Chapter 17

Gigantism, Dwarfism, and Cope's Rule: "Nothing in Evolution Makes Sense without a Phylogeny"

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ABSTRACT

Body size is of fundamental importance in understanding macroevolutionary patterns, both for extant taxa and for those with a fossil record. In this paper we describe four different kinds of body-size evolution: autapomorphic giantism, autapomorphic nanism, phyletic giantism, and phyletic nanism. The terms *giantism* and *nanism* are preferred here rather than the frequently, although incorrectly used equivalents, gigantism and dwarfism, respectively. We assert that without a known phylogeny, it is difficult or impossible to differentiate these four different kinds of body-size evolution. Case examples are presented for two groups: varanid lizards (family Varanidae) and fossil horses (family Equidae).

Previous hypotheses of body-size evolution within the Varanidae suggested that there were several cladogenic events in which some groups and isolated species became large. The most recent phylogeny of Varanidae based on mtDNA suggests otherwise. Mapping the known total body lengths onto the phylogeny indicates that varanids were already getting large early in their evolutionary history, with the crown group, *Odatria*, becoming secondarily small on mainland Australia. Although hypothesized as a giant island varanid, the komodo dragon (*Varanus komodoensis*) is discovered to be nested within a clade in which the basalmost taxon (*V. salvadorii*), also endemic to an island, reaches body lengths similar to those of the komodo dragon. Review of the Varanidae suggests that caution should be taken when characterizing taxa as island giants/dwarfs without first reviewing a phylogeny.

Fossil horses (family Equidae) are frequently cited in the literature, as well as depicted in museums, as prime examples of Cope's rule, i.e., a gradual trend toward body-size increase over time. Several recent parsimony analyses have resolved many of the phylogenetic interrelationships of North American fossil horses and have elucidated their patterns of body-size evolution. In light of these new analyses, there is no evidence for Cope's rule in fossil horses. In fact, the evolution of large body size occurred multiple times in fossil horses and exemplifies autapomorphic giantism. Body-size decrease, oftentimes considered the exception to Cope's rule, is actually widespread within multiple clades of fossil horses and is characterized by both autapomorphic and phyletic nanism.

The result of our analysis suggests that studies of body-size evolution must be intimately tied to a phylogeny before distinct patterns, if any, can be discerned. Cope's rule is not applicable to the two case examples presented herein, calling into question the most frequently cited mode of body size evolution.

INTRODUCTION

Body size is one of the most fundamental attributes of a species (Eisenberg, 1981; Peters, 1983; Brown, 1995), and arguably the most observable. The literature is replete with reports of the largest (or smallest) individual of species (x) ever found, the largest known species of group (x) ever found, is-land gigantism/dwarfism, insular gigantism, polar gigantism, phyletic gigantism/dwarfism, and even time periods that supported unusually gigantic life forms (e.g., the Carboniferous). Gigantism (and alternatively, dwarfism) has been observed in almost every taxonomic group from bacteria to dinosaurs, and because of its conspicuous nature, nu-

Autapomorphic Giantism   Autapomorphic Nanism

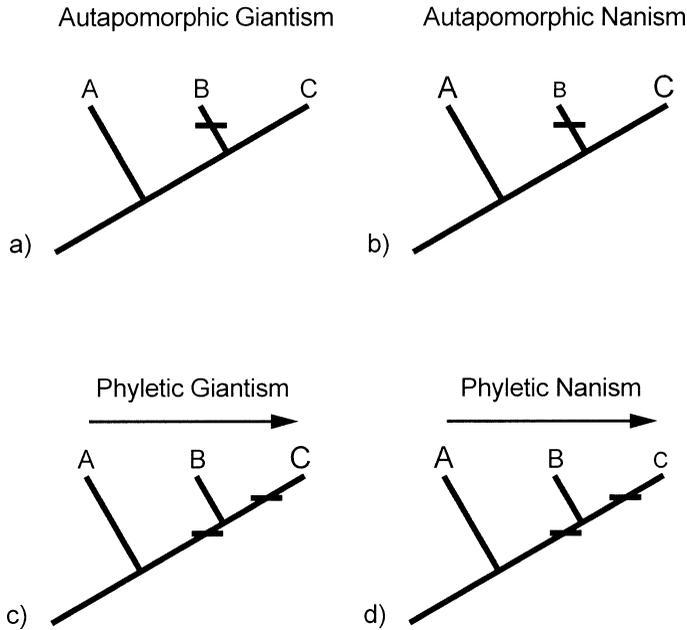Phyletic Giantism   Phyletic Nanism

Fig. 17.1.   Three-taxon statements illustrating the four kinds of body-size change discussed in the text.

merous hypotheses have been posited to describe and explain the phenomenon (e.g., Cope's rule, Bergman's rule, Rensch's rule, Island rule; see Stanley, 1975 for a historical account).

Because it is seemingly easy to discern the difference between the processes that cause gigantism (or dwarfism) in humans, on one hand, from that which results in island gigantism (or dwarfism) in hedgehogs, on the other (Freudenthal, 1972; Ruedi and Fumagalli, 1996, respectively), recognition of the various kinds of size-change manifestations is generally taken for granted by most researchers. Regardless of the obvious difference at the level at which these processes operate (ontogenetic vs. phylogenetic), the current terminology used to discriminate these body size variants is limited, generally misapplied, and has led to some confusion.

In this paper, we recognize and describe four kinds of body-size evolution reported in the literature (fig. 17.1). They include (1) **autapomorphic giantism,** in which body-size increase occurs on a single branch within a clade (fig. 17.1a); (2) **autapomorphic nanism,** in which body-size decrease occurs on only one branch within a clade (fig. 17.1b);

(3) **phyletic giantism,** in which successive body-size increase occurs in nested clades within a lineage (fig. 17.1c); and (4) **phyletic nanism,** in which successive body-size decrease occurs in nested clades within a lineage (fig. 17.1d). In this study, using known phylogenies, we seek to identify and describe more accurately these patterns of size change observed in nature under the paradigm that "body size increase in clades can only be differentiated once the phylogenetic systematics of the clade is established" (Jay M. Savage, Presidential Address at the Joint Meeting of the Society of Systematic Biologists, Society for the Study of Evolution, and the American Society of Naturalists in Boulder, Colorado, June 1997).

PATTERNS, PROCESSES, AND
NOMENCLATURE OF ORGANISMAL
SIZE INCREASE

An organism's tendency toward size increase is generally believed to be a more prevalent evolutionary process than diminution, or body-size decrease (Cope, 1887; McKinney, 1990a; Alroy, 1998, although see Salthe, 1972; Stanley, 1975; Gould, 1990,

1997; and Jablonski, 1997) and is commonly referred to as gigantism. Officially, the term *gigantism* is defined as "the condition of being much larger than normal, or of exhibiting excessive growth, often associated with polyploidy" (Lincoln et al., 2001), or "a hereditary and glandular disturbance in animals" (Merriam-Webster Dictionary Online, American Heritage Dictionary Online). In the primary biological and paleontological literature, however, the term gigantism has been broadly applied to individuals, species, and entire lineages alike, and posited to be the result of a myriad of factors, ranging from climate to predation to parasites (see Peters, 1983 and McKinney, 1986 for a more comprehensive review).

The same is true for the term *dwarfism,* which is defined as "a person that is smaller than normal and disproportionate in size; an animal or plant that is below the ordinary size of its kind or species" (Merriam-Webster Dictionary Online). Dwarfs have been reported in a multitude of taxa, from individuals (e.g., Stiger and Payri, 1999) to higher taxonomic groups (Mertens, 1942).

The most obvious manifestation of individual gigantism is noted in humans. It is a form of *acromegaly,* a condition that is caused by growth hormone-producing tumors in the anterior lobe of the pituitary gland and is characterized by large extremities and malformation of facial features. Unlike acromegaly, which occurs only in adulthood, true gigantism is a childhood disease that results in the continuous growth of the individual, both upwardly and outwardly. Dwarfism, or *achondroplasia,* is caused by a congenital disorder resulting in a lack of growth hormone and/or defects at birth. Its expression results in disproportionately short extremities.

The phenomenon of excessively large individuals within a population is not exclusive to humans. It has been reported in gastropods (Williams and Brailsford, 1990; Ballabeni, 1995; Probst and Kube, 1999), bivalves (Taskinen, 1998), fishes (Arnott et al., 2000), agave (Colunga-García Marín et. al., 1996), and tomatoes (Shaw et al., 1993), all resulting from invasive parasites. In bacteria and some bivalves, large size can be the result of polyploidy (Bresler et al., 1998), DNA re-

organization (Guo and Allen, 1994), or nutritional factors (Fankboner and Reid, 1990). And in isolated populations of zooplankton, large size has been observed in response to the mouth-gap size of their principal predators (Arumugam and Geddes, 1996). Not surprisingly, dwarfism is also reportedly caused by parasites (Lorenz, 1992), environmental perturbations such as resource shortages (Main, 1990), and genetic factors (Everts et al., 2000), causes similar to those cited for gigantism.

Irrespective of the precise causes of gigantism or dwarfism of an individual, these phenomena are all a result of some kind of aberrant modification during ontogeny, which is expressed at the tokogenetic level, not at the phylogenetic level (that is, expressed below the species level only). Although these expressions of extreme body size many seem similar, they are in fact quite different in their genesis. Current nomenclature for these expressions, however, makes no differentiation between them.

The term giant comes from fourteenth-century Greek nomenclature; the concept of giant is even older, dating back to Goliath (the giant) of the Old Testament, well before Darwin's theory of evolution. The original meaning of *giant* was most likely applied to a phenomenon that is expressed during ontogeny. Similarly, the terms *dwarf* and *dwarfism* have been applied to small people since at least the twelfth century. Given the long-standing history of these words, we recommend they be applied exclusively to single individuals within a population, and not to species or higher taxonomic groups.

The cited manifestations of giantism and nanism in species, or higher-level taxa, are not as straightforward to define and categorize. Unlike their expression in an individual, giantism or nanism expressed at or above the species level is the result not of a "condition" but of a complexity of factors (e.g., genetic drift, change in environment) ensuing in the evolution of a new species (Stanley, 1975; Benton, 1990; McKinney, 1986; Hallam, 1999). Because these phenomena occur across a wide array of taxa, hypotheses as to why species become huge or tiny are innumerable and range from symbiosis (Hakansson and Madsen, 1991) and mutualism (Dud-

ley, 1998) to territorial behavior (Case, 1975). These occurrences of extreme body size at or above the species level fall under at least one of the three most cited patterns of body-size evolution observed in nature; (1) the Island (= Insular) rule (Carlquist, 1965; Case, 1978; Damuth, 1993); (2) Cope's rule (see Peters, 1983); and the opposite of Cope's rule, (3) phyletic nanism.

The Island (Insular) rule pertains to taxa endemic to insular environments (i.e., on an island or in an equally ecologically remote area) that are either considerably larger or smaller than their more cosmopolitan sister taxa on the mainland (Mertens, 1942; Darlington, 1957; Sondaar, 1977; Case, 1978). Researchers have developed numerous hypotheses and models to explain island/insular gigantism. They range from a lack of predators concomitantly with an increase in available prey (Carlquist, 1965; Case, 1978), to sexual selection pressures (Carlquist, 1965), interference competition (Gilbert and Confer, 1986), biomechanical optimization (Song et al., 1994), digestive efficiency (Smith, 1995), and an increase in oxygen availability in polar regimes (Dudley, 1998; Cosel and Olu, 1998; Chappelle and Peck, 1999). Hypotheses for dwarfism are equally diverse; for example, the amount of time isolated on an island (Lister, 1996), high levels of salinity in open waters (Price, 1982), and environmental factors (Theodorou, 1988). Irrespective of why these organisms became large or small, the expression is always autapomorphic for a taxon within a clade (fig. 17.1a). We, therefore, recommend that island/insular gigantism be termed (autapomorphic) **giantism**: the quality or state of being a **giant,** which is defined in mainstream dictionaries as: (1) a living being of great size; and (2) having extremely large size, proportion, or power (www.yourdictionary.com). This definition suggests a considerable difference in size with respect to others of like kind (or sister taxa), that is, its expression is autapomorphic for the group.

With respect to island miniaturization or dwarfism (fig. 17.1b), we prefer the term autapomorphic **nanism** or **nanoid**; the condition of being stunted or smaller than normal, or of having restricted growth (Lincoln et al., 2001).

Cope's rule pertains to a lineage that is purported to exhibit a progressive increase in size over time (Cope, 1887), whether it be anagenic or cladogenic in nature. These size increases are measured by "state variables" (McKinney, 1990b), usually in the form of morphometric characters (the same is also applied to nanism, e.g., Roth, 1992). This phenomenon has been recorded in almost every group of mammals (Alroy, 1998), and most recently in trilobites (Trammer and Kaim, 1997), foraminifera (Arnold et al., 1995), and of course, dinosaurs (Benton, 1990; Colbert, 1993; Paul, 1998). The expression of Cope's rule is one of the most widely cited evolutionary trends and has been attributed to dozens of causal hypotheses for the optimization of body size. These hypotheses are, for the most part, related to predation and accessibility to food (see Benton, 1990; Peters, 1983; McKinney, 1986; and Hallam, 1999, for a complete review). The opposite of Cope's rule, a trend toward miniaturization or diminution, has also been observed in many diverse taxa (e.g., Pregill, 1986; MacFadden, 1987; Pianka, 1995), although the causal hypotheses for this phenomenon remain scant.

Despite widespread acceptance by most paleontologists, Cope's rule remains controversial. According to some investigators, a phyletic trend toward large size has not been adequately demonstrated in the fossil record and should be considered a "phenomenon" rather than a rule (Stanley, 1975; MacFadden, 1987; Damuth, 1993; Trammer and Kaim, 1999). Others simply reject Cope's rule as a phenomenon or otherwise (Salthe, 1972; Jablonski, 1997) and consider it an unfortunate "psychological artefact" of the discipline (Gould, 1997). No one (at least that we could find), on the other hand, seems to object to phyletic body-size decrease.

To differentiate successive increase in size within a lineage from autapomorphic giantism, we suggest **phyletic giantism** be applied to this type of manifestation of giantism because it implies the phenomenon of anagenic or cladogenic increase in size over time (fig. 17.1c). The same holds true for successive decrease in size within a lineage, i.e., **phyletic nanism** (fig. 17.1d).

REVIEWING THE PATTERNS

A phylogenetic trend is defined as a "directional morphological change between more than two species" (McNamara, 1982) within a lineage that is "elucidated by a known phylogeny" (Salthe, 1972: 152). Phylogenies are reconstructed based on shared derived (homologous) structures, i.e., "states/characters having a common ancestry but not necessarily retaining similarity of the structure, function or behavior" (Lincoln et al., 2001), irrespective of their physical form (e.g., morphology, DNA). It therefore follows that autapomorphic and phyletic size change is observable (or better, falsifiable [Popper, 2002]) only when mapped onto a phylogeny that is supported by discrete characters. Recent studies reportedly demonstrating island giantism/nanism and Cope's rule employed continuous data and statistical algorithms as the evidence for phyletic size increase (see for example, Case, 1978; Pianka, 1995; Arnold et al., 1995; Trammer and Kaim, 1997; Alroy, 1998; and Trammer, 2002). These data sets alone, however, cannot be considered statements of homology (Crowe, 1994), which is paramount in addressing any questions that pertain to historical relationships and character evolution (Hennig, 1979).

In this study, we chose two groups, varanid lizards (Varanidae) and fossil horses (Equidae), both of which have been cited in the literature as classic examples of island giantism/nanism and Cope's rule, respectively. We review their body-size evolution patterns based on their known phylogenies and test previous hypotheses of giantism, both autapomorphic and phyletic.

Varanid Lizard Evolution: A Case for Insular Gigantism/Dwarfism

Since the first descriptions of varanid lizards in 1758 (King et al., 1991), more than 50 extant species have been described (see Ast, 2001 for a review). Within the extant members of this family two distinct lineages have been recognized by investigators: the subgenus, *Varanus*, which is widely distributed and includes the largest of the extant varanids, i.e., *V. komodoensis* and *V. salvadorii*; and the dwarf (or pygmy) subgenus, *Ondatria*, which is restricted to Australia. The dichotomy in size of these two groups, in conjunction with their distribution (many of them are endemic to islands), has inspired their use as a model for investigating the processes of body-size evolution (Fuller et al., 1998; Pianka, 1968, 1995; Case and Schwaner, 1993; King, 1991; Mertens, 1942); hence, the group's inclusion in this study.

Living varanids are distributed throughout Australia, parts of Africa, central and southern mainland Asia, and the Indo-Malaysian islands (Ast, 2001), and occupy diverse habitats, including deserts, tropical rain forests, wetlands, and forest canopies (King and Green, 1999). They range in size from the smallest, *V. brevicaudata*, which is 0.2 m in length, to the giant, *V. komodoensis*, which is greater than 3 m long (Auffenberg, 1981). The largest varanid known is the fossil taxon, *Megalania prisca* from the late Pleistocene (~19,000–26,000 BP) of Australia, which is estimated to have reached 7 m in length with a body mass of over 650 kg (Auffenberg, 1980).

There are numerous hypotheses regarding the origin and the evolutionary relationships of varanids (e.g., Ast, 2001; King and Green, 1999; King et al., 1999; Fuller et al., 1998; Card and Kluge, 1995; Baverstock et al., 1993; King et al., 1991; Becker et al., 1989; King and King, 1975; Mertens, 1942). To date, however, none include the fossil taxa from the Miocene in Africa (Clos, 1995) and Australia (Hutchinson and Donnellan, 1993). The most recent phylogeny of the extant Varanidae includes the majority of the known species (see above) and is based on mitochondrial DNA characters (Ast, 2001; fig. 17.2a, note that some terminal clades have been collapsed for brevity). For the purpose of our study, we accept this hypothesis as the best estimate of phylogeny for the Varanidae among the other parsimony analyses available in the literature (e.g., Fuller et al., 1998; Card and Kluge, 1995). We base our decision on several facts: Ast's (2001) study is the most taxonomically inclusive study to date (Omland et al., 1999), her analysis considered the most base pairs among other molecular studies (see Fuller et al., 1998), and only a single well-supported most parsimonious tree was discovered.

The historical views regarding varanid body-size evolution were recently compiled and depicted on a phenogram (Pianka, 1995; fig. 17.2b). Two independent trends toward body size increase are suggested, one in the African clade (stem A) and one in the Australian clade (stem B); a nanitic event/trend in the *Odatria* lineage (stem C); and "runaway selection" for giantism in *V. komodoensis* (Pianka, 1995: 408; fig 17.2b, stem B, taxon not depicted in original figure) as opposed to the alternative hypotheses of a relic species (Auffenberg, 1981; Case, 1978; Mertens, 1942).

The most recent phylogeny of the varanids (Ast, 2001; fig. 17.2a) also recognizes three independent clades: an African clade (stem A), an Indo/Asian clade (stem B), and an Indo-Australian clade (stem C). The latter is composed of three clades: (1) *V. salvadorii* + [*V. komodoensis* + *V. varius*] (stem D): (2) the *gouldii* clade (stem E); and (3) the *Odatria* clade (stem F). When the known total body lengths of the species are mapped onto the phylogeny (fig. 17.2a; appendix 17.1), considerable variance in body size within each terminal clade is indicated. For the most part, the overall direction (either toward large or small) of body size evolution is seemingly random (compare fig. 17.2a with fig. 17.2b), with numerous independent trends occurring within the family. Despite the noted size variance, monitor lizards are (generally) between 1 to 2 m in length, with the exception of the nanoid *Odatria* clade (stem F) and *V. komodoensis* and *V. salvadorii* (stem D), the latter of which can reach up to 3 m in length. Phyletic giantism is not immediately implied by this phylogeny, although within the Indonesian clade (fig. 17.2a, stem G; appendix 17.1) there is a hint of a progressive size increase: each terminal taxon is approximately 0.25 m longer than the immediate basal taxon.

The hypothesis of insular giantism of *V. komodoensis* is also challenged. *V. komodoensis* is known from the islands of Komodo, Padar, Rintja, the western end of Flores, and the small islets of the Gili Moto and Oewada Sami (Auffenberg, 1981) and is commonly referred to as the komodo dragon. *V. salvadorii*, the basal member of the komodo clade, is also an island taxon (endemic to New Guinea) and is equally as large as *V. komodoensis*, albeit not as robust. Despite these similarities, to our knowledge, *V. salvadorii* has never been reported in the literature as an island giant. *V. varius*, the sister-taxon to the komodo dragon, is endemic to southern Australia. *V. varius* reaches lengths of only up to 2.1 m (King and Green, 1999), although it one of the largest monitor lizards on the island continent of Australia. Ast's (2001) phylogeny suggests that *V. varius* became small secondarily and that the ancestor of *V. komodoensis* was already fairly large (i.e., the relic species hypothesis). The alternate hypothesis, i.e., island giantism in *V. komodoensis*, would require an additional hypothesis to explain the independent acquisition of giant size in *V. salvadorii* in the same clade (fig. 17.2b). Under the rules of parsimony, this hypothesis is rejected.

Although the size distribution of living varanids suggests that the komodo dragon indeed defines the upper size limit for extant varanids, and that *V. brevicaudata* defines the lower limit, the vast majority of monitor lizards are small- to medium-sized animals (i.e., 1–2 m length). Despite this skewed distribution, it is not uncommon for closely related varanids to exhibit size differences of 50% in length (e.g., *V. glebopalma* + *V. pilbarensis*, stem H), nor is it apparently uncommon within a species (Case and Schwaner, 1993).

The size and distribution of members within the clade of nanoid (*Odatria*) varanids (fig. 17.2a, stem F) is curious. Considerable variance in body size within this group is evident, with the largest taxa (*V. gleopalma*, *glauteri*, and *mitchelli*) reaching lengths as long as the smallest taxa within the subgenus *Varanus* (e.g., *V. keithhorni*, stem K). In some cases, they are 50% larger than their sister taxon (e.g., see stem H), yet we do not refer to these species as giants. A comparison of mean lengths per monophyletic clade might seem more comparable, i.e., African clade (stem A [ML = 1.50 m]), Indo-Asian clades (stems J [ML = 1.42 m] and K [ML = 1.23 m]), and the Indo-Australian clades (stems D [ML = 2.70 m], E [ML = 1.75 m], and F [ML = 0.63 m]); however, these dimensions tend to exaggerate size differences between the Indo-Asian clade (stem K) and
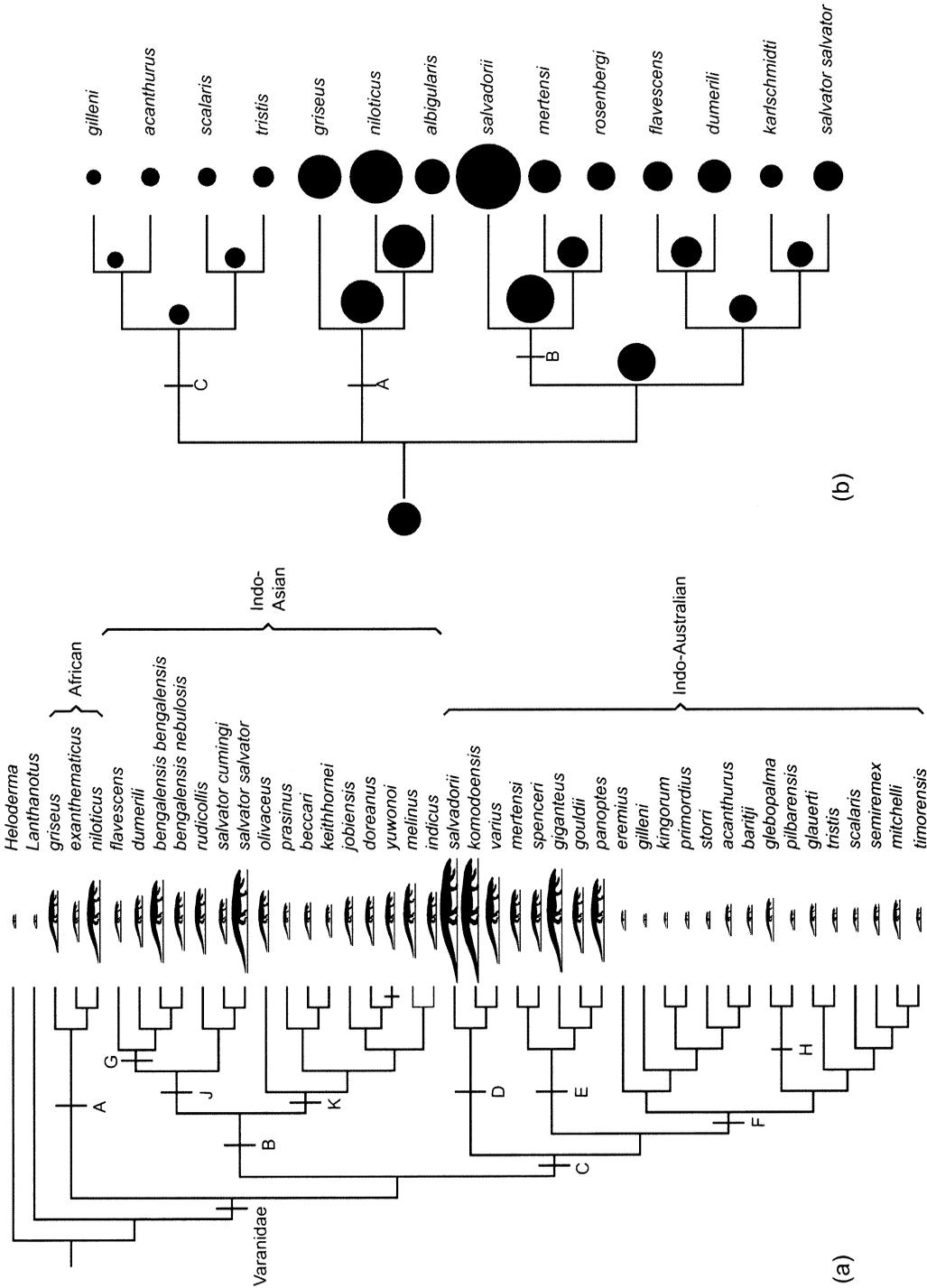
Fig. 17.2. (a) The most recent phylogenetic hypothesis of varanid relationships based on mtDNA (Ast, 2001) compared to (b) a compilation of the hypotheses of body-size evolution of varanids (taken from Pianka, 1995). The maximum total lengths for the species were retrieved from King and Green, 1999, and Mertens, 1942; these are listed in appendix 17.1. Note the following terminal clades were collapsed for the sake of brevity: *Varanus salvator togianus*, *V. salvator bivittatus*, *V. indicus*, and *V. panoptes* (*horni*).

the *Odatria* clade (stem J), and do not reflect the size variance witnessed in each group. Based on Ast's (2001) phylogeny, the *Odatria* is clearly a nanoid group.

The widely accepted outgroups for the Varanidae are the North American *Heloderma* (gila monster) and the Bornean earless monitor lizard, *Lanthanotus*, both of which only reach 0.3 m in length. Ast's (2001) phylogeny strongly suggests that the Varanidae were already medium-sized lizards early in their evolutionary history (stem Varanidae; Pianka, 1995: 408, hypothesis 2), with *Megalania* as the only known varanid that reached giant proportions relative to all other known varanids.

The size variance within the family Varanidae is notable, but does not seem to be linked to endemism on islands or in insular environments. The komodo dragon, although the largest living varanid and endemic to only a few islands, is not a giant with respect to other members within the group. Alternatively, the nanoid *Odatria* clade appears to have evolved rapidly on the mainland of Australia and not on a smaller, more insular island as would be predicted by the insular phenomenon.

Body Size Evolution in Horses

"One's mind inevitably turns to that inexhaustible textbook example, the horse sequence. This has been cited—incorrectly more than not—as evidence for practically every evolutionary principle that has ever been coined." (Kurten, 1953: 113)

Cenozoic horses (family Equidae), specifically those from North America, have one of the most continuous and robust fossil records of almost any vertebrate group. This record, combined with human's fascination for horses, has resulted in the utilization of the family Equidae for positing various kinds of macroevolutionary processes and patterns. Relevant here is that fossil horses have been used for almost a century as one of the classic examples of Cope's rule, both in the primary and popular literature (e.g., Simpson, 1953 and Rackle, 1979, respectively). In the following discussion, we continue the historical tradition of mining the family Equidae for evidence of body-size evolution and assert that fossil horses, on the contrary, do not provide a definitive example of Cope's rule

(see MacFadden, 1987), and that in fact, body-size evolution in horses is very complex.

Extant horses (family Equidae) include six to eight species (depending upon species-level interpretations) within the genus *Equus* that are native to Eurasia and Africa (e.g., Nowak, 1999). In addition to the domesticated horse, the genus also includes the extant zebras, asses, and onager. Body masses of the wild species range between 200 and 450 kg, while the domesticated breeds can attain body weights exceeding 1,000 kg (Nowak, 1999); the later is obviously an example of artificial selection.

The living diversity of the Equidae is a mere fraction of its past diversity. In North America, the family Equidae formerly consisted of some three dozen, now extinct genera and approximately 175 named species (MacFadden, 1997). During most of their 55-million-year history, horses were pandemic until they became extinct in North and South America at the end of the Pleistocene.

Interest in body-size evolution of Cenozoic horses first developed in the late nineteenth century with new collections of fossil mammals from the western territories. Huxley (see Marsh, 1895) believed that the stratigraphically ordered sequence of Marsh's fossil horses contained in the Yale Peabody Museum depicted a gradual sequence of evolutionary change and provided fundamental evidence in support of Darwin's theory of evolution (MacFadden, 1977). This early interpretation of the fossil horse sequence was represented by an orthogenetic progression from *Orohippus* to *Mesohippus* to *Miohippus* to *Protohippus* to *Pliocene* to *Equus* (e.g., Marsh, 1879; fig. 17.3), which set the stage for more than a century of discussions about their body size evolution.

By the first quarter of the twentieth century, paleontologists were using morphological proportions, particularly of the skull, teeth, and limbs, to reconstruct the body masses of individual fossil horses (e.g., Matthew, 1903; Lull, 1931). Simpson (1944, 1951, 1953) frequently used fossil horses as examples of evolution and the notion of progressive change or "improvement". As late as the 1970s, the gradual orthogenetic depiction of body size increase in fossil horses,
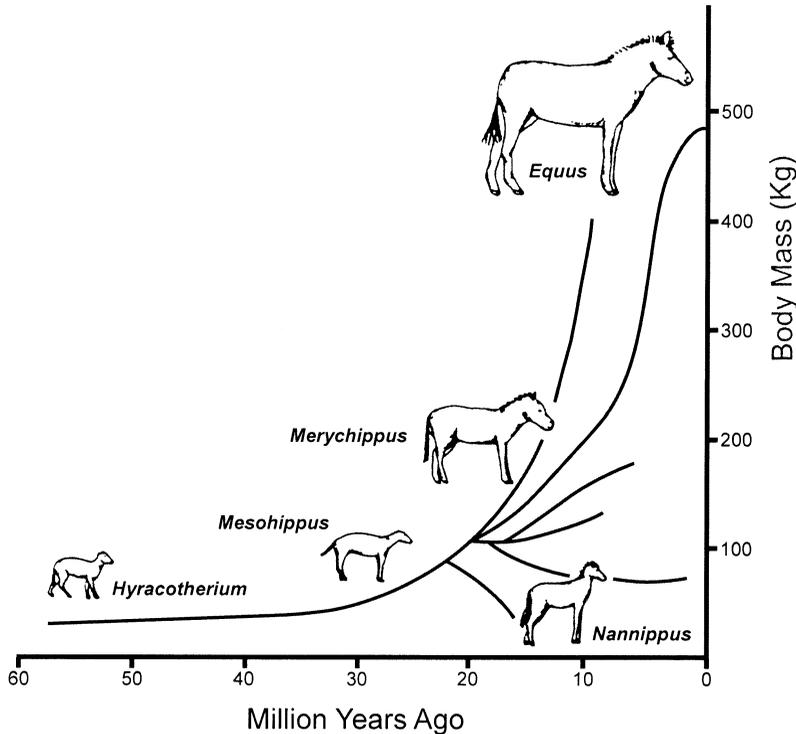
Fig. 17.3. Patterns of body-size evolution in fossil horses from North America, based on MacFadden (1987; modified figure reproduced in MacFadden, 1992). Reproduced with permission of Cambridge University Press.

i.e., the expression of Cope's rule, was still being depicted in the literature (e.g., Rackle, 1979).

The traditionally held story has been that horses started off in the Eocene "about the size of a fox terrier" (see Gould, 1988, for comments) and gradually increased in body size through time, an embodiment of the paradigm of Cope's rule. In the past 15 years, the evolutionary relationships of the Equidae have been elucidated by a variety of researchers (e.g., Evander, 1989; Hulbert, 1989; Hulbert and MacFadden, 1991; MacFadden 1992, 1997; Prado and Alberdi, 1996; Kelly, 1998; Froehlich, 1999). Rather then a gradual trend toward large size (e.g., Lull, 1931; Stirton, 1947; Simpson, 1951; Rackle, 1979), horse evolution was not gradual nor did it exhibit only a single trend.

The phylogeny presented herein (fig. 17.4) is a consensus tree derived from several sources (MacFadden, 1992, 1998; McKenna and Bell, 1997; Prado and Alberdi, 1996).

With only a few exceptions (i.e., Neogene equids), the temporal ranges are taken directly from McKenna and Bell (1997: 469–472) and MacFadden (1998; personal observation). Calibration of absolute time follows that of McKenna and Bell (1997: fig. 1). The size (or body mass) of each taxon is represented by a silhouette of the skull. These skull lengths are derived from mean tooth lengths (taken from MacFadden, 1998), which have been demonstrated to be highly correlated to body mass (MacFadden, 1987).

This phylogenetic hypothesis identifies at least three clades in which their respective members became independently large (anchitheres, hippidiforms, and *Equus*) and at least five others that exhibit some type of nanism, challenging the notion that horse evolution corroborates the macroevolutionary paradigm, Cope's rule.

The anchitheres include the genera *Kalobatippus*, *Anchitherium*, *Hypohippus*, and *Megahippus* from North America, and *An-*
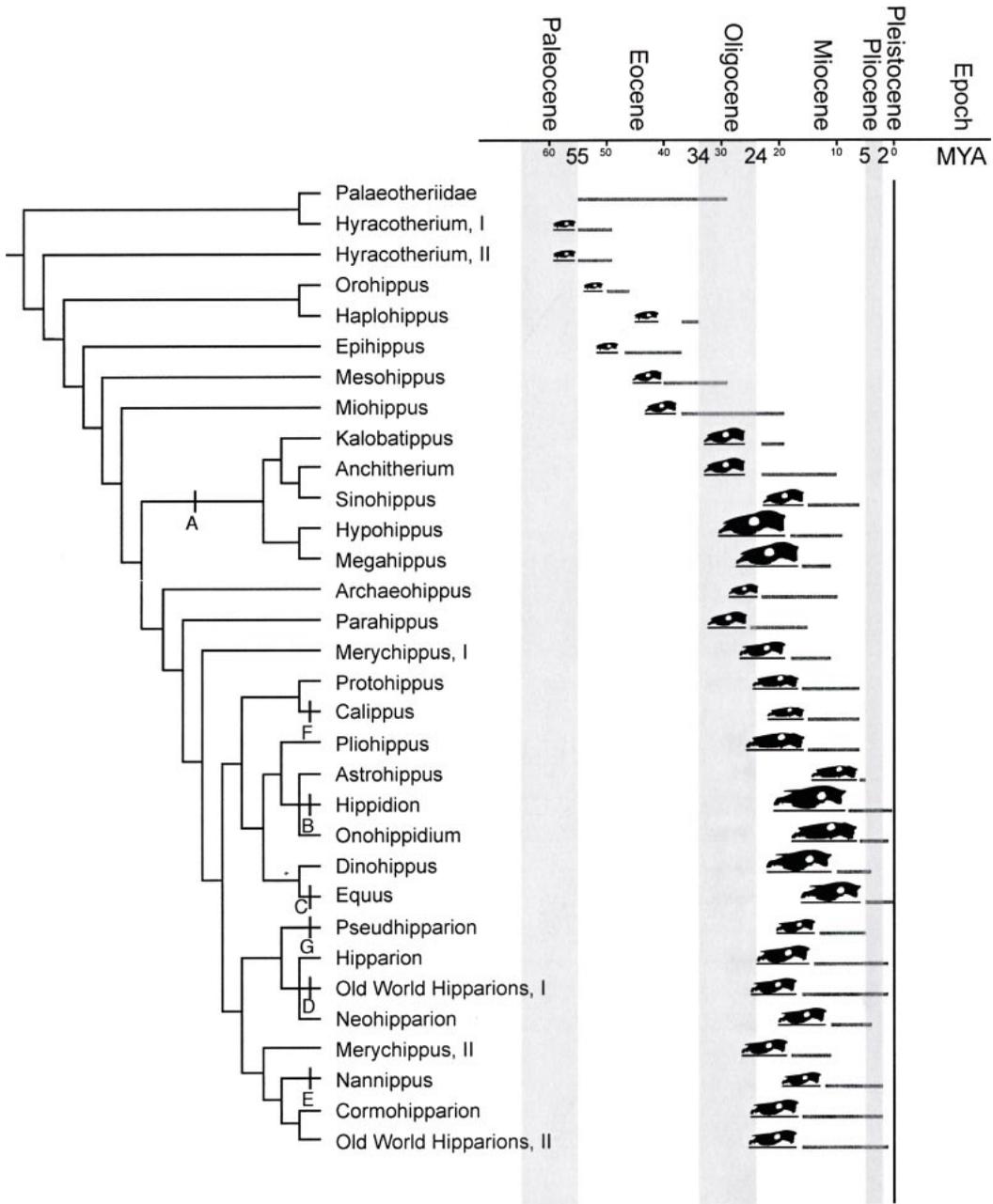
Fig. 17.4. Left, phylogeny of the Equidae, with emphasis on the North American record. Right, temporal distribution of the Equidae, with relative size indicated by skull length derived from tooth-length dimensions (see appendix 17.2 and methodology discussion in text). Branches indicated by A, B, and C represent body-size increase (giantism); D, E, F, and G represent body-size decrease (nanism).

chitherium and *Sinohippus* from the Old World (fig. 17.4, stem A). Both *Megahippus matthewi* and *Hypohippus* from the Miocene of North America were very large, with es-

timated body sizes of 266 and 403 kg, respectively (MacFadden, 1987).

Within the hippidiform radiation (fig. 17.4, stem B; MacFadden, 1997), *Hippidion prin-*

cipale from the Pleistocene of South America is estimated to have had a body mass of 462 kg (MacFadden, 1987, as *H. neogeum*).

It has been traditionally and widely accepted that members of the genus *Equus* are the largest of all the known horses, and it is estimated that *E. scotti* may have reached a body weight of 495 kg (MacFadden, 1987). However, other equines, such as the Miocene-Holocene genus *Hippidion* (fig. 17.4, stem B), rival the largest wild species of *Equus* in size (MacFadden, 1987).

Dwarfing, or nanism, has been considered the exception to the rule with respect to horse evolution. However, in fact, phyletic nanism seems to be as common as giantism. MacFadden (1987) first recognized five such instances within 24 hypothesized ancestor-descendent relationships of North American fossil horses, four of which are discussed here. In addition, recently published parsimony analyses also document instances of size decrease within the Old World hipparions (Alberdi et al., 1998; fig. 17.4, stem D), as well as within *Equus* (Alberdi et al., 1998). Among North American taxa, nanism has occurred multiple times, including within the genera *Nannippus*, *Pseudhipparion*, and *Calippus*.

Nannippus (fig. 17.4, stem E) is a group of tiny, three-toed hipparions whose range extends from the middle Miocene to the late Pliocene (McKenna and Bell, 1997). The most recent systematic review of this group (Hulbert, 1993) suggests that at least two independent size decreases occurred within in the genus: in *N. morgani* (fig. 17.5a, stem A) and in *N. aztecus* (fig. 17.5a, stem B).

Members of the genus *Calippus* ranged from the middle to late Miocene (Matthew and Stirton, 1930; Johnston, 1937; Hulbert, 1988; fig. 17.4, stem F) and were all relatively small in size. The most recent phylogenetic hypothesis posits that the clade exhibited phyletic nanism (Hulbert, 1988, 1993; fig. 17.5b), and as well, seemingly rep-
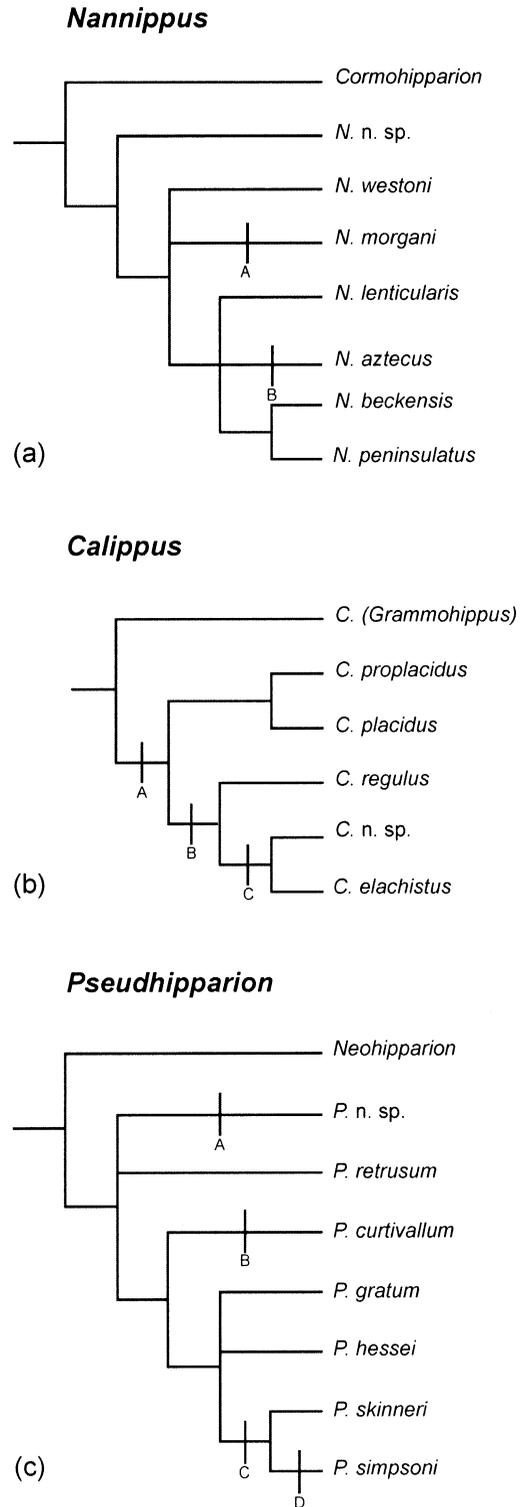
$\rightarrow$

Fig. 17.5.   Three examples of body-size evolution at the species-level: (**a**) *Nannippus*, (**b**) *Calippus*, and (**c**) *Pseudhipparion*. Modified from Hulbert (1993).

Nannippus

(a)

Calippus

(b)

Pseudhipparion

(c)

resents a chronocline. Excluding *Calippus* n. sp., which remains poorly known, the temporal series for *Calippus* demonstrates a size increase from smaller *C. proplacidus* and *C. placidus* in the late Barstovian to middle Clarendonian (~13 to 10 Ma), to intermediate-sized *C. regulus* in the middle Clarendonian (10 Ma), to the larger *C. elachistus* in the very late Clarendonian to early Hemphillian (9.0 to 6 Ma; Hulbert, 1988).

Pseudhipparion, another group of relatively small horses with a temporal range that extended from the Miocene to the early Pliocene (Webb and Hulbert, 1986; fig. 17.4, stem G), exhibits both autapomorphic nanism (i.e., in a new undescribed species, and in *P. curtivallum*, sensu Hulbert, 1993; fig. 17.5c, stems A and B, respectively), as well as phyletic nanism (i.e., *P. skinneri* and *P. simpsoni*; fig. 17.5c, stems C and D).

Finally, the genus *Archaeohippus* (fig. 17.4) has traditionally been considered a ''dwarf horse'' (i.g., Sirton, 1940; Simpson, 1941). The sister group of this taxon and the relationships within the group remain unresolved (O'Sullivan, personal communication 2002, 2003); therefore, we have omitted it from this analysis.

The discussion of horse evolution presented herein suggests that of the four potential kinds of body-size evolution reviewed in this study, the available generic and species-level relationships indicate that horses exhibit not one (i.e., phyletic giantism) but three kinds of body-size evolution: autapomorphic giantism, autapomorphic nanism, and phyletic nanism. These observations challenge the notion that horse evolution embodies the paradigm of Cope's rule.

CONCLUSIONS

Our investigation of trends in body-size evolution considered only two groups of organisms. Although our sampling size may seem meager to review such an extensive topic, these two groups have been cited many times in the literature as exemplary evidence for definable and demonstrable trends in body-size evolution. Our results of mapping body-size estimates onto character-based phylogenies refute the status of varanids and fossil horses as respective exemplars of island giantism and Cope's rule.

Recognition of the smallest and largest members of a lineage is a seemingly straightforward matter. On closer inspection, however, this is not necessarily the case. Of first order are the discrepancies in the measure of size (height, length, weight) across different analyses making comparisons difficult at best. For example, although *V. komodoensis* and *V. salvadorri* attain the same body lengths, the komodo dragon is far more robust and is therefore perceived as a giant with respect to *V. salvadorri*. Nevertheless, developmentally, lizards reach their maximum length early in ontogeny, while their body mass is both a function of resources and lifespan. Size than becomes an issue of perspective.

We also noted that the parameters of a lineage are not always clearly defined. In the case of the Equidae, some of the smallest known species of horses are nested deep within terminal clades and are generally not considered in the overall picture of horse evolution; size, therefore, becomes a function of averaging.

In the case of fossil horses, the group's evolutionary history has been intimately tied to the stratigraphic record and Simpsonian diagrams, which has lead to erroneous conclusions. For example, MacFadden (1987) calculated the body masses of 40 species of fossil horses from North America using size-correlated characters of the skeleton, skull, and molar dimensions in order to test whether North American Equidae exhibited a progressive size increase over time, i.e., Cope's rule. Based on the morphometric data and stratigraphic record, MacFadden (1987, updated in MacFadden, 1992) concluded that the first half of equid evolution was characterized by relative stasis in overall body size, with masses estimated to range between 5 kg for *Hyracotherium* (the smallest being for *H. sandrae*, Gingerich, 1989; revised from MacFadden, 1987) to about 50 kg for large species of *Miohippus* (MacFadden 1987), and thereafter, the body mass of fossil horses diversified, including several clades of large forms, e.g., *Merychippus* and *Equus* (fig. 17.3), and small forms, e.g., *Nannippus* (fig. 17.3).

Although the stratigraphic record can provide us with detailed glimpses of deep time, it cannot be used as a statement of phylogeny or homology (Frost and Kluge, 1995) or to elucidate trends in body size evolution.

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REFERENCES

Alberdi, M.T., J.E. Ortiz, and J.L. Prado. 1998. A quantitative review of European stenonoid horses. Journal of Paleontology 72(2): 371–387.

Alroy, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. Science 280(5364): 731–734.

Arnold, A.J., D.C. Kelly, and W.C. Parker. 1995. Causality and Cope's rule: evidence from the planktonic foraminifera. Journal of Paleontology 69(2): 203–210.

Arnott, S.A., I. Barber, and F. Huntingford, 2000. A parasite-associated growth enhancement in a fish-cestode system. Proceedings of the Royal Society, London, ser. B, 267(1444): 657–663.

Arumugam, P.T., and M.C. Geddes. 1996. Effects of golden perch (*Macquaria ambigua* (Richard-son)) larvae, fry and fingerlings on zooplankton communities in larval-rearing ponds: an enclosure study. Marine and Freshwater Research 47(6): 837–844.

Ast, J.C. 2001. Mitochondrial DNA evidence and evolution in Varanoidea (Squamata). Cladistics 17(3): 211–226.

Auffenberg, W.A. 1980. The herpteofauna of Komodo, with notes on adjacent areas. Bulletin of the Florida State Museum, Biological Sciences 25(2): 39–156.

Auffenberg, W.A. 1981. Behavioral ecology of the Komodo monitor. Gainesville: University Presses of Florida.

Ballabeni, P. 1995. Parasite-induced gigantism in a snail: a host adaptation? Functional Ecology 9(6): 887–893.

Baverstock, P. R., D. King, M. King, J. Birrell, and M. Krieg. 1993. The evolution of the species of the Varanidae: microcomplement fixation analysis of serum albumins. Australian Journal of Zoology 41(6): 621–638.

Becker, H.O., W. Böhme, and S.F. Perry. 1989. Die Lungenmorphologie der Warane (Reptilia: Varanidae) und ihre systematisch-stammesgeschichtliche Bedeutung. Bonner Zoologische Beiträge 40(1): 27–56.

Benton, M. 1990. Evolution of large size. In D.E.G. Briggs and P.R. Crowther (editors), Paleobiology: a synthesis: 147–152. Oxford: Blackwell.

Bresler, V., W.L. Montgomery, L. Fishelson, and P.E. Pollak. 1998. Gigantism in a bacterium, *Epulopiscium fishelsoni*, correlates with complex patterns in arrangement, quantity, and segregation of DNA. Journal of Bacteriology 180(21): 5601–5611.

Brown, J. F. 1995. Macroecology. Chicago: University Chicago Press.

Card, W., and A.G. Kluge. 1995. Hemipenial bones and varanid lizard systematics. Journal of Herpetology 29(2): 275–280.

Carlquist, S.J. 1965. Island life: a natural history of the islands of the world. Garden City, NY: Natural History Press.

Case, T.J. 1975. Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf on California. Ecology 56: 3–18.

Case, T. J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. Ecology 59: 1–18.

Case, T.J., and T.D. Schwaner. 1993. Island/mainland body size differences in Australian varanid lizards. Oecologia 94(1): 102–109.

Chapelle, G. and L.S. Peck. 1999. Polar gigantism dictated by oxygen availability. Nature 399(6732): 114–115.

Clos, L.M. 1995. A new species of *Varanus* (Reptilia: Sauria) from the Miocene of Kenya. Journal of Vertebrate Paleontology 15: 254–267.

Colbert, E.H. 1993. Feeding strategies and metabolism in elephants and sauropod dinosaurs. American Journal of Science 293(A): 1–19.

Colunga-García Marín, P., E.L. Estrada, and M.P. Filogonio. 1996. Patterns of morphological variation, diversity, and domestication of wild and cultivated populations of Agave in Yucatan, Mexico. American Journal of Botany 83(8): 1069–1082.

Cope, E.D. 1887. The origin of the fittest: essays on evolution. New York: D. Appleton.

Cosel, R., and K. Olu. 1998. Gigantism in Mytilidae. A new Bathymodiulus from cold seep areas on the Barbados Accretionary Prism. Compte Rendus de l'Académie des Sciences, sér. 3, 321(8): 655–663.

Crowe, T.M. 1994. Morphometrics, phylogenetic models and cladistics: means to an end or much to do about nothing? Cladistics 10(1): 77–84.

Damuth, J. 1993. Cope's rule, the island rule and the scaling of mammalian population density. Nature 365(6448): 748–750.

Darlington, P.J. 1957. Zoogeography: the geographical distribution of animals. New York: John Wiley.

Dudley, R. 1998. Atmospheric oxygen, giant Paleozoic insects and the evolution of aerial locomotor performance. Journal of Experimental Biology 201(8): 1043–1050.

Eisenberg, J.F. 1981. The mammalian radiations: an analysis of trends in evolution, adaptations, and behavior. Chicago: University of Chicago Press.

Evander, R.L. 1989. Phylogeny of the Family Equidae. *In* D.R. Prothero and R.M. Schoch (editors), The evolution of perissodactyls: 109–127. Oxford: Clarendon Press.

Everts, R.E., H.A.W. Hazewinkel, J. Rothuizen, and B.A. van Ost. 2000. Bone disorders in the dog: a review of modern genetic strategies to find the underlying causes. Veterinary Quarterly 22(2): 63–70.

Fankboner, P.V. and R. G. B. Reid. 1990. Nutrition in giant clams (Tridacnidae). *In* B. Morten (editor), The Bivalvia. Proceedings of a memorial symposium in honor of Sir Charles Maurice Yonge (1899–1996): 195–209. Edinburgh: University Press.

Freudenthal, M. 1972. *Deinogalerix koenigswaldi* nov. gen., nov. spec., giant insectivore from the Neogene of Italy. Scripta Geologica 14: 1–17.

Froehlich, D.J. 1999. Phylogenetic systematics of basal perissodactyls. Journal of Vertebrate Paleontology 19: 140–159.

Frost, D.R., and A.G. Kluge. 1995. A consideration of epistemology in systematic biology, with special reference to species. Cladistics 10: 259–294.

Fuller, S., P. Baverstock, and D. King, 1998. Biogeographic origins of Goannas (Varanidae): a molecular perspective. Molecular genetics and evolution 9(2): 294–307.

Gidley, J.W. 1906. A new genus of horse from the Mascall beds, with notes on a small collection of equine teeth in the University of California. Bulletin of the American Museum of Natural History 22: 395–388.

Gilbert, J.J., and J.L. Confer. 1986. Gigantism and the potential for interference competition in the rotifer genus *Asplanchna*. Oecologia 70(4): 549–554.

Gingerich, P.D. 1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sampled high-floodplain assemblage. University of Michigan Papers in Paleontology 28: 1–97.

Gould, S.J. 1988. The case of the creeping fox terrier clone. Natural History 97: 16–24.

Gould, S.J. 1990. Speciation and sorting as the source of evolutionary trends, or 'things are seldom what them seem.' *In* K.J. McNamara (editor), Evolutionary trends in body size evolution: 3–27. London: Belhaven Press.

Gould, S.J. 1997. Cope's rule as a psychological artefact. Nature 385: 199–200.

Guo, X., and S.K. Allen, Jr. 1994. Sex determination and polyploid gigantism in the dwarf surfclam (*Mulinia lateralis* Say). Genetics 138(4): 1199–1206.

Hakansson, E., and L. Madsen, 1991. Symbiosis—a plausible explanation of gigantism in Permian trepostome bryozoans. Bulletin de la société des sciences natureles de l'ouest de la France, Memoire hors de serie 1: 151–159.

Hallam, A. 1999. Speciation patterns and trends in the fossil record. Geobios 30(7): 921–930.

Hennig, W. 1979. Phylogenetic systematics. Translated by D.D. Davis and R. Zangerl. Urbana: University of Illinois Press.

Hulbert, R.C., Jr. 1988. *Calippus* and *Protohippus* (Mammalia, Perissodactyla, Equidae) from the Miocene (Barstovian-early Hemphillian) of the Gulf Coastal Plain. Bulletin of the Florida Museum of Natural History 32(3): 221–340.

Hulbert, R.C., Jr. 1989. Phylogenetic interrelationships and evolution of North American late Neogene Equidae. *In* D.R Prothero and R.M. Schoch (editors), The evolution of perissodactyls: 176–196. Oxford: Clarendon Press.

Hulbert, R.C., Jr. 1993. Late Miocene *Nannippus* (Mammalia: Perissodactyla) from Florida, with a description of the smallest hipparionine spe-

cies. Journal of Vertebrate Paleontology 13(3): 350–366.

Hulbert, R.C., Jr., and B.J. MacFadden. 1991. Morphological transformation and cladogenesis at the base of the adaptive radiation of Miocene hypsodont horses. American Museum Novitates 3000: 1–61.

Hutchinson, M.N., and S.C. Donnellan, 1993. Biogeography and phylogeny of the Squamata. *In* G.J.B. Ross (editor), Fauna of Australia. Vol. 2A, Amphibia, Reptilia, Aves: 210–220. Canberra: Australian Biological and Environmental Survey.

Jablonski, D. 1997. Body-size evolution in Cretaceous mollusks and the status of Cope's rule. Nature 385(6613): 250–252.

Johnston, C.S. 1937. *Calippus regulus* from the Clarendon beds of Donley County, Texas. American Midland Naturalist 18(5): 905–907.

Kelly, T. 1998. New middle Miocene equid crania from California and their implications for the phylogeny of the Equini. Contributions to Science, Natural History Museum of Los Angeles County 473: 1–43.

King, D. 1991. The effect of body size on the ecology of varanid lizards. Mertensiella. Advances in Monitor Research No. 2: 204–210.

King, D., and M. King. 1975. Chromosomal evolution in the lizard genus *Varanus* (Reptilia). Australian Journal of Biological Sciences 28: 89–108.

King, D., M, King, and P. Baverstock. 1991. A new phylogeny of the Varanidae. *In* W. Böhme and H.-G. Horn (editors), Advances in Monitor Research. Mertensiella 2: 211–219.

King, D., S. Fuller, and P. Baverstock. 1999. The biogeographic origins of varanid lizards. *In* H.-G. Horn and W. Böhme (editors), Advances in monitor research II. Mertensiella 11: 43–49.

King, D., and B. Green. 1999. Monitors: the biology of varanid lizards, 2nd ed. Malabar, FL: Krieger Publishing Company.

Kurten, B. 1953. On the variation and population dynamics of fossil and recent mammal populations. Acta Zoologica Fennica 76(1): 1–122.

Lincoln, R., G. Boxshall, and P. Clark. 2001. A Dictionary of ecology, evolution, and systematics, 2nd ed. Cambridge: Cambridge University Press.

Lister, A.M. 1996. Dwarfing in island elephants and deer: processes in relation to time of isolation. Symposia of the Zoological Society of London 69: 277–292.

Lister, A.M. 1995. Sea-levels and the evolution of island endemics: the dwarf red deer of Jersey. U.S. Geological Society Special Publication 96: 151–172.

Lorenz, F., Jr. 1992. On the identity of *Cypraea tortirostris* Sowerby III 1906. Parasitism as a possible reason for malformations in Cypraeidae and some new facts on *E. chinensis*. Schriften zur Malakozoologie aus dem Haus der Natur-Cismar 5: 63–66.

Lull, R.S. 1931. The evolution of the horse family. Yale Peabody Museum of Natural History, Special Guide 1: 1–31.

MacFadden, B.J. 1977. ''*Eohippus*'' to *Equus*: fossil horses in the Yale Peabody Museum. Discovery 12(2): 69–76.

MacFadden, B.J. 1984. Systematics and phylogeny of *Hipparion*, *Neohipparion*, *Nannippus*, and *Cormohipparion* (Mammalia, Equidae) from the Miocene and Pliocene of the New World. Bulletin of the American Museum of Natural History 179(1): 1–196.

MacFadden, B.J. 1987. Fossil horses from ''*Eohippus*'' (*Hyracotherium*) to *Equus*: scaling, Cope's law, and the evolution of body size. Paleobiology 12(4): 355–369.

MacFadden, B.J. 1992. Fossil horses: systematics, paleobiology, and evolution of the family Equidae. New York: Cambridge University Press.

MacFadden, B.J. 1997. Pleistocene horses from Tarija, Bolivia, and validity of the genus †*Onohippidium* (Mammalia: Equidae). Journal of Vertebrate Paleontology 17(2): 199–218.

MacFadden, B.J. 1998. Chapter 37. Equidae. *In* C. M. Janis, K. M. Scott, and L. L. Jacobs (editors), Evolution of Tertiary mammals of North America: 537–559. New York: Cambridge University Press.

Main, B.V. 1990. Dwarf males in mygalomorph spiders: adaptations to environmental hazards. Acta Zoologica Fennica 190: 273–278.

Marsh, O.C. 1879. Polydactyl horses, recent and extinct. American Journal of Science 17: 499–505.

Marsh, O.C. 1895. Thomas Henry Huxley. American Journal of Science 50(296): 177–183.

Matthew, W.D. 1903. The evolution of the horse. Guide leaflet, Supplement to the American Museum Journal 3: 1–30.

Matthew, W.D. 1926. The evolution of the horse: a record and its interpretation. Quarterly Review of Biology 1(2): 139–185.

Matthew, W.D. and R.A. Stirton. 1930. Equidae from the Pliocene of Texas. University of California Publications, Bulletin of the Department of Geological Sciences 19(17): 349–396.

McKenna, M.C., and S.K. Bell. 1997. Classification of mammals above the species level. New York: Columbia University Press.

McKinney, M.L. 1986. Ecological causation of heterochrony: a test and implications for evolutionary theory. Paleobiology 12(3): 282–289.

McKinney, M.L. 1990a. Classifying and analyz-

ing evolutionary trends. *In* K.J. McNamara (editor), Evolutionary trends: 29–58. London: Belhaven Press.

McKinney, M.L. 1990b. Trends in body size evolution. *In* K.J. McNamara (editor), Evolutionary trends: 75–117. London: Belhaven Press.

McNamara, K.J. 1982. Heterochrony and phylogenetic trends. Paleobiology 8(2): 130–142.

Mertens, R. 1942. Die familie der warane (Varanidae). Teil 1–3: Taxonomie. Abhandlungen Senckenbergischen Naturforschenden Gesellschaft 462: 1–116, 465: 117–234, 446: 235–391.

Nowak, R.M. 1999. Walker's Mammals of the World, Vol. 2, 6th ed. Baltimore: The Johns Hopkins University Press.

Omland, K.E., S.M. Lanyon, and S.J. Fritz. 1999. A molecular phylogeny of the New World orioles (*Icterus*): the importance of dense sampling. Molecular Phylogenetics and Evolution 12(2): 224–239.

Osborn, H. F. 1918. Equidae of the Oligocene, Miocene, and Pleistocene of North America, iconographic type revision. Memoir of the American Museum of Natural History, new ser., 2: 1–326.

O'Sullivan, J.A. 2003. A new species of *Archaeohippus* (Mammalia, Equidae) from the Arikareean of Central Florida. Journal of Vertebrate Paleontology 23(4): 877–885.

Paul, G.S. 1998. Terramegathermy and Cope's Rule in the land of titans. Modern Geology (Special Issue) 23(1–4): 179–217.

Peters, R.H. 1983. The ecological implications of body size. Cambridge: Cambridge University Press.

Pianka, E.R. 1995. Evolution of body size: varanid lizards as a model system. American Naturalist 146(3): 398–414.

Pianka, E.R. 1968. Notes of the biology of *Varnus eremius*. West Australian Nature 11: 141–144.

Popper, K. 2002. The logic of scientific discovery, 15th ed. London: Routledge.

Prado, J., and M. T. Alberdi. 1996. A cladistic analysis of the horses of the tribe Equini. Palaeontology 39(3): 663–680.

Pregill, G.K. 1986. Body size of insular lizards: a pattern of Holocene dwarfism. Evolution 40(5): 997–1008.

Price, A.R.G. 1982. Western Arabian Gulf echinoderms in high salinity waters and the occurrences of dwarfism. Journal of Natural History 16(4): 519–527.

Probst, S., and J. Kube. 1999. Histopathological effects of larval trematode infections in mudsnails and their impact on host growth: what causes gigantism in *Hydrobia ventrosa* (Gastropoda: Prosobranchia)? Journal of Experimental Marine Biology and Ecology 238(1): 49–68.

Rackle, F.A. 1979. Introduction to evolution. Engelwood Cliffs, NJ: Prentice-Hall.

Roth, V.L. 1992. Inferences from allometry and fossils: dwarfing of elephants on islands. Oxford Surveys in Evolutionary Biology 8: 259–288.

Ruedi, M., and L. Fumagalli,. 1996. Genetic structure of gymnures (genus *Hylomys*; Erinaceidae) on continental islands of southeast Asia: historical effects of fragmentation. Journal of Zoological Systematics and Evolutionary Research 34: 153–162.

Salthe, S.N. 1972. Evolutionary biology. New York: Holt, Rinehart and Winston.

Shaw, M.E., B.C. Kirkpatrick, and D.A. Golino. 1993. The beet leafhopper-transmitted virescence agent causes tomato big bud disease in California. Plant Disease 77(3): 290–295.

Simpson, G.G. 1944. Tempo and mode in evolution. New York: Columbia University Press.

Simpson, G.G. 1951. Horses: the story of the horse family in the modern world and through sixty million years of history. New York: Oxford University Press.

Simpson, G.G. 1953. The major features of evolution. New York: Columbia Univ. Press.

Smith, F.A. 1995. Scaling of digestive efficiency with body mass in *Neotoma*. Functional Ecology 9(2): 299–305.

Sondaar, P.Y. 1977. Insularity and its effect on mammal evolution. *In* M.K. Hecht, P.C. Goody, and B.M. Hecht (editors), Major patterns in vertebrate evolution: 671–707. New York: Plenum.

Song, Y., R.G. Black, and J.H. Lipps. 1994. Morphological optimization in the largest living foraminifera: implications from finite element analysis. Paleobiology 20(1): 14–26.

Stanley, S.M. 1975. An explanation for Cope's rule. Evolution 27(1): 1–26.

Stiger, V., and C.E. Payri. 1999. Spatial and seasonal variations in the biological characteristics of two invasive brown algae, *Turbinaria ornata* (Turner) J. Agardh, and *Sargassum mangarevense* (Grunow), stechel (Sargassacea fucales) spreading on the reefs of Tahiti. Botanica Marina 42(3): 295–306.

Stirton, R.A. 1940. Phylogeny of North American Equidae. University of California Publications, Bulletin of the Department of Geological Sciences 25(4): 165–198.

Stirton, R.A. 1947. Observations on evolutionary rates in hypsodonty. Evolution 1(1): 32–41.

Taskinen, J. 1998. Influence of trematode parasitism on the growth of a bivalve host in the field. International Journal for Parasitology 28(4): 599–602.

Theodorou, G.E. 1988. Environmental factors af-

fecting the evolution of island endemics: the Tilos example from Greece. Modern Geology 13(2): 183–189.

Trammer, J. 2002. Power formula for Cope's rule. Evolutionary Ecology Research 4: 147–153.

Trammer, J., and A. Kaim. 1997. Body size and diversity exemplified by three trilobite clades. Acta Palaeontologica Polonica 42(1): 1–12.

Trammer, J., and A. Kaim. 1999. Active trends, passive trends, Cope's Rule and temporal scaling: new categorization of cladogenetic changes in body size. Historical Biology 13(2–3): 113–125.

Webb, S.D., and R.C. Hulbert, Jr. 1986. Systematics and evolution of *Pseudhipparion* (Mammalia, Equidae) from the late Neogene of the Gulf Coastal Plain and the Great Plains. *In* K.M. Flanagan and J.A. Lillegraven (editors), Vertebrates, phylogeny, and philosophy. Contributions to Geology, Univ. of Wyoming, Special Paper 3: 237–272.

Williams, G.A., and T.J. Brailsford. 1990. The relationship between flat periwinkle life histories and digenean infections. In K. Johannesson, D.G. Raffaelli, and C. J. Hannaford Ellis (editors), Progress in littorinid and muricid biology. Hydrobiologia 193: 183–190.

APPENDIX 17.1

ESTIMATED SIZES OF VARANID TAXA (REFER TO FIG. 17.2)

Taxon	Length (mm)	Source
Heloderma	300	Green and King, 1999
Lanthanotus	300	Green and King, 1999
Varanus griseus	1500	Mertens, 1942
V. exanthematicus	1000	Mertens, 1942
V. niloticus	2000	Mertens, 1942
V. flavescens	1000	Mertens, 1942
V. dumerili	1250	Mertens, 1942
V. bengalensis bengalensis	2000	Mertens, 1942
V. bengalensis nebulosis	1430	Mertens, 1942
V. rudicollis	1600	Mertens, 1942
V. salvator cumingi	1100	Mertens, 1942
V. salvator salvator	2500	Mertens, 1942
V. olivaceus	1500	Mertens, 1942
V. prasinus	900	Mertens, 1942
V. beccari	900	Mertens, 1942
V. keithhornei	800	M. K. Bayless, personal commun.
V. jobiensis	1200	Mertens, 1942
V. doreanus	1200	M. K. Bayless, personal commun.
V. yuwonoi	1400	M. K. Bayless, personal commun.
V. melinus	1800	Mertens, 1942
V. indicus	1400	Mertens, 1942
V. salvadorii	3000	Mertens, 1942
V. komodoensis	3000	Mertens, 1942
V. varius	2100	Mertens, 1942
V. mertensi	1170	Mertens, 1942
V. spenceri	1500	Mertens, 1942
V. giganteus	2500	Mertens, 1942
V. gouldii	1600	Mertens, 1942
V. panoptes	2000	M. K. Bayless, personal commun.
V. eremius	500	Green and King, 1999
V. gilleni	340	Green and King, 1999
V. kingorum	400	Green and King, 1999
V. primordius	420	Green and King, 1999
V. storri	440	Green and King, 1999
V. acanthurus	780	Green and King, 1999
V. baritji	720	Green and King, 1999
V. glebopalma	1060	Green and King, 1999
V. pilbarensis	500	Green and King, 1999
V. glauerti	800	Green and King, 1999
V. tristis	600	Green and King, 1999
V. scalaris	590	Green and King, 1999
V. semiremex	760	Green and King, 1999
V. mitchelli	960	Green and King, 1999
V. timorensis	600	Green and King, 1999

APPENDIX 17.2

TEMPORAL RANGES AND MOLAR LENGTHS OF EQUID TAXA (REFER TO FIG. 17.4)

Taxon[a]	Temporal Range		Molar length (mm)[b]
	Geologic age[a]	Million years[a]	
Palaeotheriidae	E. Eocene–E. Oligocene	55–29	
Hyracotherium, I	E. Eocene	55–49	9
Hyracotherium, II	E. Eocene	55–49	9
Orohippus	E.–M. Eocene	50–46	8
Haplohippus	L. Eocene	37–34	10
Epihippus	M. Eocene	47–37	9
Mesohippus	M. Eocene–E. Oligocene	40–29	12
Miohippus	L. Eocene–E. Miocene	37–19	13
Kalobatippus	E. Miocene	23–19	17
Anchitherium	E.–L. Miocene	23–10	17
Sinohippus	M.–L. Miocene	15–6	17
Hypohippus	E.–L. Miocene	18–10	28
Megahippus	M. Miocene	16–11	26
Archaeohippus	E.–L. Miocene	23–10	12
Parahippus	L. Oligocene–M. Miocene	25–15	16
Merychippus, I	E.–M. Miocene	18–11	19
Protohippus	M.–L. Miocene	16–6	19
Calippus	M.–L. Miocene	15–6	15
Pliohippus	M.–L. Miocene	15–6	24
Astrohippus	L. Miocene–E. Pliocene	6–5	19
Hippidion	L. Miocene–Holocene	8–0[c]	30
Onohippidium	L. Miocene–L. Pleistocene	6–<1	27
Dinohippus	L. Miocene–E. Pliocene	10–4	27
Equus	E. Pliocene–Recent	5–0	25
Pseudhipparion	M. Miocene–E. Pliocene	13–5	16
Neohipparion	M. Miocene–E. Pliocene	13–4	22
Hipparion	M. Miocene–M. Pleistocene	14–1	19
Old World Hipparions, I	M. Miocene–M. Pleistocene	16–1	20
Merychippus, II	E.–M. Miocene	18–11	19
Nannippus	M. Miocene–L. Pliocene	12–2	16
Cormohipparion	M. Miocene–L. Pliocene	16–2	20
Old World Hipparions, II	M. Miocene–M. Pleistocene	16–1	20

[a] Nomenclature follows McKenna and Bell (1997) and/or MacFadden (1998); geologic and age in million years follow McKenna and Bell (1997) and/or MacFadden (1998; personal obs.).

[b] Approximate mean molar (1st or 2nd) length taken from MacFadden (1998) and used as a proxy indication for skull length and general size.

[c] Although extinct today, range extends into Holocene.