8321 ¹	0.77	0.64
Hind	ThP	18	0.7571	0.72	20	0.7971 ¹	0.72	0.57
Fore	STL	18	0.9057	0.93	19	0.8948 ¹	0.91	0.81
Hind	STL	18	0.8881	0.79	20	0.8951 ¹	0.85	0.76
<u>A. senicula</u>								
Fore	ThP	14	0.7799	0.86	18	0.8146 ¹	0.72	0.59
Hind	ThP	14	0.8362	0.53	17	0.8592 ¹	0.44	0.38
Fore	STL	14	0.7136	1.01	18	0.7670 ¹	0.97	0.74
Hind	STL	14	0.7566	0.72	17	0.7945 ¹	0.59	0.47
<u>A. palliata</u>								
Fore	ThP	8	0.2521	-0.34	9	0.3006*	0.64	0.19
Hind	ThP	8	0.0670	-0.88	8	0.0178*	0.78	0.01
Fore	STL	8	0.7023	0.67	12	0.9005 ¹	0.81	0.73
Hind	STL	8	0.6418	1.73	11	0.9109 ¹	0.98	0.90

Table V.4 Allometry of forelimb and hindlimb lengths in three species of Alouatta; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; N, number of skeletons; b, allometric coefficient; r, correlation coefficient; Fore, forelimb length; Hind, hindlimb length; ThP thoraco-pelvic length; STL, skeletal trunk length; WT, body weight; ¹, r = p < 0.001; *, r = not significant (p > 0.05).

<u>y</u>	<u>x</u>	<u>MA</u>			<u>N</u>	<u>RMA</u>			<u>LSQ</u>
		<u>N</u>	<u>r</u>	<u>b</u>		<u>r</u>	<u>b</u>	<u>b</u>	
HL	ThP	15	0.8068	1.54	17	0.7319 ¹	1.37	1.01	
RL	ThP	15	0.7962	1.27	17	0.7975 ¹	1.02	0.82	
FL	ThP	15	0.8414	1.45	18	0.8100 ¹	1.17	0.95	
TL	ThP	15	0.8615	1.29	18	0.8077	1.14	0.92	
HL	STL	18	0.9232	1.10	20	0.8864 ¹	1.29	1.14	
RL	STL	18	0.9087	0.91	19	0.9097 ¹	0.96	0.87	
FL	STL	18	0.9292	1.03	21	0.9274 ¹	1.10	1.02	
TL	STL	18	0.8685	0.92	21	0.8615 ¹	1.07	0.92	
HD	HL	18	0.7202	0.72	20	0.7101 ¹	0.72	0.51	
RD	RL	19	0.6100	1.10	19	0.6174 ²	1.23	0.76	
FD	FL	18	0.8420	1.04	21	0.8500 ¹	1.04	0.88	
TD	TL	18	0.6700	1.51	21	0.8864 ¹	1.30	0.89	

Aotus trivirigatus

Table V.5 Allometry of limb segment lengths and widths in Aotus trivirigatus; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; N, number of skeletons; b, allometric coefficient; r, correlation coefficient; HL, RL, FL, TL, lengths of humerus, radius, femur and tibia, respectively; HD, RD, FD, TD, diameters of humerus, radius, femur and tibia, respectively; ThP, thoraco-pelvic length; STL, skeletal trunk length; ¹, $r = p < 0.001$; ², $r = p < 0.01$.

y	x	MA			N	r	RMA	LSQ
		N	r	b			b	b
HL	ThP	14	0.4947	0.63	18	0.6496 ²	0.58	0.37
RL	ThP	14	0.5052	0.77	20	0.6771 ¹	0.62	0.42
FL	ThP	14	0.6229	0.87	20	0.7290 ¹	0.67	0.49
TL	ThP	14	0.5102	0.65	18	0.5741 ²	0.45	0.26
HL	STL	14	0.5353	0.54	18	0.6236 ²	0.63	0.40
RL	STL	14	0.6884	0.69	20	0.7669 ¹	0.68	0.52
FL	STL	14	0.6946	0.76	20	0.7828 ¹	0.74	0.58
TL	STL	14	0.6571	0.59	18	0.6941 ¹	0.50	0.34
HD	HL	17	0.6652	2.76	21	0.7571 ¹	2.04	1.55
RD	RL	17	0.8979	2.34	23	0.8842 ¹	2.02	1.78
FD	FL	17	0.6360	1.23	23	0.7139 ¹	1.45	1.03
TD	TL	17	0.8715	2.23	21	0.8679 ¹	2.11	1.83
HL	WT	16	0.7011	0.10	20	0.7246 ¹	0.16	0.11
RL	WT	16	0.7417	0.12	22	0.6525 ¹	0.17	0.11
FL	WT	16	0.6782	0.12	21	0.6270 ¹	0.18	0.12
TL	WT	16	0.7495	0.10	19	0.7069 ¹	0.12	0.09
HD	WT	16	0.7587	0.26	20	0.7424 ²	0.32	0.24
RD	WT	16	0.7595	0.28	22	0.7525 ²	0.34	0.26
FD	WT	16	0.6115	0.16	21	0.6120 ²	0.27	0.16
TD	WT	16	0.7184	0.21	19	0.6379 ²	0.26	0.17

Saimiri sciureus

Table V.6 Allometry of limb segment lengths and widths in Saimiri sciureus; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; N, number of skeletons; b, allometric coefficient; r, correlation; HL, RL, FL, TL, lengths of humerus, radius, femur and tibia, respectively; HD, RD, FD, TD, diameters of humerus, radius, femur and tibia, respectively; ThP, thoraco-pelvic length; STL, skeletal trunk length; WT, body weight; 1, $r = p < 0.001$; 2, $r = p < 0.01$.

<u>y</u>	<u>x</u>	<u>MA</u>			<u>N</u>	<u>RMA</u>			<u>LSQ</u>
		<u>N</u>	<u>r</u>	<u>b</u>		<u>r</u>	<u>b</u>	<u>b</u>	
HL	ThP	10	0.5859	0.78	11	0.5988 ²	0.74	0.44	
RL	ThP	10	0.6708	0.89	11	0.6630 ²	0.77	0.51	
FL	ThP	10	0.6961	0.75	11	0.6836 ²	0.69	0.47	
TL	ThP	10	0.5984	0.76	11	0.6183 ²	0.63	0.39	
HL	STL	10	0.8350	0.80	11	0.8400 ¹	1.03	0.87	
RL	STL	10	0.9249	0.92	11	0.9218 ¹	1.08	0.99	
FL	STL	10	0.8987	0.78	11	0.8954 ¹	0.96	0.86	
TL	STL	10	0.9145	0.78	11	0.9180 ¹	0.89	0.81	
HD	HL	10	0.8117	1.72	22	0.8463 ¹	1.72	1.46	
RD	RL	10	0.9419	1.46	22	0.9025 ¹	1.82	1.64	
FD	FL	10	0.9335	1.29	22	0.8350 ¹	1.65	1.38	
TD	TL	10	0.8762	1.07	22	0.8850 ¹	1.86	1.65	
HL	WT	10	0.8102	0.19	20	0.8849 ¹	0.21	0.19	
RL	WT	10	0.9220	0.21	20	0.9436 ¹	0.22	0.21	
FL	WT	10	0.8487	0.18	20	0.8558 ¹	0.20	0.17	
TL	WT	10	0.8500	0.18	20	0.8983 ¹	0.18	0.16	
HD	WT	10	0.8816	0.32	20	0.9376 ¹	0.36	0.34	
RD	WT	10	0.9119	0.31	20	0.9410 ¹	0.40	0.38	
FD	WT	10	0.9195	0.23	20	0.9462 ¹	0.32	0.31	
TD	WT	10	0.7026	0.19	20	0.8607 ¹	0.34	0.29	

Cebus apella

Table V.7 Allometry of limb segment lengths and widths in Cebus apella; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; N, number of skeletons; b, allometric coefficient; r, correlation coefficient; HL, TL, FL, TL, lengths of humerus, radius, femur and tibia, respectively; HD, RD, FD, TD, diameters of humerus, radius, femur, and tibia, respectively; ThP, thoracopelvic length; STL, skeletal trunk length; WT, body weight; ¹, $r = p < 0.001$; ², $r = p < 0.01$.

<u>MA</u>					<u>RMA</u>		<u>LSQ</u>
<u>y</u>	<u>x</u>	<u>N</u>	<u>r</u>	<u>b</u>	<u>N</u>	<u>r</u>	<u>b</u>
HL	ThP	18	0.8373	0.85	18	0.8373 ¹	0.78
RL	ThP	18	0.7931	0.85	20	0.8126 ¹	0.79
FL	ThP	18	0.7644	0.69	20	0.7920 ¹	0.69
TL	ThP	18	0.7216	0.76	20	0.7643 ¹	0.76
HL	STL	18	0.8919	0.97	19	0.8810 ¹	0.92
RL	STL	18	0.8843	0.94	21	0.8747 ¹	0.93
FL	STL	18	0.8636	0.76	20	0.8664 ¹	0.81
TL	STL	18	0.8787	0.84	21	0.8906 ¹	0.90
HD	HL	18	0.8510	1.78	21	0.8575 ¹	1.74
RD	RL	18	0.7963	2.03	21	0.8000 ¹	1.78
FD	FL	18	0.6352	1.66	21	0.6845 ¹	1.55
TD	TL	18	0.7652	2.05	21	0.7980 ¹	1.67

Alouatta caraya

Table V.8 Allometry of limb segment lengths and widths in Alouatta caraya; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; N, number of skeletons; b, allometric coefficient; r, correlation coefficient; HL, RL, FL, TL, lengths of humerus, radius, femur and tibia, respectively; HD, RD, FD, TD, diameters of humerus, radius, femur and tibia, respectively; ThP, thoraco-pelvic length; STL, skeletal trunk length; ¹, r = p < 0.001.

<u>y</u>	<u>x</u>	<u>MA</u>			<u>N</u>	<u>RMA</u>			<u>LSQ</u>
		<u>N</u>	<u>r</u>	<u>b</u>		<u>r</u>	<u>b</u>	<u>b</u>	
HL	ThP	14	0.8942	0.89	18	0.8315 ¹	0.70	0.58	
RL	ThP	14	0.7444	0.97	19	0.7879 ¹	0.75	0.59	
FL	ThP	14	0.8570	0.55	18	0.8846 ¹	0.47	0.42	
TL	ThP	14	0.7960	0.52	17	0.8331 ¹	0.44	0.37	
HL	STL	14	0.7299	1.35	18	0.7801 ¹	0.95	0.74	
RL	STL	14	0.6866	1.48	19	0.7433 ¹	1.01	0.75	
FL	STL	14	0.7660	0.83	18	0.8247 ¹	0.64	0.52	
TL	STL	14	0.7294	0.81	17	0.7756 ¹	0.59	0.46	
HD	HL	14	0.8907	0.96	28	0.8438 ¹	1.10	0.93	
RD	RL	14	0.7422	1.15	33	0.7467 ¹	1.34	1.00	
FD	FL	14	0.8988	1.62	32	0.8453 ¹	1.60	1.35	
TD	TL	14	0.8662	1.58	31	0.7371 ¹	1.59	1.17	

Alouatta senicula

Table V.9 Allometry of limb segment lengths and widths in Alouatta senicula; MA, reduced major axis method; RMA, reduced major axis method; LSQ, least squares method; N, number of skeletons; b, allometric coefficient; r, correlation coefficient; HL, RL, FL, TL, lengths of humerus, radius, femur and tibia, respectively; HD, RD, FD, TD, diameters of humerus, radius, femur and tibia, respectively; ThP, thoraco-pelvic length; STL, skeletal trunk length; ¹, $r = p < 0.001$.

<u>y</u>	<u>x</u>	<u>MA</u>			<u>RMA</u>			<u>LSQ</u>
		<u>N</u>	<u>r</u>	<u>b</u>	<u>N</u>	<u>r</u>	<u>b</u>	<u>b</u>
HL	ThP	8	0.2069	-0.08	9	0.2876*	0.67	0.26
RL	ThP	8	0.2297	-0.62	9	0.2065*	0.66	0.14
FL	ThP	8	0.1269	-0.98	9	0.0689*	0.77	0.05
TL	ThP	8	-0.0305	-0.77	8	-0.1051*	0.80	-0.08
HL	STL	11	0.8480	0.84	12	0.8480 ¹	0.84	0.71
RL	STL	11	0.9167	0.94	12	0.8893 ¹	0.84	0.74
FL	STL	11	0.9120	1.06	12	0.8711 ¹	0.97	0.84
TL	STL	11	0.8736	1.12	11	0.8736 ¹	0.97	0.85
HD	HL	11	0.4648	2.82	12	0.4860*	2.06	0.96
RD	RL	11	0.5401	2.91	12	0.5264*	2.45	1.29
FD	FL	11	0.7378	1.78	12	0.7237 ¹	2.45	1.29
TD	TL	11	0.6752	1.69	11	0.6782 ²	1.41	0.96

Alouatta palliata

Table V.10 Allometry limb segment lengths and widths in Alouatta palliata; MA, major axis method; RMA, reduced major axis method; LSQ, least squares method; N, number of skeletons; b, allometric coefficient; r, correlation coefficient; HL, RL, FL, TL, Lengths of humerus, radius, femur and tibia, respectively; HD, RD, FD, TD, diameters of humerus, radius, femur and tibia, respectively; ThP, thoraco-pelvic length; STL, skeletal trunk length; ¹, $r = p < 0.001$; ², $r = p < 0.01$; *, $r = \text{not significant}$ ($p > 0.05$).

FIGURES

Figure I.1 Distribution of intermembral index with
body weight in strepsirhine (*), platyrrhine (●) and
catarrhine (○) primates (data from Napier and Napier
1967).

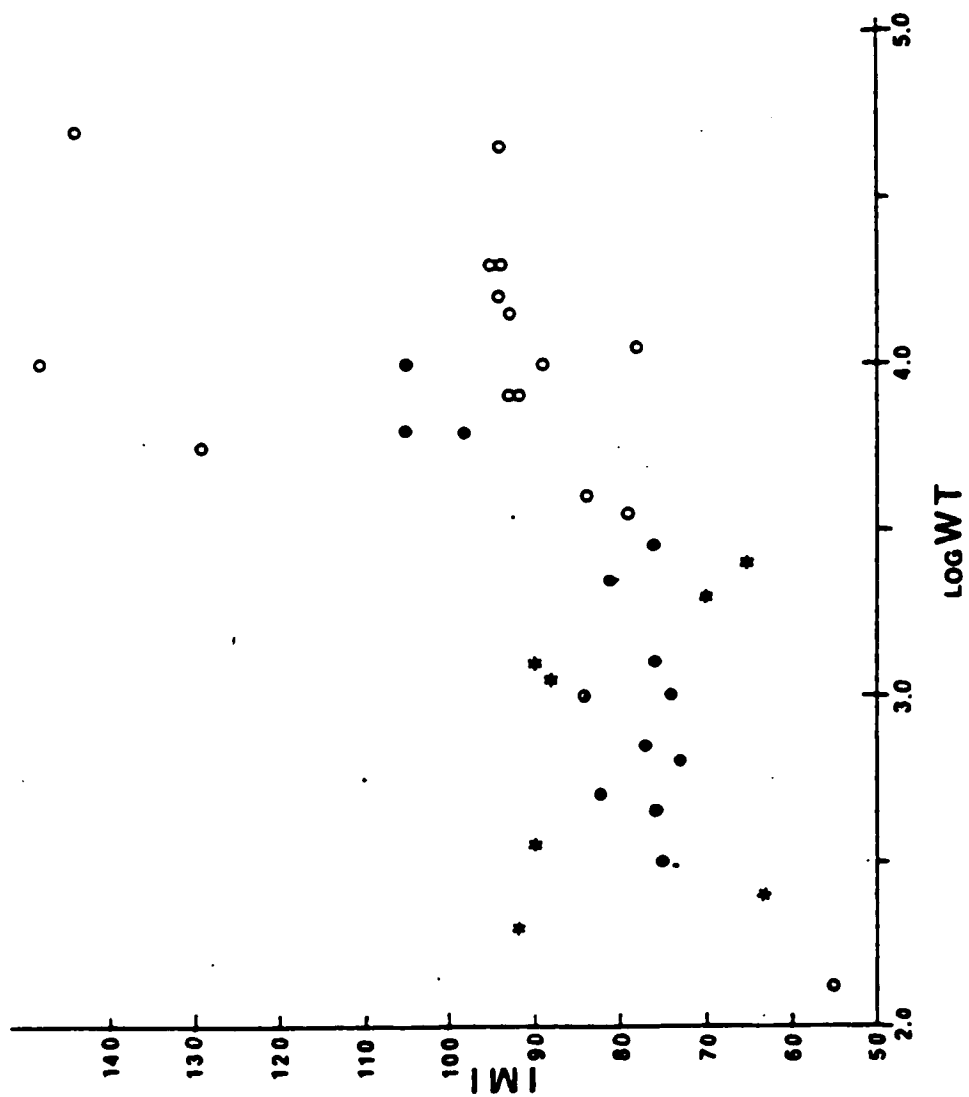


Figure I.1

Figure 1.2 Distribution of intermembral index with head and body length in strepsirrhine (*), platyrrhine (●) and catarrhine (○) primates (data from Napier and Napier 1967).

Figure I.2

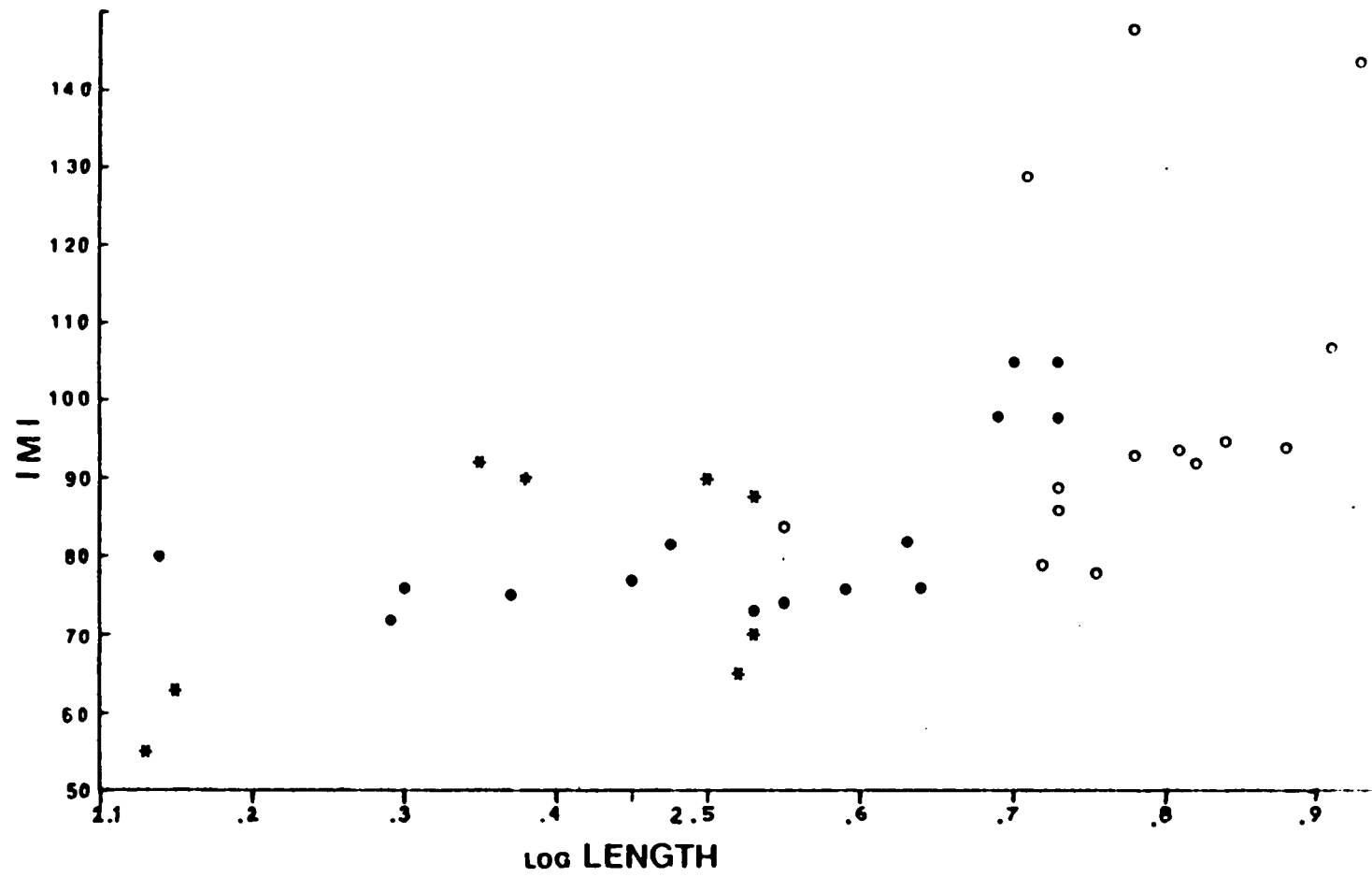


Figure 1.3 Distribution of intermembral index in primate genera arranged by taxonomic group (from top to bottom) and body size (head and body length); IMI, intermembral index; (data from Napier and Napier (1967)).

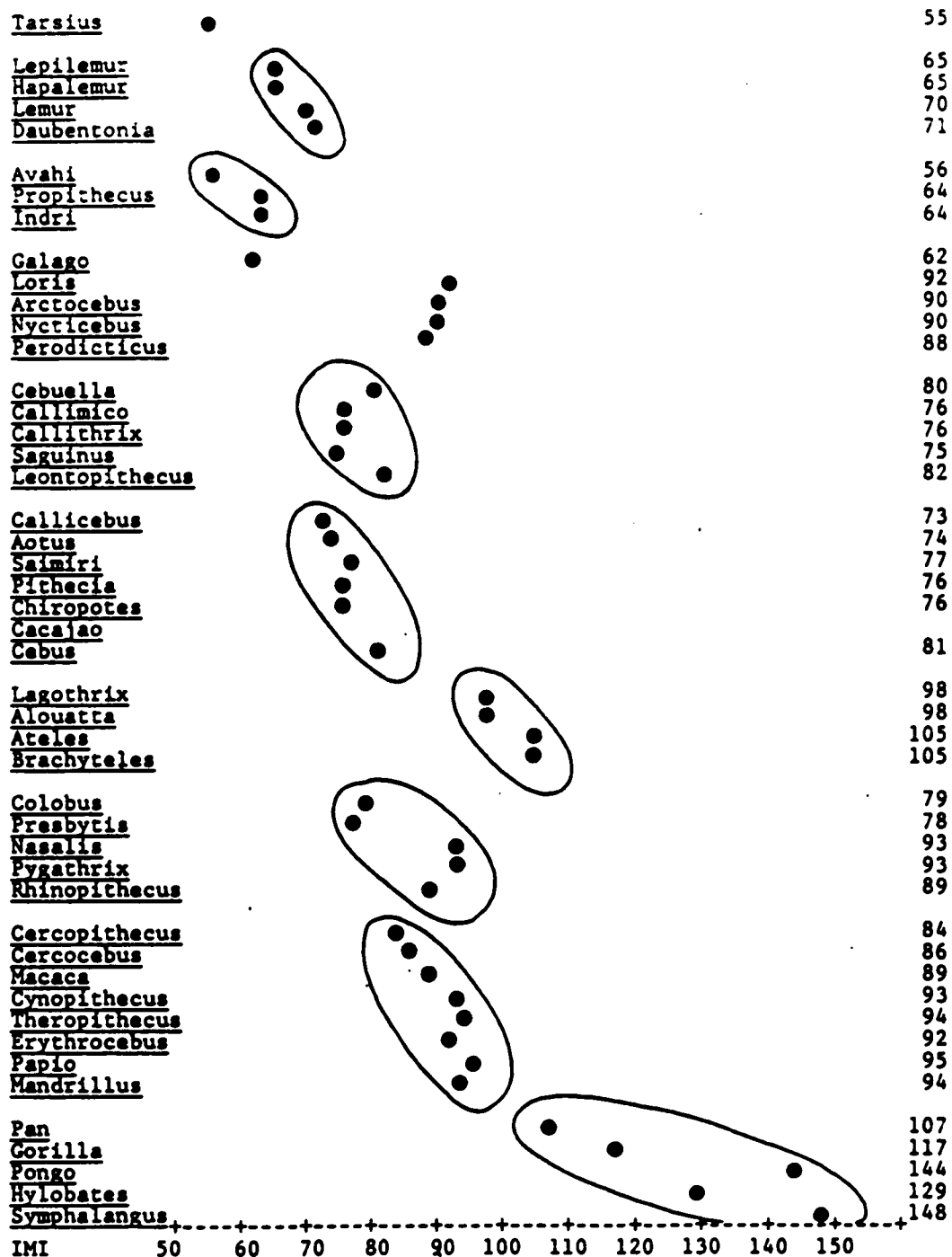


Figure I.3

Figure III.1 Allometry of Mean Trunk Length Variables to Mean Weight; T, thoracic length (by facet); P, pelvic length; L, lumbar length (LuF, by facet); *, thoraco-pelvic length (ThP); V, skeletal trunk length (STL); WT, body weight; A, Alouatta; B, Aotus; C, Ateles; D, Cacajao; E, Callicebus; F, Callimico; G, Callithrix; H, Cebuella; I, Cebus; J, Chiropotes; K, Lagothrix; L, Leontopithecus; M, Pithecia; N, Saguinus; O, Saimiri. Slopes are drawn for skeletal trunk length, lumbar length and thoraco-pelvic length only.

Figure III.1

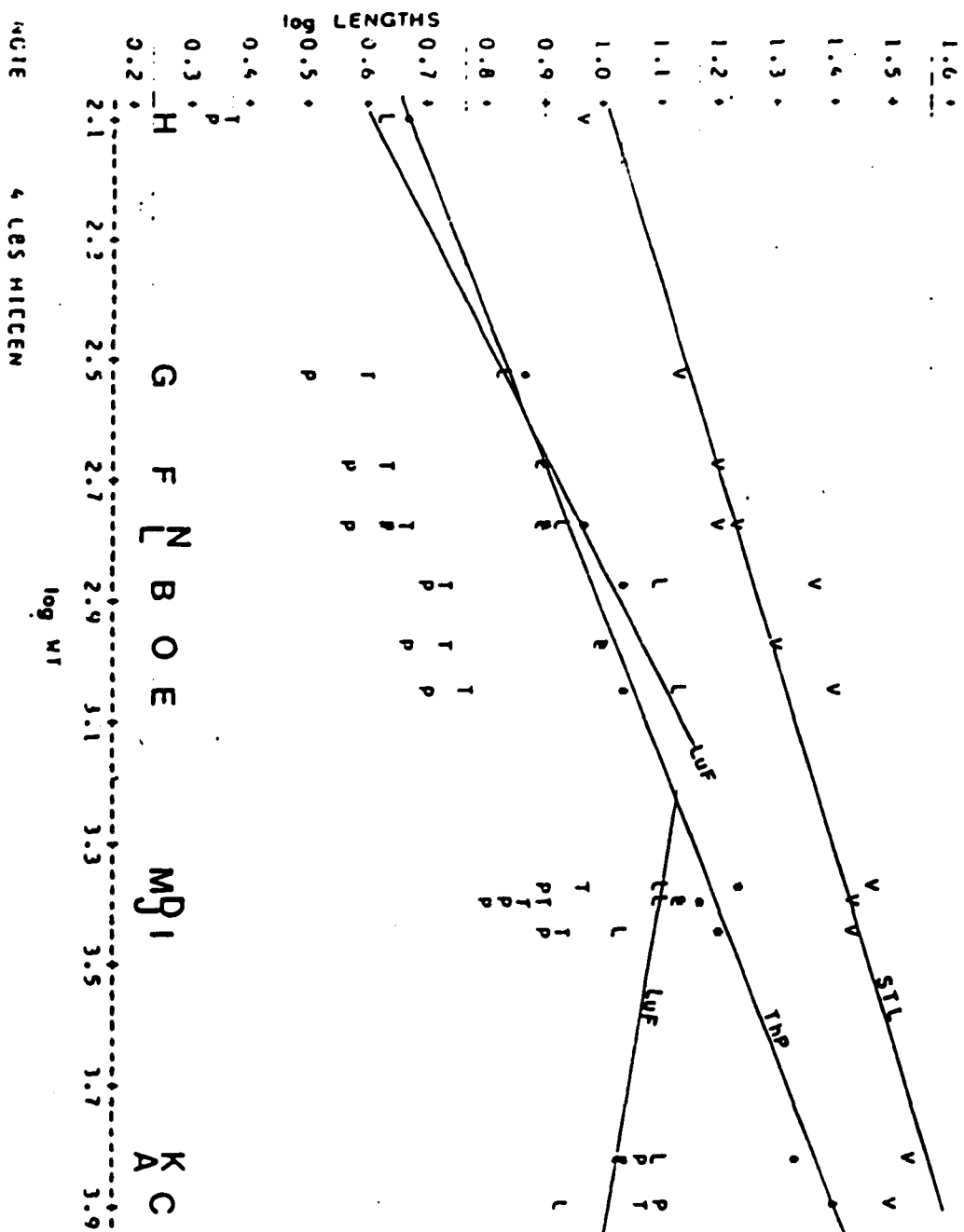


Figure IV.1 Allometry of mean forelimb segment lengths to mean weight; H, humerus length; R, radius length; M, metacarpal III length; WT, body weight; A, Alouatta; B, Aotus; C, Ateles; D, Cacajao; E, Callicebus; F, Callimico; G, Callithrix; H, Cebuella; I, Cebus; J, Chiropotes; K, Lagothrix; L, Leontopithecus; M, Pithecia; N, Saguinus; O, Saimiri.

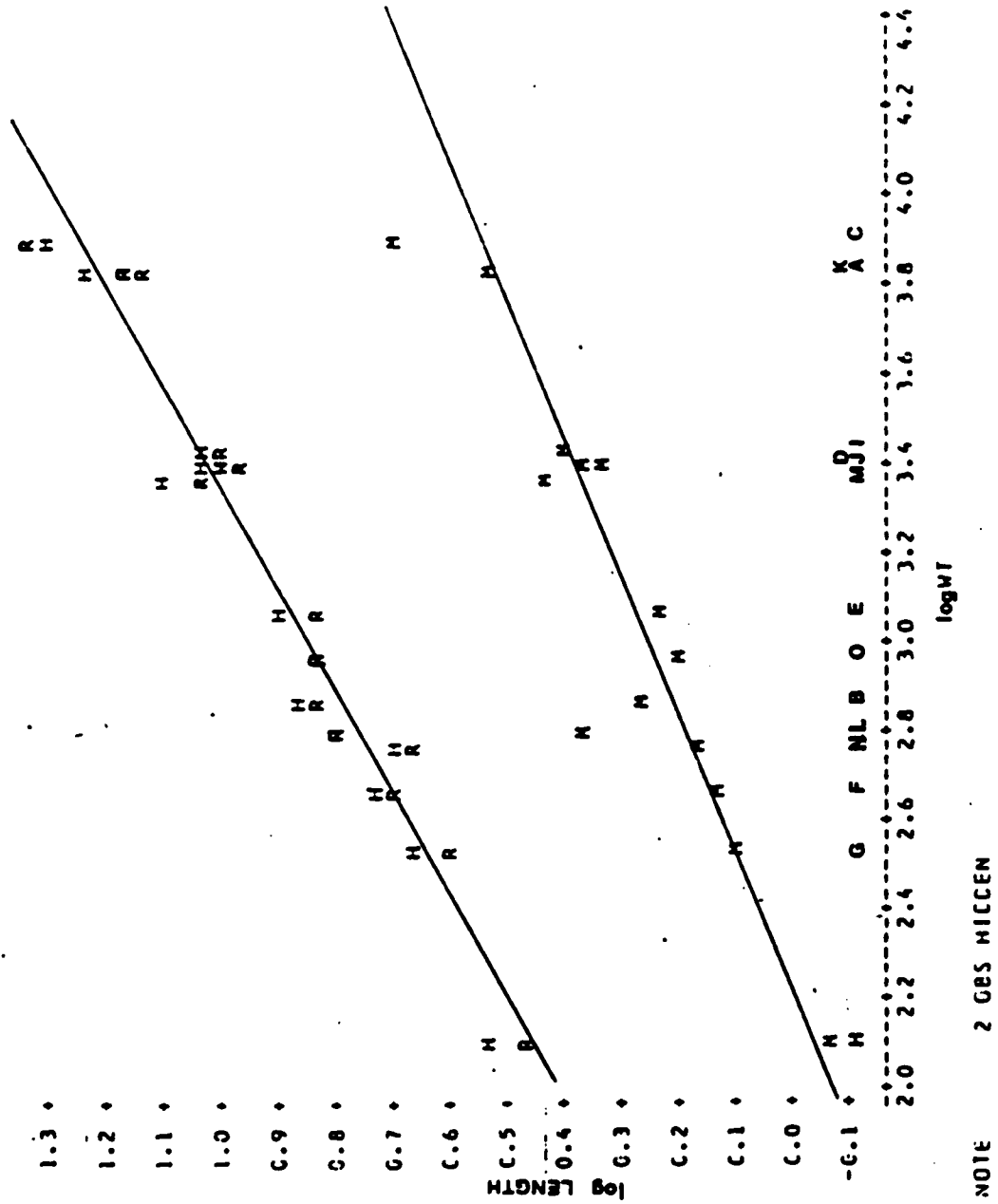
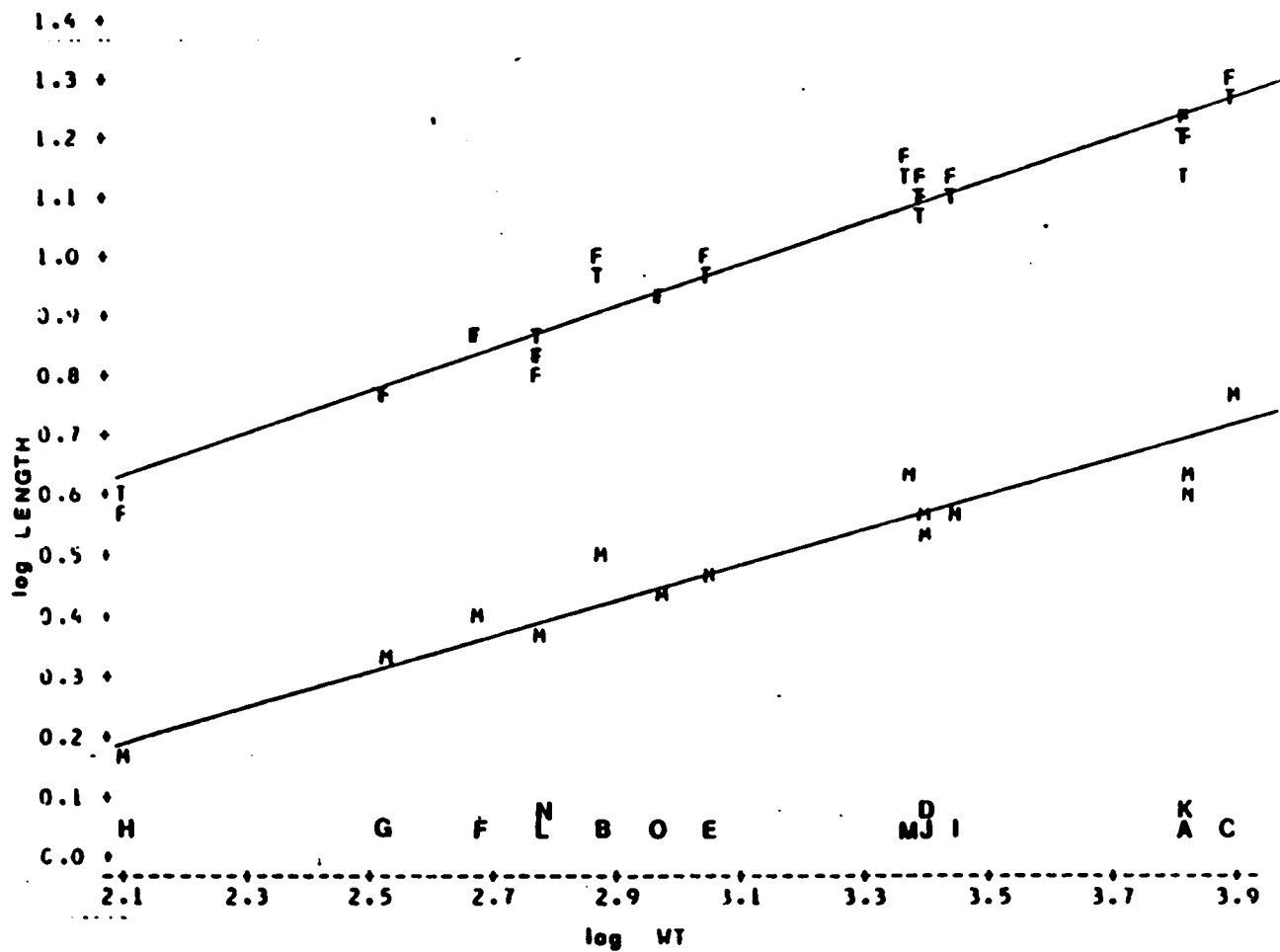


Figure IV.1

Figure IV.2 Allometry of mean hindlimb segment lengths to mean weight; F, femur length; T, tibia length; M, metatarsal III length; WT, body weight; A, Alouatta; B, Aotus; C, Ateles; D, Cacajao; E, Callicebus; F, Callimico; G, Callithrix; H, Cebuella; I, Cebus; J, Chiropotes; K, Lagothrix; L, Leontopithecus; M, Pithecia; N, Saguinus; O, Saimiri.

Figure IV.2



NOTE 1 GRS HICEN

Figure IV.3 Allometry of mean forelimb and hindlimb lengths to mean weight; $\circ$, forelimb length; $\bullet$, hindlimb length; WT, body weight; A, Alouatta; B, Aotus; C, Ateles; D, Cacajao; E, Callicebus; F, Callimico; G, Callithrix; H, Cebuella; I, Cebus; J, Chiropotes; K, Lagothrix; L, Leontopithecus; M, Pithecia; N, Saguinus; O, Saimiri.

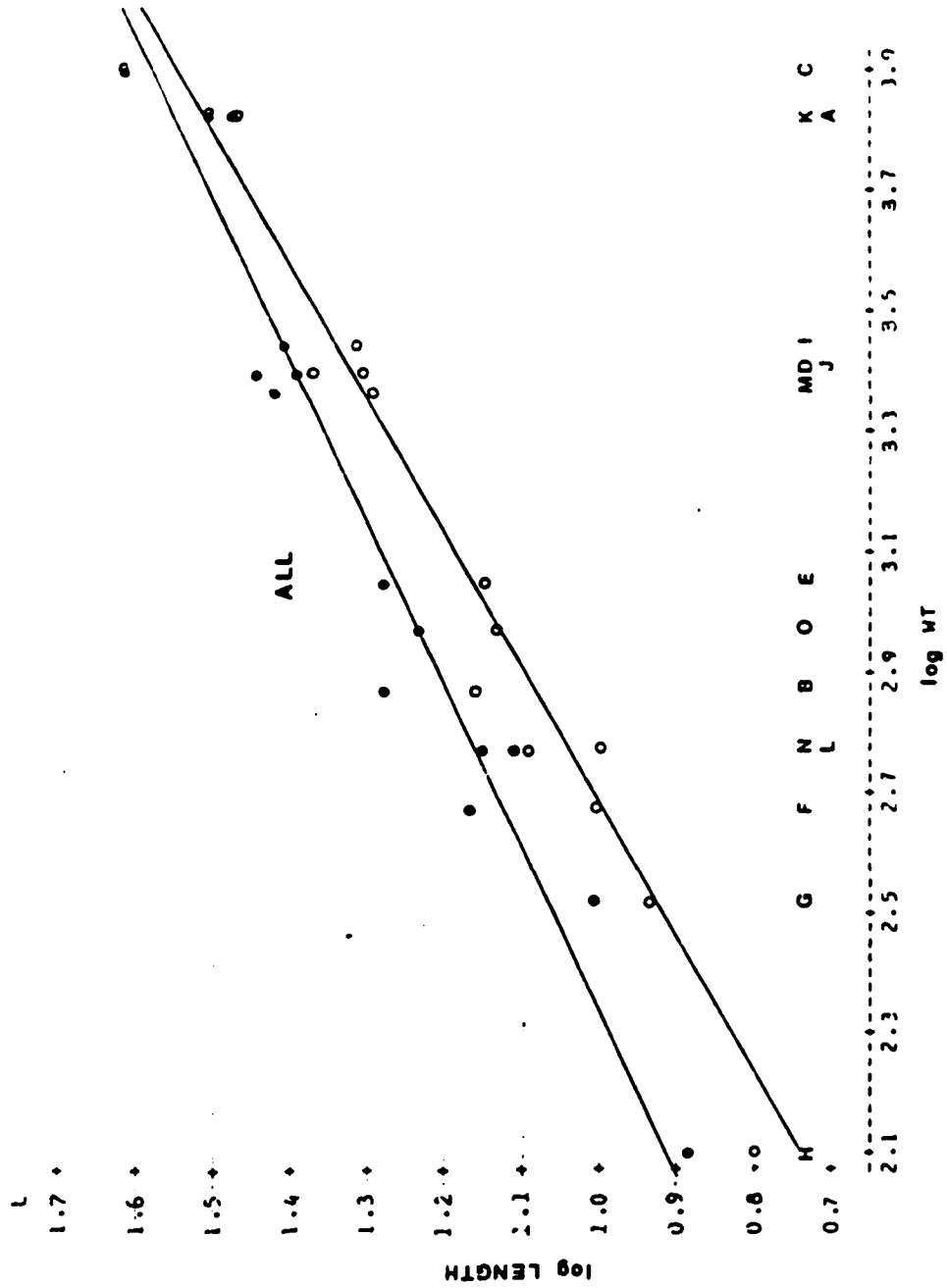


Figure IV.3

Figure IV.4 Allometry of mean forelimb and hindlimb lengths to mean thoraco-pelvic length; °, forelimb length; ● hindlimb length; ThP, thoraco-pelvic length; A, Alouatta; B, Aotus; C, Ateles; D, Cacajao; E, Callicebus; F, Callimico; G, Callithrix; H, Cebuella; I, Cebus; J, Chiropotes; K, Lagothrix; L, Leontopithecus; M, Pithecia; N, Saguinus; O, Saimiri.

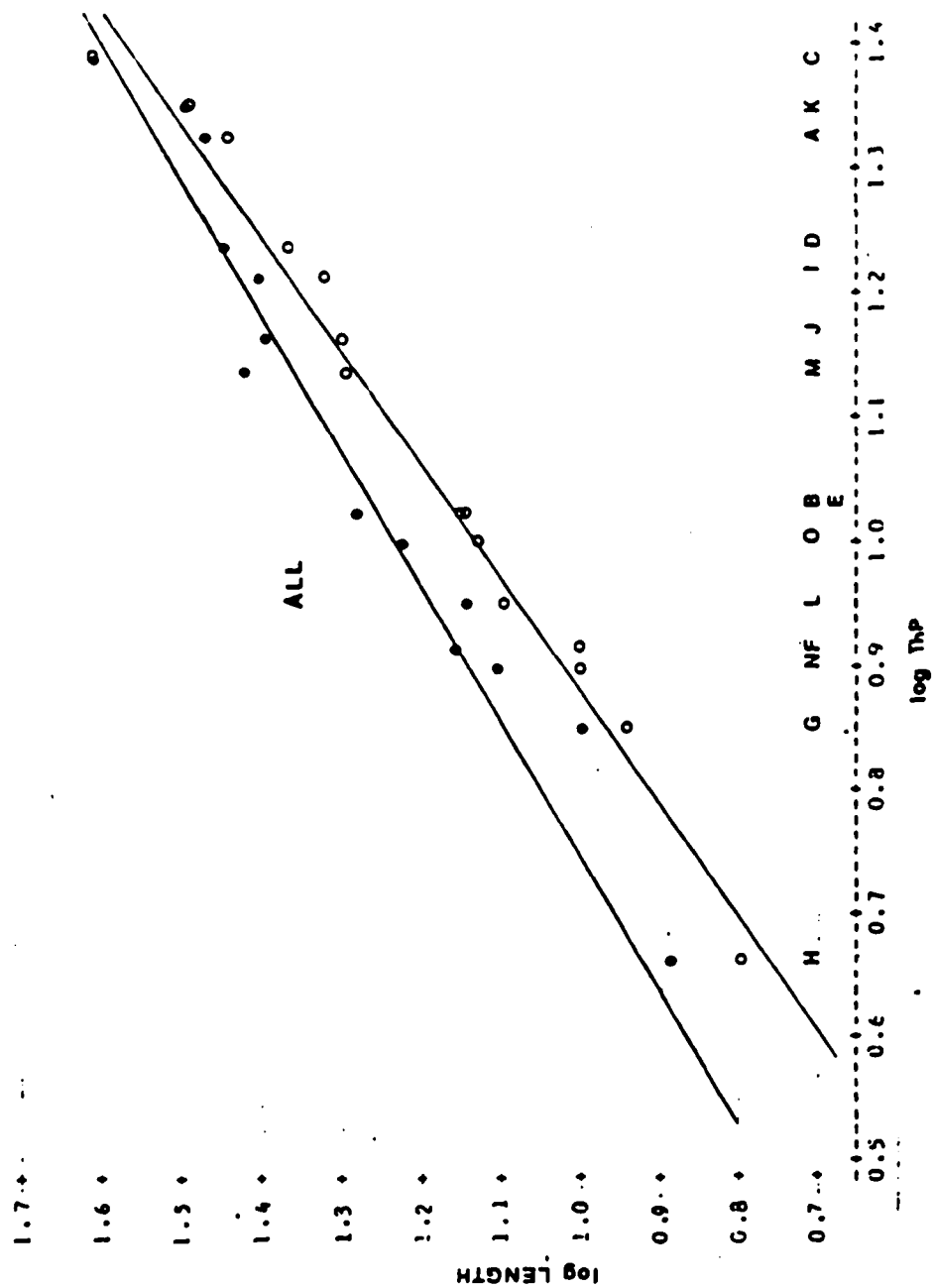


Figure IV.4

Figure IV.5 Allometry of mean forelimb and hindlimb lengths to mean weight in NOATELS: $\circ$, forelimb length; $\bullet$, hindlimb length; WT, body weight; B, Aotus; D, Cacajao; E, Callicebus; F, Callimico; G, Callithrix; H, Cebuella; I, Cebus; J, Chiropotes; L, Leontopithecus; M, Pithecia; N, Saguinus; O, Saimiri.

Figure IV.5

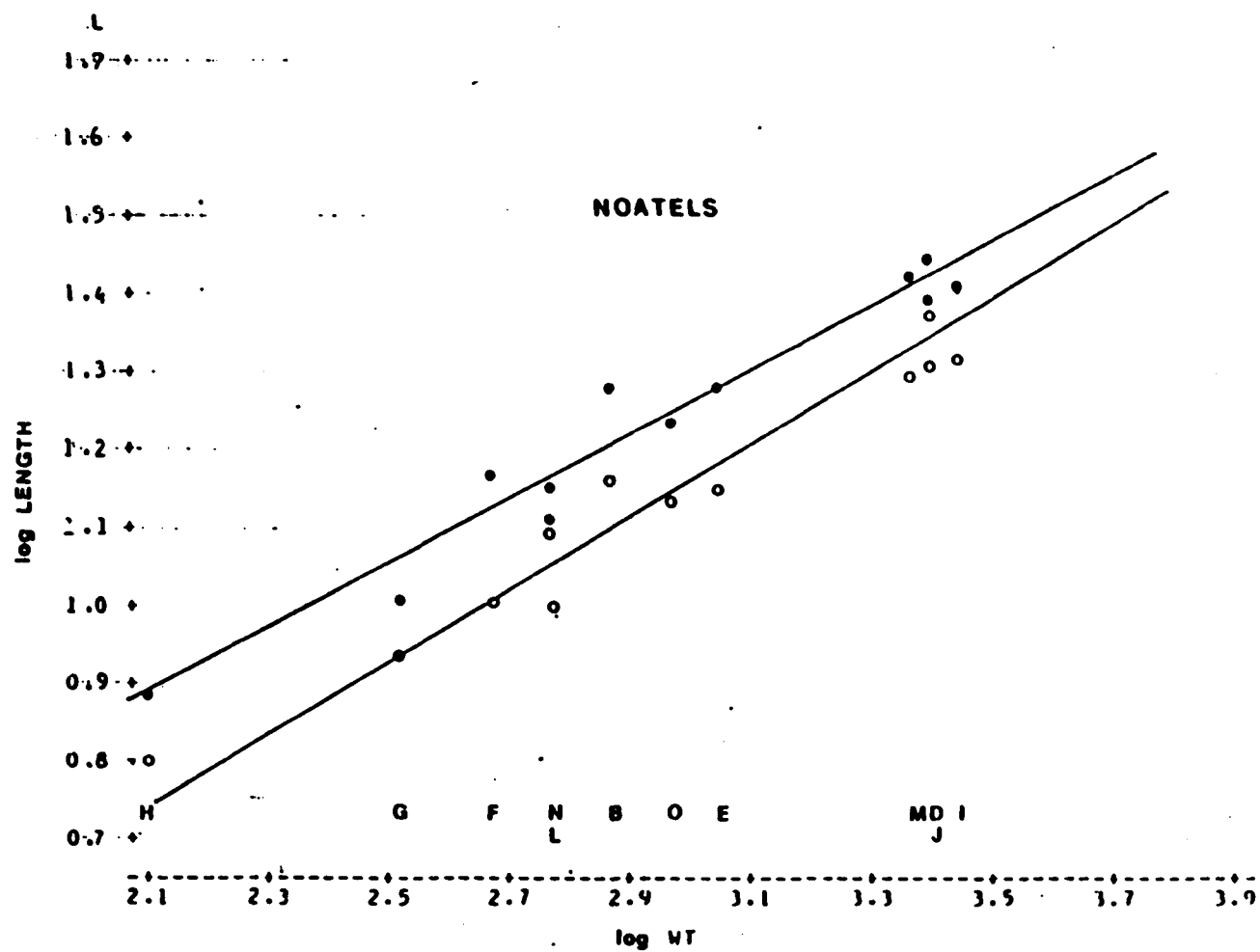


Figure IV.6 Allometry of mean forelimb and hindlimb lengths to mean weight in the traditional platyrrhine families, Callitrichidae and Cebidae; °, forelimb length; •, hindlimb length; WT, body weight; Callitrichidae: (F) Callimico, (G) Callithrix, (H) Cebuella, (L) Leontopithecus, (N) Saguinus; Cebidae: (A) Alouatta, (B) Aotus, (C) Ateles, (D) Cacajao, (E) Callicebus, (I) Cebus, (J) Chiropotes, (K) Lagothrix, (O) Saimiri.

Figure IV.6

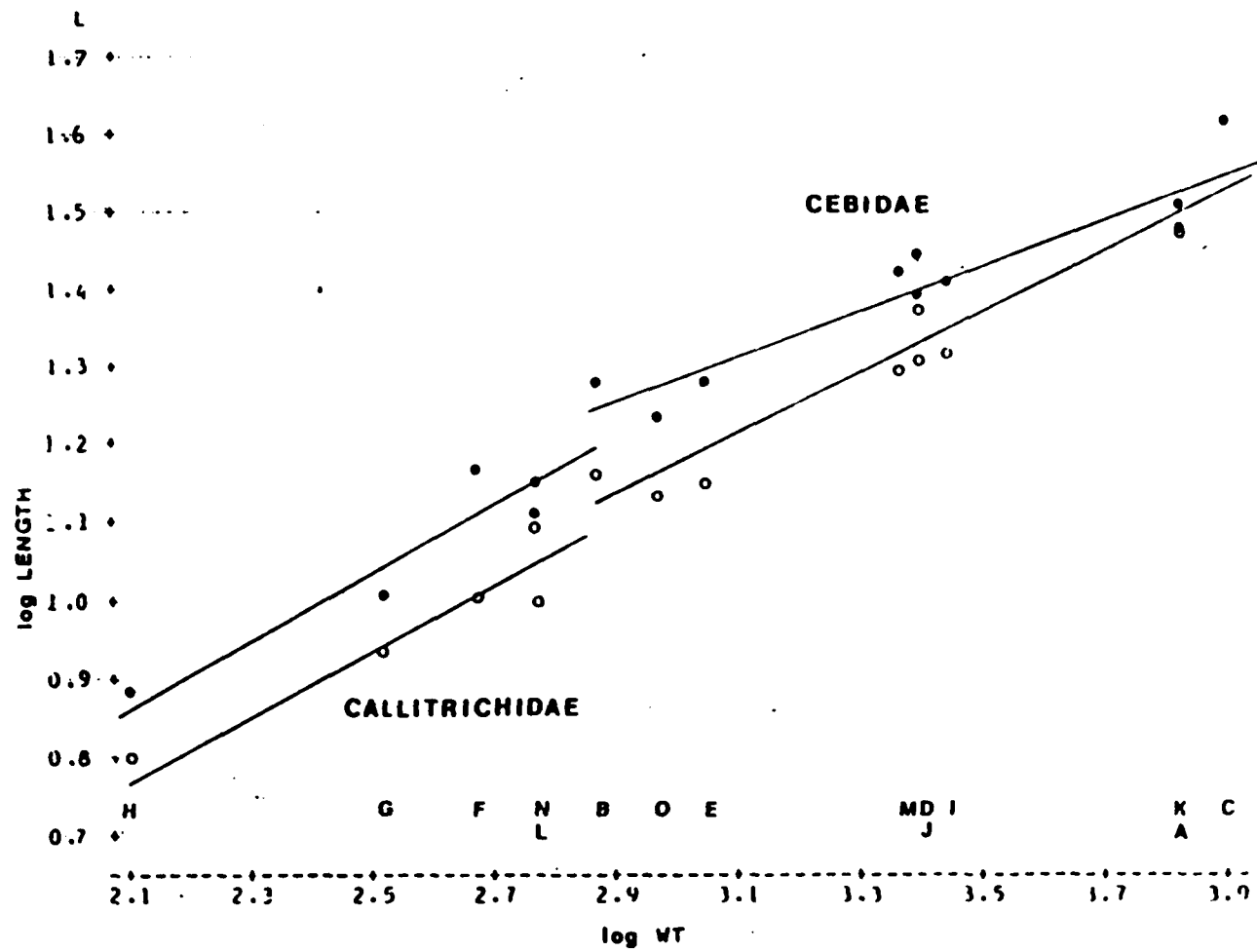


Figure IV.7 Allometry of mean forelimb and hindlimb lengths to mean weight in "Cebidae" and "Atelidae"; (Rosenberger 1979); °, forelimb length; •, hindlimb length; WT, body weight; "Cebidae": (F) Callimico, (G) Callithrix, (H) Cebuella, (I) Cebus, (L) Leontopithecus, (N) Saguinus, (O) Saimiri; "Atelidae": (A) Alouatta, (B) Aotus, (C) Ateles, (D) Cacajao, (E) Callicebus, (J) Chiropotes, (K) Lagothrix, (M) Pithecia.

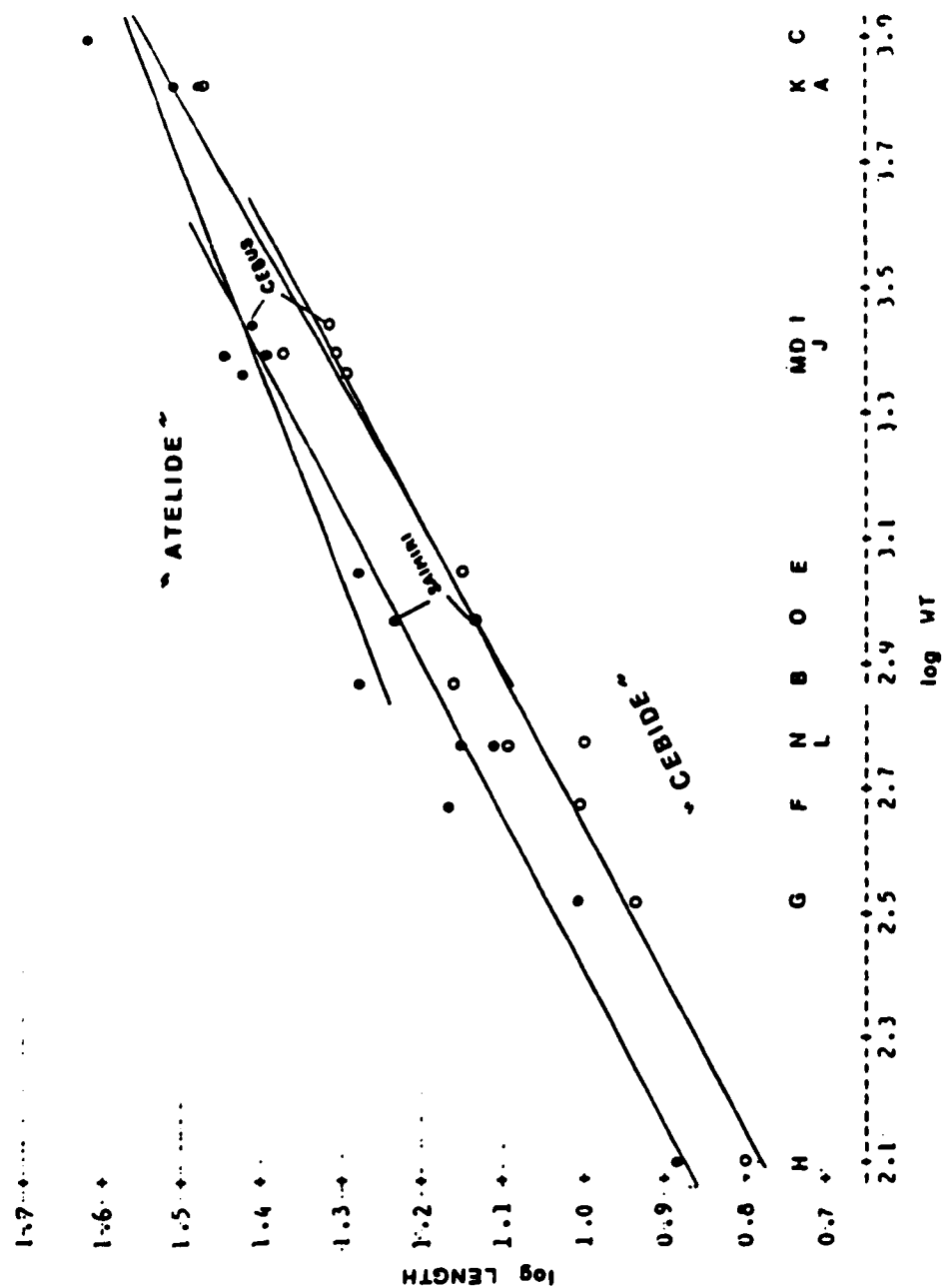


Figure IV.7

Figure IV.8 Allometry of mean forelimb and hindlimb lengths to mean weight in "derived" Platyrrhines proposed by Ford (1980); ○, forelimb length; ●, hindlimb length; WT, body weight; A, Alouatta; C, Ateles; D, Cacajao; F, Callimico; G, Callithrix; H, Cebueella; J, Chiropotes; K, Lagothrix; L, Leontopithecus; M, Pithecia; N, Saguinus.

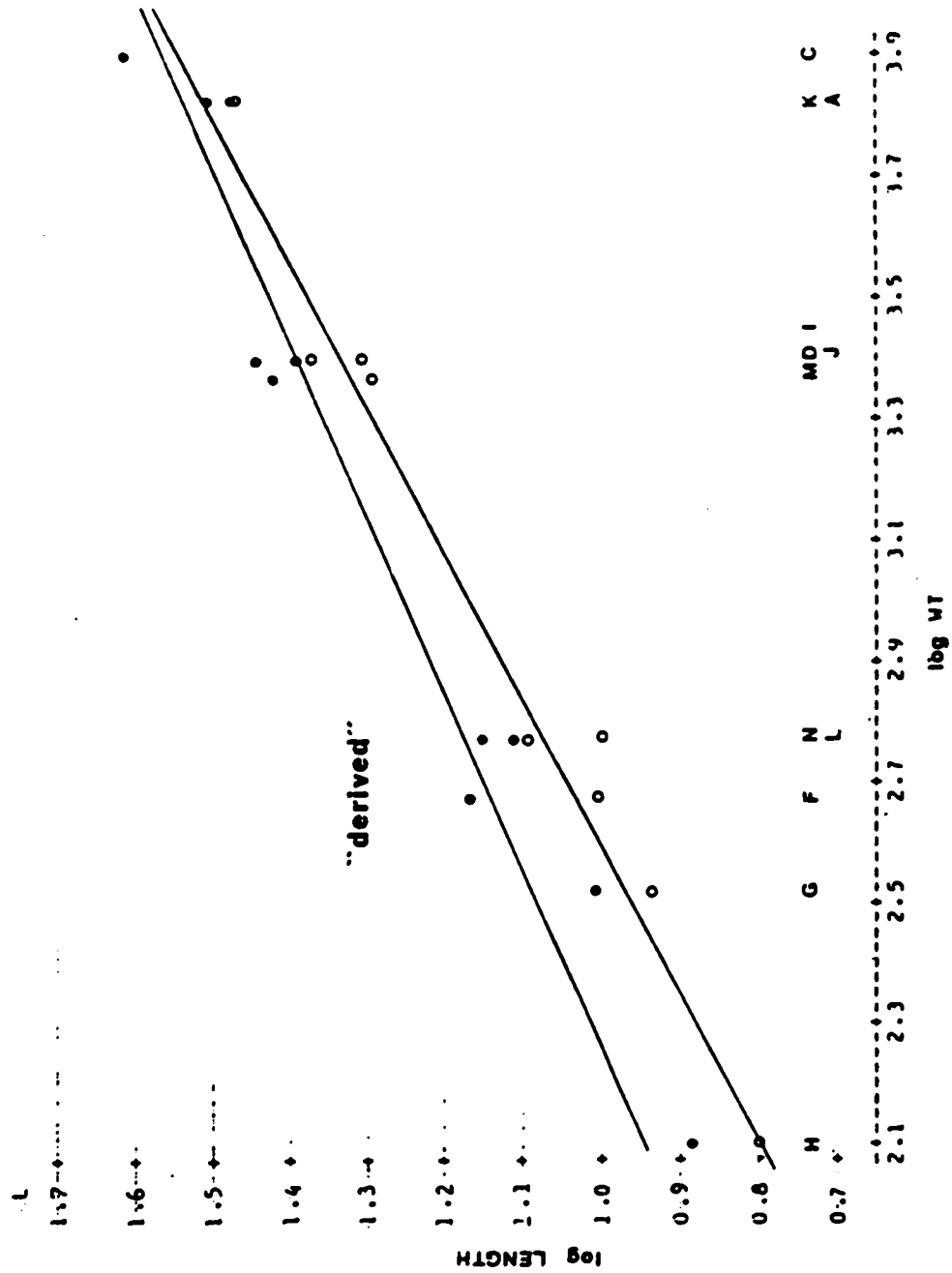


Figure IV.8

Figure IV.9 Allometry of mean forelimb segment diameters to mean weight; H, humerus; R, radius; M, metacarpal III; WT, body weight; A, Alouatta; B, Aotus; C, Ateles; D, Cacajao; E, Callicebus; F, Callimico; G, Callithrix; H, Cebuella; I, Cebus; J, Chiropotes; K, Lagothrix; L, Leontopithecus; M, Pithecia; N, Saguinus; O, Saimiri.

Figure 1 is a log-log plot showing the relationship between log diameter (y-axis) and log weight (x-axis). The y-axis ranges from -1.4 to 0.0, and the x-axis ranges from 2.0 to 4.4. Three parallel lines are drawn through the data points, representing different stages of development. Data points are labeled with letters: H, R, B, M, D, K, A, C, G, F, N, L, O, E, M, J, I. The lines show a positive correlation between log diameter and log weight.

Figure IV.10 Allometry of mean hindlimb segment diameters to mean weight; F, femur; T, tibia; M, metatarsal III; WT, body weight; A, Alouatta; B, Aotus; C, Ateles; D, Cacajao; E, Callicebus; F, Callimico; G, Callithrix; H, Cebuella; I, Cebus; J, Chiropotes; K, Lagorhix; L, Leontopithecus; M, Pithecia; N, Saguinus; O, Saimiri.

Figure IV.10

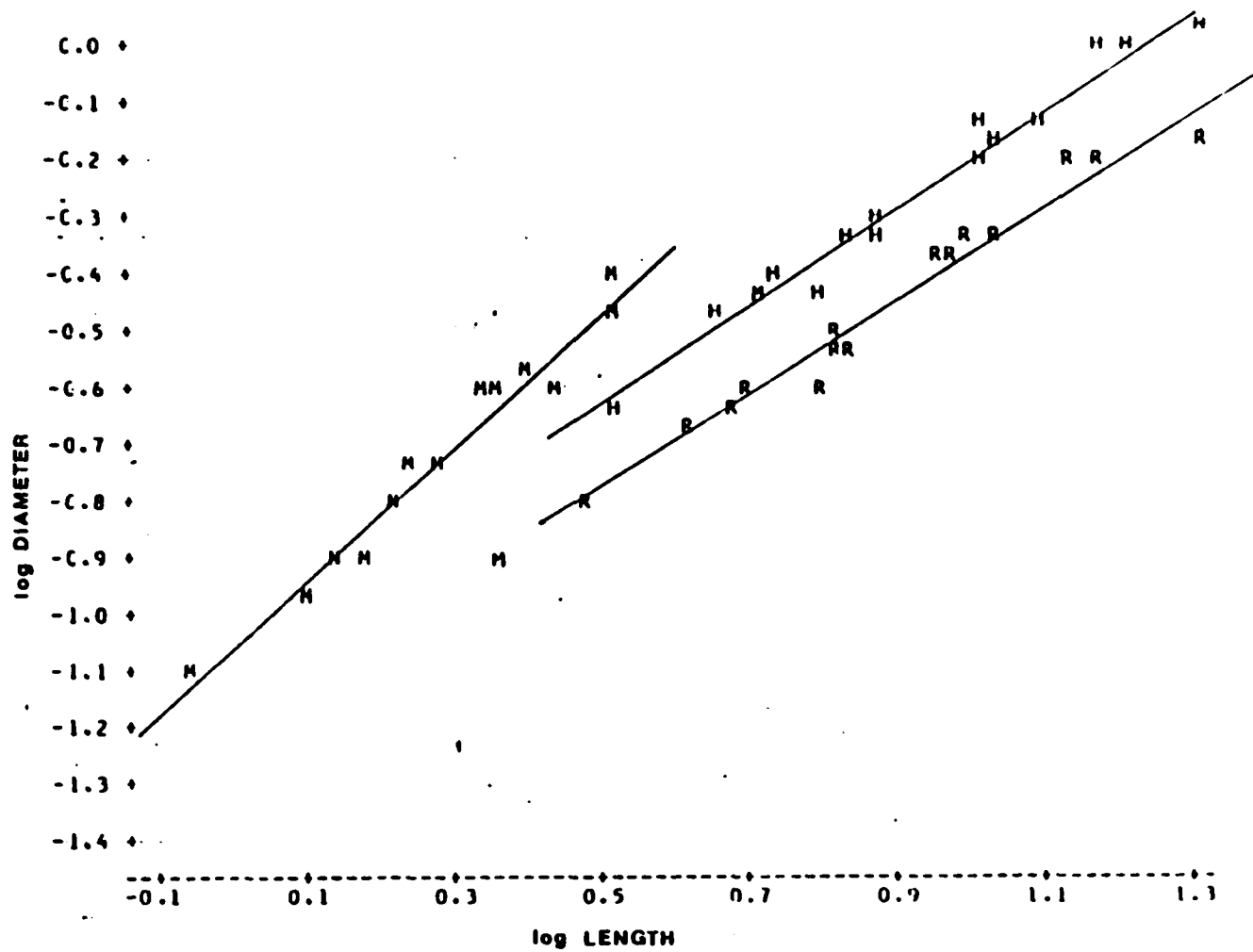


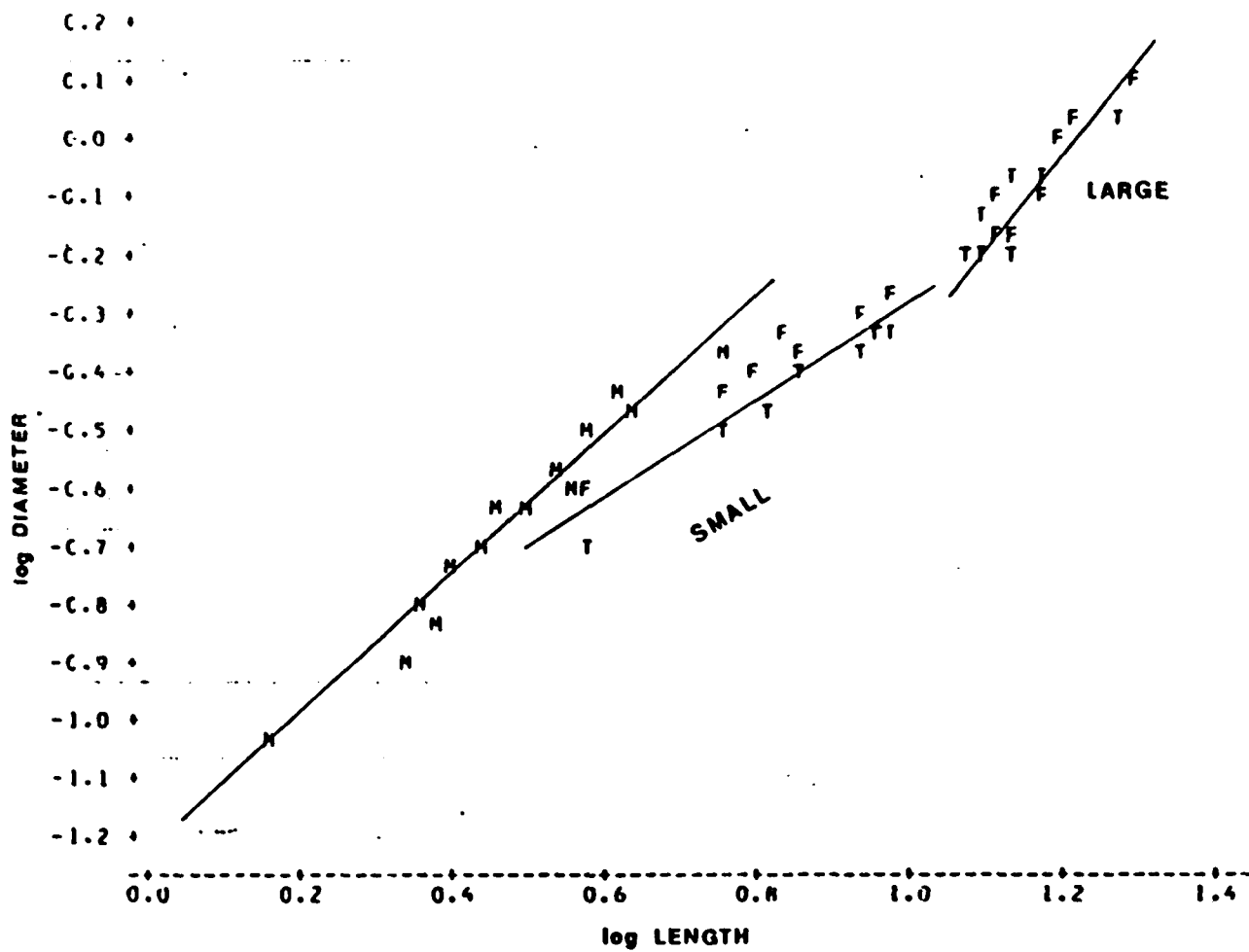
Figure IV.11 Allometry of mean forelimb segment diameters to mean segment lengths; H, humerus; R, radius; M, metacarpal III.

Figure 1 is a scatter plot showing the relationship between log DIAMETER (Y-axis) and log WT (X-axis). The Y-axis ranges from -1.2 to 0.2, and the X-axis ranges from 2.0 to 4.4. Two regression lines are shown: a solid line for the upper group of points and a dashed line for the lower group. Data points are labeled with letters: F, T, M, G, N, L, B, O, E, D, M, J, I, K, A, C. The upper group (solid line) includes points F, T, M, G, N, L, B, O, E, D, M, J, I. The lower group (dashed line) includes points M, G, N, L, B, O, E, D, M, J, I, K, A, C.

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Figure IV.12 Allometry of mean hindlimb segment diameters to mean segment lengths; F, femur; T, tibia; M, metatarsal III.

Figure IV.12



NOTE 3 OBS HIDDEN

APPENDIX I

The following gives localities (by country)*, where known, and numbers of skeletons () for designated genera, species and subspecies.

<u>genus</u>	<u>species</u>	<u>subspecies</u>	<u>locality</u>
<u>Alouatta</u>	<u>senicula</u>	<u>senicula</u>	Colombia (16)
<u>A.</u>	<u>s.</u>	<u>s.</u>	Bolivia (9) Peru (2)
<u>A.</u>	<u>s.</u>	<u>straminea</u>	Venezuela (3)
<u>A.</u>	<u>s.</u>	<u>s.</u>	British Guiana (3)
<u>A.</u>	<u>caraya</u>		Bolivia (22)
<u>A.</u>	<u>c.</u>		Brazil (1)
<u>A.</u>	<u>palliata</u>		Panama (4)
<u>A.</u>	<u>p.</u>		Barro Colorado (7)
<u>A.</u>	<u>p.</u>		Guatemala (1)
	<u>belzebul</u>		Brazil (1)
<u>Aotus</u>	<u>trivirigatus</u>		Bolivia (11)
<u>A.</u>	<u>t.</u>		Colombia (4)
<u>A.</u>	<u>t.</u>		Brazil (1)
<u>Ateles</u>			Venezuela (1)
<u>A.</u>			Mexico (1)
<u>A.</u>			British Guiana (1)
<u>A.</u>			Costa Rica (1)
<u>A.</u>	<u>belzebul</u>	<u>belzebul</u>	Venezuela (1)
<u>A.</u>	<u>geoffroyi</u>	<u>villerosus</u>	Mexico (2)
<u>A.</u>	<u>g.</u>	<u>ornatus</u>	Costa Rica (1)
<u>A.</u>	<u>paniscus</u>	<u>paniscus</u>	British Guiana (1)

* The only more specific locality given is Barro Colorado Island, as apart from mainland Panama, for certain skeletons of Alouatta palliata.

<u>genus</u>	<u>species</u>	<u>subspecies</u>	<u>locality</u>
<u>Callicebus</u>	<u>moloch</u>		Bolivia (6)
<u>C.</u>	<u>m.</u>		Brazil (1)
<u>C.</u>	<u>m.</u>		Colombia (3)
<u>C.</u>	<u>m.</u>		Equador (1)
<u>Callithrix</u>	<u>argentata</u>	<u>leucipe</u>	Brazil (1)
<u>C.</u>	<u>jacchus</u>		Brazil (3)
<u>C.</u>			Brazil (1)
<u>Cebuella</u>	<u>pygmaea</u>		Peru (1)
<u>Cebus</u>	<u>albifrons</u>		Bolivia (3) Peru (1)
<u>C.</u>	<u>a.</u>		Colombia (3)
<u>C.</u>	<u>apella</u>		Bolivia (4)
<u>C.</u>	<u>a.</u>		Brazil (3)
<u>C.</u>	<u>a.</u>	<u>paraguayanus</u>	Brazil (12)
<u>C.</u>	<u>nigrivittatus</u>	<u>apiculatus</u>	Venezuela (4)
<u>C.</u>	<u>n.</u>	<u>castaneus</u>	British Guiana (4)
<u>Lagothrix</u>	<u>lagotricha</u>		Peru (1)
<u>L.</u>	<u>l.</u>	<u>poeppigii</u>	Peru (1)
<u>Pithecia</u>	<u>pithecia</u>		British Guiana (2)
<u>Saguinus</u>			Peru (5) Brazil (1)
<u>S.</u>			Panama (3)
<u>S.</u>			Bolivia (1)
<u>S.</u>			British Guiana (1)
<u>Saimiri</u>	<u>sciureus</u>		Bolivia (22)
			Peru (1) Brazil (1)

APPENDIX II: THE DATA

The following pages give all measurements for all skeletons used in this study; OBS, observation; GEN, genus; SP, species; CAT, catalog number; S, sex; chapter II (ii) and Table II.1 for other abbreviations.

URS	GEN	SP	CAT	S	WT	STL	ThF	LuF	ThR	LuR	Pol	ThP
1	A	BE	133544	F	6300	33.56	10.12	12.78	14.10	8.80	10.66	20.78
2	A	CA	133875	.	.	.	.	.	.	.	.	.
3	A	CA	209917	M	.	35.99	11.65	11.83	15.90	7.58	12.51	24.16
4	A	CA	211495	F	6100	31.23	10.22	10.32	12.62	7.92	10.69	20.91
5	A	CA	211496	M	8900	34.37	10.77	11.26	14.87	7.16	12.34	23.11
6	A	CA	211497	F	.	.	10.13	10.69	12.76	8.06	.	.
7	A	CA	211498	M	.	33.72	10.13	12.76	14.26	8.63	10.83	20.96
8	A	CA	211499	M	.	32.45	11.73	9.43	13.08	8.08	11.29	23.00
9	A	CA	211501	F	.	28.76	8.75	9.96	11.71	7.00	10.05	18.80
10	A	CA	211502	F	.	32.00	10.54	11.18	13.01	8.71	10.28	20.82
11	A	CA	211504	M	8300	34.59	11.12	13.10	15.17	9.05	10.37	21.49
12	A	CA	211508	M	9000	34.55	11.55	11.85	14.30	9.10	11.15	22.70
13	A	CA	211510	M	.	34.64	11.40	11.62	14.13	8.89	11.62	23.02
14	A	CA	211512	F	.	31.60	10.40	10.36	12.74	8.02	10.84	21.24
15	A	CA	211513	M	.	36.00	12.23	14.54	14.92	9.10	11.98	24.21
16	A	CA	211519	M	.	38.77	13.44	13.33	16.48	10.29	12.00	25.44
17	A	CA	211520	F	.	30.88	10.37	10.74	12.80	8.31	9.77	20.14
18	A	CA	211522	F	.	30.87	10.42	10.62	13.10	7.94	9.83	20.25
19	A	CA	211523	M	.	33.97	11.13	11.84	13.84	9.13	11.00	22.13
20	A	CA	211524	F	.	32.27	.	.	13.82	8.75	9.70	.
21	A	CA	211525	M	7500	33.34	11.64	9.86	14.52	6.98	11.84	23.48
22	A	CA	211585	F	6140	31.01	9.95	11.95	13.80	8.10	9.11	19.06
23	A	CA	215060	F	.	29.58	9.16	9.89	11.35	7.70	10.53	19.69
24	A	CA	215061	M	.	30.43	9.12	10.78	12.29	7.61	10.53	19.65
25	A	PA	240407	M	.	35.19	11.92	13.17	16.13	8.96	10.10	22.02
26	A	PA	240408	.	.	34.65	8.95	15.20	14.33	9.82	10.50	19.45
27	A	PA	244870	M	.	41.37	.	.	16.58	11.49	13.30	.
28	A	PA	25309	.	.	37.54	12.23	14.34	16.65	9.92	10.97	23.20
29	A	PA	257307	F	.	35.39	10.99	14.10	15.18	9.58	10.63	21.62
30	A	PA	257359	.	.	34.66	11.18	13.11	15.23	9.06	10.37	21.55
31	A	PA	257404	.	.	35.97	11.02	13.56	15.15	9.43	11.39	22.41
32	A	PA	258313	F	.	35.05	10.88	13.47	15.11	9.24	10.70	21.58
33	A	PA	258314	.	.	36.03	.	.	16.07	9.06	10.90	.
34	A	PA	397108	.	.	33.90	10.09	12.81	14.02	8.88	11.00	21.09
35	A	PA	397112	.	.	36.78	10.64	16.24	14.99	11.89	9.90	20.54
36	A	PA	397113	.	.	36.49	.	.	15.77	10.02	10.70	.
37	A	SE	132790	M	.	38.65	13.45	13.38	16.53	10.30	11.82	25.27
38	A	SE	187994	F	.	28.30	9.15	12.21	11.68	9.68	6.94	16.09
39	A	SE	188006	F	.	33.26	9.91	13.07	14.18	8.80	10.28	20.19
40	A	SE	211527	F	4770	30.67	9.01	12.64	12.51	9.14	9.02	18.03
41	A	SE	211528	M	6360	34.64	12.40	12.00	13.80	10.60	10.10	22.50
42	A	SE	211531	F	5910	34.05	10.34	12.79	14.44	8.69	10.92	21.26
43	A	SE	211532	M	8640	36.10	11.55	12.76	15.66	8.65	11.79	23.34
44	A	SE	211535	F	5230	32.64	9.10	13.93	14.09	8.94	9.61	18.71
45	A	SE	211538	F	6140	30.14	9.75	11.49	12.17	9.07	8.90	18.65
46	A	SE	211540	F	5000	31.49	10.01	11.98	13.84	8.15	9.50	19.51
47	A	SE	211542	M	8640	37.12	12.40	13.20	15.31	10.29	11.52	23.92
48	A	SE	211543	F	5450	28.81	8.53	10.88	10.72	8.69	9.40	17.93
49	A	SE	23330	F	.	32.67	10.95	12.01	12.34	10.62	9.71	20.66
50	A	SE	23334	M	.	35.91	12.08	12.72	15.10	9.70	11.11	23.19
51	A	SE	23341	.	.	.	.	.	.	.	.	.
52	A	SE	23342	.	.	.	.	.	.	.	.	.
53	A	SE	23351	.	.	.	.	.	.	.	.	.

UHS	GEN	SP	CAT	S	WT	STL	ThF	LuF	ThR	LuR	Pol	ThP
1	A	BE	133544	F	6300	33.56	10.12	12.78	14.10	8.80	10.66	20.78
2	A	CA	133875	.	.	.	.	.	.	.	.	.
3	A	CA	209917	M	.	35.99	11.65	11.83	15.90	7.58	12.51	24.16
4	A	CA	211495	F	6100	31.23	10.22	10.32	12.62	7.92	10.69	20.91
5	A	CA	211496	M	8900	34.37	10.77	11.26	14.87	7.16	12.34	23.11
6	A	CA	211497	F	.	.	10.13	10.69	12.76	8.06	.	.
7	A	CA	211498	M	.	33.72	10.13	12.76	14.26	8.63	10.83	20.96
8	A	CA	211499	M	.	32.45	11.73	9.43	13.08	8.08	11.29	23.02
9	A	CA	211501	F	.	28.76	8.75	9.96	11.71	7.00	10.05	18.80
10	A	CA	211502	F	.	32.00	10.54	11.18	13.01	8.71	10.28	20.82
11	A	CA	211504	M	8300	34.59	11.12	13.10	15.17	9.05	10.37	21.49
12	A	CA	211508	M	9000	34.55	11.55	11.85	14.30	9.10	11.15	22.70
13	A	CA	211510	M	.	34.64	11.40	11.62	14.13	8.89	11.62	23.02
14	A	CA	211512	F	.	31.60	10.40	10.36	12.74	8.02	10.84	21.24
15	A	CA	211513	M	.	36.00	12.23	14.54	14.92	9.10	11.98	24.21
16	A	CA	211519	M	.	38.77	13.44	13.33	16.48	10.29	12.00	25.44
17	A	CA	211520	F	.	30.88	10.37	10.74	12.80	8.31	9.77	20.14
18	A	CA	211522	F	.	30.87	10.42	10.62	13.10	7.94	9.83	20.25
19	A	CA	211523	M	.	33.97	11.13	11.84	13.84	9.13	11.00	22.13
20	A	CA	211524	F	.	32.27	.	.	13.82	8.75	9.70	.
21	A	CA	211525	M	7500	33.34	11.64	9.86	14.52	6.98	11.84	23.48
22	A	CA	211585	F	6140	31.01	9.95	11.95	13.80	8.10	9.11	19.06
23	A	CA	215060	F	.	29.58	9.16	9.89	11.35	7.70	10.53	19.69
24	A	CA	215061	M	.	30.43	9.12	10.78	12.29	7.61	10.53	19.65
25	A	PA	240407	M	.	35.19	11.92	13.17	16.13	8.96	10.10	22.02
26	A	PA	240408	.	.	34.65	8.95	15.20	14.33	9.82	10.50	19.45
27	A	PA	244870	M	.	41.37	.	.	16.58	11.49	13.30	.
28	A	PA	25309	.	.	37.54	12.23	14.34	16.65	9.92	10.97	23.20
29	A	PA	257307	F	.	35.39	10.99	14.10	15.18	9.58	10.63	21.62
30	A	PA	257359	.	.	34.66	11.18	13.11	15.23	9.06	10.37	21.55
31	A	PA	257404	.	.	35.97	11.02	13.56	15.15	9.43	11.39	22.41
32	A	PA	258313	F	.	35.05	10.88	13.47	15.11	9.24	10.70	21.58
33	A	PA	258314	.	.	36.03	.	.	16.07	9.06	10.90	.
34	A	PA	397108	.	.	33.90	10.09	12.81	14.02	8.88	11.00	21.09
35	A	PA	397112	.	.	36.78	10.64	16.24	14.99	11.89	9.90	20.54
36	A	PA	397113	.	.	36.49	.	.	15.77	10.02	10.70	.
37	A	SE	132790	M	.	38.65	13.45	13.38	16.53	10.30	11.82	25.27
38	A	SE	187994	F	.	28.30	9.15	12.21	11.68	9.68	6.94	16.09
39	A	SE	188006	F	.	33.26	9.91	13.07	14.18	8.80	10.28	20.19
40	A	SE	211527	F	4770	30.67	9.01	12.64	12.51	9.14	9.02	18.03
41	A	SE	211528	M	6360	34.64	12.40	12.00	13.80	10.60	10.10	22.50
42	A	SE	211531	F	5910	34.05	10.34	12.79	14.44	8.69	10.92	21.26
43	A	SE	211532	M	8640	36.10	11.55	12.76	15.66	8.65	11.79	23.34
44	A	SE	211535	F	5230	32.64	9.10	13.93	14.09	8.94	9.61	18.71
45	A	SE	211538	F	6140	30.14	9.75	11.49	12.17	9.07	8.90	18.65
46	A	SE	211540	F	5000	31.49	10.01	11.98	13.84	8.15	9.50	19.51
47	A	SE	211542	M	8640	37.12	12.40	13.20	15.31	10.29	11.52	23.92
48	A	SE	211543	F	5450	28.81	8.53	10.88	10.72	8.69	9.40	17.93
49	A	SE	23330	F	.	32.67	10.95	12.01	12.34	10.62	9.71	20.66
50	A	SE	23334	M	.	35.91	12.08	12.72	15.10	9.70	11.11	23.19
51	A	SE	23341	.	.	.	.	.	.	.	.	.
52	A	SE	23342	.	.	.	.	.	.	.	.	.
53	A	SE	23351	.	.	.	.	.	.	.	.	.

OBS	GEN	SP	CAT	S	WT	STL	ThF	LuF	ThR	LuR	PeI	ThP
54	A	SE	23355		.	.	.	.	.	.	.	.
55	A	SE	23361		.	.	.	.	.	.	.	.
56	A	SE	23370		.	.	.	.	.	.	.	.
57	A	SE	23371		.	.	.	.	.	.	.	.
58	A	SE	23377	F	.	.	.	.	.	.	.	.
59	A	SE	23378	F	.	.	.	.	.	.	.	.
60	A	SE	23382	F	.	.	.	.	.	.	.	.
61	A	SE	23386		.	.	.	.	.	.	.	.
62	A	SE	23549	F	.	.	.	.	.	.	.	.
63	A	SE	23556		.	.	.	.	.	.	.	.
64	A	SE	30193	M	.	39.32	13.61	13.34	16.58	10.37	12.37	25.98
65	A	SE	42313		.	36.13	11.93	13.43	16.15	9.21	10.77	22.70
66	A	SE	42316	F	.	34.87	10.01	12.61	13.97	8.65	12.25	22.26
67	A	SE	48119	F	5680	35.39	10.39	14.24	15.47	9.16	10.76	21.15
68	A	SE	69591		.	.	12.58	15.12	15.58	12.12	10.51	23.09
69	A	SE	70088	M	.	34.62	11.52	12.94	14.65	9.81	10.16	21.68
70	A	SE	99657	F	.	.	.	.	.	.	.	.
71	B	TR	10	M	.	20.86	5.36	10.87	7.77	8.46	4.63	9.99
72	B	TR	1442		.	20.78	5.17	11.03	7.33	8.87	4.58	9.75
73	B	TR	209916	F	.	20.83	4.87	11.06	6.98	8.95	4.90	9.77
74	B	TR	211464	M	1500	25.44	6.02	13.75	8.56	11.21	5.67	11.69
75	B	TR	211477	F	.	23.25	5.46	12.44	7.75	10.15	5.35	10.81
76	B	TR	21153		.	21.34	5.45	11.25	7.03	9.67	4.64	10.09
77	B	TR	215048	F	.	23.87	5.88	12.67	8.32	10.23	5.32	11.20
78	B	TR	215050	F	.	24.26	5.75	13.32	8.33	10.74	5.19	10.94
79	B	TR	215051	M	.	25.38	6.12	13.50	8.65	10.97	5.76	11.88
80	B	TR	215052	M	.	23.93	5.22	13.75	8.57	10.40	4.96	10.18
81	B	TR	215053	F	.	23.78	5.23	13.09	7.67	10.67	5.46	10.69
82	B	TR	215054	M	.	24.17	5.91	12.90	8.34	10.47	5.36	11.27
83	B	TR	215056	F	.	25.27	6.27	13.98	9.00	11.25	5.22	11.49
84	B	TR	215057	M	.	24.52	5.43	14.07	8.88	10.62	5.02	10.45
85	B	TR	215059	M	.	23.69	.	.	7.84	10.66	5.19	.
86	B	TR	396505	M	.	22.93	6.22	13.40	7.98	9.97	4.98	11.20
87	B	TR	396702	F	.	20.32	5.05	9.99	7.02	8.47	4.83	9.88
88	B	TR	39675	F	.	21.67	.	.	7.02	9.38	5.27	.
89	B	TR	451		.	22.25	5.68	11.41	7.22	9.87	5.16	10.84
90	B	TR	937	F	.	22.71	.	.	7.56	9.65	5.50	.
91	B	TR	938	F	.	21.95	5.37	11.24	7.76	8.85	5.34	10.71
92	C		12		.	.	.	.	.	.	.	.
93	C		12		.	.	.	.	.	.	.	.
94	C		140	M	.	32.49	11.08	8.46	13.47	6.07	12.95	24.03
95	C		154189		.	31.78	.	.	12.73	5.81	13.24	.
96	C		183	M	.	.	11.69	9.67	15.23	6.13	.	.
97	C		184	M	.	32.22	11.90	8.55	14.33	6.12	11.77	23.67
98	C		277		.	33.63	.	.	12.94	7.52	13.17	.
99	C		292	F	.	.	.	.	.	.	.	.
100	C		3768	M	.	32.55	10.93	8.66	13.45	6.14	12.96	23.89
101	C		810	F	.	.	.	.	.	.	.	.
102	C	BE	259	F	.	32.82	11.62	7.72	12.96	6.38	13.48	25.10
103	C	BE	30192	M	.	.	.	.	.	.	.	.
104	C	GE	14128		.	.	.	.	16.55	6.72	.	.
105	C	GE	172985		.	.	.	.	.	.	.	.
106	C	GE	244863		.	34.56	12.15	8.96	14.83	6.28	13.45	25.60

OBS	GEN	SF	CAT	S	WT	STL	ThF	LuF	ThR	LuR	PeI	ThP
107	C	GE	276631	F	.	31.20	11.43	7.03	12.63	5.83	12.74	24.17
108	C	GE	276657	F	.	.	.	.	.	.	.	.
109	C	FA	361027	M	.	.	.	.	.	.	.	.
110	D		1566	F	.	28.55	9.92	10.40	11.12	9.20	8.23	18.15
111	D		1571		.	31.40	.	.	13.01	10.46	7.93	.
112	D		1572		.	30.36	9.20	13.61	11.68	11.13	7.55	16.75
113	D		1573		.	.	.	.	.	.	.	.
114	D		1574		.	28.71	9.15	12.03	11.73	9.45	7.53	16.68
115	D		1575		.	.	.	.	.	.	.	.
116	D		1576		.	30.42	.	.	11.98	10.49	8.95	.
117	D		1577		.	.	.	.	.	.	.	.
118	D		1578		.	30.14	9.51	12.41	11.95	9.97	8.22	17.73
119	D		1584		.	26.57	7.70	11.05	9.91	8.84	7.82	15.52
120	D		1585		.	30.09	9.36	12.64	11.89	10.11	8.09	17.45
121	D		1866		.	.	7.66	12.19	10.68	9.17	7.21	14.87
122	D	RU	302626	M	.	.	8.26	14.01	10.68	11.59	.	.
123	D	RU	519570	F	.	30.49	8.92	12.77	11.37	10.32	8.80	17.72
124	D	RU	70192	M	.	32.75	9.90	13.95	12.63	11.22	8.90	18.80
125	E		119625	M	.	24.36	5.39	13.97	8.44	10.92	5.00	10.39
126	E		1273	M	.	27.13	.	.	9.73	12.24	5.16	.
127	E		136208	M	.	.	.	.	.	.	.	.
128	E		211492	M	1430	22.38	5.40	12.43	8.03	9.80	5.55	10.95
129	E		659		.	23.49	.	.	8.03	10.64	4.82	.
130	E		997	F	.	23.46	6.05	12.46	8.03	10.48	4.95	11.00
131	E		998		.	.	.	.	.	.	.	.
132	E	MO	130361		.	24.95	6.02	13.79	8.24	11.57	5.14	11.16
133	E	MO	136217	M	.	22.38	6.03	11.82	8.00	9.85	4.53	10.56
134	E	MO	211487	M	907	23.33	5.12	13.51	8.09	10.54	4.70	9.82
135	E	MO	211488	M	907	23.16	5.45	13.28	8.45	10.28	4.43	9.88
136	E	MO	211489	F	907	23.19	5.49	12.91	8.34	10.06	4.79	10.28
137	E	MO	211490	F	907	23.24	6.14	12.44	9.04	9.54	4.66	10.80
138	E	MO	211493	M	907	23.52	5.60	13.40	8.70	10.30	4.40	10.00
139	E	MO	240088	F	.	28.86	6.44	16.63	10.15	12.92	5.79	12.23
140	E	MO	269827	M	.	24.77	5.74	14.02	8.82	10.94	5.01	10.75
141	E	MO	397933	M	1400	23.53	5.42	13.14	8.24	10.32	4.97	10.39
142	E	MO	94977	M	.	23.80	5.40	13.67	8.52	10.55	4.73	10.13
143	E	TO	398212	F	.	25.49	6.84	13.01	10.32	9.53	5.64	12.48
144	F	GO	1829		.	.	.	.	.	.	.	.
145	F	GO	183289		.	16.54	4.48	8.16	6.65	5.99	3.90	8.38
146	F	GO	303323	M	.	.	4.38	7.72	5.73	6.37	.	.
147	F	GO	395455	M	.	15.97	4.37	7.95	6.51	5.81	3.65	8.02
148	G		1279	M	.	15.22	3.96	7.83	5.29	6.50	3.43	7.39
149	G		1280	M	.	15.02	3.74	7.81	5.50	6.05	3.47	7.21
150	G		1290	M	.	.	.	.	.	.	.	.
151	G		1298	M	.	.	.	.	.	.	.	.
152	G		1314	F	.	.	.	.	.	.	.	.
153	G		1323	M	.	12.70	3.62	6.00	4.77	4.85	3.08	6.70
154	G		1325	F	.	13.28	3.50	6.59	5.31	4.78	3.19	6.69
155	G		1329	M	.	13.70	3.60	6.92	5.49	5.03	3.18	6.78
156	G		1330	F	.	13.56	3.69	6.81	5.66	4.84	3.06	6.75
157	G		1336	F	.	14.49	3.74	7.40	5.70	5.44	3.35	7.09
158	G		1339	M	.	14.55	3.88	7.26	5.79	5.35	3.41	7.29
159	G		293	F	.	15.49	4.44	7.69	5.78	6.35	3.36	7.80

ORS	GEN	SF	CAT	S	WT	STL	ThF	LuF	ThR	LuR	Pe1	ThP
160	G		49480		.	13.67	3.45	7.18	5.08	5.55	3.04	6.49
161	G		66		.	14.32	4.19	6.95	5.42	5.72	3.18	7.37
162	G		68	F	.	13.97	4.05	6.77	5.25	5.57	3.10	7.15
163	G		95127	M	.	14.63	4.30	6.88	5.98	5.20	3.45	7.75
164	G	AR	133712		310	.	.	.	.	.	.	.
165	G	AR	184689		.	13.44	3.88	6.37	5.62	4.63	3.19	7.07
166	G	CH	241197	F	.	14.02	4.22	6.26	6.50	4.98	3.54	7.76
167	G	JA	133688	F	250	13.72	3.97	6.79	5.11	5.65	2.96	6.93
168	G	JA	133694	M	.	.	.	.	.	.	.	.
169	G	JA	133698	F	.	.	.	.	.	.	.	.
170	G	JA	35529		.	14.04	3.76	6.93	5.57	5.12	3.35	7.11
171	H	PY	244101		.	8.16	1.94	4.20	2.90	3.24	2.02	3.96
172	H	PY	303037	M	.	8.89	2.34	4.28	3.46	3.16	2.27	4.61
173	H	PY	305778	M	.	9.10	2.49	4.42	3.73	3.18	2.19	4.68
174	H	PY	314966	F	.	10.11	2.61	4.87	3.90	3.58	2.63	5.24
175	H	PY	336325	M	.	9.12	2.51	4.49	3.75	3.25	2.12	4.63
176	H	PY	337947	M	.	9.24	2.51	4.57	3.72	3.36	2.16	4.67
177	H	PY	337948	M	.	8.68	2.31	4.25	3.44	3.12	2.12	4.43
178	H	PY	673		.	.	.	.	3.87	3.56	2.44	.
179	H	PY	693	M	.	.	.	.	.	.	.	.
180	H	PY	694	M	.	.	.	.	.	.	.	.
181	H	PY	695	M	.	.	.	.	.	.	.	.
182	H	PY	696		.	.	.	.	.	.	.	.
183	H	PY	697	M	.	.	.	.	.	.	.	.
184	H	PY	699	M	.	.	.	.	.	.	.	.
185	H	PY	699	F	.	.	.	.	.	.	.	.
186	H	PY	701	F	.	.	.	.	.	.	.	.
187	H	PY	734		.	.	1.91	3.30	2.61	2.33	1.95	3.86
188	H	PY	923	F	.	.	.	.	.	.	.	.
189	I	AL	188018	F	.	27.22	7.59	11.37	10.73	8.23	8.26	15.85
190	I	AL	209923	F	2000	25.43	7.76	10.38	9.81	8.33	7.29	15.05
191	I	AL	209924	M	.	26.86	8.12	10.32	11.41	7.03	8.42	16.54
192	I	AL	209925	M	.	28.83	8.75	11.48	12.27	7.96	8.60	17.35
193	I	AL	23392	M	.	28.77	8.45	11.90	11.83	8.52	8.42	16.87
194	I	AL	23401	F	.	26.96	7.64	11.28	10.61	8.31	8.05	15.69
195	I	AL	23402		.	27.43	8.22	11.59	11.46	8.35	7.62	15.84
196	I	AP	133606	M	3900	28.75	7.52	12.98	11.68	8.92	8.15	15.67
197	I	AP	133620	M	3250	.	.	.	.	.	.	.
198	I	AP	133622	M	3120	27.15	8.76	10.88	10.89	8.75	7.51	16.27
199	I	AP	133623	M	2750	.	.	.	.	.	.	.
200	I	AP	133624	M	3000	.	.	.	.	.	.	.
201	I	AP	133626	F	1830	.	.	.	.	.	.	.
202	I	AP	133628	M	3320	26.85	9.64	9.49	10.67	8.46	7.72	17.36
203	I	AP	133631	F	2070	.	.	.	.	.	.	.
204	I	AP	133637	M	3250	27.20	8.71	11.91	12.07	7.56	7.57	16.28
205	I	AP	133665	M	3390	26.51	6.84	12.06	11.25	7.65	7.61	14.45
206	I	AP	133806	F	2100	.	.	.	.	.	.	.
207	I	AP	133810	F	1700	.	.	.	.	.	.	.
208	I	AP	133813	F	1850	.	.	.	.	.	.	.
209	I	AP	133851	M	3850	28.17	8.81	11.45	12.36	7.90	7.91	16.72
210	I	AP	133862	M	2900	.	.	.	.	.	.	.
211	I	AP	133864	M	1800	.	.	.	.	.	.	.
212	I	AP	209926	F	1771	23.23	7.01	9.25	9.95	6.31	6.97	13.98

URS	GEN	SP	CAT	S	WT	STL	ThF	LuF	ThR	LuR	PeI	ThP
213	I	AF	207927	F	2200	25.14	6.90	10.88	9.77	8.01	7.36	14.26
214	I	AF	211578	M	3900	28.38	8.98	10.82	12.41	7.39	8.58	17.56
215	I	AF	211579	M	4090	27.97	8.52	10.66	11.76	7.42	8.79	17.31
216	I	AF	270361	M	.	28.19	9.23	10.41	11.68	7.96	8.55	17.78
217	I	AF	95129	M	.	.	10.55	10.92	13.06	8.41	.	.
218	I	NI	30195	M	.	29.28	8.33	12.43	11.58	9.18	8.52	16.85
219	I	NI	30196	F	.	.	8.22	11.94	11.42	8.74	.	.
220	I	NI	30197	M	.	.	.	.	.	.	.	.
221	I	NI	30198	M	.	.	.	.	.	.	.	.
222	I	NI	361020	M	.	.	.	.	.	.	.	.
223	I	NI	361021	F	.	24.46	7.41	10.09	9.45	8.05	6.96	14.37
224	I	NI	42873	F	.	28.50	8.32	12.46	11.58	9.20	7.72	16.04
225	I	NI	42884	M	.	28.29	7.87	12.27	12.62	7.52	8.15	16.02
226	J	.	1198	.	.	25.29	6.44	12.36	10.24	8.56	6.49	12.93
227	J	.	1199	.	.	27.26	7.78	12.47	9.85	10.40	7.01	14.79
228	J	.	1200	.	.	27.93	8.34	12.92	11.70	9.56	6.67	15.01
229	J	.	1201	M	.	.	.	.	.	.	.	.
230	J	.	1202	F	.	.	.	.	.	.	.	.
231	J	.	1864	M	.	27.54	8.54	11.79	12.06	8.27	7.21	15.75
232	J	.	1867	F	.	28.13	9.13	11.64	11.45	9.32	7.36	16.49
233	J	.	1868	.	.	.	6.68	14.38	11.07	9.99	7.72	14.40
234	J	.	1909	F	.	27.64	7.81	12.68	10.93	9.56	7.15	14.96
235	J	.	1912	F	.	26.65	.	.	10.44	9.26	6.95	.
236	J	.	1918	M	.	22.29	6.60	12.20	10.24	8.56	6.49	13.09
237	K	.	163	M	.	31.49	.	.	13.61	6.41	11.47	.
238	K	.	164	M	.	34.01	12.38	10.07	15.41	7.04	11.56	23.94
239	K	.	165	.	.	32.07	.	.	13.66	8.40	10.01	.
240	K	.	177	.	.	33.69	11.68	9.83	14.62	6.89	12.18	23.86
241	K	.	178	.	.	34.61	10.89	11.98	15.52	7.35	11.74	22.63
242	K	.	180	.	.	.	.	.	.	.	.	.
243	K	.	355	M	.	34.87	10.83	11.91	13.60	9.14	12.13	22.96
244	K	.	555	F	.	32.86	11.43	9.97	14.43	6.97	11.46	22.89
245	K	.	675	M	.	33.58	10.02	12.52	15.65	6.89	11.04	21.06
246	K	.	676	M	.	33.04	.	.	14.06	6.73	12.25	.
247	K	.	677	M	.	31.32	8.64	11.57	13.75	6.50	11.07	19.71
248	K	.	970	.	.	.	10.44	10.61	14.53	6.52	10.57	21.01
249	K	LA	188153	F	.	31.28	10.31	9.76	13.15	7.92	10.21	20.52
250	K	LA	188162	F	.	30.42	10.48	9.07	13.13	6.42	10.87	21.35
251	K	LA	35752	M	.	33.54	11.71	10.79	14.36	8.14	11.04	22.75
252	K	LA	397774	F	.	38.98	11.42	15.26	17.16	9.52	12.30	23.72
253	K	LA	397775	M	.	30.71	10.39	9.02	14.45	4.96	11.30	21.69
254	K	LA	70404	M	.	35.17	11.75	11.61	14.75	8.61	11.81	23.56
255	L	.	185347	.	.	17.48	.	.	6.05	7.03	4.40	.
256	L	RO	269705	F	.	17.10	4.77	8.35	6.25	6.87	3.98	8.75
257	M	.	129	F	.	.	.	.	.	.	.	.
258	M	.	1417	.	.	24.62	6.15	12.75	9.32	9.58	5.72	11.87
259	M	.	1445	F	.	25.26	6.95	11.87	10.14	8.68	6.44	13.39
260	M	.	1450	.	.	.	.	.	.	.	.	.
261	M	.	154	F	.	30.34	8.52	14.94	12.03	11.43	6.88	15.40
262	M	.	660	.	.	.	9.51	16.02	13.80	11.73	7.41	16.92
263	M	.	661	M	.	28.92	.	.	12.13	10.12	6.67	.
264	M	.	667	F	.	28.31	7.94	13.71	11.50	10.15	6.66	14.60
265	M	PA	241007	F	.	24.76	6.43	12.36	9.37	9.42	5.97	12.40

OBS	GEN	SF	CAT	S	WT	STL	ThF	LuF	ThR	LuR	Pol	ThP
266	M	PA	300794		.	24.24	6.86	11.61	9.94	8.53	5.77	12.63
267	M	PA	339659	F	.	.	.	.	.	.	.	.
268	M	PA	64088	M	.	26.41	7.48	12.72	9.64	10.56	6.21	13.69
269	M	PA	70377	M	.	25.80	6.81	13.39	10.11	10.09	5.60	12.41
270	N		148454		.	17.61	4.65	8.44	6.10	6.99	3.79	8.44
271	N		180091		.	15.53	4.38	7.49	6.44	5.43	3.66	8.04
272	N		207726		.	17.52	.	.	6.49	7.25	3.78	.
273	N		35516		.	16.27	4.61	8.17	6.04	6.74	3.49	8.10
274	N		77693		.	16.50	4.60	8.10	6.01	6.69	3.80	8.40
275	N		97316	M	.	16.56	4.76	8.12	6.22	6.66	3.68	8.44
276	N	M	1146		.	16.59	4.59	8.05	5.99	6.65	3.95	8.54
277	N	M	1148		.	.	4.86	8.34	6.02	6.88	.	.
278	N	M	25313		.	15.64	5.17	6.55	5.94	5.78	3.92	9.09
279	N	MB	1448		.	.	4.57	8.76	5.94	7.39	.	.
280	N	ML	148322		.	15.37	4.20	7.54	5.47	6.27	3.63	7.83
281	N	ML	292294	F	.	15.48	4.60	7.54	5.95	6.19	3.34	7.94
282	N	ML	439	F	.	16.64	4.57	8.18	6.78	5.97	3.89	8.46
283	N	O	117	F	.	.	.	.	5.91	6.56	.	.
284	N	O	121	M	.	15.52	4.38	7.70	5.71	6.37	3.44	7.82
285	N	O	442	F	.	.	.	.	6.00	6.82	.	.
286	N	O	445	F	.	16.21	4.38	7.61	5.76	6.23	4.22	8.60
287	N	O	648	F	.	15.68	4.13	7.80	5.48	6.45	3.75	7.88
288	N	O	654	M	.	15.80	4.49	7.86	5.87	6.48	3.45	7.94
289	N	O	708	F	.	16.36	4.63	8.03	6.11	6.55	3.70	8.33
290	N	OG	148336	M	.	16.35	4.80	8.61	7.10	6.31	3.94	8.74
291	N	OG	240425		.	.	4.47	7.94	5.87	6.54	.	.
292	N	OG	257345		.	16.01	4.56	7.62	5.90	6.28	3.83	8.39
293	N	OG	49389		.	16.49	4.51	7.80	6.71	5.96	3.82	8.33
294	N	OO	446	F	.	15.69	4.34	7.83	5.67	6.50	3.52	7.86
295	N	S	726	M	.	12.99	3.71	6.40	4.86	5.25	2.88	6.59
296	N	S	728	M	.	14.48	3.99	6.99	5.94	5.04	3.50	7.49
297	N	S	733	F	.	14.06	3.81	6.91	4.99	5.73	3.34	7.15
298	N	S	735	F	.	15.05	4.39	7.39	5.71	6.07	3.27	7.66
299	N	SD	148453	M	.	17.08	4.41	8.50	6.65	6.26	4.17	8.58
300	N	SD	362118		.	16.17	4.66	8.11	6.07	6.70	3.40	8.06
301	N	SF	461267	M	.	15.52	4.27	7.52	5.62	6.17	3.73	8.00
302	N	SI	336299	F	.	14.80	4.09	7.16	6.04	5.21	3.55	7.64
303	N	SI	336301	F	.	15.91	4.57	7.61	5.85	6.33	3.73	8.30
304	N	SN	147433		.	15.01	4.00	7.78	5.95	5.83	3.23	7.23
305	N	SY	188171	M	.	13.74	3.68	6.83	4.89	5.62	3.23	6.91
306	N	SY	188177	M	.	13.46	3.66	6.80	5.49	4.97	3.00	6.66
307	N	SY	238258	M	.	13.86	3.67	6.77	5.45	4.99	3.42	7.09
308	N	OG	49397		.	.	.	.	.	.	.	.
309	O	SC	188080	F	.	19.73	5.10	10.10	7.49	7.71	4.53	9.63
310	O	SC	188110	F	.	21.29	6.03	10.21	7.72	8.52	5.05	11.08
311	O	SC	209928	F	647	18.70	4.19	10.13	6.85	7.47	4.38	8.57
312	O	SC	209930	M	1400	20.88	6.05	10.07	7.65	8.47	4.76	10.81
313	O	SC	209933	F	641	19.06	4.56	9.98	6.61	7.93	4.52	9.08
314	O	SC	209934	M	920	21.45	5.69	11.26	8.18	8.77	4.50	10.19
315	O	SC	209935	M	973	22.19	5.87	11.38	8.50	8.75	4.94	10.81
316	O	SC	211591	F	752	19.02	5.37	8.78	6.85	7.30	4.87	10.24
317	O	SC	211592	M	1850	21.33	6.19	10.03	7.81	8.41	5.21	11.40
318	O	SC	211594	M	1070	22.17	5.91	11.87	7.55	10.23	4.39	10.30

ORIS	GEN	SP	CAT	S	WT	STL	ThF	LuF	ThR	LuR	Pol	ThP
319	O	SC	211596	M	939	19.91	5.63	9.54	7.15	8.02	4.74	10.37
320	O	SC	211597	M	1136	21.14	5.83	10.39	7.40	8.82	4.92	10.75
321	O	SC	211600	M	1108	20.18	5.84	9.97	7.54	8.17	4.47	10.31
322	O	SC	211601	M	1100	.	5.59	.	7.95	.	4.41	10.00
323	O	SC	211606	F	735	18.26	4.23	9.33	6.30	7.26	4.70	8.93
324	O	SC	211609	F	670	18.29	.	.	6.60	7.26	4.43	.
325	O	SC	211613	F	1136	18.88	4.67	9.60	6.81	7.46	4.61	9.28
326	O	SC	211614	F	562	17.36	4.80	8.11	6.17	6.74	4.45	9.25
327	O	SC	211615	F	801	.	4.89	10.27	7.09	8.07	.	.
328	O	SC	211616	F	816	18.68	4.88	9.34	6.28	7.94	4.46	9.34
329	O	SC	211618	M	866	.	6.14	9.67	7.66	8.15	.	.
330	O	SC	211624	M	909	19.95	5.23	10.06	7.43	7.86	4.66	9.89
331	O	SC	211627	M	821	20.46	5.08	10.78	7.33	8.53	4.60	9.68
332	O	SC	211628	M	827	21.36	6.19	10.47	7.86	8.80	4.70	10.89
333	O	SC	211639	F	640	19.04	5.29	8.97	6.75	7.51	4.78	10.07

ORG	GEN	SP	CAT	S	MUL	HL	RL	FL	TL	ML	HD	RD
1	A	RE	133544	F	15.8	14.50	16.3	14.4	.	4.17	1.040	0.650
2	A	CA	133875		14.5	13.30	15.3	13.5	.	.	0.830	0.555
3	A	CA	209917	M	17.2	15.30	17.6	15.6	3.65	4.40	1.080	0.760
4	A	CA	211495	F	14.6	12.92	14.8	13.3	.	.	0.940	0.610
5	A	CA	211496	M	16.2	15.30	16.5	15.2	.	.	1.130	0.755
6	A	CA	211497	F	13.8	12.70	14.5	12.9	.	.	0.860	0.570
7	A	CA	211498	M	16.8	14.90	17.3	15.1	.	.	1.170	0.755
8	A	CA	211499	M	15.8	14.00	15.9	13.9	.	.	1.050	0.715
9	A	CA	211501	F	14.1	12.38	14.5	12.7	.	.	0.860	0.540
10	A	CA	211502	F	14.7	13.30	15.5	13.5	.	.	0.950	0.630
11	A	CA	211504	M	16.1	14.80	16.7	15.9	3.43	.	0.985	0.655
12	A	CA	211508	M	16.5	14.80	16.8	14.8	.	.	1.100	0.740
13	A	CA	211510	M	16.7	15.00	16.8	14.9	3.35	4.25	1.185	0.745
14	A	CA	211512	F	.	13.70	15.9	13.8	3.03	3.83	.	0.650
15	A	CA	211513	M	16.2	15.10	17.1	14.9	3.53	4.43	1.125	0.750
16	A	CA	211519	M	.	15.50	17.5	15.9	3.52	4.39	.	0.720
17	A	CA	211520	F	14.4	12.80	15.1	13.2	3.15	3.88	0.955	0.635
18	A	CA	211522	F	14.3	13.70	15.7	13.8	3.50	4.00	0.895	0.520
19	A	CA	211523	M	16.0	14.80	16.6	14.7	3.43	4.30	1.195	0.760
20	A	CA	211524	F	14.7	13.40	.	13.8	3.09	3.83	1.000	0.675
21	A	CA	211525	M	16.4	14.80	17.0	14.7	3.32	4.24	1.090	0.680
22	A	CA	211585	F	14.5	13.60	15.3	13.6	3.05	3.98	0.985	0.655
23	A	CA	215060	F	15.0	13.90	15.8	14.0	3.26	4.00	0.920	0.600
24	A	CA	215061	M	14.8	13.60	16.0	13.7	3.18	3.80	0.850	0.575
25	A	PA	240407	M	14.3	13.40	14.7	12.8	.	3.97	1.045	0.660
26	A	PA	240408		14.9	13.60	15.5	13.5	.	3.95	1.070	0.725
27	A	PA	244870	M	17.0	15.70	17.5	15.6	3.58	4.58	1.175	0.745
28	A	PA	25309		15.1	14.50	15.8	13.6	.	.	1.050	0.745
29	A	PA	257307	F	15.0	14.40	15.9	.	.	3.94	0.980	0.640
30	A	PA	257359		15.1	14.00	15.1	13.2	.	4.32	1.055	0.690
31	A	PA	257404		15.2	13.80	15.4	13.7	3.16	4.13	0.945	0.615
32	A	PA	258313	F	14.9	13.70	14.7	12.9	3.29	4.03	0.855	0.565
33	A	PA	258314		15.2	14.00	15.6	13.4	3.22	4.10	0.910	0.590
34	A	PA	397108		14.5	13.70	14.4	13.3	.	3.75	1.025	0.650
35	A	PA	397112		14.8	14.50	15.2	13.5	.	.	1.025	0.660
36	A	PA	397113		15.7	14.60	15.7	13.9	.	4.25	1.140	0.815
37	A	SE	132790	M	16.8	15.10	17.7	15.8	3.45	4.40	1.080	0.760
38	A	SE	187994	F	10.3	9.00	13.4	12.2	.	.	0.710	0.435
39	A	SE	188006	F	.	13.10	.	.	3.32	4.25	.	0.610
40	A	SE	211527	F	13.8	12.40	14.2	12.7	2.86	3.43	0.840	0.525
41	A	SE	211528	M	14.8	14.10	15.8	14.5	3.44	4.01	.	0.625
42	A	SE	211531	F	14.6	12.80	15.7	13.3	3.07	3.79	0.855	0.525
43	A	SE	211532	M	16.5	15.00	17.5	15.2	3.89	4.47	.	0.715
44	A	SE	211535	F	14.2	13.80	15.3	13.7	3.32	3.92	0.920	0.550
45	A	SE	211538	F	15.3	13.90	16.0	14.5	3.45	4.03	0.945	0.585
46	A	SE	211540	F	13.9	12.90	14.6	13.0	3.20	3.73	0.860	0.495
47	A	SE	211542	M	17.0	15.80	17.6	15.8	3.67	4.43	.	0.725
48	A	SE	211543	F	14.3	13.40	15.5	13.6	3.27	3.92	0.850	0.500
49	A	SE	23330	F	14.2	13.70	15.7	14.1	3.35	4.19	0.985	0.650
50	A	SE	23334	M	15.2	14.00	16.1	14.1	2.99	4.03	0.975	0.665
51	A	SE	23341		14.9	13.70	15.7	14.4	.	.	1.045	0.635
52	A	SE	23342		15.6	14.50	16.6	14.9	3.70	4.10	1.010	0.635
53	A	SE	23351		14.7	13.10	16.2	14.0	3.32	3.97	1.000	0.555

OBS	GEN	SP	CAT	S	HL	RL	FL	TL	MCL	MTL	HD	RD
54	A	SE	23355		15.30	13.50	15.80	14.00	.	.	1.005	0.655
55	A	SE	23361		15.20	13.90	16.20	14.10	.	.	1.000	0.650
56	A	SE	23370		15.60	13.90	16.60	14.40	.	.	1.030	0.610
57	A	SE	23371		15.50	14.60	16.30	14.40	.	.	1.115	0.695
58	A	SE	23377	F	14.90	13.50	15.80	13.80	.	.	0.970	0.650
59	A	SE	23378	F	15.20	14.10	16.40	14.50	.	.	0.935	0.665
60	A	SE	23382	F	17.00	15.20	15.50	13.20	.	.	1.080	0.675
61	A	SE	23384		14.50	13.20	15.30	13.70	.	.	0.915	0.575
62	A	SE	23549	F	15.70	13.50	15.60	14.00	3.39	4.13	1.010	0.615
63	A	SE	23556		15.30	14.30	16.20	14.10	.	.	0.910	0.600
64	A	SE	30193	M	16.40	15.10	17.70	.	3.58	.	1.115	0.715
65	A	SE	42313		15.60	14.60	16.20	14.50	3.30	3.80	0.945	0.595
66	A	SE	42316	F	15.40	14.00	16.50	14.60	3.30	4.22	0.975	0.555
67	A	SE	48119	F	14.90	14.10	15.50	14.10	3.19	4.02	0.950	0.560
68	A	SE	49591		.	.	.	.	.	.	.	.
69	A	SE	70088	M	15.00	13.90	15.80	13.90	3.39	4.13	0.905	0.550
70	A	SE	99657	F	14.80	13.60	15.40	14.10	.	.	0.945	0.695
71	B	TR	10	M	6.42	6.37	8.48	8.60	.	.	0.435	0.270
72	B	TR	1442		6.45	5.95	8.36	8.28	.	.	0.415	0.265
73	B	TR	209916	F	6.79	6.47	8.75	8.84	.	.	0.455	0.300
74	B	TR	211464	M	8.09	7.30	10.80	10.51	.	.	0.485	0.325
75	B	TR	211477	F	8.05	7.47	10.32	9.90	2.00	.	0.455	0.285
76	B	TR	21153		6.57	.	8.72	8.65	1.64	2.69	0.415	.
77	B	TR	215048	F	8.13	7.40	9.83	10.10	1.90	3.21	0.485	0.280
78	B	TR	215050	F	.	7.25	10.14	10.01	1.95	3.26	.	0.320
79	B	TR	215051	M	8.23	7.52	10.40	10.42	2.03	3.39	0.520	0.340
80	B	TR	215052	M	7.74	7.27	9.91	10.13	.	3.29	0.490	0.325
81	B	TR	215053	F	8.04	7.22	10.30	10.11	1.93	3.16	0.465	0.290
82	B	TR	215054	M	7.90	7.16	10.20	10.12	1.93	3.20	0.500	0.320
83	B	TR	215056	F	8.06	7.40	10.39	10.32	1.97	3.31	0.465	0.325
84	B	TR	215057	M	7.82	7.33	10.00	9.04	1.93	3.17	0.505	0.325
85	B	TR	215059	M	7.88	7.27	10.25	10.16	1.97	3.36	0.470	0.290
86	B	TR	396505	M	7.25	7.10	9.74	9.70	.	.	0.495	0.300
87	B	TR	396702	F	6.60	6.21	8.66	8.66	1.62	2.64	0.430	0.275
88	B	TR	39675	F	7.36	6.69	9.53	9.29	1.86	2.98	0.445	0.280
89	B	TR	451		6.39	.	8.84	8.60	.	.	0.460	.
90	B	TR	937	F	7.43	7.06	9.85	9.79	.	.	0.460	0.280
91	B	TR	938	F	7.32	6.89	9.34	9.46	.	.	0.425	0.255
92	C		12		21.90	21.97	20.96	19.18	.	.	0.965	0.650
93	C		12		19.44	20.25	19.14	18.80	.	.	0.960	0.655
94	C		140	M	19.13	18.29	19.08	18.67	.	.	1.040	0.755
95	C		154189		22.00	21.90	22.00	.	5.37	.	0.975	0.610
96	C		183	M	21.75	21.68	22.88	20.25	.	.	1.045	0.715
97	C		184	M	.	18.14	18.89	17.35	.	.	.	0.610
98	C		277		19.57	19.57	19.43	18.11	.	.	1.140	0.780
99	C		292	F	19.29	.	18.58	17.20	.	.	0.950	.
100	C		3768	M	20.70	20.10	21.80	19.50	5.18	6.18	1.035	0.750
101	C		810	F	20.36	.	19.66	18.35	.	.	1.085	.
102	C	BE	259	F	20.70	21.00	.	19.20	5.00	5.52	0.965	.
103	C	BE	30192	M	20.20	20.80	20.20	19.40	.	.	1.260	0.855
104	C	GE	14128		20.10	21.20	18.70	19.40	4.98	5.51	1.075	0.770
105	C	GE	172985		21.70	22.20	22.00	20.50	5.54	6.00	1.105	0.700
106	C	GE	244863		19.60	20.80	19.00	18.30	5.16	5.64	1.020	0.685

ORS	GEN	SP	CAT	S	HL	RL	FL	TL	MCL	MTL	HD	RD
107	C	GE	276631	F	19.70	20.70	19.50	18.30	5.20	5.70	0.955	0.635
108	C	GE	276657	F	20.90	21.70	20.80	19.50	5.45	5.95	1.010	0.640
109	C	FA	361027	M	22.20	21.90	.	.	4.93	.	1.100	0.725
110	D		1566	F	12.20	10.28	14.02	12.77	.	.	0.685	0.420
111	D		1571		12.48	10.67	15.08	13.53	.	.	0.740	0.490
112	D		1572		12.07	10.36	14.52	12.90	.	.	0.700	0.455
113	D		1573		12.14	10.52	14.56	13.20	.	.	0.705	0.410
114	D		1574		11.93	10.08	13.97	12.69	.	.	0.655	0.400
115	D		1575		12.80	10.96	.	13.68	.	.	0.700	0.435
116	D		1576		12.41	10.93	15.26	13.54	.	.	0.775	0.485
117	D		1577		13.00	10.98	14.92	.	.	.	0.790	0.505
118	D		1578		13.12	11.27	15.30	14.00	.	.	0.785	0.525
119	D		1584		11.93	10.17	13.84	12.62	.	.	0.660	0.410
120	D		1585		12.35	10.47	14.32	13.39	.	.	0.755	0.460
121	D		1866		.	.	.	.	.	.	.	.
122	D	RU	302626	M	14.43	12.76	16.82	15.14	.	4.43	0.885	0.595
123	D	RU	519570	F	12.91	11.74	.	13.82	.	.	0.770	0.550
124	D	RU	70192	M	13.70	12.20	15.70	14.50	2.77	4.36	0.815	0.565
125	E		119625	M	7.81	.	10.14	.	.	.	0.495	.
126	E		1273	M	8.31	.	10.73	.	.	.	0.550	.
127	E		136208	M	7.50	7.52	9.28	9.13	1.67	2.65	0.530	0.250
128	E		211492	M	7.15	6.17	9.32	8.83	.	.	0.480	0.290
129	E		659		7.25	.	8.90	8.61	.	.	0.500	.
130	E		997	F	7.74	6.44	9.61	9.45	.	.	0.450	0.290
131	E		998		7.66	6.65	9.70	9.33	.	.	0.475	0.285
132	E	MO	130361		7.57	6.36	9.59	9.30	1.63	2.71	0.440	0.270
133	E	MO	136217	M	7.30	6.18	9.02	8.71	1.65	2.71	0.465	0.285
134	E	MO	211487	M	.	6.49	9.47	9.32	1.66	.	.	0.290
135	E	MO	211488	M	7.62	6.45	9.57	9.28	1.70	2.93	0.445	0.280
136	E	MO	211489	F	.	6.41	.	9.05	1.66	2.84	.	0.255
137	E	MO	211490	F	7.26	5.95	9.18	8.88	1.52	2.80	0.450	0.265
138	E	MO	211493	M	7.37	6.14	9.31	9.16	1.56	.	0.455	0.305
139	E	MO	240088	F	8.60	7.39	11.54	11.18	2.05	3.28	0.610	0.385
140	E	MO	269827	M	8.01	7.00	10.16	10.08	1.75	3.01	0.530	0.325
141	E	MO	397933	M	7.72	6.62	.	9.37	1.70	2.71	0.465	0.300
142	E	MO	94977	M	7.35	6.28	9.41	9.10	1.72	2.76	0.435	0.265
143	E	TO	398212	F	8.11	6.99	10.65	9.64	1.85	3.03	0.535	0.350
144	F	GO	1829		5.65	5.44	7.50	7.98	.	2.90	0.435	0.300
145	F	GO	183289		5.42	4.98	7.39	7.33	1.45	2.14	0.365	0.240
146	F	GO	303323	M	5.44	4.84	7.23	7.12	1.41	2.48	0.405	0.255
147	F	GO	395455	M	5.27	4.82	7.04	7.11	1.32	2.45	0.375	0.240
148	G		1279	M	.	.	6.00	6.10	.	.	.	.
149	G		1280	M	.	4.41	6.30	6.42	.	.	.	0.225
150	G		1290	M	5.15	4.25	6.56	6.69	.	.	0.365	0.220
151	G		1298	M	4.65	4.24	5.85	5.93	.	.	0.350	0.235
152	G		1314	F	4.88	4.33	.	.	.	.	0.380	0.230
153	G		1323	M	4.28	3.84	5.25	5.47	.	.	0.285	0.175
154	G		1325	F	4.32	3.85	5.39	5.44	.	.	0.345	0.220
155	G		1329	M	4.38	3.99	5.50	5.69	.	.	0.335	0.205
156	G		1330	F	.	3.96	5.69	.	.	.	.	0.200
157	G		1336	F	4.97	3.95	5.55	5.85	.	.	0.355	0.210
158	G		1339	M	4.51	3.95	5.49	5.72	.	.	0.370	0.225
159	G		293	F	4.87	4.35	5.92	6.00	.	.	0.365	0.260

OBS	GEN	SF	CAT	S	HL	RL	FL	TL	MCL	MTL	MD	RD
213	I	AP	209927	F	10.00	9.10	12.60	11.40	.	.	0.660	0.430
214	I	AP	211578	M	11.00	10.50	14.00	12.80	.	.	0.775	0.530
215	I	AP	211579	M	10.90	10.10	13.20	12.20	2.42	3.56	0.765	0.490
216	I	AP	270361	M	10.98	10.25	13.26	12.52	2.62	3.91	0.865	0.515
217	I	AP	95129	M	11.82	11.30	14.24	12.89	2.60	3.93	0.810	0.515
218	I	NI	30195	M	11.70	11.70	14.70	13.90	2.72	4.44	0.750	0.450
219	I	NI	30196	F	10.80	10.90	13.40	13.00	2.58	4.15	0.695	0.450
220	I	NI	30197	M	11.90	11.00	14.20	13.70	2.63	4.11	0.770	0.495
221	I	NI	30198	M	11.60	.	14.20	13.20	.	.	0.760	.
222	I	NI	361020	M	10.77	10.35	13.12	12.18	.	3.79	0.815	0.515
223	I	NI	361021	F	9.74	9.03	11.73	11.05	2.16	3.21	0.625	0.395
224	I	NI	42873	F	11.70	11.20	14.70	13.80	2.73	4.31	0.720	0.495
225	I	NI	42884	M	11.70	11.30	14.00	13.80	2.61	4.29	0.765	0.510
226	J		1198		10.66	8.73	12.44	11.20	.	.	0.645	0.430
227	J		1199		10.59	8.59	12.78	11.69	.	.	0.630	0.420
228	J		1200		10.95	9.18	12.92	11.81	2.26	3.31	0.670	0.425
229	J		1201	M	11.79	10.21	14.16	12.94	.	.	0.715	0.485
230	J		1202	F	11.00	9.49	12.97	11.71	.	.	0.710	0.455
231	J		1864	M	11.23	8.93	13.23	11.79	2.29	3.45	0.780	0.470
232	J		1867	F	10.97	.	.	11.50	2.10	3.61	0.700	.
233	J		1868		.	.	.	.	.	.	.	.
234	J		1909	F	10.29	10.20	12.72	11.62	2.62	3.52	0.650	0.435
235	J		1912	F	.	.	.	.	2.00	3.39	.	.
236	J		1918	M	10.74	8.71	.	.	2.68	3.94	0.655	0.415
237	K		163	M	15.50	.	15.31	14.10	.	.	0.990	.
238	K		164	M	16.36	.	16.86	15.46	.	.	1.005	.
239	K		165		16.28	.	16.44	14.70	3.13	4.04	0.990	.
240	K		177		16.30	14.38	16.40	14.93	.	.	1.000	0.625
241	K		178		16.62	14.97	16.34	15.40	.	4.22	1.035	0.640
242	K		180		16.71	.	.	15.40	.	.	0.900	.
243	K		355	M	15.95	14.73	16.38	15.08	3.20	4.50	0.880	0.585
244	K		555	F	16.86	.	17.08	15.40	.	4.45	1.000	.
245	K		675	M	15.75	14.65	16.32	15.40	3.04	4.05	1.005	0.605
246	K		676	M	16.31	15.23	16.99	15.80	3.40	4.30	1.000	0.660
247	K		677	M	16.43	14.83	16.67	15.13	3.25	.	1.020	0.640
248	K		970		.	.	.	.	.	.	.	.
249	K	LA	188153	F	16.50	14.70	16.10	15.20	.	.	0.955	0.630
250	K	LA	188162	F	.	.	.	.	3.43	4.33	.	.
251	K	LA	35752	M	17.70	16.20	17.60	16.80	3.47	4.71	1.025	0.630
252	K	LA	397774	F	17.40	16.30	17.30	16.40	3.50	4.56	1.045	0.650
253	K	LA	397775	M	16.20	14.60	17.10	.	3.60	4.70	0.900	0.605
254	K	LA	70404	M	18.10	16.40	18.20	17.00	.	5.05	1.040	0.665
255	L		185347		6.33	6.41	7.06	7.40	2.24	2.85	0.390	0.250
256	L	RD	269705	F	6.15	6.07	6.70	7.18	.	2.17	0.370	0.240
257	M		129	F	11.27	9.93	13.86	13.05	.	.	0.785	0.475
258	M		1417		9.77	9.64	13.07	12.67	.	.	0.630	0.445
259	M		1445	F	9.91	9.15	13.69	12.82	2.25	3.40	0.610	0.425
260	M		1450		10.29	9.74	13.76	13.22	.	.	0.660	0.455
261	M		154	F	11.70	9.84	14.74	13.00	.	.	0.685	0.430
262	M		660		.	.	.	.	.	.	.	.
263	M		661	M	11.08	9.30	.	12.98	2.28	3.82	0.635	0.425
264	M		667	F	.	9.25	13.80	12.45	2.16	3.57	.	0.440
265	M	PA	241007	F	10.46	9.70	13.87	13.38	2.16	.	0.635	0.395

OBS	GEN	SP	CAT	S	HL	RL	FL	TL	MCL	MTL	HD	RD
160	G		49480		4.39	3.91	5.47	5.19	.	.	0.335	0.210
161	G		66		4.13	3.70	5.25	5.35	.	.	0.340	0.210
162	G		68	F	4.39	3.91	5.47	5.19	.	.	0.335	0.210
163	G		95127	M	5.05	4.56	6.12	6.30	1.32	2.23	0.345	0.250
164	G	AR	133712		5.02	4.47	6.28	6.28	.	.	0.355	0.250
165	G	AR	184689		4.77	.	5.79	.	.	.	0.355	.
166	G	CH	241197	F	4.49	.	5.61	.	.	.	0.375	.
167	G	JA	133688	F	4.53	4.06	5.79	5.92	1.24	2.23	0.320	0.210
168	G	JA	133694	M	4.33	3.85	5.44	5.50	.	.	0.315	0.210
169	G	JA	133698	F	4.44	4.01	5.59	5.70	1.15	2.11	0.315	0.215
170	G	JA	35529		4.55	4.08	5.64	5.83	1.23	2.15	0.305	0.210
171	H	PY	244101		2.92	2.70	.	3.49	0.87	1.38	0.235	0.145
172	H	PY	303037	M	3.27	2.87	3.71	3.83	0.87	.	0.245	0.170
173	H	PY	305778	M	3.36	.	3.75	3.81	.	.	0.235	.
174	H	PY	314966	F	3.56	3.27	4.10	4.24	0.90	1.56	0.245	0.175
175	H	PY	336325	M	3.20	2.93	3.70	3.81	0.86	1.43	0.235	0.150
176	H	PY	337947	M	3.37	3.00	3.82	3.87	0.80	1.35	0.260	0.165
177	H	PY	337948	M	3.35	2.99	3.83	3.77	0.83	.	0.230	0.135
178	H	PY	673		.	.	.	.	.	.	.	.
179	H	PY	693	M	3.44	.	3.90	4.13	0.86	.	0.245	.
180	H	PY	694	M	3.15	2.88	3.51	3.67	.	.	0.240	0.160
181	H	PY	695	M	3.25	3.03	3.67	3.68	.	.	0.255	0.160
182	H	PY	696		.	2.92	.	.	.	.	.	0.150
183	H	PY	697	M	3.24	2.89	3.59	3.77	.	.	0.225	0.145
184	H	PY	699	M	3.34	.	.	.	.	.	0.230	.
185	H	PY	699	F	.	2.97	3.86	3.99	.	.	.	0.155
186	H	PY	701	F	.	.	3.95	4.07	.	.	.	.
187	H	PY	734		.	.	.	.	.	.	.	.
188	H	PY	923	F	.	3.07	3.87	4.03	.	.	.	0.165
189	I	AL	188018	F	11.20	10.80	14.40	13.30	2.76	4.20	0.745	0.455
190	I	AL	209923	F	10.30	9.80	12.50	12.00	2.43	3.69	0.665	0.440
191	I	AL	209924	M	10.20	9.70	12.50	11.60	2.39	3.55	0.725	0.500
192	I	AL	209925	M	10.90	10.70	13.40	13.00	2.60	3.78	0.865	0.475
193	I	AL	23392	M	11.60	11.40	14.40	14.30	.	.	0.825	0.546
194	I	AL	23401	F	11.60	11.20	14.80	13.70	.	.	0.720	0.500
195	I	AL	23402		10.60	10.20	13.20	12.80	.	3.87	0.740	0.470
196	I	AP	133606	M	11.50	10.80	13.80	13.30	2.50	3.70	0.870	0.520
197	I	AP	133620	M	10.49	10.02	13.94	12.20	2.40	3.58	0.770	0.475
198	I	AP	133622	M	10.80	10.10	13.10	12.20	2.47	3.71	0.770	0.465
199	I	AP	133623	M	10.34	9.88	12.90	12.03	2.47	3.70	0.740	0.455
200	I	AP	133624	M	10.49	10.18	12.73	12.06	.	3.49	0.785	0.495
201	I	AP	133626	F	9.60	9.02	12.03	11.12	2.17	3.26	0.655	0.415
202	I	AP	133628	M	10.65	10.12	13.21	11.95	2.57	3.84	0.745	0.515
203	I	AP	133631	F	9.82	9.29	12.24	11.39	2.32	3.58	0.650	0.420
204	I	AP	133637	M	9.91	9.80	12.40	11.76	2.40	3.64	0.745	0.470
205	I	AP	133665	M	10.50	10.10	12.80	11.90	2.35	3.40	0.825	0.505
206	I	AP	133806	F	10.19	9.32	12.43	11.72	2.26	3.48	0.665	0.410
207	I	AP	133810	F	9.47	8.80	11.55	10.85	2.16	3.32	0.620	0.350
208	I	AP	133813	F	10.04	9.42	12.68	11.37	2.19	3.26	0.605	0.380
209	I	AP	133851	M	11.52	10.65	13.46	12.52	2.52	3.82	0.800	0.535
210	I	AP	133862	M	10.61	10.05	13.17	12.35	2.52	3.80	0.750	0.470
211	I	AP	133864	M	9.34	8.94	11.67	10.97	.	.	0.630	0.375
212	I	AP	209926	F	9.70	9.00	11.60	11.00	.	.	0.630	0.410

ORR	GEN	SP	CAT	S	HL	RL	FL	TL	MCL	MTL	HD	RD
266	M	PA	300794		9.86	9.25	13.16	11.96	2.33	3.95	0.530	0.360
267	M	PA	339659	F	9.08	8.56	.	11.96	.	.	0.640	0.385
268	M	PA	64088	M	.	.	13.00	.	.	.	.	.
269	M	PA	70377	M	10.10	9.80	13.00	13.00	2.16	3.75	0.610	0.400
270	N		148454		5.20	4.56	6.60	6.53	1.38	2.32	0.435	0.270
271	N		180091		5.24	4.85	6.38	6.47	1.58	2.38	0.385	0.255
272	N		207726		5.58	5.06	6.94	7.06	1.53	2.38	0.405	0.290
273	N		35516		5.17	4.65	6.41	6.62	1.47	2.52	0.330	0.215
274	N		77693		5.38	4.92	7.00	7.00	1.49	2.44	0.385	0.245
275	N		97316	M	5.51	5.08	6.93	7.19	1.56	2.46	0.395	0.255
276	N	M	1146		5.59	.	7.01	7.20	.	.	0.390	.
277	N	M	1148		5.69	5.00	7.26	7.33	.	.	0.425	0.270
278	N	M	25313		.	4.93	6.98	7.01	1.53	2.51	.	0.275
279	N	MB	1448		.	.	.	.	.	.	.	.
280	N	ML	148322		5.15	4.60	6.60	6.60	1.49	2.33	0.375	0.230
281	N	ML	292294	F	4.92	4.56	6.17	6.58	1.43	2.33	0.355	0.225
282	N	ML	439	F	5.21	4.80	6.71	6.63	.	.	0.420	0.235
283	N	O	117	F	5.38	.	6.97	6.91	.	.	0.385	.
284	N	O	121	M	4.94	.	6.39	.	.	.	0.365	.
285	N	O	442	F	5.26	.	6.67	6.85	.	.	0.385	.
286	N	O	445	F	5.25	.	6.40	6.54	.	.	0.365	.
287	N	O	648	F	5.38	4.94	6.76	6.88	.	.	0.375	0.230
288	N	O	654	M	5.55	4.55	6.15	6.27	.	.	0.370	0.235
289	N	O	708	F	4.98	4.47	6.22	6.35	.	.	0.375	0.230
290	N	OG	148336	M	.	4.99	.	7.02	.	.	.	0.275
291	N	OG	240425		5.13	.	6.57	6.68	.	.	0.370	.
292	N	OG	257345		.	4.71	6.62	6.75	1.32	2.33	.	0.285
293	N	OG	49389		5.26	4.71	6.51	6.55	1.49	.	0.400	0.265
294	N	OO	446	F	5.10	4.50	6.35	6.41	.	.	0.370	0.235
295	N	S	726	M	4.58	4.30	5.60	5.93	.	.	0.285	0.185
296	N	S	728	M	4.74	4.17	5.90	6.07	.	.	0.320	0.225
297	N	S	733	F	4.65	4.24	5.67	5.88	.	.	0.290	0.190
298	N	S	735	F	4.76	4.43	5.92	5.90	.	.	0.330	0.210
299	N	SD	148453	M	5.45	4.89	7.09	6.89	1.47	2.41	0.400	0.250
300	N	SD	362118		5.36	4.76	6.54	6.73	1.45	2.30	0.345	0.255
301	N	SF	461267	M	5.16	4.89	6.25	6.59	1.37	2.44	0.365	0.220
302	N	SI	336299	F	4.75	4.40	5.84	5.88	1.35	2.43	0.315	0.195
303	N	SI	336301	F	5.51	5.01	6.43	6.70	1.95	2.35	0.370	0.235
304	N	SN	147433		5.06	4.78	6.19	6.60	1.59	2.43	0.370	0.250
305	N	SY	188171	M	4.79	4.50	5.79	6.30	1.37	2.14	0.325	0.210
306	N	SY	188177	M	4.70	4.31	5.61	5.76	1.35	2.12	0.305	0.215
307	N	SY	238258	M	4.91	4.55	5.89	.	.	.	0.345	0.215
308	N	OG	49397		5.08	.	6.39	6.46	.	.	0.345	.
309	O	SC	188080	F	.	.	8.42	8.49	1.63	2.76	.	.
310	O	SC	188110	F	7.32	6.70	9.00	8.99	1.64	2.78	0.475	0.310
311	O	SC	209928	F	6.43	6.05	7.90	.	.	.	0.420	0.275
312	O	SC	209930	M	7.53	.	8.88	.	.	.	0.520	.
313	O	SC	209933	F	6.62	6.35	7.88	8.23	.	.	0.415	0.275
314	O	SC	209934	M	7.43	6.92	.	8.95	.	.	0.510	0.345
315	O	SC	209935	M	.	7.26	9.48	.	.	.	.	0.350
316	O	SC	211591	F	6.55	6.17	7.86	8.40	.	.	0.410	0.260
317	O	SC	211592	M	7.50	7.21	9.20	9.24	.	2.78	0.530	0.360
318	O	SC	211594	M	7.01	6.83	8.48	8.79	1.60	2.71	0.500	0.320

OBS	GEN	SP	CAT	S	HL	RL	FL	TL	MCL	MTL	HD	RD
319	0	SC	211596	M	6.80	6.56	8.38	8.46	1.62	2.69	0.475	0.310
320	0	SC	211597	M	.	6.77	.	8.95	.	2.86	.	0.320
321	0	SC	211600	M	7.19	6.74	8.54	.	1.70	2.78	0.485	0.330
322	0	SC	211601	M	7.32	6.97	8.96	9.05	.	.	0.480	0.325
323	0	SC	211606	F	6.88	6.61	8.21	8.70	1.66	2.70	0.460	0.295
324	0	SC	211609	F	6.82	6.43	8.13	8.38	.	2.62	0.415	0.275
325	0	SC	211613	F	7.12	6.63	8.39	8.78	1.68	2.80	0.430	0.290
326	0	SC	211614	F	6.88	6.41	8.16	8.32	1.55	.	0.410	0.270
327	0	SC	211615	F	6.84	6.61	8.36	8.61	.	.	0.440	0.285
328	0	SC	211616	F	.	6.24	8.10	8.39	.	.	.	0.280
329	0	SC	211618	M	6.90	6.64	8.42	8.52	.	.	0.485	0.335
330	0	SC	211624	M	7.32	7.02	8.97	9.24	1.71	.	0.520	0.325
331	0	SC	211627	M	7.02	6.70	8.83	8.81	.	.	0.455	0.300
332	0	SC	211628	M	7.08	6.96	8.82	8.87	.	.	0.465	0.330
333	0	SC	211639	F	7.05	6.55	8.50	8.56	.	.	0.400	0.275

ORS	GEN	SP	CAT	S	RN	HX	RN	FD	TD	MCD	MTD
1	A	BE	133544	F	0.96	1.12	0.60	1.005	0.925	.	0.360
2	A	CA	133875		0.76	0.90	0.52	0.885	0.740	.	.
3	A	CA	209917	M	1.03	1.13	0.74	1.090	0.970	0.400	0.400
4	A	CA	211495	F	0.84	1.04	0.56	0.965	0.830	.	.
5	A	CA	211496	M	1.03	1.23	0.70	1.050	0.920	.	.
6	A	CA	211497	F	0.82	0.90	0.55	0.875	0.725	.	.
7	A	CA	211498	M	1.10	1.24	0.70	1.085	0.990	.	.
8	A	CA	211499	M	1.00	1.10	0.67	0.990	0.875	.	.
9	A	CA	211501	F	0.82	0.90	0.50	0.910	0.765	.	.
10	A	CA	211502	F	0.91	0.99	0.56	0.990	0.820	.	.
11	A	CA	211504	M	0.93	1.04	0.62	0.975	0.895	0.375	.
12	A	CA	211508	M	1.03	1.17	0.70	1.100	0.955	.	.
13	A	CA	211510	M	1.14	1.23	0.70	1.110	0.960	0.330	0.405
14	A	CA	211512	F	.	.	0.62	1.035	0.840	0.395	0.385
15	A	CA	211513	M	1.04	1.21	0.70	1.100	0.955	0.425	0.410
16	A	CA	211519	M	.	.	0.69	1.045	0.935	0.395	0.420
17	A	CA	211520	F	0.91	1.00	0.59	0.935	0.765	0.335	0.335
18	A	CA	211522	F	0.85	0.94	0.49	0.905	0.735	0.365	0.320
19	A	CA	211523	M	1.11	1.28	0.67	1.100	0.945	0.400	0.400
20	A	CA	211524	F	0.93	1.07	0.62	.	0.825	0.370	0.370
21	A	CA	211525	M	1.00	1.18	0.65	1.010	0.920	0.360	0.415
22	A	CA	211585	F	0.93	1.04	0.60	1.060	0.830	.	0.365
23	A	CA	215060	F	0.85	0.99	0.55	0.895	0.730	0.340	0.335
24	A	CA	215061	M	0.80	0.90	0.51	0.845	0.715	0.380	0.320
25	A	PA	240407	M	1.00	1.09	0.61	0.980	0.805	.	0.360
26	A	PA	240408		1.02	1.12	0.67	1.045	0.825	.	0.390
27	A	PA	244870	M	1.09	1.26	0.65	1.180	0.915	0.430	0.395
28	A	PA	25309		0.98	1.12	0.67	1.015	0.905	.	.
29	A	PA	257307	F	0.96	1.00	0.62	0.995	.	.	0.385
30	A	PA	257359		1.03	1.08	0.66	0.920	0.820	.	0.465
31	A	PA	257404		0.89	1.00	0.58	0.990	0.815	0.350	0.365
32	A	PA	258313	F	0.83	0.88	0.50	0.865	0.725	0.365	0.370
33	A	PA	258314		0.86	0.96	0.55	0.945	0.780	0.360	0.380
34	A	PA	397108		0.95	1.10	0.62	1.005	0.835	.	0.385
35	A	PA	397112		0.98	1.07	0.60	1.025	0.830	.	.
36	A	PA	397113		1.09	1.19	0.74	1.030	0.935	.	0.430
37	A	SE	132790	M	1.06	1.10	0.66	1.105	0.990	0.430	0.430
38	A	SE	187994	F	0.66	0.76	0.41	0.740	0.655	.	.
39	A	SE	188006	F	.	.	0.53	.	.	0.375	0.390
40	A	SE	211527	F	0.81	0.87	0.48	0.840	0.730	0.380	0.335
41	A	SE	211528	M	.	.	0.58	0.940	0.835	0.260	0.330
42	A	SE	211531	F	0.84	0.87	0.51	0.860	0.760	0.355	0.350
43	A	SE	211532	M	.	.	0.68	1.070	0.915	0.465	0.415
44	A	SE	211535	F	0.87	0.97	0.52	0.915	0.750	0.380	0.355
45	A	SE	211538	F	0.90	0.99	0.55	0.950	0.855	0.385	0.345
46	A	SE	211540	F	0.81	0.91	0.45	0.825	0.745	0.370	0.335
47	A	SE	211542	M	.	.	0.67	1.020	0.910	0.415	0.395
48	A	SE	211543	F	0.83	0.87	0.45	0.830	0.710	0.370	0.330
49	A	SE	23330	F	0.88	1.09	0.54	1.005	0.850	0.435	0.400
50	A	SE	23334	M	0.90	1.05	0.63	0.965	0.900	0.395	0.405
51	A	SE	23341		0.97	1.12	0.58	0.955	0.830	.	.
52	A	SE	23342		0.93	1.09	0.57	1.020	0.835	0.425	0.375
53	A	SE	23351		0.96	1.04	0.55	0.995	0.850	0.415	0.395

ONS	GEN	SP	CAT	S	HN	EX	RN	FD	TI	MCI	MTD
54	A	SE	23355		0.94	1.07	0.61	1.085	0.955	.	.
55	A	SE	23361		0.95	1.05	0.58	1.045	0.895	.	.
56	A	SE	23370		0.97	1.09	0.52	1.055	0.870	.	.
57	A	SE	23371		1.00	1.23	0.58	1.100	0.925	.	.
58	A	SE	23377	F	0.91	1.03	0.59	0.950	0.870	.	.
59	A	SE	23378	F	0.90	0.97	0.61	1.015	0.845	.	.
60	A	SE	23382	F	0.97	1.19	0.60	0.965	0.865	.	.
61	A	SE	23386		0.85	0.98	0.52	0.920	0.825	.	.
62	A	SE	23549	F	0.92	1.10	0.56	0.940	0.850	0.390	0.395
63	A	SE	23556		0.86	0.96	0.55	0.950	0.830	.	.
64	A	SE	30193	M	1.07	1.16	0.69	1.145	.	0.440	.
65	A	SE	42313		0.88	1.01	0.58	0.980	0.785	0.400	0.290
66	A	SE	42316	F	0.87	1.08	0.53	1.035	0.800	0.405	0.370
67	A	SE	48119	F	0.91	0.99	0.52	0.970	0.810	0.400	0.375
68	A	SE	69591		.	.	.	.	.	.	.
69	A	SE	70088	M	0.83	0.98	0.50	0.940	0.810	0.365	0.390
70	A	SE	99657	F	0.92	0.97	0.58	0.980	0.850	.	.
71	B	TR	10	M	0.41	0.46	0.25	0.465	0.425	.	.
72	B	TR	1442		0.40	0.43	0.25	0.465	0.380	.	.
73	B	TR	209916	F	0.45	0.46	0.26	0.545	0.440	.	.
74	B	TR	211464	M	0.47	0.50	0.31	0.585	0.525	.	.
75	B	TR	211477	F	0.45	0.46	0.28	0.535	0.480	0.170	.
76	B	TR	21153		0.40	0.43	.	0.470	0.420	0.170	0.200
77	B	TR	215048	F	0.46	0.51	0.27	0.535	0.455	0.200	0.230
78	B	TR	215050	F	.	.	0.29	0.570	0.490	0.200	0.235
79	B	TR	215051	M	0.51	0.53	0.34	0.600	0.525	0.205	0.245
80	B	TR	215052	M	0.48	0.50	0.31	0.535	0.500	.	0.230
81	B	TR	215053	F	0.45	0.48	0.27	0.565	0.470	0.195	0.240
82	B	TR	215054	M	0.48	0.52	0.31	0.575	0.530	0.200	0.235
83	B	TR	215056	F	0.46	0.47	0.30	0.575	0.530	0.190	0.240
84	B	TR	215057	M	0.47	0.54	0.30	0.560	0.535	0.190	0.215
85	B	TR	215059	M	0.45	0.49	0.28	0.545	0.460	0.200	0.250
86	B	TR	396505	M	0.48	0.51	0.26	0.535	0.455	.	.
87	B	TR	396702	F	0.43	.	0.26	0.460	0.410	0.160	0.180
88	B	TR	39675	F	0.43	0.46	0.26	0.525	0.470	0.180	0.210
89	B	TR	451		0.43	0.49	.	0.515	0.465	.	.
90	B	TR	937	F	0.44	0.48	0.26	0.500	0.445	.	.
91	B	TR	938	F	0.41	0.44	0.24	0.490	0.400	.	.
92	C		12		0.91	1.02	0.59	1.210	1.115	.	.
93	C		12		0.92	1.00	0.56	1.135	1.065	.	.
94	C		140	M	1.01	1.07	0.71	1.310	1.090	.	.
95	C		154189		0.92	1.03	0.56	1.190	.	0.360	.
96	C		183	M	0.98	1.11	0.66	1.230	1.085	.	.
97	C		184	M	.	.	0.57	1.395	1.220	.	.
98	C		277		1.10	1.18	0.75	1.300	1.395	.	.
99	C		292	F	0.93	0.97	.	1.380	0.990	.	.
100	C		3768	M	0.99	1.08	0.70	1.205	1.100	0.385	0.450
101	C		810	F	1.06	1.11	.	1.375	1.125	.	.
102	C	BE	259	F	0.91	1.02	.	.	1.040	0.340	0.415
103	C	BE	30192	M	1.23	1.29	0.80	1.355	1.200	.	.
104	C	GE	14128		1.04	1.11	0.72	1.280	1.005	0.370	0.405
105	C	GE	172985		1.10	1.11	0.65	1.270	1.095	0.400	0.460
106	C	GE	244863		0.96	1.08	0.66	1.190	1.010	0.350	0.425

OBS	GEN	SP	CAT	S	HN	HX	RN	FD	TD	MCI	MTD
107	C	GE	276631	F	0.92	0.99	0.59	1.150	1.040	0.380	0.405
108	C	GE	276657	F	0.97	1.05	0.59	1.190	1.040	0.390	0.420
109	C	PA	361027	M	1.03	1.17	0.67	.	.	0.390	.
110	D		1566	F	0.66	0.71	0.39	0.685	0.600	.	.
111	D		1571		0.71	0.77	0.44	0.800	0.645	.	.
112	D		1572		0.66	0.74	0.40	0.720	0.610	.	.
113	D		1573		0.67	0.74	0.38	0.710	0.610	.	.
114	D		1574		0.63	0.68	0.37	0.710	0.600	.	.
115	D		1575		0.65	0.75	0.41	.	0.645	.	.
116	D		1576		0.73	0.82	0.45	0.805	0.670	.	.
117	D		1577		0.75	0.83	0.46	0.810	.	.	.
118	D		1578		0.74	0.83	0.50	0.785	0.685	.	.
119	D		1584		0.64	0.68	0.39	0.690	0.575	.	.
120	D		1585		0.71	0.80	0.43	0.810	0.650	.	.
121	D		1866		.	.	.	.	.	.	.
122	D	RU	302626	M	0.85	0.92	0.57	0.900	0.750	.	0.340
123	D	RU	519570	F	0.73	0.81	0.51	.	0.695	.	.
124	D	RU	70192	M	0.78	0.85	0.46	0.825	0.705	0.260	0.320
125	E		119625	M	0.47	0.52	.	0.560	.	.	.
126	E		1273	M	0.50	0.60	.	0.620	.	.	.
127	E		136208	M	0.53	.	0.22	0.475	0.400	.	.
128	E		211492	M	0.44	0.52	0.24	0.505	0.435	.	.
129	E		659		0.47	0.53	.	0.540	0.475	.	.
130	E		997	F	0.44	0.46	0.25	0.550	0.455	.	.
131	E		998		0.45	0.50	0.24	0.535	0.455	.	.
132	E	MO	130361		0.43	0.45	0.24	0.490	0.425	0.180	0.220
133	E	MO	136217	M	0.44	0.49	0.26	0.505	0.425	0.175	0.225
134	E	MO	211487	M	.	.	0.25	0.525	0.465	0.180	.
135	E	MO	211488	M	0.42	0.47	0.24	0.470	0.435	0.170	0.205
136	E	MO	211489	F	.	.	0.20	.	0.430	0.180	0.225
137	E	MO	211490	F	0.44	0.46	0.22	0.500	0.440	0.170	0.210
138	E	MO	211493	M	0.44	0.47	0.24	0.515	0.430	0.180	.
139	E	MO	240088	F	0.59	0.63	0.35	0.665	0.585	0.210	0.270
140	E	MO	269827	M	0.51	0.55	0.31	0.605	0.525	0.195	0.255
141	E	MO	397933	M	0.46	0.47	0.27	.	0.460	0.190	0.240
142	E	MO	94977	M	0.41	0.46	0.26	0.490	0.450	0.160	0.200
143	E	TO	398212	F	0.52	0.55	0.29	0.585	0.540	0.215	0.240
144	F	GO	1829		0.42	0.45	0.26	0.490	0.450	.	0.220
145	F	GO	183289		0.36	0.37	0.23	0.420	0.390	0.120	0.160
146	F	GO	303323	M	0.38	0.43	0.21	0.425	0.370	0.130	0.170
147	F	GO	395455	M	0.36	0.39	0.23	0.435	0.365	0.125	0.160
148	G		1279	M	.	.	.	0.400	0.345	.	.
149	G		1280	M	.	.	0.18	0.385	0.330	.	.
150	G		1290	M	0.35	0.38	0.18	0.400	0.340	.	.
151	G		1298	M	0.34	0.36	0.18	0.375	0.350	.	.
152	G		1314	F	0.36	0.40	0.19	.	.	.	.
153	G		1323	M	0.26	0.31	0.15	0.275	0.265	.	.
154	G		1325	F	0.32	0.37	0.18	0.360	0.285	.	.
155	G		1329	M	0.32	0.35	0.17	0.360	0.310	.	.
156	G		1330	F	.	.	0.17	0.345	.	.	.
157	G		1336	F	0.34	0.37	0.16	0.375	0.310	.	.
158	G		1339	M	0.34	0.40	0.17	0.375	0.320	.	.
159	G		293	F	0.36	0.37	0.22	0.390	0.335	.	.

OBS	GEN	SP	CAT	S	HN	EX	RN	FD	TD	MCD	MTD
160	G		49480		0.31	0.36	0.18	0.360	0.305	.	.
161	G		66		0.33	0.35	0.15	0.340	0.305	.	.
162	G		68	F	0.31	0.36	0.18	0.360	0.305	.	.
163	G		95127	M	0.33	0.36	0.21	0.385	0.360	0.110	0.140
164	G	AR	133712		0.34	0.37	0.21	0.395	0.355	.	.
165	G	AR	184689		0.34	0.37	.	0.380	.	.	.
166	G	CH	241197	F	0.37	0.38	.	0.385	.	.	.
167	G	JA	133688	F	0.32	.	0.19	0.340	0.300	0.100	0.130
168	G	JA	133694	M	0.31	0.32	0.16	0.355	0.310	.	.
169	G	JA	133698	F	0.30	0.33	0.16	0.365	0.320	0.090	0.110
170	G	JA	35529		0.30	0.31	0.16	0.340	0.310	0.120	0.130
171	H	PY	244101		0.21	0.26	0.11	.	0.200	0.060	0.080
172	H	PY	303037	M	0.24	0.25	0.13	0.270	0.200	0.090	.
173	H	PY	305778	M	0.23	0.24	.	0.240	0.195	.	.
174	H	PY	314966	F	0.24	0.25	0.14	0.275	0.220	0.090	0.090
175	H	PY	336325	M	0.22	0.25	0.12	0.235	0.200	0.090	0.090
176	H	PY	337947	M	0.24	0.28	0.13	0.250	0.195	0.080	0.100
177	H	PY	337948	M	0.21	0.25	0.12	0.260	0.190	0.070	.
178	H	PY	673		.	.	.	.	.	.	.
179	H	PY	693	M	0.23	0.26	.	0.250	0.215	0.080	.
180	H	PY	694	M	0.22	0.26	0.14	0.240	0.180	.	.
181	H	PY	695	M	0.23	0.28	0.13	0.250	0.190	.	.
182	H	PY	696		.	.	0.14	.	.	.	.
183	H	PY	697	M	0.20	0.25	0.11	0.220	0.175	.	.
184	H	PY	699	M	0.22	0.24	.	.	.	.	.
185	H	PY	699	F	.	.	0.13	0.255	0.200	.	.
186	H	PY	701	F	.	.	.	0.270	0.180	.	.
187	H	PY	734		.	.	.	.	.	.	.
188	H	PY	923	F	.	.	0.13	0.255	0.195	.	.
189	I	AL	188018	F	0.72	0.77	0.44	0.865	0.780	0.295	0.325
190	I	AL	209923	F	0.62	0.71	0.40	0.740	0.630	0.265	0.290
191	I	AL	209924	M	0.70	0.75	0.47	0.765	0.710	0.290	0.310
192	I	AL	209925	M	0.83	0.90	0.46	0.855	0.805	0.320	0.340
193	I	AL	23392	M	0.78	0.87	0.47	0.875	0.790	.	.
194	I	AL	23401	F	0.67	0.77	0.43	0.850	0.695	.	.
195	I	AL	23402		0.69	0.79	0.41	0.780	0.730	.	0.315
196	I	AP	133606	M	0.84	0.90	0.49	0.875	0.825	0.300	0.325
197	I	AP	133620	M	0.75	0.79	0.45	0.815	0.725	0.270	0.270
198	I	AP	133622	M	0.73	0.81	0.42	0.780	0.705	0.280	0.300
199	I	AP	133623	M	0.71	0.77	0.40	0.755	0.685	0.260	0.300
200	I	AP	133624	M	0.76	0.81	0.47	0.815	0.715	.	0.315
201	I	AP	133626	F	0.64	0.67	0.40	0.665	0.620	0.235	0.260
202	I	AP	133628	M	0.69	0.80	0.49	0.800	0.700	0.280	0.320
203	I	AP	133631	F	0.64	0.66	0.38	0.690	0.665	0.240	0.270
204	I	AP	133637	M	0.72	0.77	0.45	0.780	0.715	0.280	0.310
205	I	AP	133665	M	0.80	0.85	0.47	0.810	0.740	0.295	0.330
206	I	AP	133806	F	0.63	0.70	0.37	0.730	0.655	0.240	0.280
207	I	AP	133810	F	0.60	0.64	0.32	0.650	0.550	0.200	0.260
208	I	AP	133813	F	0.58	0.63	0.35	0.635	0.570	0.225	0.255
209	I	AP	133851	M	0.75	0.85	0.50	0.835	0.720	0.280	0.320
210	I	AP	133862	M	0.72	0.78	0.43	0.780	0.750	0.270	0.325
211	I	AP	133864	M	0.61	0.65	0.33	0.655	0.585	.	.
212	I	AP	209926	F	0.61	0.65	0.35	0.705	0.675	.	.

OBS	GEN	SP	CAT	S	RN	HX	RN	FD	TD	MCD	MTD
213	I	AP	209927	F	0.63	0.69	0.37	0.745	0.655	.	.
214	I	AP	211578	M	0.74	0.81	0.51	0.865	0.795	.	.
215	I	AP	211579	M	0.74	0.79	0.46	0.815	0.715	0.290	0.310
216	I	AP	270361	M	0.84	0.89	0.48	0.855	0.765	0.285	0.325
217	I	AP	95129	M	0.78	0.84	0.48	0.845	0.750	0.290	0.340
218	I	NI	30195	M	0.72	0.78	0.42	0.795	0.735	0.290	0.335
219	I	NI	30196	F	0.68	0.71	0.41	0.755	0.670	0.280	0.300
220	I	NI	30197	M	0.73	0.81	0.45	0.905	0.795	0.305	0.350
221	I	NI	30198	M	0.71	0.81	.	0.835	0.755	.	.
222	I	NI	361020	M	0.79	0.84	0.45	0.815	0.750	.	0.335
223	I	NI	361021	F	0.60	0.65	0.37	0.725	0.605	0.235	0.275
224	I	NI	42873	F	0.69	0.75	0.42	0.825	0.790	0.300	0.320
225	I	NI	42884	M	0.75	0.78	0.45	0.835	0.745	0.310	0.340
226	J		1198		0.60	0.69	0.37	0.685	0.630	.	.
227	J		1199		0.60	0.66	0.37	0.680	0.605	.	.
228	J		1200		0.64	0.70	0.39	0.675	0.645	0.240	0.250
229	J		1201	M	0.67	0.76	0.42	0.730	0.695	.	.
230	J		1202	F	0.66	0.76	0.41	0.705	0.640	.	.
231	J		1864	M	0.75	0.81	.	0.740	0.700	0.300	0.300
232	J		1867	F	0.67	0.73	.	.	0.620	0.270	0.285
233	J		1868		.	.	.	.	.	.	.
234	J		1909	F	0.63	0.67	0.37	0.680	0.575	0.240	0.300
235	J		1912	F	.	.	.	.	.	0.240	0.270
236	J		1918	M	0.63	0.68	0.37	.	.	0.250	0.270
237	K		163	M	0.95	1.03	.	1.030	0.830	.	.
238	K		164	M	0.90	1.11	.	1.060	0.865	.	.
239	K		165		0.93	1.05	.	1.025	0.835	0.360	0.360
240	K		177		0.96	1.04	0.59	0.975	0.810	.	.
241	K		178		1.03	1.04	0.62	1.080	0.900	.	0.360
242	K		180		0.86	0.94	.	.	0.800	.	.
243	K		355	M	0.86	0.90	0.57	0.935	0.790	0.330	0.360
244	K		555	F	0.95	1.05	.	1.050	0.845	.	0.370
245	K		675	M	0.96	1.05	0.56	0.980	0.830	0.300	0.355
246	K		676	M	0.97	1.03	0.62	1.070	0.875	0.355	0.375
247	K		677	M	0.97	1.07	0.58	1.040	0.865	0.340	.
248	K		970		.	.	.	.	.	.	.
249	K	LA	188153	F	0.92	0.99	0.60	1.080	0.815	.	.
250	K	LA	188162	F	.	.	.	.	.	0.325	0.325
251	K	LA	35752	M	1.00	1.05	0.61	1.155	0.900	0.360	0.365
252	K	LA	397774	F	1.00	1.09	0.50	1.145	0.925	0.355	0.360
253	K	LA	397775	M	0.85	0.95	0.54	0.960	.	0.295	0.315
254	K	LA	70404	M	0.99	1.09	0.63	1.145	0.975	.	0.350
255	L		185347		0.37	0.41	0.23	0.470	0.405	0.130	0.180
256	L	RD	269705	F	0.35	0.39	0.22	0.475	0.400	.	0.125
257	M		129	F	0.74	0.83	0.45	0.680	0.680	.	.
258	M		1417		0.62	0.64	0.43	0.745	0.630	.	.
259	M		1445	F	0.54	0.68	0.38	0.695	0.635	0.260	0.260
260	M		1450		0.63	0.69	0.41	0.770	0.680	.	.
261	M		154	F	0.67	0.70	0.40	0.710	0.615	.	.
262	M		660		.	.	.	.	.	.	.
263	M		661	M	0.61	0.66	0.38	.	0.620	0.270	0.250
264	M		667	F	.	.	0.39	0.665	0.610	0.280	0.260
265	M	PA	241007	F	0.58	0.69	0.37	0.710	0.605	0.250	.

OBS	GEN	SP	CAT	S	RN	HX	RN	FL	TU	MCD	MTD
266	M	PA	300794		0.51	0.55	0.32	0.640	0.585	0.215	0.260
267	M	PA	339659	F	0.59	0.69	0.33	.	0.575	.	.
268	M	PA	64088	M	.	.	.	0.715	.	.	.
269	M	PA	70377	M	0.53	0.69	0.37	0.645	0.585	0.225	0.250
270	N		148454		0.41	0.46	0.24	0.430	0.400	0.150	0.150
271	N		180091		0.38	0.39	0.23	0.425	0.350	0.110	0.140
272	N		207726		0.39	0.42	0.25	0.480	0.395	0.120	0.150
273	N		35516		0.32	0.34	0.20	0.360	0.315	0.130	0.140
274	N		77693		0.36	0.41	0.23	0.435	0.370	0.130	0.150
275	N		97316	M	0.39	0.40	0.24	0.425	0.375	0.130	0.150
276	N	M	1146		0.37	0.41	.	0.430	0.390	.	.
277	N	M	1148		0.40	0.45	0.24	0.470	0.380	.	.
278	N	M	25313		.	.	0.26	0.470	0.425	0.150	0.170
279	N	MB	1448		.	.	.	.	.	.	.
280	N	ML	148322		0.36	0.39	0.22	0.390	0.345	0.120	0.140
281	N	ML	292294	F	0.34	0.37	0.20	0.375	0.345	0.135	0.145
282	N	ML	439	F	0.40	0.44	0.21	0.415	0.355	.	.
283	N	O	117	F	0.36	0.41	.	0.420	0.380	.	.
284	N	O	121	M	0.35	0.38	.	0.380	.	.	.
285	N	O	442	F	0.38	0.39	.	0.420	0.355	.	.
286	N	O	445	F	0.35	0.38	.	0.385	0.350	.	.
287	N	O	648	F	0.36	0.39	0.20	0.395	0.335	.	.
288	N	O	654	M	0.35	0.39	0.22	0.380	0.350	.	.
289	N	O	708	F	0.36	0.39	0.21	0.395	0.380	.	.
290	N	OG	148336	M	.	.	0.26	.	0.395	.	.
291	N	OG	240425		0.35	0.39	.	0.375	0.355	.	.
292	N	OG	257345		.	.	0.26	0.415	0.380	0.150	0.165
293	N	OG	49389		0.39	0.41	0.23	0.425	0.390	0.140	.
294	N	OO	446	F	0.35	0.39	0.21	0.380	0.335	.	.
295	N	S	726	M	0.28	0.29	0.17	0.340	0.290	.	.
296	N	S	728	M	0.31	0.33	0.20	0.365	0.325	.	.
297	N	S	733	F	0.28	0.30	0.18	0.340	0.295	.	.
298	N	S	735	F	0.32	0.34	0.20	0.400	0.330	.	.
299	N	SD	148453	M	0.39	0.41	0.23	0.440	0.370	0.125	0.150
300	N	SD	362118		0.32	0.37	0.24	0.390	0.350	0.130	0.160
301	N	SF	461267	M	0.35	0.38	0.20	0.405	0.370	0.110	0.145
302	N	SI	336299	F	0.31	0.32	0.19	0.370	0.325	0.100	0.135
303	N	SI	336301	F	0.36	0.38	0.22	0.410	0.375	0.120	0.160
304	N	SN	147433		0.34	0.40	0.24	0.420	0.370	0.120	0.160
305	N	SY	188171	M	0.30	0.35	0.20	0.350	0.295	0.100	0.120
306	N	SY	188177	M	0.30	0.31	0.19	0.340	0.300	0.100	0.130
307	N	SY	238258	M	0.34	0.35	0.20	0.385	.	.	.
308	N	OG	49397		0.34	0.35	.	0.375	0.315	.	.
309	O	SC	188080	F	.	.	.	0.460	0.435	0.165	0.195
310	O	SC	188110	F	0.45	0.50	0.29	0.515	0.455	0.160	0.200
311	O	SC	209928	F	0.41	0.43	0.25	0.430	.	.	.
312	O	SC	209930	M	0.48	0.56	.	0.530	.	.	.
313	O	SC	209933	F	0.40	0.43	0.26	0.455	0.395	.	.
314	O	SC	209934	M	0.49	0.53	0.32	.	0.490	.	.
315	O	SC	209935	M	.	.	0.35	0.550	.	.	.
316	O	SC	211591	F	0.40	0.42	0.25	0.510	0.385	.	.
317	O	SC	211592	M	0.52	0.54	0.32	0.550	0.490	.	0.210
318	O	SC	211594	M	0.45	0.55	0.30	0.470	0.475	0.175	0.190

ORS	GEN	SP	CAT	S	RV	FX	RW	FU	TD	MCD	MTU
319	0	SC	211596	M	0.46	0.49	0.28	0.480	0.435	0.175	0.190
320	0	SC	211597	M	.	.	0.30	.	0.455	.	0.200
321	0	SC	211600	M	0.47	0.50	0.30	0.535	.	0.170	0.205
322	0	SC	211601	M	0.47	0.49	0.29	0.510	0.460	.	.
323	0	SC	211606	F	0.44	0.48	0.28	0.505	0.430	0.160	0.200
324	0	SC	211609	F	0.40	0.43	0.26	0.465	0.410	.	0.195
325	0	SC	211613	F	0.40	0.46	0.28	0.490	0.430	0.150	0.190
326	0	SC	211614	F	0.37	0.45	0.26	0.440	0.385	0.150	.
327	0	SC	211615	F	0.43	0.45	0.27	0.475	0.420	.	.
328	0	SC	211616	F	.	.	0.26	0.490	0.415	.	.
329	0	SC	211618	M	0.46	0.51	0.29	0.515	0.450	.	.
330	0	SC	211624	M	0.48	0.56	0.31	0.575	0.485	0.140	.
331	0	SC	211627	M	0.43	0.48	0.28	0.490	0.455	.	.
332	0	SC	211628	M	0.45	0.48	0.31	0.500	0.455	.	.
333	0	SC	211639	F	0.37	0.43	0.26	0.470	0.440	.	.

OPS	GEN	SP	CAT	S	RX	FN	FX	TN	TX	FORE	HIND
1	A	RE	133544	F	0.70	0.96	1.05	0.79	1.06	30.30	30.7
2	A	CA	133875		0.59	0.80	0.97	0.65	0.83	27.80	28.8
3	A	CA	209917	M	0.78	1.00	1.18	0.87	1.07	32.50	33.2
4	A	CA	211495	F	0.66	0.90	1.03	0.75	0.91	27.52	28.1
5	A	CA	211496	M	0.81	1.00	1.10	0.83	1.01	31.50	31.7
6	A	CA	211497	F	0.59	0.81	0.94	0.66	0.79	26.50	27.4
7	A	CA	211498	M	0.81	0.97	1.20	0.87	1.11	31.70	32.4
8	A	CA	211499	M	0.76	0.88	1.10	0.81	0.94	29.80	29.8
9	A	CA	211501	F	0.58	0.88	0.94	0.68	0.85	26.48	27.2
10	A	CA	211502	F	0.70	0.90	1.08	0.77	0.87	28.00	29.0
11	A	CA	211504	M	0.69	0.92	1.03	0.76	1.03	30.90	32.6
12	A	CA	211508	M	0.78	1.03	1.17	0.91	1.00	31.30	31.6
13	A	CA	211510	M	0.79	1.03	1.19	0.88	1.04	31.70	31.7
14	A	CA	211512	F	0.68	0.95	1.12	0.77	0.91	.	29.7
15	A	CA	211513	M	0.80	1.00	1.20	0.88	1.03	31.30	32.0
16	A	CA	211519	M	0.75	0.99	1.10	0.85	1.02	.	33.4
17	A	CA	211520	F	0.68	0.90	0.97	0.72	0.81	27.20	28.3
18	A	CA	211522	F	0.55	0.82	0.99	0.63	0.84	28.00	29.5
19	A	CA	211523	M	0.85	1.01	1.19	0.89	1.00	30.80	31.3
20	A	CA	211524	F	0.73	.	.	0.69	0.96	28.10	.
21	A	CA	211525	M	0.71	0.92	1.10	0.86	0.98	31.20	31.7
22	A	CA	211585	F	0.71	0.95	1.17	0.74	0.92	28.10	28.9
23	A	CA	215060	F	0.65	0.84	0.95	0.66	0.80	28.90	29.8
24	A	CA	215061	M	0.64	0.79	0.90	0.67	0.76	28.40	29.7
25	A	PA	240407	M	0.71	0.88	1.08	0.67	0.94	27.70	27.5
26	A	PA	240408		0.78	0.98	1.11	0.70	0.95	28.50	29.0
27	A	PA	244870	M	0.84	1.02	1.34	0.81	1.02	32.70	33.1
28	A	PA	25309		0.82	0.94	1.09	0.74	1.07	29.60	29.4
29	A	PA	257307	F	0.66	0.93	1.06	.	.	29.40	.
30	A	PA	257359		0.72	0.91	0.93	0.71	0.93	29.10	28.3
31	A	PA	257404		0.65	0.90	1.08	0.70	0.93	29.00	29.1
32	A	PA	258313	F	0.63	0.79	0.94	0.66	0.79	28.60	27.6
33	A	PA	258314		0.63	0.86	1.03	0.69	0.87	29.20	29.0
34	A	PA	397108		0.68	0.91	1.10	0.71	0.96	28.20	27.7
35	A	PA	397112		0.72	0.93	1.12	0.72	0.94	29.30	28.7
36	A	PA	397113		0.89	0.98	1.08	0.79	1.08	30.30	29.6
37	A	SE	132790	M	0.86	0.98	1.23	0.80	1.18	31.90	33.5
38	A	SE	187994	F	0.46	0.72	0.76	0.56	0.75	19.30	25.6
39	A	SE	188006	F	0.69	.	.	.	.	.	.
40	A	SE	211527	F	0.57	0.79	0.89	0.64	0.82	26.20	26.9
41	A	SE	211528	M	0.67	0.85	1.03	0.70	0.97	28.90	30.3
42	A	SE	211531	F	0.54	0.80	0.92	0.64	0.88	27.40	29.0
43	A	SE	211532	M	0.75	0.95	1.19	0.75	1.08	31.50	32.7
44	A	SE	211535	F	0.58	0.80	1.03	0.65	0.85	28.00	29.0
45	A	SE	211538	F	0.62	0.86	1.04	0.68	1.03	29.20	30.5
46	A	SE	211540	F	0.54	0.78	0.87	0.61	0.88	26.80	27.6
47	A	SE	211542	M	0.78	0.91	1.13	0.77	1.05	32.80	33.4
48	A	SE	211543	F	0.55	0.75	0.91	0.59	0.83	27.70	29.1
49	A	SE	23330	F	0.76	0.90	1.11	0.76	0.94	27.90	29.8
50	A	SE	23334	M	0.70	0.86	1.07	0.83	0.97	29.20	30.2
51	A	SE	23341		0.69	0.86	1.05	0.72	0.94	28.60	30.1
52	A	SE	23342		0.70	0.92	1.12	0.77	0.90	30.10	31.5
53	A	SE	23351		0.56	0.90	1.09	0.77	0.93	27.80	30.2

ORS	GEN	SP	CAT	S	RX	FN	FX	TI	TX	FORE	HIND
54	A	SE	23355		0.70	0.95	1.22	0.81	1.10	28.80	29.80
55	A	SE	23361		0.72	0.95	1.14	0.78	1.01	29.10	30.30
56	A	SE	23370		0.70	0.94	1.17	0.72	1.02	29.50	31.00
57	A	SE	23371		0.81	0.95	1.25	0.79	1.06	30.10	30.70
58	A	SE	23377	F	0.71	0.86	1.04	0.72	1.02	28.40	29.60
59	A	SE	23378	F	0.72	0.91	1.12	0.71	0.98	29.30	30.90
60	A	SE	23382	F	0.75	0.88	1.05	0.74	0.99	32.20	28.70
61	A	SE	23386		0.63	0.80	1.04	0.79	0.86	27.70	29.00
62	A	SE	23549	F	0.67	0.85	1.03	0.72	0.98	29.20	29.60
63	A	SE	23556		0.65	0.88	1.02	0.70	0.96	29.60	30.30
64	A	SE	30193	M	0.74	1.07	1.22	.	.	31.50	.
65	A	SE	42313		0.61	0.88	1.08	0.67	0.90	30.20	30.70
66	A	SE	42316	F	0.58	0.97	1.10	0.68	0.92	29.40	31.10
67	A	SE	48119	F	0.60	0.87	1.07	0.70	0.92	29.00	29.60
68	A	SE	69591		.	.	.	.	.	.	.
69	A	SE	70088	M	0.60	0.85	1.03	0.79	0.83	28.90	29.70
70	A	SE	99657	F	0.81	0.87	1.09	0.70	1.00	28.40	29.50
71	B	TR	10	M	0.29	0.44	0.49	0.35	0.50	12.79	17.08
72	B	TR	1442		0.28	0.45	0.48	0.32	0.44	12.40	16.64
73	B	TR	209916	F	0.34	0.53	0.56	0.35	0.53	13.26	17.59
74	B	TR	211464	M	0.34	0.57	0.60	0.39	0.66	15.39	21.31
75	B	TR	211477	F	0.29	0.50	0.57	0.43	0.53	15.52	20.22
76	B	TR	21153		.	0.45	0.49	0.32	0.52	.	17.37
77	B	TR	215048	F	0.29	0.50	0.57	0.38	0.53	15.53	19.93
78	B	TR	215050	F	0.35	0.54	0.60	0.42	0.56	.	20.15
79	B	TR	215051	M	.	0.55	0.65	0.45	0.60	15.75	20.82
80	B	TR	215052	M	0.34	0.51	0.56	0.41	0.59	15.01	20.04
81	B	TR	215053	F	0.31	0.52	0.61	0.39	0.55	15.26	20.41
82	B	TR	215054	M	0.33	0.54	0.61	0.41	0.65	15.06	20.32
83	B	TR	215056	F	0.35	0.56	0.59	0.41	0.65	15.46	20.71
84	B	TR	215057	M	0.35	0.53	0.59	0.42	0.65	15.15	19.04
85	B	TR	215059	M	0.30	0.53	0.56	0.40	0.52	15.15	20.41
86	B	TR	396505	M	0.34	0.52	0.55	0.40	0.51	14.35	19.44
87	B	TR	396702	F	0.29	0.46	.	0.33	0.49	12.81	17.32
88	B	TR	39675	F	0.30	0.52	0.53	0.34	0.60	14.05	18.82
89	B	TR	451		.	0.49	0.54	0.36	0.57	.	17.44
90	B	TR	937	F	0.30	0.50	.	0.37	0.52	14.49	19.64
91	B	TR	938	F	0.27	0.46	0.52	0.30	0.50	14.21	18.80
92	C		12		0.71	1.18	1.24	0.94	1.29	43.87	40.44
93	C		12		0.75	1.08	1.19	0.88	1.25	39.69	37.94
94	C		140	M	0.80	1.28	1.34	0.95	1.23	37.42	37.75
95	C		154189		0.66	1.11	1.27	.	.	43.90	.
96	C		183	M	0.77	1.13	1.33	0.92	1.25	43.43	43.13
97	C		184	M	0.65	1.06	1.73	0.72	1.72	.	36.24
98	C		277		0.81	1.18	1.42	0.99	1.80	39.14	37.54
99	C		292	F	.	1.19	1.57	0.80	1.18	.	35.78
100	C		3768	M	0.80	1.08	1.33	0.83	1.37	40.80	41.30
101	C		810	F	.	1.35	1.40	0.95	1.30	.	38.01
102	C	BE	259	F	.	.	.	0.86	1.22	41.70	.
103	C	BE	30192	M	0.91	1.32	1.39	1.05	1.35	41.00	39.60
104	C	GE	14128		0.82	1.18	1.38	0.83	1.18	41.30	38.10
105	C	GE	172985		0.75	1.17	1.37	0.91	1.28	43.90	42.50
106	C	GE	244863		0.71	1.07	1.31	0.83	1.19	40.40	37.30

ORS	GEN	SP	CAT	S	RX	FN	FX	TN	TX	FORE	HINT
107	C	GE	276631	F	0.68	1.08	1.22	0.82	1.26	40.40	37.80
108	C	GE	276657	F	0.69	1.07	1.31	0.85	1.23	42.60	40.30
109	C	PA	361027	F	0.78	.	.	.	.	44.10	.
110	D		1566		0.45	0.67	0.70	0.55	0.65	22.48	26.79
111	D		1571		0.54	0.78	0.82	0.55	0.74	23.15	28.61
112	D		1572		0.51	0.70	0.74	0.52	0.70	22.43	27.42
113	D		1573		0.44	0.70	0.72	0.54	0.68	22.66	27.76
114	D		1574		0.43	0.70	0.72	0.50	0.70	22.01	26.66
115	D		1575		0.46	.	.	0.56	0.73	23.76	.
116	D		1576		0.52	0.78	0.83	0.57	0.77	23.34	28.80
117	D		1577		0.55	0.79	0.83	.	.	23.98	.
118	D		1578		0.55	0.76	0.81	0.59	0.78	24.39	29.30
119	D		1584		0.43	0.66	0.72	0.50	0.65	22.10	26.46
120	D		1585		0.49	0.78	0.84	0.59	0.71	22.82	27.71
121	D		1866		.	.	.	.	.	.	.
122	D	RU	302626	M	0.62	0.87	0.93	0.65	0.85	27.19	31.96
123	D	RU	519570	F	0.59	.	.	0.58	0.81	24.65	.
124	D	RU	70192	M	0.67	0.80	0.85	0.65	0.76	25.90	30.20
125	E		119625	M	.	0.52	0.60	.	.	.	.
126	E		1273	M	0.28	0.57	0.67	0.32	0.48	15.02	18.41
127	E		136208	M	0.34	0.46	0.49	0.36	0.51	13.32	18.15
128	E		211492	M	0.34	0.44	0.57	0.42	0.53	14.18	19.06
129	E		659		.	0.50	0.58	0.38	0.53	14.31	18.89
130	E		997	F	0.33	0.52	0.58	0.38	0.53	14.18	19.06
131	E		998		0.33	0.50	0.57	0.38	0.53	13.93	17.73
132	E	MO	130361	M	0.30	0.46	0.52	0.36	0.49	14.07	18.85
133	E	MO	136217	M	0.31	0.48	0.53	0.36	0.49	13.51	18.47
134	E	MO	211487	M	0.33	0.48	0.57	0.36	0.57	13.48	18.79
135	E	MO	211488	F	0.32	0.44	0.50	0.38	0.49	14.07	18.85
136	E	MO	211489	F	0.31	.	.	0.37	0.49	13.21	18.06
137	E	MO	211490	F	0.31	0.47	0.53	0.35	0.53	13.51	18.47
138	E	MO	211493	M	0.37	0.49	0.54	0.37	0.49	13.51	18.47
139	E	MO	240088	F	0.42	0.63	0.70	0.46	0.71	15.99	22.72
140	E	MO	269827	M	0.34	0.56	0.65	0.43	0.62	15.01	20.24
141	E	MO	397933	M	0.33	.	0.52	0.36	0.56	14.34	.
142	E	MO	94977	M	0.27	0.46	0.52	0.39	0.51	13.63	18.51
143	E	TO	398212	F	0.41	0.57	0.60	0.46	0.62	15.10	20.29
144	F	GO	1829		0.34	0.47	0.51	0.36	0.54	11.09	15.48
145	F	GO	183289	M	0.25	0.39	0.45	0.30	0.48	10.40	14.72
146	F	GO	303323	M	0.30	0.40	0.45	0.31	0.43	10.28	14.35
147	F	GO	395455	M	0.25	0.42	0.45	0.29	0.44	10.09	14.15
148	G		1279	M	.	0.39	0.41	0.30	0.39	.	12.10
149	G		1280	M	0.27	0.35	0.42	0.27	0.39	.	12.72
150	G		1290	M	0.26	0.37	0.43	0.30	0.38	9.40	13.25
151	G		1298	M	0.29	0.35	0.40	0.28	0.42	8.89	11.78
152	G		1314	F	0.27	.	.	.	.	9.21	.
153	G		1323	M	0.20	0.26	0.29	0.21	0.32	8.12	10.72
154	G		1325	F	0.26	0.33	0.39	0.24	0.33	8.17	10.83
155	G		1329	M	0.24	0.35	0.37	0.26	0.36	8.37	11.19
156	G		1330	F	0.23	0.33	0.36	.	.	.	.
157	G		1336	F	0.26	0.35	0.40	0.27	0.35	8.92	11.40
158	G		1339	M	0.28	0.36	0.39	0.27	0.37	8.46	11.21
159	G		293	F	0.30	0.36	0.42	0.29	0.38	9.22	11.92

OBS	GEN	SP	CAT	S	RX	FN	FX	TN	TX	FORE	HIND
160	G		49480		0.24	0.35	0.37	0.26	0.35	8.30	10.66
161	G		66		0.27	0.34	.	0.25	0.36	7.83	10.60
162	G		68	F	0.24	0.35	0.37	0.26	0.35	8.30	10.66
163	G		95127	M	0.29	0.37	0.40	0.32	0.40	9.61	12.42
164	G	AR	133712		0.29	0.39	0.40	0.29	0.42	9.49	12.56
165	G	AR	184689		.	0.36	0.40	.	.	.	.
166	G	CH	241197	F	.	0.37	0.40	.	.	.	.
167	G	JA	133688	F	0.23	0.32	0.36	0.27	0.33	8.59	11.71
168	G	JA	133694	M	0.26	0.35	0.36	0.27	0.35	8.18	10.94
169	G	JA	133698	F	0.27	0.36	0.37	0.26	0.38	8.45	11.29
170	G	JA	35529		0.26	0.33	0.35	0.25	0.37	8.63	11.47
171	H	PY	244101		0.18	.	.	0.16	0.24	5.62	.
172	H	PY	303037	M	0.21	0.26	0.28	0.17	0.23	6.14	7.54
173	H	PY	305778	M	.	0.23	0.25	0.16	0.23	.	7.56
174	H	PY	314966	F	0.21	0.26	0.29	0.18	0.26	6.83	8.34
175	H	PY	336325	M	0.18	0.22	0.25	0.17	0.23	6.13	7.51
176	H	PY	337947	M	0.20	0.23	0.27	0.17	0.22	6.37	7.69
177	H	PY	337948	M	0.15	0.24	0.28	0.16	0.22	6.34	7.60
178	H	PY	673		.	.	.	.	.	.	.
179	H	PY	693	M	.	0.25	.	0.18	0.25	.	8.03
180	H	PY	694	M	0.18	0.23	0.25	0.16	0.20	6.03	7.18
181	H	PY	695	M	0.19	0.24	0.26	0.16	0.22	6.28	7.35
182	H	PY	696		0.16	.	.	.	.	.	.
183	H	PY	697	M	0.18	0.21	0.23	0.14	0.21	6.13	7.36
184	H	PY	699	M	.	.	.	.	.	.	.
185	H	PY	699	F	0.18	0.24	0.27	0.17	0.23	.	7.85
186	H	PY	701	F	.	0.25	0.29	0.17	0.19	.	8.02
187	H	PY	734		.	.	.	.	.	.	.
188	H	PY	923	F	0.20	0.24	0.27	0.16	0.23	.	7.90
189	I	AL	188018	F	0.47	0.81	0.92	0.68	0.88	22.00	27.70
190	I	AL	209923	F	0.48	0.72	0.76	0.48	0.78	20.10	24.50
191	I	AL	209924	M	0.53	0.73	0.80	0.51	0.91	19.90	24.10
192	I	AL	209925	M	0.49	0.83	0.88	0.63	0.98	21.60	26.40
193	I	AL	23392	M	0.61	0.81	0.94	0.65	0.93	23.00	28.70
194	I	AL	23401	F	0.57	0.78	0.92	0.58	0.81	22.80	28.50
195	I	AL	23402		0.53	0.74	0.82	0.60	0.86	20.80	26.00
196	I	AP	133606	M	0.55	0.80	0.95	0.62	1.03	22.30	27.10
197	I	AP	133620	M	0.50	0.80	0.83	0.58	0.87	20.51	26.14
198	I	AP	133622	M	0.51	0.76	0.80	0.55	0.86	20.90	25.30
199	I	AP	133623	M	0.51	0.73	0.78	0.57	0.80	20.22	24.93
200	I	AP	133624	M	0.52	0.79	0.84	0.61	0.82	20.67	24.79
201	I	AP	133626	F	0.43	0.64	0.69	0.50	0.74	18.62	23.15
202	I	AP	133628	M	0.54	0.78	0.82	0.58	0.82	20.77	25.16
203	I	AP	133631	F	0.46	0.68	0.70	0.49	0.84	19.11	23.63
204	I	AP	133637	M	0.49	0.76	0.80	0.55	0.88	19.71	24.16
205	I	AP	133665	M	0.54	0.79	0.83	0.64	0.84	20.60	24.70
206	I	AP	133806	F	0.45	0.69	0.77	0.51	0.80	19.51	24.15
207	I	AP	133810	F	0.38	0.63	0.67	0.48	0.62	18.27	22.40
208	I	AP	133813	F	0.41	0.62	0.65	0.46	0.68	19.46	24.05
209	I	AP	133851	M	0.57	0.79	0.88	0.58	0.86	22.17	25.98
210	I	AP	133862	M	0.51	0.76	0.80	0.59	0.91	20.66	25.52
211	I	AP	133864	M	0.42	0.64	0.67	0.45	0.72	18.28	22.64
212	I	AP	209926	F	0.47	0.66	0.75	0.49	0.86	18.70	22.60

ORS	GEN	SP	CAT	S	RX	FN	FX	TN	TX	FORE	HIND
213	I	AP	209927	F	0.49	0.73	0.76	0.50	0.81	19.10	24.00
214	I	AP	211578	M	0.55	0.84	0.89	0.59	1.00	21.50	26.80
215	I	AP	211579	M	0.52	0.79	0.84	0.57	0.86	21.00	25.40
216	I	AP	270361	M	0.55	0.82	0.89	0.56	0.97	21.23	25.78
217	I	AP	95129	M	0.55	0.79	0.90	0.60	0.90	23.12	27.13
218	I	NI	30195	M	0.48	0.73	0.86	0.62	0.85	23.40	28.60
219	I	NI	30196	F	0.49	0.73	0.78	0.59	0.75	21.70	26.40
220	I	NI	30197	M	0.54	0.85	0.96	0.65	0.94	22.90	27.90
221	I	NI	30198	M	.	0.80	0.87	0.62	0.89	.	27.40
222	I	NI	361020	M	0.58	0.75	0.88	0.59	0.91	21.12	25.30
223	I	NI	361021	F	0.42	0.69	0.76	0.50	0.71	18.77	22.78
224	I	NI	42873	F	0.57	0.76	0.89	0.63	0.85	22.90	28.50
225	I	NI	42884	M	0.57	0.79	0.88	0.65	0.84	23.00	27.80
226	J		1198		0.49	0.67	0.70	0.53	0.73	19.39	23.64
227	J		1199		0.47	0.63	0.73	0.50	0.71	19.18	24.47
228	J		1200		0.46	0.65	0.70	0.55	0.74	20.13	24.73
229	J		1201	M	0.55	0.69	0.77	0.59	0.80	22.00	27.10
230	J		1202	F	0.50	0.67	0.74	0.54	0.74	20.49	24.68
231	J		1864	M	0.47	0.74	.	0.60	0.80	20.16	25.02
232	J		1867	F	.	.	.	0.53	0.71	.	.
233	J		1868	.	.	.	.	.	.	.	.
234	J		1909	F	0.50	0.64	0.72	0.50	0.65	20.49	24.34
235	J		1912	F	.	.	.	.	.	.	.
236	J		1918	M	0.46	.	.	.	.	19.45	.
237	K		163	M	.	0.99	1.07	0.76	0.90	.	29.61
238	K		164	M	.	0.99	1.13	0.72	1.01	.	32.32
239	K		165	.	.	0.95	1.10	0.75	0.92	.	31.14
240	K		177		0.66	0.92	1.03	0.67	0.95	30.68	31.33
241	K		178		0.66	0.99	1.17	0.80	1.00	31.59	31.74
242	K		180		.	.	.	0.68	0.92	.	.
243	K		355	M	0.60	0.90	0.97	0.70	0.88	30.68	31.46
244	K		555	F	.	1.00	1.10	0.76	0.93	.	32.48
245	K		675	M	0.65	0.92	1.04	0.71	0.95	30.40	31.72
246	K		676	M	0.70	0.99	1.15	0.73	1.02	31.54	32.79
247	K		677	M	0.70	0.99	1.09	0.74	0.99	31.26	31.80
248	K		970	.	.	.	.	.	.	.	.
249	K	LA	188153	F	0.66	1.04	1.12	0.70	0.93	31.20	31.30
250	K	LA	188162	F	.	.	.	.	.	.	.
251	K	LA	35752	M	0.65	1.08	1.23	0.85	0.95	33.90	34.40
252	K	LA	397774	F	0.80	1.09	1.20	0.76	1.09	33.70	33.70
253	K	LA	397775	M	0.67	0.87	1.05	.	.	30.80	.
254	K	LA	70404	M	0.70	1.10	1.19	0.88	1.07	34.50	35.20
255	L		185347		0.27	0.45	0.49	0.35	0.46	12.74	14.46
256	L	RO	269705	F	0.26	0.46	0.49	0.35	0.45	12.22	13.88
257	M		129	F	0.50	0.67	0.69	0.55	0.81	21.20	26.91
258	M		1417		0.46	0.70	0.79	0.53	0.73	19.41	25.74
259	M		1445	F	0.47	0.66	0.73	0.52	0.75	19.06	26.51
260	M		1450		0.50	0.75	0.79	0.57	0.79	20.03	26.98
261	M		154	F	0.46	0.69	0.73	0.52	0.71	21.54	27.74
262	M		660	.	.	.	.	.	.	.	.
263	M		661	M	0.47	.	.	0.53	0.71	20.38	.
264	M		667	F	0.49	0.65	0.68	0.53	0.69	.	26.25
265	M	PA	241007	F	0.42	0.69	0.73	0.51	0.70	20.16	27.25

OBS	GEN	SP	CAT	S	RX	FN	FX	TN	TX	FORE	HIND
266	M	PA	300794		0.40	0.62	0.66	0.51	0.66	19.11	25.12
267	M	PA	339659	F	0.44	.	.	0.47	0.68	17.64	.
268	M	PA	64088	M	.	0.70	0.73	.	.	.	.
269	M	PA	70377	M	0.43	0.62	0.67	0.52	0.65	19.90	26.00
270	N		148454		0.30	0.40	0.46	0.33	0.47	9.76	13.13
271	N		180091		0.28	0.41	0.44	0.31	0.39	10.09	12.85
272	N		207726		0.33	0.46	0.50	0.33	0.46	10.64	14.00
273	N		35516		0.23	0.36	.	0.27	0.36	9.82	13.03
274	N		77693		0.26	0.42	0.45	0.30	0.44	10.30	14.00
275	N		97316	M	0.27	0.42	0.43	0.31	0.44	10.59	14.12
276	N	M	1146		0.30	0.46	0.48	0.31	0.47	.	14.21
277	N	M	1148		0.30	0.46	0.48	0.31	0.45	10.69	14.59
278	N	M	25313		0.29	0.43	0.51	0.34	0.51	.	13.99
279	N	MB	1448		.	.	.	.	.	.	.
280	N	ML	148322		0.24	0.36	0.42	0.28	0.41	9.75	13.20
281	N	ML	292294	F	0.25	0.35	0.40	0.29	0.40	9.48	12.75
282	N	ML	439	F	0.26	0.37	0.46	0.30	0.41	10.01	13.34
283	N	O	117	F	.	0.41	0.43	0.32	0.44	.	13.88
284	N	O	121	M	.	0.36	0.40	.	.	.	.
285	N	O	442	F	.	0.39	0.45	0.29	0.42	.	13.52
286	N	O	445	F	.	0.37	0.40	0.29	0.41	.	12.94
287	N	O	648	F	0.26	0.39	0.40	0.28	0.39	10.32	13.64
288	N	O	654	M	0.25	0.37	0.39	0.28	0.42	10.10	12.42
289	N	O	708	F	0.25	0.38	0.41	0.33	0.43	9.45	12.57
290	N	OG	148336	M	0.29	.	.	0.35	0.44	.	.
291	N	OG	240425		.	0.36	0.39	0.30	0.41	.	13.25
292	N	OG	257345		0.31	0.40	0.43	0.32	0.44	.	13.37
293	N	OG	49389		0.30	0.41	0.44	0.33	0.45	9.97	13.06
294	N	OO	446	F	0.26	0.36	0.40	0.29	0.38	9.60	12.76
295	N	S	726	M	0.20	0.31	0.37	0.25	0.33	8.88	11.53
296	N	S	728	M	0.25	0.34	0.39	0.28	0.37	8.91	11.97
297	N	S	733	F	0.20	0.32	0.36	0.25	0.34	8.89	11.55
298	N	S	735	F	0.22	0.38	0.42	0.29	0.37	9.19	11.82
299	N	SD	148453	M	0.27	0.40	0.48	0.32	0.42	10.34	13.98
300	N	SD	362118		0.27	0.37	0.41	0.29	0.41	10.12	13.27
301	N	SF	461267	M	0.24	0.38	0.43	0.30	0.44	10.05	12.84
302	N	SI	336299	F	0.20	0.35	0.39	0.27	0.38	9.15	11.72
303	N	SI	336301	F	0.25	0.40	0.42	0.32	0.43	10.52	13.13
304	N	SN	147433		0.26	0.41	0.43	0.32	0.42	9.84	12.79
305	N	SY	188171	M	0.22	0.33	0.37	0.25	0.34	9.29	12.09
306	N	SY	188177	M	0.24	0.34	.	0.25	0.35	9.01	11.57
307	N	SY	238258	M	0.23	0.37	0.40	.	.	9.46	.
308	N	OG	49397		.	0.35	0.40	0.25	0.38	.	12.85
309	O	SC	188080	F	.	0.45	0.47	0.36	0.51	.	16.91
310	O	SC	188110	F	0.33	0.49	0.54	0.38	0.53	14.02	17.99
311	O	SC	209928	F	0.30	0.43	.	.	.	12.48	.
312	O	SC	209930	M	.	0.52	0.54	.	.	.	.
313	O	SC	209933	F	0.29	0.45	0.46	0.33	0.46	12.97	16.11
314	O	SC	209934	M	0.37	.	.	0.42	0.56	14.35	.
315	O	SC	209935	M	.	0.52	0.58	.	.	.	.
316	O	SC	211591	F	0.27	0.49	0.53	0.32	0.45	12.72	16.26
317	O	SC	211592	M	0.40	0.54	0.56	0.41	0.57	14.71	18.44
318	O	SC	211594	M	0.34	0.46	0.48	0.38	0.57	13.84	17.27

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OBS	GEN	SF	CAT	S	RX	FM	FX	TN	TX	FORE	MINU
319	0	SC	211596	M	0.34	0.46	0.50	0.35	0.52	13.36	16.84
320	0	SC	211597	M	0.34	.	.	0.37	0.54	.	.
321	0	SC	211600	M	0.36	0.53	0.54	0.36	0.56	13.93	18.01
322	0	SC	211601	M	0.31	0.50	0.51	0.36	0.50	13.49	16.91
323	0	SC	211606	F	0.29	0.46	0.47	0.33	0.49	13.25	16.51
324	0	SC	211609	F	0.29	0.48	0.50	0.34	0.52	13.75	17.17
325	0	SC	211613	F	0.28	0.42	0.46	0.31	0.46	13.29	16.48
326	0	SC	211614	F	0.30	0.46	0.49	0.33	0.51	13.45	16.97
327	0	SC	211615	F	0.30	0.49	.	0.34	0.49	.	16.49
328	0	SC	211616	M	0.38	0.49	0.54	0.35	0.55	13.54	16.94
329	0	SC	211618	M	0.34	0.56	0.59	0.38	0.59	14.34	18.21
330	0	SC	211624	M	0.32	0.47	0.51	0.35	0.56	13.72	17.64
331	0	SC	211627	M	0.35	0.48	0.52	0.36	0.55	14.04	17.69
332	0	SC	211628	M	0.29	0.46	0.48	0.36	0.52	13.60	17.06
333	0	SC	211639	F	0.29	0.46	0.48	0.36	0.52	13.60	17.06

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