Systematics and Phylogeny of the Horse

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The Order Perissodactyla

The order Perissodactyla, known as odd-toed hoofed mammals, are characterized by the relative enlargement of digit III on each extremity. Other characteristics include, in the skull, the persistence of the tuber maxillare, and, in the dentition, the basic π-shape of the occlusal pattern of the maxillary molars (modified in living Equidae, but extremely useful for recognizing primitive fossil perissodactyls).

The order contains three living groups, the horses, tapirs and rhinos, and two major extinct groups, the brontotheres (or titanotheres) and the ancylopods (or chalicotheres). The brontotheres arose in the Early Eocene and survived into the Oligocene but no longer; the ancyclopods arose in the late Eocene and survived into the Pleistocene. Tapirs and rhinos differentiated in the Late Eocene.

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The following outline classification of the Perissodactyla is based on Prothero and Schoch (1989), but excludes the hyraxes which (contrary to the classification of Prothero and Schoch) are not perissodactyls but are related to the elephants and sirenians.

Order Perissodactyla
  Suborder Titanotheriomorpha – brontotheres
  Suborder Hippomorpha
    Superfamily Pachynolophoidea
    Superfamily Equioidea
      Family Palaeotheriidae
      Family Equidae
  Suborder Moropomorpha
    Parvorder Ancylopoda – chalicotheres
    Parvorder Ceratomorpha – tapirs and rhinos

The Pachynolophoidea, restricted to the Eocene, were small perissodactyls with simple teeth, but with some development of the complexity of the cheek teeth which characterizes equids; in particular, the premolars were somewhat molarized (meaning that they had come to resemble the molars to some degree). The Palaeotheriidae, from the Late Eocene and Early Oligocene, were larger (some of them tapir-sized) and longer necked, but still extremely primitive; they include *Palaeotherium*, which was described by Georges Cuvier in 1804, and was one of the very first fossil mammals to be discovered.

The Family Equidae

The Equidae are known from the earliest Eocene. The famous *Hyracotherium*, described by Richard Owen in 1841, is very primitive, and the various species which have been included within it, and which differ only very slightly from each other, are now regarded as probable ancestors to the Pachynolophoidea, the Palaeotheriidae and probably the Moropomorpha as well as the Equidae, so many authors now place them on cladistic grounds into different genera. The species described by Owen, *Hipparion leporinum*, is thought by Hooker (1984) to be the ancestor of the Palaeotheriidae. The ancestor of the Equidae, according to Hooker, is the species formerly known as *Hyracotherium cuniculum*, which he places in a new genus *Cymbalophus*.

The general outline of the evolution of the Equidae is summarized by Evander (1989). After *Cymbalophus* of the earliest Eocene (54 million years ago (mya)) of Europe, the line moves to North America, and goes more or less straight through a series of genera which (except for the last two, which do overlap) simply mark points on the tree which are represented by good fossil material: *Orohippus* (Early Eocene, 50–47 mya), *Epihippus* (Middle and Late Eocene, 47–40 mya), *Mesohippus* (Late Eocene and Early Oligocene, 40–30 mya), and *Miohippus* (Latest Eocene and Oligocene, 37–25 mya). The line leading to modern horses had thus gone through more than half of its evolutionary history with hardly any branching until the latest stages. The narrow basicranium so characteristic of modern horses was absent in the primitive stages but had been developed by *Mesohippus*, and the dentition of each is advanced over its predecessor(s): more complex, with more cusp development, but still without any uniting of the cusps into ridges.

The line then, at the beginning of the Oligocene some 25 mya branched into the Anchitheriinae and the Equinae. Both these lines were advanced in having molar ridges, unlike their predecessors; the Anchitheriinae, which lasted until about 12 mya in North America and 7 mya in Asia, lost some features of the molars and the foot skeleton which the Equinae retained, while the Equinae developed a close-packed foot skeleton suitable for running in open grasslands.

The line of the Equinae continued through to the Middle Miocene (15 mya) via *Kalobatippus, Archaeohippus* and *Parahippus*, with increasingly complex molars. From *Archaeohippus* on, the skull developed a post-orbital bar, a complete strut of bone behind the orbit, separating it from the temporal fossa. From the later species of *Parahippus* on, the crowns of the molar and premolars had become high, covered with cementum, and suitable for shearing silica-rich grasses, and the radius and ulna had become fused. The line then, about 15 mya, split into three branches: the Protohippini, Hipparionini and Equini, though Hulbert (1989) considers that the Protohippini are actually a composite, made up of stem forms of the other two tribes and of their common ancestors, and includes *Protohippus* itself in the Equini; all these late groups are difficult to work out, and there was a good deal of parallel evolution in such features as large size, development of a pre-orbital fossa and retraction of the nasal notch. However, the Equini were the only horses to reduce their toes to one on each foot (with the laterals, represented by metapodials II and IV, retained as ‘splint bones’), whereas the Hipparionini developed their lateral toes into support digits, perhaps for marshy country. The Hipparionini, the last of the three-toed horses, lived in North America until the beginning of the Pliocene, 5 mya, but survived in the Old World until about 1 mya, disappearing last from Africa.

Evander’s (1989) classification of the family is (abbreviated and slightly modified) as follows:

- Family Equidae
  - *Cymbalophus*
  - *Orohippus*
  - *Epihippus*
  - *Mesohippus*
  - *Miohippus*
  - Subfamily Anchitheriinae
  - Subfamily Equinae
    - *Kalobatippus*
    - *Archaeohippus*
    - *Parahippus*

Tribe Protohippini
Tribe Hipparionini
Tribe Equini
  Dinohippus
  Hippidion
  Onohippidion
  Astrohippus
  Pliohippus
  Equus

In this classification, the five unranked genera coordinate with the two subfamilies, and the three coordinate with the three tribes of Equinae, are given the status of Plesion: a category which means that they are of limited diversity (one or a few species in each), and primitive for that group (and very likely ancestral to the remainder).

The genus *Dinohippus*, which lived in North America between about 8 and 5 mya, is the stem genus of *Equus*, and Hulbert (1989) even includes it in *Equus*. It emerged gradually from *Pliohippus*, which lived in North America from about 14.5 to 6 mya; *Astrohippus* lived in the same region from about 6 to 4.5 mya. *Hippidion* and *Onohippidion* were large single-toed horses that lived in South America from the Early Pliocene until the end of the Pleistocene; their earliest species lived in North America about 5 mya.

Genetics of the Equidae

Studies of chromosomes and DNA have provided a rich source of information for interpretation of morphological and palaeontological data (George and Ryder, 1986; Ryder *et al.*, 1978; Oakenfull *et al.*, unpublished observations). The phylogenetic analysis of DNA sequence data sheds new light on the systematics and taxonomy of *Equus* and is highly relevant for conservation action plans for equid taxa (Oakenfull, equid action plan).

The first DNA-based studies of *Equus* involved the analysis of mitochondrial DNA restriction maps and required purification of mitochondrial DNA (George and Ryder, 1986). With the advent of the polymerase chain reaction (PCR), DNA sequence data have become the accepted standard in studies of molecular evolution; PCR also allows a wide variety of samples previously unusable for genetic analysis to be utilized in genetic studies. The complete 16,660 nucleotide sequence of a domestic horse mitochondrial DNA has been published (Xu and Arnason, 1994).

The first extinct organism to have its DNA cloned was the quagga, *Equus* (*burchelli*) *quagga*, an event of technical wizardry made even more remarkable for its accomplishment before PCR was invented (Higuchi *et al.*, 1984). Samples of dried tissue, a residue of a roughshod taxidermy, provided sufficient DNA for the construction of a library that included quagga DNA sequences.

Today, bone and tissue fragments, dried blood and dung samples provide routine sources of DNA for comparative genetic studies. Despite these advances, it is still the case that DNA sequence data are lacking for some equid populations and named taxa that confound the assembly of a clear picture of the systematic relationships of extant and recently extinct taxa. The Somali wild ass, Syrian, Indian and Mongolian wild asses, and the kiang have yet to be the subject of reports utilizing molecular methods on wild populations. Although most equid taxa have been the subject of at least preliminary DNA sequencing studies, the amount of data is still rather small, may not include nuclear loci and may incorporate limited sampling of the potential variability within extant wild populations. The investigation of molecular genetics of captive and wild equids is an area of great current interest. Thus, we can anticipate that new findings will soon become available (Oakenfull *et al.*, unpublished observations) and that as more intensive analysis incorporating additional loci and more extensive sampling of extant populations is carried out, a more refined picture of evolutionary relationships and the resultant taxonomy will emerge.

The most definitive genetic data pertinent to equid evolution collected to date involve sequence analysis of mitochondrial DNA. The region of the circular mitochondrial DNA at which strand displacement for the initiation of DNA replication takes place (the d-loop) is thought to be the most rapidly evolving portion of the approximately 16,500 bp molecule. Accordingly, this region can identify recent divergences due to mutations. Other portions of the mitochondrial DNA, such as the 12S region and the cytochrome *b* gene, accumulate mutations at a slower rate and there is a proportionally smaller chance that the same sequence of nucleotides is present as a result of two mutations (a ‘forward’ mutation and a ‘back’ mutation). For this reason, evidence of the divergence of lineages at the base of the phylogenetic tree may be derived less ambiguously from more slowly evolving sequences.

Generic Limits

While most specialists have been content to include all living equids in a single genus, *Equus*, from time to time different authors have proposed to set aside one or more species into separate genera, on the general grounds that they were ‘different enough’. Part of the philosophy was no doubt that horses, asses, onagers and zebras are all the living species that we have in the family Equidae, and there is sufficient ‘taxonomic room’ for several genera. The wish to divide up the genus in this way persists in the modern era: Trumler (1961), Groves and Mazák (1967) and Bennett (1980) are examples of this. A different philosophy is behind Quinn’s (1957) multigeneric scheme: that author – incorrectly, as most specialists now concur – saw the different modern groups as the end points of lineages which could be traced back deep into the Miocene, and had even achieved monodactyly independently.

Although proposals have been made to link taxonomic ranking to time depth, these have not achieved general acceptance, and the only widely acknowledged criterion for taxonomic categories (above the species level, at least) is monophyly. The single versus multigeneric schemes are essentially a matter of taste. The fossil record of the Equidae is one of the best known among mammals, and is replete at every level with genera, leaving much less 'room' for multiple genera among the living fauna. There is also some doubt what these genera would actually be: will *Equus, Asinus* and *Hippotigris* suffice, or must we have *Hemionus*, *Dolichohippus* and *Quagga* as well? What, really, are the interrelationships of the living species? We are of the opinion, in accord with most other equid specialists, that the less formal category of subgenus will have to do; but the question remains, what are they? The question in general narrows down to asking, what are the monophyletic groups and how well-supported are they? Below, we argue that three subgenera, *Equus* (horses), *Asinus* (asses and hemiones) and *Hippotigris* (zebras), adequately represent the major monophyletic groupings among living species, although the diversity of species makes it necessary to recognize species-groups within the latter two.

Early History of the Genus *Equus*

Before examining the living members of *Equus*, a brief survey of fossil forms is in order. Like the family as a whole, the genus *Equus* evolved in North America, and spread from there into the Old World. It is likely that horses, asses and zebras all evolved in North America, and separately spread into the Old World when the Bering land bridge was open, from the mid-Pliocene onward. Azzaroli (1998) has reviewed the North American species. The earliest, *Equus simplicidens*, which lived from 4 to 2.5 mya, was very primitive, with many *Dinohippus*-like features, and was probably ancestral to all subsequent species; it is conventionally placed in a separate subgenus, *Allohippus.* The subgenus *Equus* was represented by an indigenous species, *E. niobrarensis*, in the Middle Pleistocene, and the immigrant *E. ferus* in the Late Pleistocene, surviving into the Holocene in Alaska. The subgenus *Asinus* had emerged by 2 mya, and was well known by fossils by 1.2 mya (*E. semiplicatus*) and survived into the Middle Pleistocene (*E. francisci*). Possible representatives of the subgenus *Hippotigris* were *E. idahoensis* (Late Pliocene to Early Pleistocene, 2.6–1.0 mya), *E. excelsus* and *E. occidentalis* (Middle and Late Pleistocene, respectively). A further subgenus, *Amerhippus*, is represented by early remains at 2 mya, by a Middle Pleistocene species (*E. fraternus*) and one or two Late Pleistocene species (*E. conversidens* and, possibly, *E. mexicanus*). Why equids eventually became extinct in North America is unknown, but the last of them, *E. occidentalis* (known from many skeletons from the tar pits at Rancho La Brea, Los Angeles, California), was perhaps exterminated by the first human inhabitants in the Early Holocene.

It is worth noting, too, that one branch of *Equus* entered South America in the Late Pliocene. This is the zebra-like subgenus *Amerhippus*, which diversified into a variety of pampas and even Andean species (seven in number, according to Azzaroli, 1992a), which survived alongside *Hippidion* and *Onohippidion* until the Late Pleistocene, and finally died out for reasons that are unclear; however, Azzaroli (1992b) has argued that it was a case of 'prehistoric overkill', i.e. overhunting by early humans, perhaps abetted by climatic change.

In both Europe and Asia, the earliest certain appearance of monodactyl equids is at about 2.5 mya, apparently part of a major faunal turnover as forest mammals disappeared and open-country fauna took their place (Azzaroli, 1990); they entered Africa around 2 mya (Azzaroli, 1998). The earliest species (*E. stenonis* and its relatives) were nearly identical to North American *E. simplicidens* and are placed in the subgenus *Allohippus*. After 1 mya, they began to be replaced by species related to modern forms: by the Middle Pleistocene, both the subgenus *Equus* (*E. mosbachensis* and later species) and the subgenus *Asinus* (*E. altidens*, a member of the *E. hemionus* group) had entered Eurasia; and in the Late Pleistocene, *E. graziosii*, a member of the *E. asinus* group known only from Italy, and the widespread but still very poorly known *E. hydruntinus*, which may be either a hemione or a zebra.

The African fossil representatives of *Equus* are almost entirely zebras. From 2 mya on, one or several large species related to *E. grevyi* were widespread throughout east and south Africa (*E. capensis, E. oldowayensis, E. koobiforensis*). Remains of other zebra groups are rare, becoming common only in the Late Pleistocene. A fossil ass is known from Olduvai Bed II (~2 mya) and from the Middle (*E. tabeti*) and Late (*E. melkiensis*) Pleistocene of the Maghreb. Fragmentary horse remains (*E. algericus*) also occur in the Maghreb in the Late Pleistocene.

The species question

Most non-taxonomists still operate on a misunderstanding of the biological species concept (BSC) of Mayr (1942). The popular misapprehension is that different species cannot interbreed; some go a step further, believing that species are sometimes able to interbreed, but hybrids between them are sterile. The six universally recognized 'species' (here, species-groups) of *Equus* therefore qualify under any rubric as valid species: hybrids between horses and asses, for example, are (almost always) sterile. Many commentators would go on to say that if hybrids between Indian and Persian wild asses prove to be fertile, this would indicate that they, by contrast, are not valid species.

This is not in fact what Mayr said: he proposed that species 'do not interbreed under natural conditions', and emphasized that this reproductive isolation might be the result of either pre- or post-mating isolating mechanisms. The post-mating mechanisms are those which cause hybrids to be sterile; the pre-mating ones include such things as ethological mechanisms (different courtship displays, for example), which can be broken down under unnatural conditions, such as captivity. If the pre-mating mechanisms break down, we may well discover that post-mating mechanisms are not in place – and perfectly fertile hybrids will result.

Clearly, sympatry between two taxa is *prima facie* evidence for the existence of reproductive isolating mechanisms between them; but, under the BSC, allopatric taxa are simply not amenable to being assessed objectively, unless we are able to conduct breeding experiments in captivity. Even then, if crossing them is unsuccessful, or hybrids between them are sterile, we can say that they are reproductively isolated and so are distinct species; but if they interbreed to give fertile hybrids, we are *not* at liberty to claim that they are members of the same species. All too often, of course, breeding experiments are simply not feasible, which means in practice that the majority of sexually reproducing species cannot even be tested. This is the case with living equids: hybrids are known in captivity between (for example) Indian and Persian wild asses, but their fertility has not been tested; and, today, the concern has always been to preserve the pure gene pool, and multigeneration crossing is of low priority.

Several variants of the BSC have been proposed, but when all is said and done the biologist needs an operational definition of this concept, the species, which we all agree is so basic. Cracraft (1983) gave voice to such thoughts when he pointed out what an arbitrary decision it could be to assess whether two taxa might or might not interbreed were their ranges to meet, and proposed the phylogenetic species concept (PSC), whose operational criterion is simply the diagnosability (the consistency) of the candidates for species status.

This is the attitude we take here: where two taxa are consistently different, given the available evidence, we rank them as separate species. This is why we recognize four species of the *E. hemionus* group, and two of the *E. zebra* group, and why we do not recognize more than one species in the *E. quagga* group, whose subspecies merge insensibly into each other.

The potential importance of the reproductive factor is unquestioned, but it can never in itself be a criterion. We usually do not know whether there is interbreeding between two species, or we may even know that there actually is; the significant factor is that, if there is interbreeding, any resulting gene flow does not affect the character discontinuity between them.

The subspecies question

Conceptually, there is no disagreement that subspecies are geographic segments of a species which are morphologically differentiated to some extent. They are geographic: by definition, they can never be sympatric. They are morphologically differentiated, but not consistently, not 100%: this would, under the PSC, make them different species. Mayr's 75% rule, i.e. that three-quarters of individuals of one subspecies must be distinguishable from all individuals of all the others, is usually upheld, but this is a rule-of-thumb.

The subspecies is just a point on the continuum of degrees of differentiation at which it becomes helpful (or desirable, or simply convenient) to recognize that differentiation with a trinomial.

Subspecies are often the steps on a stepped cline. The subspecies of *E. quagga* are an example here. On a stepped cline (as within *E. africanus*), one can say, within limits, where subspecies A ends and subspecies B begins, and between the two points is a more rapid change in gene frequencies, metrical averages, whatever one is talking about. If the clinal gradient is insensibly smooth, obviously to dignify its two ends as subspecies is rather arbitrary: and this is why we recognize a single living subspecies of *E. quagga* south of the Zambezi.

Note that either a species has at least two subspecies, or it has none. Subspecies exist in relation to one another: there is no such thing as a species having one single subspecies. One of the subspecies is called the nominotypical subspecies, and its subspecific name repeats its specific name; this will be the subspecies that exists at the species' own type locality. There is no assumption that one subspecies is more 'typical' of the species than another.

Nomenclature of Domestic Animals

Groves (1995) has argued that there is, and can be, no definitive answer to the question of whether domestic animals are the same species as their wild relatives, or different species. They are not subspecies because they are sympatric; they are not, or generally not, different species because except in a few outstanding cases they are not diagnosably different. Groves (1995) has called them **paraspecies**. Corbet and Clutton-Brock (1984) argued that, in most cases, it is convenient to maintain the fiction that, for nomenclatural purposes at least, they are different species.

The wild species may have subspecies; the domestic species does not. Domestic breeds, however distinct they are, are sympatric; they arise and merge within very short periods of time.

A Taxonomy of the Genus *Equus*

C.P.G. collected a number of characters from the literature (mainly Bennett, 1980; Groves and Willoughby, 1981; Eisenmann, 1986), but found that most of the unique states are clearly autapomorphic: the elongated metapodials of *Hemionus*, and so on. As in Bennett (1980), *Dinohippus* is taken as the outgroup. In the end, 26 characters seem to yield phylogenetically informative information (Table 1.1). The data matrix is given in Table 1.2.

The resulting cladogram (Fig. 1.1) separates the living equids into three clades: horses, zebras, and asses plus hemiones. These same three clades are found by studies of mitochondrial DNA (George and Ryder, 1986), whereas a repetitive DNA sequence placed ass, hemione and the zebra group as three

Table 1.1. Morphological interrelationships within living *Equus*.

1. Presence and development of isthmus on lower molars (B, no. 6)
2. Presence and development of infundibulum on third lower incisor (B, no. 11)
3. Presence of ‘cranial broadening complex’ (B, no. 12)
4. Degree of cranial flexion (B, no. 13)
5. Relationships of mastoid, paramastoid and mastoid temporal (B, no. 14)
6. Orientation of post-orbital bar relative to horizontal plane (B, no. 15)
7. Presence of frontal doming (B, no. 18)
8. Relative skull breadth (B, no. 19)
9. Scapula length > 102% of radius, humerus length < 86% of scapula (GW) – polarity unknown
10. Forefoot terminal phalanx breadth > 125% of length (GW)
11. Forefoot terminal phalanx length > 55% of proximal phalanx, > 14% of radius (GW)
12. Forefoot terminal phalanx plantar length > 125% of height (GW)
13. Proximal humerus bicipital grooves deep (GW) – polarity unknown
14. Skull vertex length > 560 where basal length standardized = 500 mm (GW)
15. Palate–vomer length < vomer–basion (GW, E)
16. Tooth row length > 170 where basal length standardized = 500 mm (GW)
17. Occipital height > 298 (state 1), > 320 (state 2) where basal length standardized = 500 mm (GW)
18. Nasal end of pre-maxilla narrowed, insinuated between nasal and maxilla (GW)
19. Choanal opening horseshoe-shaped (GW) – polarity unknown
20. Hypostylid present on third lower deciduous molar (GW) – polarity unknown
21. Shape of wolf tooth (GW) – polarity unknown
22. Ectoloph styles angle into walls (GW)
23. Palate length < 52% of basal length (E)
24. Muzzle length > 50% of palate length (E)
25. Choanal length > 15% of basal length (E)
26. Choanal breadth > 8.5% of basal length (E)

Morphological characters used in the cladistic analysis of species-groups of living equids (B = Bennett, 1980; GW = Groves and Willoughby, 1981; E = Eisenmann, 1986; in general, the derived states are described).

Table 1.2. Matrix of character states.

Horse	12111100111110110010100001
Hemione	21000001011001010010001001
Ass	20000000010001001100111001
Mountain zebra	00111100000001002001011110
Quagga	00111111011001102111100100
Grévy’s zebra	00111111111111000001111110

The characters are listed in rows 1–26 as per Table 1.1. State 0 denotes the primitive state, state 1 the derived, state 2 (where relevant) most derived.

equal branches of a non-horse clade (Sakagami *et al*., 1999). A striking point of agreement is that the zebras form a monophyletic group; the common ancestor of the three extant species was probably a striped animal and each taxon of

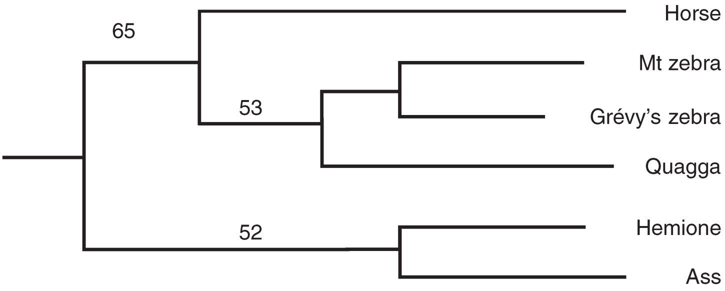

Fig. 1.1. Cladogram of living species-groups of *Equus*, based on the matrix of Table 1.2. The single most parsimonious tree has length 48, consistency index 0.604, retention index 0.486. The numbers above the lines are bootstrap values based on 1000 replicates. The horse/zebra clade is defined by derived states of characters 3, 4, 5 and 6; the hemione/ass clade by the derived state of character 1; the zebra clade by derived states of characters 7, 20 and 24; and the mountain/Grévy's clade by derived states of characters 22, 23, 25 and 26.

zebra is more closely related to other zebras than it is to any other equid. A minor difference is that the ass/hemione clade separates first in the morphological tree, the horse clade in the genetic tree. Another possible area of disagreement is that asses and hemiones are associated unequivocally in the morphological tree, but less definitely in the genetic tree: whether hemiones and African ('true') wild asses are more closely related to horses or whether they are most closely related to each other and form a separate lineage has yet to be resolved unequivocally by the DNA data, and note that in the morphological data they are united by only a single derived condition (Fig. 1.1).

In what follows, we have adopted the cladistic results (above), and lumped all zebras into one subgenus, all 'asses' into another, with the horses in a third. We briefly survey the evidence for species within each, giving less attention to subspecies.

Subgenus **Equus***: horses*

Externally, horses are recognizable by the long-haired tail; the mane that is both long and thick and tends, at least in winter and/or with increasing age, to fall to one side; the rounded croup; the usual presence of chestnuts on hindlimbs as well as forelimbs; the broad, rounded hooves; and the poor countershading, weak dorsal stripe and dark lower limbs with general traces of stripes on carpus and tarsus. Cranially, they have a relatively small skull, reduced cranial flexion, long diastema (the gap between the incisors and the cheek teeth), large pterygopalatine fossa (behind the hard palate) and a long, rounded occipital crest. The nasal end of the pre-maxilla is truncated or rounded, so that the nasal bone forms the angle of the narial notch. Postcranially, they have a long scapula and stout metapodials and phalanges. The metacarpus is short compared with the metatarsus, so that their hindlegs are longer than their forelegs. The pelvis is broad and splayed compared with other subgenera; the biischial breadth is high compared with the biacetabular (i.e. it is flared at the haunch compared with the hip joint); the height of the pelvic inlet is strongly sexually dimorphic, increasing the width of the female's birth canal.

Groves (1986, 1993) argued that all horses that survived into historic times belonged to one species, *Equus ferus* Boddaert, 1785, with three subspecies: *E. f. ferus* (Steppe tarpan), *E. f. sylvestris* (Forest tarpan) and *E. f. przewalskii* (Przewalski horse). The evidence that the Przewalski horse is the eastern representative of the species that contained the European tarpan is admittedly inferential: an apparent gradation of colours from west to east, and apparently the occasional appearance of Przewalski-like colours in Europe (including, as many people have noticed, on the walls of terminal Pleistocene caves such as Lascaux). This needs to be tested further (if possible!), but it does seem at the moment as if there was a continuum across Eurasia.

A large number of species of wild horse have been described from the Late Pleistocene and Early Holocene of Europe, Siberia and China (see Forsten, 1988, and, for a recent survey, see Azzaroli, 1998). Eisenmann (1996) examined characters that have commonly been used to differentiate wild horse species; very few actually seem to characterize credible taxonomic units. Przewalski horses have a short vomer compared with other horses, both wild and domestic, including tarpans, and differ in the metacarpal proportions. On the other hand Przewalski horses and tarpans have shorter proximal phalanges compared with the metapodials (i.e. their feet are short compared with their lower limbs) than do the Late Pleistocene wild horses of France, Ukraine and Russia; however, the Portugese wild horses and the European Bronze Age (presumably domestic) horses resemble Przewalski horse and the tarpan.

Przewalski's horses have $2n = 66$ chromosomes, while normal domestic horses possess $2n = 64$ chromosomes.

There is no evidence that there were differentiated subspecies within what conventionally has been considered the range of *E. f. przewalskii.* Analysis of the stud book of the Przewalski's horses identifies that just four mitochondrial DNA haplotypes may descend from the 13 founders. However, DNA sequence analysis of the control region of these four matrilines suggests that only two distinct haplotypes survive (Oakenfull and Ryder, 1998). Previous studies of a single mitochondrial control region haplotype of Przewalski's horses in comparison with domestic horses resulted in the suggestion that Przewalski's horses may have been derived from domestic horses (Ishida *et al.*, 1995), but more recent studies involving all surviving mitochondrial DNA control region haplotypes suggest that insufficient information exists to identify the phylogenetic relationships of Przewalski's horses based on mitochondrial DNA. Erect mane, lack of forelock and moulting of the hair at the base of the tail are all primitive characteristics noted in wild, but not domestic, equids that are typical features for Przewalski's horses. Studies of nuclear genetic variation in domestic and Przewalski's horses may shed additional light on to the phylogeny of caballine horses. Of particular interest will be studies of domestic horses in Mongolia whose mitochondrial and nuclear diversity may provide otherwise unavailable insights into the relationship of Przewalski's and domestic horses.

Subgenus **Asinus***: ass, onager and kiang*

These are characterized externally by having a tufted tail, chestnuts on forelimbs only and at least some degree of countershading. Cranially they are characterized by the squared, upturned occipital crest and wide external auditory meatus. Post-cranially, they have a short scapula; and, like horses, the metacarpus is short compared with the metatarsus, the biischial breadth is high compared with the biacetabular, and the height of the pelvic inlet is strongly sexually dimorphic.

We can divide this subgenus into two certainly monophyletic species-groups, the *E. hemionus* group and the *E. asinus* group. This is necessary because of the existence of more than one living species of 'hemiones', and of multiple fossil species of 'true asses'.

Equus hemionus *group*

The *E. hemionus* group (onagers or hemiones or Asian wild asses) are characterized externally by the short, clipped-appearing mane, short erect hair forming a broad dorsal stripe 50–100 mm broad, and white underparts and lower limbs. Cranially, they are characterized by the very narrow squared upturned occipital crest, shortened brain case, long vomer, short diastema and short pterygopalatine fossa. The nasal end of the pre-maxilla is truncated or rounded, so that nasal bone forms the angle of the narial notch. The tuber maxillae extend back, hiding the pterygopalatine fossa in the ventral view, like quaggas and unlike other equids. Post-cranially, they are distinguished by the short humerus and femur, the elongated, slender metapodials (so that the lower limb segments are long and fine) and the elongated distal phalanx.

Groves and Mazák (1967) argued that the kiang, of the Tibetan plateau, is a distinct species (*E. kiang*) from the onagers (*E. hemionus*) of the more low-lying Asian deserts. The differences are very striking, and this separation has been widely followed. The subspecies *onager, kulan, castaneus* and *hemionus* form an intergrading series, overlapping (at the extremes) in their traits but each strongly distinct as a unit. The two other taxa usually placed as subspecies of *E. hemionus*, i.e. *hemippus* and *khur*, are in fact diagnosable taxa (in the PSC sense) and are here regarded as distinct species.

The number of chromosomes in Asiatic wild asses varies from $2n = 56$ to $2n = 50$. This is a large amount of numerical and structural chromosomal polymorphism to be segregating within a single species. Tibetan kiangs, *Equus kiang holdereri*, apparently have fixed chromosomal differences from other subspecies of Asiatic wild asses, based on the available chromosomal data (Ryder *et al.*, 1978; Ryder, 1986; Ryder and Chemnick, 1990). Mitochondrial DNA studies, including restriction fragment length polymorphism (RFLP) analysis (Ryder and Chemnick, 1990) and control region and 12S RNA sequence data (Oakenfull *et al.*, unpublished observations), find that named *E. hemionus* subspecies are paraphyletic. Phylogenetic analysis identifies mitochondrial lineages encompassing the examined diversity of Asiatic wild asses that are present in multiple subspecies. Based on available data, extant mitochondrial DNA variation appears to reside largely within the named subspecies and not to be partitioned between onagers, kulans and kiangs.

Subspecies of *E. hemionus* may hybridize, and be fertile, in spite of the chromosomal polymorphism (Pohle, stud book), providing evidence that reproductive isolation has not yet developed. The implication from mitochondrial DNA analyses is that the extant subspecies share a common pool of mitochondrial variation; divergence and genetic isolation are minimal, implying that these processes have begun only recently. The most divergent of the Asiatic wild asses based upon genetic analysis is the kiang, supporting their status as a separate species.

Significant gaps exist, though, in the genetic studies of the hemione group. In particular, the khur of the Little Rann of Kutch has not been the subject of published molecular studies. Mongolian wild asses and the western and southern kiang similarly are absent from the literature on molecular evolution in *Equus*. Accordingly, there are opportunities for additional studies and a need to provide a more detailed view of nuclear and mitochondrial variation in Asiatic wild asses for conservation assessments, monitoring and management.

Equus kiang *Moorcroft, 1841: Kiang* The kiang or Tibetan wild ass is of large size; it has a large head and thick muzzle, a relatively long mane and long hairs not restricted to the tail tuft but extending some way up either side of the tail. The pattern of contrasting dark (reddish) body blocks and white underside is characteristic: the demarcation between them on the flank is oblique from stifle to croup, and the white rump patch is infused with the reddish tone of the haunch. The dorsal stripe is thin and never bordered with white; it extends to the tail tuft. There is a dark ring round the hoof. The ear is 165–178 mm long.

The skull resembles that of *E. hemionus*, except that the incisors tend to sit more vertically in the jaws (except in aged individuals, in which alveolar recession tends to reveal the oblique roots), and the highest point on the cranial profile is often directly above the posterior rim of the orbit, instead of behind it.

There are three subspecies, which differ (as a whole, but not absolutely) as follows:

1. *Equus kiang kiang* Moorcroft, 1841. Western kiang. Dark red-brown colour in summer, dark brown in winter; the legs have brown tones. Size large; nasal bones short; tooth row relatively short. The southwestern corner of Tibet, into India (Ladakh) and Pakistan.

2. *Equus kiang holdereri* Matschie, 1911. Eastern kiang. Colour not so dark: strong red in summer, darker red-brown in winter; the legs are pure white. Size large; nasals very long; tooth row long. Eastern Tibet (Lhasa district) to Chinghai, Ganssu and the Seshu region of Sichuan.

3. *Equus kiang polyodon* (Hodgson, 1847). Southern kiang. Colour dark as in *E.k. kiang*; size very small; nasals and tooth row long as in *E. k. holdereri*. The Gayam Tso region of Tibet, into Sikkim.

Equus hemionus *Pallas, 1775: Onager* The onager varies from kiang-sized to khur-sized. The mane is very short and 'clipped'; the dorsal stripe is thick, often bordered with a white line on either side; the white of the rump is not infused; the demarcation between the reddish flank block and whitish underside runs parallel to the body outline, before turning sharply up towards the dorsal stripe. The dorsal stripe extends to the tail tuft. There is a dark ring round the hoof. The nasal bones are relatively straight, the skull resembles that of *E. kiang*.

The number and definition of the subspecies are disputed, but the following seem recognizable:

1. *Equus hemionus hemionus* Pallas, 1775. Mongolian wild ass. This is the least endangered subspecies, still found throughout the Mongolian desert regions, and formerly into Transbaikalia. Height 110–130 cm; poor demarcation of dark and light (off-white) areas; the only subspecies usually lacking a white border to the dorsal stripe. The concept that Groves and Mazák (1967) and Groves (1986) used was: (i) a disruptively coloured subspecies, occupying a northerly distribution extending from Transbaikalia to Kazakhstan, and (ii) a grading-toned one, called *E. h. luteus*, restricted to the Gobi desert. However, Denzau and Denzau (1999) have shown that the type illustration of Pallas's *E. hemionus*, which was from Transbaikalia, in fact corresponds to the grading subspecies. The disruptively patterned 'northern' subspecies therefore never extended to Transbaikalia but was purely western in range, and must be called:

Equus hemionus castaneus (Lydekker, 1905). Probably now extinct: formerly from Dzungaria through Kazakhstan to Uzbekistan. Also large; clear demarcation of coloured and white areas; much white on body and head.

2. *Equus hemionus kulan* (Groves and Mazák, 1967). Turkmenian wild ass or kulan. Badkhyz Reserve, Turkmenia. Smaller: height 108–120 cm. Coloured and white areas strongly demarcated like *castaneus*. Relatively larger teeth than the large Mongolian/Kazakhstan forms.

3. *Equus hemionus onager* Boddaert, 1785. Persian wild ass. Iran, east of the Zagros Range. Also small; demarcation between coloured and white areas less strong than in *kulan*, from which it differs in pattern details. Broader occipital crest; even larger teeth. This still occurs in the Bahram-e-Gur and Touran Reserves in Iran; according to Denzau and Denzau (1999), these two remnant populations differ in size.

4. *Equus hemionus blanfordi* Pocock, 1947. Probably now extinct; formerly, known only from Sham Plains (Pakistan) and Kandahar (Afghanistan). Also small, and large-toothed; with relatively narrow occipital crest and long nasals; extensive dark areas on flanks; the dorsal stripe fades out halfway down the tail.

Equus khur *Lesson, 1827; Khur (Indian wild ass)* The Indian wild ass or khur is sharply distinct from *E. hemionus*, and because it can always be distinguished from other forms we recognize it as a full species. The coloured blocks on the flank and haunch are very small, so the predominant colour is white, and the lower 45% or more of flank is whitish; the demarcation on the lower haunch slants upward from the front (stifle) to the back. There is a dorsal stripe with a clear white border on either side. The white wedge between the haunch and flank blocks nearly or fully reaches the spine. The legs are pure white. The dorsal stripe fades out halfway down the tail. There is no dark ring round the hoof.

The facial profile is concave; the nasal bones are raised (making the whole facial profile strongly concave), and comparatively short (Groves, 1986, Figure 1); and the teeth are small. The skull is noticeably high crowned. The choanae are small and the orbits are high. Height at withers is 110–130 cm. The metapodials are less elongated than in *E. hemionus*. The ear is very long: 187–210 mm.

The ass survives in the Rann of Kutch, Gujarat, India; formerly known from the Sind deserts, Pakistan.

Equus hemippus *I. Geoffroy St Hilaire, 1855: Syrian wild ass* The extinct Syrian wild ass or achdari was likewise diagnostically different from other hemiones. It was very small in size; the evidence suggests that this difference has come about since the end of the Pleistocene (Turnbull, 1986). The height at the withers was about 1 m. Colour was very grading; a sandy-brown flank patch extended well down, grading into off-white on the underside; only the lower 20% or less of flank was whitish. There was a dorsal stripe with a clear white border on either side; this became obfuscated with age, and eventually disappeared. The white wedge between the haunch and flank blocks was vague, strongly infused with body tone. The legs were strongly infused with body tone. The dorsal stripe faded out halfway down the tail. There was no dark ring round the hoof.

The nasal bones were raised, and relatively longer than in other onagers (Groves, 1986, Fig. 1.1); the teeth were relatively large. Otherwise the skull, with its concave profile, high-placed orbit, and high crown, resembled a small *E. khur*. The metapodials were more elongated than those of other species; the terminal phalanges were shortened.

It was known from Syria and northern Iraq.

Equus asinus *group*

The *Equus asinus* group (true asses or donkeys) are characterized externally by a long, thin ‘scruffy’ mane, thin dorsal stripe, usually traces of stripes on the legs (at least fetlocks) and a restricted white (or pale) region on the underside. Cranially they have a very long cranium, short palate, long diastema, large pterygopalatine fossa and a squared, upturned occipital crest. The nasal end of the pre-maxilla is narrow, insinuated into a corner of the narial notch. The orbit is high, rounded and not anteroposteriorly elongated like other equids except mountain zebras. Post-cranially, there are very short, narrow distal phalanges, translating externally to small, narrow hooves.

Eisenmann (1995) reviewed recently the palaeontological evidence for the evolution of this species group, and the evidence for extinct Early Holocene populations.

There is one wild species:

Equus africanus *Heuglin and Fitzinger, 1866: African wild ass* All African wild asses tend to be more reddish in summer, greyer in winter, with contrastingly white legs and a less contrastingly whitish underside; the white wedges behind the shoulder and in front of the haunch, so prominent in hemiones, are evanescent.

Groves (1986) showed that, to some degree, there is clinal change from the Atbara population via the Red Sea coastal populations to Somalia. There is quite a marked change, a distinct step in the cline, between northern and southern Eritrea, perhaps representing a bottleneck to gene flow in the Massawa region, where the Highlands approach the sea, and this justifies the recognition of at least two subspecies. A supposed wild ass was described as *Asinus taeniopus* Heuglin (type locality: Little Dobar, south of Berbera), and even today this is sometimes recognized as a subspecies, but no such wild ass actually exists: it was based on a cross between a Somali wild ass and a domestic ass.

A north African wild ass, with strong, often doubled, shoulder-cross and well-marked leg stripes was depicted in both rock art and Roman era mosaics, and was stated to survive at Siwa, on the Libyan–Egyptian border, by Hufnagel (1965). It is often called *Equus africanus atlanticus*, but should not be, as that name was first given to a fossil north African zebra. Eisenmann (1995) discusses whether the name *Equus melkiensis* (described from a genuine fossil ass, from the Late Pleistocene of Allobroges, Algeria) might apply to this form, though one ought to be rather cautious in associating Pleistocene fossils with Holocene rock depictions.

In the earliest Holocene, wild asses were also present in northern Arabia (Ducos, 1986; Groves, 1986); a subspecies *Equus africanus mureybeti* Ducos, 1986 has been described from pre-pottery levels in Iraq, but Eisenmann (1995) is not convinced that the remains are ass rather than onager.

Only the Somali wild ass has been studied genetically, and there are significant doubts that any other forms of African wild ass survive. Chromosomal polymorphisms in Somali wild asses have been described (Houck *et al*., 1998). Mitochondrial DNA analyses place Somali wild ass as a sister group to domestic donkey but, without additional study, the phylogenetics and systematics of African wild asses remain tentative.

There are several subspecies:

1. *Equus africanus africanus* Heuglin and Fitzinger, 1866. Nubian wild ass. From Atbara River to Red Sea coast and northernmost Eritrea. May be extinct. Shoulder height 115–121 cm. A dorsal stripe is always present, and nearly always complete from mane to tail tuft; crossed by an usually thin, fairly short shoulder stripe. Leg stripes, where present are restricted to a few bands at the fetlocks. The diastema is relatively short, and the post-orbital constriction well marked. The nasal process of the pre-maxilla ends bluntly. There is never a 'bridge' between metaconid and metastylid in the lower premolars and molars. Groves (1986) found that specimens from the Atbara differ on average from those from the Red Sea Hills (Sudan) and Eritrea, and they could be subspecifically distinct. The Nubian wild ass is probably not, contrary to 'received opinion', the ancestor of the domestic donkey.

2. *Equus africanus somaliensis* Noack, 1884. Somali wild ass. Ears shorter, 187–200 mm; shoulder height 120–125 cm; the dorsal stripe is often absent, and when present is often incomplete, broken at some point along the dorsum. Shoulder-cross often absent. Leg stripes are present from hooves to above the carpus and tarsus. Diastema is relatively long, and the post-orbital constriction less marked. There is a thickened bar of bone behind the orbits, marking the highest point on the profile. The nasal process of the pre-maxilla is thin and pointed. There is always at least a trace of a 'bridge' between metaconid and metastylid in the lower premolars and molars. Somali asses seem to be longer legged, and shorter bodied than Nubian ones. Differences between Somalian and Danakil plus Djibouti populations exist, but are less marked than those between the two populations of *E. a. africanus.* Somali wild asses still exist in two small population nuclei: in the Afar (Danakil) country of southern Eritrea, and in the Nogal valey, northern Somalia.

3. *Equus africanus* subsp. Saharan wild ass. Still more a rumour than a fact, but best authenticated for Ahaggar, Tibesti and Fezzan; the appearance of the (apparently indigenous) wild ass of the Sahara was reconstructed by Groves (1986) as closest to *E. a. africanus* but smaller and greyer, and with a long, thin shoulder-cross.

Subgenus **Hippotigris***: zebras*

These are characterized externally by the long, rather thick upright mane, tufted tail, chestnuts on forelimbs only, and striking black and white stripes.

Cranially, the occiput is high and raised; the post-orbital constriction is deep; the muzzle long; and the vomer long. Post-cranially, the metacarpus is long compared with the metatarsus, so that the forelimbs are longer than the hindlimbs. The biischial breadth is low compared with the biacetabular, so that the hip joints are further apart, giving zebras a fat-rumped appearance; the height of the pelvic inlet is not strongly sexually dimorphic, so that males, as well as females, have a large, high space corresponding to the birth canal.

Chromosomal and molecular data, as well as the morphological analysis presented here, all support the position of monophyly for zebras – that all extant zebras share a recent common ancestor with each other. Mitochondrial DNA RFLP study suggested that plains zebra and Grévy's zebra are sister taxa, as did study of a repeated sequence (Sakagami *et al.*, 1999), but in another study involving control region and 12S gene sequencing, the mountain zebra and plains zebra were identified as sister taxa (Oakenfull and Ryder, 1998). The morphological tree, however, places mountain and Grévy's zebras closer.

Equus zebra *group*
The *E. zebra* group (mountain zebras) is characterized externally by the long, rather thick upright mane, small dewlap, and stripes absent from venter, forming what has been called a 'gridiron' pattern (short transverse stripes meeting the uppermost of a long, thick, oblique/longitudinal series) on the croup.

Cranially, the nasal end of the pre-maxilla is truncated or rounded, so that the nasal bone forms the angle of the narial notch. The external auditory meatus is wide, and (uniquely) directed horizontally instead of upward and backward, probably connected with the large external ears. The ventral bar of the orbit is slender and the orbit is high, rounded like that of asses. Postcranially, the scapula is short; the distal phalanges are short and narrow, so that the hoof is small and fine like that of a donkey. The skull is relatively large compared with the rest of the skeleton.

The two forms usually ranked as subspecies of a single species, *E. zebra*, should certainly be regarded as distinct species. They are strikingly different externally, and some of the skull measurements do not overlap, although note that sample sizes are small. For example, occipital crest breadth is 63–71 mm in male *zebra*, 74–78 mm in male *hartmannae* ($n = 5$ of each); in females, 63–68 mm in *zebra*, 70–86 mm in *hartmannae* ($n = 3$ and 6, respectively). In the present sample, there is a sexual size difference in *zebra* (mean skull length 516.0 mm in males, 530.8 mm in females), but not in *hartmannae* (548.0 and 549.9 mm, respectively).

Equus zebra *Linnaeus, 1758. Cape mountain zebra.* Mountains of the southern Cape (Skead, 1980). It was nearly extinct in the 1950s but has been very successfully preserved and reintroduced over much of its former range.

Size smaller; black stripes broader than white interspaces. Occipital crest narrow; females apparently larger than males.

Equus hartmannae *Matschie, 1898. Hartmann's mountain zebra* Arid, hilly regions from southern Angola formerly to northwestern Cape. It still occurs in Angola and northern Namibia, but is very much less numerous than formerly.

Size much larger; black stripes narrower than white interspaces. Occipital crest broad. Sexes equal in size.

Equus quagga *group*
The *E. quagga* group (plains zebras) have a mane varying from long, thick, neat to shorter, thinner, and even absent altogether; striping varies from dark brown and white on head and neck only to striking black and white over the whole body, including the venter, and a simple oblique/longitudinal pattern on the croup and haunch.

The post-orbital constriction is relatively narrow, the vomer long, the diastema long, the teeth relatively small, and the occiput extremely raised. The narial notch is less deep than that of other zebras. The interorbital part of the frontal bone is strongly convex, so that these zebras have a forehead that is rounded and convex from side to side. The bizygomatic width (cheekbones behind eyes) generally exceeds the biorbital width, so that the eyes do not protrude like those of other equids. The nasal end of the pre-maxilla is narrow, insinuated into the corner of the narial notch. Pre-maxillae, unlike those of other zebras, are curved downward below the level of the alveolar line of the cheek teeth, so that the upper lip is unusually deep. The tuber maxillae extends back, hiding the pterygopalatine fossa in the ventral view, like *Hemionus* and unlike other equines. The foramen magnum (the hole through which the spinal cord enters the brain case) is an unusual, uniquely rectangular shape. The metapodials are somewhat lengthened, so that the lower legs are relatively long. Distal phalanges are less reduced than in the *E. zebra* group, translating to larger, broader hooves.

The cranial differences between plains and mountain zebras are given by Eisenmann and de Giuli (1974) and Smuts and Penzhorn (1988), who agree in most respects, though the latter add a few characters, notably the important difference in the foramen magnum, in which this species group is unlike any other subgenus.

Although in this species group two species, *E. quagga* and *E. burchelli*, are often recognized, they grade insensibly into each other; some of the skins described and illustrated by Rau (1974), especially the Mainz female 'true quagga' and another specimen in Mainz, the type of *paucistriatus* Hilzheimer, are difficult to allocate to one or the other. There seems no prospect of breaking the cline from the Cape to Sudan and Somalia, into species; though, the cline being stepped, the subspecies seem clear enough. The quagga was in fact the first extinct organism from which DNA was extracted (Higuchi *et al.*, 1984); the result showed clearly its close affiliation to living plains zebras.

The plains zebra is the most abundant wild equid and, though it can be divided into several fairly clear-cut subspecies, there is no clear picture to present from the genetic perspective until nuclear and mitochondrial DNA studies of populations across the range of the species has been undertaken.

Equus quagga quagga *Gmelin, 1788* The extinct true quagga lived west of the Drakensberg and south of the Vaal-Orange system (Skead, 1980). It had head and neck stripes, but on the body the stripes were incomplete at best; body colour was fawn, but legs were white. The available museum material was fully discussed by Rau (1974, 1978), who showed that there are some specimens that are so intermediate between 'true quagga' and *burchelli* that we cannot recognize any species distinction. The physical geographic barriers between the two are, however, sufficient to make a strong step in the cline, and so confirm their subspecific distinction. I have measured only three adult male skulls from the wild (Leiden, Berlin and Frankfurt). They range from 485 to 528 mm in length, and so average smaller than other subspecies apart from *boehmi.*

Equus quagga burchellii *Gray, 1824* Known in different regions as Burchell's, Chapman's, Wahlberg's and Damara zebra. From Kwazulu-Natal and the Vaal-Orange system north to the Zambezi and Namibia. They are large in size. Three or four stripes (very rarely two or five) meet (sometimes they do not quite meet) the median ventral line between the elbow and the stripe that bends back to form the 'saddle' of the lumbar region. Colour is ochrey or off-white, never pure white; shadow stripes are usually well marked; leg stripes are absent or poor, almost never complete to the hooves. The infundibulum ('cup') on the lower incisors is better expressed than in other subspecies. The mane is well developed. Northerly populations (Zimbabwe, northern Mozambique) are paler, with less strikingly marked shadow stripes and more complete leg stripes than other populations. Those from Kwazulu-Natal and also northern Namibia (Etosha and Kaokoveld) are more ochrey with stronger shadow stripes and fewer leg stripes. There is simply no prospect of breaking up this subspecies as has usually been done. The least striped phenotype, which even lacks stripes on the lower haunches, occurs in both Etosha and Kwazulu-Natal and formerly occurred in the Free State; it has sometimes been called 'true Burchell's zebra', but there was never a population even predominantly characterized by this type, and 'true Burchell's zebra' has never existed as a discrete population.

Equus quagga crawshayi *de Winton, 1896* From north of the Zambezi and east of the Luangwa: so, in easternmost Zambia, Malawi, northern Mozambique and southern Tanzania. They are of large size. Stripes are numerous and narrow; there are always at least five stripes (often six to eight) meeting the median ventral line between the elbow and 'saddle' stripe; body tone is white or off-white; almost never even traces of shadow stripes; leg stripes complete to hooves.

Equus quagga zambeziensis *Prazak, 1898* From Angola and Zambia east to the Luangwa, and perhaps into Shaba. Large in size. Stripes are broad; only three or four meet the median ventral line between the elbow and 'saddle' stripe; colour varies from ochrey through off-white to white; shadow stripes vary from fairly prominent to absent; leg stripes are usually complete, or nearly so.

Equus quagga boehmi *Matschie, 1892: Grant's or Boehm's zebra* Small in size. Externally it resembles the previous form closely, but is separated from it by *E. q. crawshayi* and by Lake Tanganyika. The infundibulum is generally absent. It intergrades with *crawshayi* in southern Tanzania, and then ranges north through Tanzania and Kenya into southern Somalia and Ethiopia, Karamoja (Uganda) and southeast Sudan, east of the Nile. Most northerly populations of this subspecies have high frequencies of manelessness, and the ears are either very vaguely striped or completely white; they could perhaps be separated as a different subspecies but there are differences among them: (i) manelessness appears to be fixed in the northeastern ones (northeast of Mount Kenya, into Somalia), but merely high frequency (especially frequent in males) in the northwestern ones (Baringo, Karamoja and Sudan), and apparently does not occur at all in Ethiopia or around Lake Turkana, and (ii) whereas northeastern zebras are as small as other *boehmi* or even slightly smaller, northwestern ones are larger, as big as the more southerly subspecies such as *zambeziensis*. If it is felt that they should be recognized as different subspecies: the name for the northeastern one would be *granti*, for the northwestern, *borensis*.

Equus grevyi *group*
The *E. grevyi* group, Grévy's zebra, has a long thick upright mane, very small chestnuts, short erect black hairs along the dorsal stripe and narrow, almost dazzling, black and white stripes on the whole body except for the venter and croup, forming a complex triradial pattern on the haunch. The skull is very elongated, exceeding the cervical spine in length. The nasal end of the pre-maxilla is rounded, wedged into the nasal bone. Post-cranially, the scapula is lengthened, the metapodials somewhat lengthened, and distal phalanges small.

There is only one living species, i.e. *Equus grevyi* Oustalet, 1882. Grévy's zebra. Provisionally, two subspecies can be recognized, based entirely on size, although they need to be tested on larger samples: (i) *Equus grevyi grevyi* Oustalet, 1882. Greatest skull length 529–615 mm. From the Somali Arid zone proper: Harar region to northernmost Kenya; and (ii) *Equus grevyi* subsp. Larger: greatest skull length 608–639 mm. From the Guaso Nyiro district, Kenya.

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