

**PART 3**  
**Equid Biology and Ecology**

# Taxonomy of Living Equidae<sup>1</sup>

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Taxonomy, like any other branch of science, is dynamic and subject to change as our understanding changes. There is not, and cannot be, any one “official” taxonomy. It is subject to fluctuation as past errors are corrected, as new data accumulate, and as concepts change. The following examples illustrate this.

## 8.1 Past errors

### 8.1.1 Individual variation

The explorers and big-game hunters of the 19th and early 20th centuries were certainly wont to mow down the large mammals of Africa in great numbers, but rarely did they think to preserve more than one or two for scientific study. So we have Matschie, Lydekker, Pocock, and others erecting new species and subspecies of plains zebra based on single specimens that looked different from any they had seen previously. Turn-of-the-century taxonomists had no idea what the variation from one individual to another encompassed; nowadays we do – and we can often see several of these “subspecies” in a single photograph of living zebras in an East African reserve!

### 8.1.2 Age-related variation

Again, our predecessors had little idea how an animal changed as it matured. Wild asses, onagers and plains zebras were becoming more common in Europe by the early years of the century; Grévy’s zebra, however, was still a rare beast in zoos, and Pocock was not to know that sub-adults of that species have brownish rather than jet-black striping, so he described *Equus grevyi berberensis*, a brown-striped race from further north than specimens previously seen by him. Ironically, the type specimen of *Equus grevyi* itself is a brown-striped sub-adult – a fact perhaps not sufficiently stressed by the describer, Oustalet.

### 8.1.3 Erroneous identification

Lydekker (1905) described and figured some living onagers in the Duke of Bedford’s collection, including a specimen said to have come from Meshed (now Mashhad) in north-eastern Iran, which he incorrectly identified as the Ghor

Khar or Indian onager and named *Equus onager indicus*; and a specimen of unknown origin, which he ascribed to the Persian onager and named *Equus onager onager*. The Mashhad animal in Lydekker’s figure has an extensive coloured zone on the flanks, and the boundary between white and coloured areas on the face follows the contour of the jaw angle; it is surely a Persian onager. His “Persian onager”, however, has the white extension well up on the flanks and the high crown and raised nasals, typical of the Indian form. In other words, he had got them the wrong way round.

Pocock (1947), who by that time used the generic name *Microhippus* for onagers, accepted Lydekker’s identifications. The only three Iranian specimens that Pocock had actually seen were three skins from Yezd (now Yazd) in the British Museum; because they were unlike Lydekker’s supposed *Equus onager onager*, he described a new subspecies *Microhippus hemionus bahram* based on them. It is a pity to quash such a poetically inspired name, but Pocock, misled by Lydekker’s erroneous identification, had simply redescribed the ordinary Persian onager.

### 8.1.4 Odd philosophies

Some of our predecessors were a little bit eccentric, and none more so than Paul Matschie, who worked in the Berlin Museum from about 1890 until his death in 1924. When he started work, Darwinian evolution was only 30 years old and there were a few hold-outs, mostly of the older generation – but not all. For Matschie, the elucidation of species and subspecies and their geographic distribution was the discovery of the Lord’s masterplan. As he had no truck with evolution, so he did not believe in individual variation either – the localities must be wrong or insufficiently precise, that’s all. Matschie is known as a great “splitter”, a describer of vast numbers of (mostly spurious) species and subspecies, and that is why. In his final days, he came to believe that the Great Plan was probably connected with half-degree units, so that if two specimens of a species or genus came from localities more than half a degree apart they must be taxonomically different, even if he was the only one who could detect exactly what the differences were. In equids, he described *Microhippus tafeli* which, because it came from the specified distance away from what he called *Microhippus holdereri*

1. Taxonomy in this chapter differs from the official Red List taxonomy. As Colin Groves points out, taxonomy is an evolving science and with new techniques, data, and theory, current categories will be questioned, reviewed, and perhaps changed.

(now *Equus hemionus holdereri*), simply must be distinct. I should perhaps add that I have seen the types of both *tafeli* and *holdereri*, and they are very similar.

## 8.2 Changes in viewpoint

### 8.2.1 Generic limits

The genus *Equus* was proposed by Linnaeus (1758) to include *E. caballus* (horse), *E. asinus* (ass) and *E. zebra* (mountain zebra), and the type species was tacitly accepted by his successors as the first of these. From time to time during the 19th century different authors proposed to set aside one or more species of living equids into genera other than *Equus* on the general grounds that they were “different enough”. Part of the philosophy was, no doubt, that horses, ass, 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. There is a different philosophy behind Quinn’s (1957) multigeneric scheme: the author saw the different modern groups as the end-points of lineages that could be traced back deep into the Miocene, and had even achieved monodactyly independently.

Quinn was wrong. 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. So, the single v. 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 inter-relationships of the living species? For the moment, the less formal category of subgenus will have to do and I suggest that, because the six living species-groups are very clearly separate and there are fossil species to accommodate as well, six subgenera may be appropriate, at least until we learn more about the finer degrees of relationship. Groves and Ryder (2000) proposed to reduce this to three, and further studies are needed to confirm relationships.

It is worth adding that Pocock was a great splitter of genera, as he was of subspecies, but rather a lumpner at the species level, with the result that he ended up with a lot of monotypic genera. He placed onagers in a genus *Microhippus* following Matschie, but the name *Microhippus* was originally proposed by von Reichenow (1915) for Przewalski’s horse. So, Matschie and Pocock

were both wrong. As Trumler (1961) pointed out, the earliest available generic name for onagers is *Hemionus* (Stehlin and Graziosi 1935).

### 8.2.2 The species question: what is a species?

Most non-taxonomists still operate on a misunderstanding of the Biological Species Concept (BSC) of Mayr (1942). The popular misconception 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. This is not in fact what Mayr said. He proposed that species “do not interbreed under natural conditions”, and emphasised that this reproductive isolation might be the result of either pre- or post-mating isolating mechanisms. The post-mating mechanisms are those that cause hybrids to be sterile; the pre-mating ones include such things as ethological mechanisms (e.g. different courtship displays), 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; under the BSC, however, allopatric taxa are simply not amenable to being objectively assessed 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. Alternatively, if they interbreed to give fertile hybrids, we are not thereby enabled to claim the converse, namely that they are members of the same species. In any case, usually breeding experiments are simply not feasible, which in practice means that the vast majority of sexually reproducing species cannot even be tested.

We must remember, too, that we are faced with a dynamic biological reality, where reproductive isolating mechanisms may be partial, so that we can speak of hybrid fertility being reduced, but not abolished; and, at times, we can even demonstrate that some well-established species are themselves of hybrid origin. *Rana esculenta*, the Edible Frog, is perhaps the best known example of this.

Several variants of the BSC have been proposed, for example, to extend the concept to asexually reproducing organisms; and Simpson’s Evolutionary Species Concept – that a species has its own unitary evolutionary role and history – gives the BSC a time depth. But is this really applicable in practice? Don’t we need an operational definition of this concept, the species, which we all agree is so basic?

When I survey drawers full of sad skins in a museum, and try to sort them into species and subspecies, I have

no difficulty with the sympatric ones: they are consistently different, they coexist geographically, they are (inferentially!) reproductively isolated. They are distinct species. Excellent. Now what about the allopatric ones? – they may well differ, but at what level should I represent this taxonomically? The heretical thought has surely occurred to every museum taxonomist at some time or other: should I not apply exactly the same criterion? If they are consistently different, should not they too be classified as distinct species? 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 (or, as I put it above, the consistency) of the candidates for species status.

Where does this leave the reproductive factor? Its potential importance is unquestioned but, in itself, it can never 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.

### 8.2.3 The subspecies question

Conceptually, there is no disagreement about what subspecies are: they are geographic segments of a species that are morphologically differentiated to some extent. They are geographic; by definition, they can never be sympatric. They are morphologically differentiated – by how much? Not consistently 100% which, under the PSC, would make them different species. Mayr's 75% rule – 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 recognise that differentiation with a trinomial.

Subspecies are often the steps on a stepped cline. If the clinal gradient is insensibly smooth, obviously to dignify its two ends as subspecies is rather arbitrary. A stepped cline, however, is something else; one can say that, within limits, subspecies A ends *here* and subspecies B begins *there*, and between the two points is a more rapid change in gene frequencies, metrical averages, or whatever one is talking about.

NB: 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.

### 8.2.4 Nomenclature of domestic animals: are domestic animals the same species as their wild relatives, or different species?

I have argued that there is and can be no definitive answer to this (Groves 1995). 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. I have 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.

## 8.3 Subgenera

### 8.3.1 Subgenus *Equus*: horses

Externally, horses are recognisable by a number of features: 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 hoofs; and the poor countershading, weak dorsal stripe, and dark lower limbs with generally traces of stripes on carpus and tarsus. Cranially, they have a relatively small skull, reduced cranial flexion, long diastema, large pterygopalatine fossa, and long, rounded occipital crest. The nasal end of the premaxilla is truncated or rounded, so that it forms the angle of the narial notch. Postcranially they have a long scapula and stout metapodials and phalanges, and the metacarpus is short compared to the metatarsus. The pelvis is broad and splayed compared to other subgenera, biischial breadth being high compared to biacetabular. Finally, the height of the pelvic inlet is strongly sexually dimorphic.

Groves (1986, 1994) argued that all horses that survived into historic times belonged to one species, *Equus ferus* Boddaert 1785, with three subspecies: *E. f. ferus*, *E. f. sylvestris*, and *E. f. przewalskii*. The evidence that the Przewalski's horse is the eastern representative of the species that contained the European tarpan is admittedly inferential; a 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 like Lascaux, France).

There is no evidence that there were any subspecies within what has conventionally been considered the range of *E. f. przewalskii*.

### 8.3.2 Subgenus *Hemionus*: onager and kiangs; Asian wild asses

The subgenus is characterised externally by the short, seemingly clipped mane, tufted tail, chestnuts (which are very large) on forelimbs only, short erect hair forming a broad dorsal stripe 50–100mm broad, and white underparts and lower limbs. Cranially, by the very narrow, squared, upturned occipital crest, shortened braincase, long vomer, short diastema, and short pterygopalatine fossa. The nasal end of the premaxilla is truncated or rounded, so that it forms the angle of the narial notch. The tuber maxillae extends back, hiding the pterygopalatine fossa in ventral view, like *Quagga* and unlike other subgenera. Postcranially, the subgenus is distinguished by the short scapula, humerus and femur, the elongated, slender metapodials and the elongated distal phalanx. The metacarpus is short compared to the metatarsus, the biischial breadth high compared to the biacetabular, and the height of the pelvic inlet is strongly sexually dimorphic.

Groves and Mazák (1967) argued that the kiang, of the Tibetan plateau, is a distinct species from the onagers of the more low-lying Asian deserts. The differences are very striking and this separation has been widely followed. The subspecies *onager*, *kulan*, *hemionus*, and *castaneus* form an intergrading series, overlapping (at the extremes) in their traits, but each strongly distinct as a unit. The subspecies *hemippus* is much smaller than any other and as a result is in fact a diagnosable taxon (in the PSC sense), while the supposed subspecies *E. h. khur* is also, unexpectedly, diagnosable.

***Equus kiang*** Moorcroft 1841: kiang

**Description:** The kiang or Tibetan wild ass is of large size, with its large head and thick muzzle, a relatively long mane, and long hairs, which are not restricted to the tail

tuft, but extend some way up either side of tail. The pattern on the contrasting dark (reddish) body blocs and white underside is characteristic; the demarcation between them on the flank is oblique from withers to mid-flank, and the white rump patch is infused with the reddish tone of the haunch. The dorsal stripe is thin and never bordered with white, and it extends to tail tuft. A dark ring surrounds each hoof, whilst the ear measures 165–178mm long.

The skull resembles *E. hemionus*, although 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.

For skull measurements, see Table 8.1.

1. ***Equus kiang kiang*** Moorcroft 1841: Western kiang

1841 *Equus kiang* Moorcroft. Eastern Ladakh.

**Colour:** The colour is dark red-brown in summer, dark brown in winter. The size is large, the nasal bones short, and the tooththrow relatively short.

**Localities:** “Little Tibet” (=Ladakh); Shooshal, Ruckshal; Kuluang and Chibra, both Hanle; L.Tsor Chum and Takalung, both Rupshu; Spanglung; Apo Tso, Sundschilling Plain; Gunlay, >5,000m; Gnari Khorsum.

2. ***Equus kiang holdereri*** Matschie 1911: Eastern kiang

1911 *Equus (Asinus) kiang holdereri* Matschie. Kuku Nor.  
1924 *Microhippus tafeli* Matschie. Tosson Nor.

**Colour:** The colour is not so dark, and is a strong red in summer, whilst darker red-brown in winter. The white of the underside advances higher up the flanks, and the size is large, the nasals very long, and the tooththrow also long.

<b>Table 8.1. Skull measurements of <i>Equus kiang</i> (mm).</b>			
	<i>E. h. kiang</i>	<i>E. h. holdereri</i>	<i>E. h. polyodon</i>
<b>Males</b>	10	6	4
Greatest length	518.4 (492–537)	533.5 (525–547)	475.0 (473–479)
Nasal length	200.3 (179–217)	220.2 (214–226)	195.5 (191–197)
Tooththrow length	161.1 (155–167)	168.3 (164–173)	158.8 (153–165)
<b>Females</b>	5	8	3
Greatest length	514.2 (504–531)	552.1 (495–538)	481.0 (474–494)
Nasal length	203.7 (200–208)	223.3 (212–238)	198.3 (192–205)
Tooththrow length	154.0 (145–163)	165.1 (158–171)	155.7 (151–160)

**Localities:** Tosson Nor; Wahou Mts., 4,000–4,500m, north-east of Tosson Nor; Kuku Nor (=Ching Hai); Seshu, Sichuan; Lhasa.

3. *Equus kiang polyodon* Hodgson 1847: Southern kiang

1847 *Asinus polyodon* Hodgson. Tibet, just north of the Sikkim border (fixed by Groves and Mazák, 1967).  
1959 *Hemionus kiang nepalensis* Trumler. “Nepal”; more probably the region of Tibet just north of the Sikkim border (see Groves and Mazák, 1967, who discuss the status of the skin and skull of the type specimen).

**Colour:** The colour is as dark as in *E. k. kiang*, the size very small, and the nasals and toothrow are long, as with *E. k. holdereri*.

**Localities:** Gyam Tso (=Lake); Sikkim.

***Equus hemionus* Pallas 1775: onager**

**Description:** The onager varies from kiang-sized to khur-sized. The mane is very short – “clipped”, and 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 bloc and whitish underside runs parallel to the body outline, before turning sharply up towards the dorsal stripe; the dorsal stripe extends to tail tuft; and there is a dark ring round each hoof. Nasal bones are relatively straight and the skull resembles *E. kiang*.

For skull measurements, see Table 8.2.

1. *Equus hemionus castaneus* Lydekker 1905: Xinjiang kulan or dziggetai

1905 *Equus onager castaneus* Lydekker. Supposedly from Kirghis Nor, Kobdo (now Jirgalanta)

1911 *Equus (Asinus) hemionus finschi* Matschie. North-east of Zaisan Nor

**Description:** The height at withers is 110–130cm. The dorsal stripe has a clear white border on either side, which becomes obfuscated with age and eventually disappears. At least the lower 30% of flank is whitish. The white wedge between the haunch and flank is clear, white, but does not reach the spine. The legs are strongly infused with body tone. The white zone on the muzzle occupies nearly half of the snout-to-ear distance. On the head, the demarcation between reddish tone of the face and the white of the interramal region cuts diagonally across the jaw angle. In the skull, the orbit sits high and tends to interrupt the dorsal outline, whilst the nasals are low and straight; the highest point on the profile is just behind the posterior margin of the orbits.

**Localities:** Urungu, 350km south-west of Kobdo; Ebi Nor; Dzungaria; “Desert Kirgisorum”; Kichik-Ulan-Ussu, west of L. Barkul, N. Tienshan. A head-skin in the London collection from Golodnaig Steppe, Bokhara (London Zoo, 1907–1916) is identified with this subspecies, rather than *E. h. kulan*, because the white on the muzzle extends fully halfway to the eye, and the same is true of two skins from the Zaisan Nor region in Berlin (one of them being the type of *finschi*).

Groves and Mazák (1967) called this subspecies *Equus hemionus hemionus*, but recently it has been argued by Denzau and Denzau (1999) that Transbaikalian dziggetai were “grading”, like those from the Gobi, so the disruptively-coloured form has to be called *E. h. castaneus*. Groves and Ryder (2000) accepted this argument.

There is, unfortunately, no recent evidence that this attractively patterned subspecies continues to exist.

**Table 8.2. Skull measurements of *Equus hemionus* (mm).**

	<i>E. h. hemionus</i>	<i>E. h. castaneus</i>	<i>E. h. kulan</i>	<i>E. h. onager</i>	<i>E. h. Blanfordi</i>
<b>Males</b>	13–15	1	4–8	8–9	1
Greatest length	518.0 (504–544)	518	495.7 (487–503)	491.1 (479–501)	484
Occiput br.	54.1 (50–58)	59	52.0 (45–55)	59.8 (57–66)	42
Diastema l.	80.5 (76–90)	91	77.4 (70–83)	72.6 (63–82)	70
Nasal l.	215.0 (205–226)	205	199.5 (195–203)	202.8 (186–214)	245
Toothrow	166.3 (153–171)	152	156.1 (149–163)	164.1 (159–176)	-
<b>Females</b>	12–13	4–5	7–8	5–6	1
Greatest length	510.4 (489–527)	516.0 (497–525)	492.0 (475–502)	487.5 (469–509)	498
Occiput br.	53.9 (47–64)	56.4 (52–63)	48.7 (45–51)	53.8 (51–59)	53
Diastema l.	83.1 (75–102)	81.0 (70–94)	80.3 (68–93)	74.3 (56–85)	72
Nasal l.	213.4 (193–232)	214.8 (199–231)	195.4 (189–205)	198.2 (174–214)	198
Toothrow	165.9 (158–174)	168.3 (163–174)	161.8 (152–175)	154.8 (145–168)	158

2. *Equus hemionus hemionus* Pallas 1775: (= *E. h. luteus*) Gobi kulan or dzigetgai

1775 *Equus hemionus* Pallas. Tarei Nor, Transbaikalia  
1911 *Equus (Asinus) hemionus luteus* Matschie. Surin Gol, Ganssu

1911 *Equus (Asinus) hemionus bedfordi* Matschie. Supposedly from Kobdo (now Jirglanata), Mongolia

**Description:** The size is as in *castaneus*. The colour pattern is very graded, with hardly any real demarcation between the sandy tone of the flanks and the yellow-white of the underside; only the lower 20% or less of the flank is whitish. No white border exists to the dorsal stripe at any age. The white wedge between the haunch- and flank- blocs is vague and strongly infused with body tone. The legs are very strongly infused with body tone. The white zone on the muzzle occupies less than 30% of the snout-to-ear distance. On the head, the demarcation between the reddish tone of the face and the white of the interramal region follows the curve of the jaw angle. The skull resembles *E. h. castaneus* in size, nasal form, and in the position of the highest point, but the orbit sits low on the profile because of the greater convexity of the interorbital space.

**Localities:** Transbaikalia; Surin Gol, between Chami (=Hami) and Su-tschou; Tsagan Nor, north of Bago Bogdo, eastward limit of Altay; Gobi Altay; Artsa Bogdo; Ikhe Bogdo; Loh; Tacin Gol. Denzau and Denzau have published some excellent, close-up photos of living examples taken at Chonin Us, Dzungarian Gobi, Mongolia.

The type specimen of *bedfordi* Matschie was figured by Lydekker (1905); it was a living animal shipped from Kobdo to the Duke of Bedford's collection; it was later donated to London Zoo, where it died in 1918. The skin and skull are now BM 1939.2472.

3. *Equus hemionus kulan* Groves and Mazák 1967: Turkmenistan kulan

1967 *Asinus hemionus kulan* Groves and Mazák. Badkhyz, Turkmenistan

**Description:** The height at withers is 108–120cm. It is less red than *E. h. hemionus*; in winter, the dark brown of the body is strongly demarcated from the white of the underside; in summer, the contrast is less strong. The dorsal stripe has a clear white border on either side; this becomes obfuscated with age and eventually disappears. On the head, the demarcation between the reddish tone of the face and the white of the interramal region cuts diagonally across the jaw angle.

The lower 30% at least of flank is whitish. The white wedge between the haunch- and flank-blocs is clear white, but does not quite reach the spine. Legs are strongly infused with body tone, and the white zone on the muzzle occupies nearly 40% of the snout-to-ear distance.

The skull is smaller than in *E. h. hemionus* and *castaneus*, but proportionally similar except for relatively larger teeth; the orbit is low like *E. h. castaneus*; the highest point may be back on the crown; the nasal ends may be slightly raised.

**Localities:** Badkhyz.

4. *Equus hemionus onager* Boddaert 1785: Persian onager or Gur

1785 *Equus onager* Boddaert. Qazvin, Iran  
1947 *Microhippus hemionus bahram* Pocock. Yazd, Iran

**Description:** The height at withers is 108–126cm; the weight of six adults (not extremely aged) from Hamburg Zoo was between 179–220kg. The demarcation between the brown of the body and the white of the underside is less strong with more grading at comparable seasons, than in *E. h. kulan*. The dorsal stripe has a clear white border on either side, which becomes obfuscated with age and eventually disappears. On the head, the demarcation between the reddish tone of the face and the white of the interramal region follows the curve of the jaw angle. At least 30% of the lower flank is whitish. The white wedge between the haunch- and flank-blocs is vague, and strongly infused with body tone. The legs are strongly infused with body tone. The white zone on the muzzle occupies 30% or less of the snout-to-ear distance.

The skull size and general shape are the same as those of *E. h. kulan*, but with a broader occipital crest. The male has even larger teeth. The orbit is high-placed – the highest point always being on the crown. Eisenmann and Shah (1996), using larger samples than those available to Groves and Mazák (1967), confirm that this subspecies differs craniometrically from *E. h. kulan*, but also note that it exhibits unusually wide variability.

**Localities:** Abarguh; Siakuh, west of Tehran; Siah Parde, near Tehran (now in Kavir National Park); Damghan Province, near Semnan; 50km south-west of Garmab, Dasht-i-Kavir. A clear, close-up photo taken by Mr Bijan Dareshuri in Touran Reserve, north-east Semnan Province, Iran, shows an animal with more white on the jaw angle than those from these more westerly localities (including the Hagenbeck-import

zoo stock, and a clear photo by the same photographer taken in Bahram-e-Gur Protected Area), and it also appears to have more white on the muzzle; this suggests some approach towards *E. h. kulan*. The graded coloration and inconspicuous stifle-wedge are, however, very typical of *onager*.

5. *Equus hemionus blanfordi* Pocock 1947

1947 *Microhippus hemionus blanfordi* Pocock. Sham Plains, Baluchistan

**Description:** These have a skull size similar to *E. h. kulan* and *onager*, with a relatively narrow occipital crest, and long nasals that end slightly raised; the orbit is high-placed; the highest point on the skull is either just behind the orbit or on the crown.

This subspecies is not, *contra* Groves and Mazák (1967), intermediate between *onager* and *khur*. It has the low flat nasals, short diastema, large teeth, and extensive dark areas on flanks that are characteristic of what is here regarded as the species *Equus hemionus*. The main point of similarity with *E. khur* is that the dorsal stripe fades out halfway down the tail.

**Localities:** Sham Plains, near Quetta; Kandahar.

***Equus khur*** Lesson 1827: (= *Equus hemionus khur*)  
Khur; Indian wild ass

1827 *Equus khur* Lesson. Little Rann of Kutch (fixed by Groves and Mazák, 1967)

1862 *Asinus indicus* George 1869. India

**Description:** The Indian wild ass or khur is sharply distinct from *E. hemionus*. The coloured blocs on the flank and haunch are very small, so the predominant colour is white, and the lower 45% or more of the flank is whitish; the demarcation on the lower haunch slants upward from front (stifle) to back. The dorsal stripe has a clear white

border on either side, which becomes obfuscated with age, but probably never entirely disappears. The white wedge between haunch- and flank-blocs nearly or fully reaches the spine. Legs are pure white. The white zone on the muzzle occupies nearly 40% of the snout-to-ear distance. On the head, the demarcation between the reddish tone of face and the white of the interramal region cuts diagonally across the jaw angle. The dorsal stripe fades out halfway down tail. There are no dark rings around the hooves.

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

For skull measurements, see Table 8.3.

**Localities:** Kutch; Thar Parkur, Sind.

***Equus hemippus*** I. Geoffroy St Hilaire 1855: (= *Equus hemionus hemippus*) Syrian wild ass

1855 *Equus hemippus* I. Geoffroy St. Hilaire. Syria

1869 *Equus hemionus* var. *syriacus* Milne-Edwards. Damascus.

The extinct Syrian Wild ass or Achdari was very small in size; the evidence implies that this difference has come about since the end of the Pleistocene (Turnbull 1986).

**Description:** The height at withers is about one metre. The colour is very grading: the sandy-brown flank patch extends well down, grading into off-white on the underside; only the lower 20% or less of the flank is whitish. The dorsal stripe has a clear white border on either side, which becomes obfuscated with age, and eventually disappears. The white wedge between the haunch- and flank-blocs is vague and strongly infused with the body tone. The legs

**Table 8.3. Skull measurements of *Equus khur* and *E. hemippus* (mm).**

	<i>E. khur</i>	<i>E. hemippus</i>
<b>Males</b>	3	3
Greatest length	505.3 (493–519)	412.7 (403–419)
Occiput breadth	60.0 (57–62)	44.3 (35–49)
Diastema length	86.3 (82–92)	52.7 (50–55)
Nasal length	189.3 (184–194)	179.3 (174–189)
Toothrow length	149.3 (140–156)	142.3 (140–145)
<b>Females</b>	6	5–6
Greatest length	492.3 (468–511)	423.0 (409–439)
Occiput breadth	54.2 (49–60)	47.0 (44–49)
Diastema length	79.5 (71–92)	58.5 (52–61)
Nasal length	181.8 (171–198)	189.7 (183–198)
Toothrow length	155.4 (152–160)	146.7 (145–149)



are also strongly infused with body tone. The white zone on the muzzle occupies under 30% of the snout-to-ear distance. On the head, the demarcation between the reddish tone of the face and the white of the interramal region follows the curve of the jaw angle. The dorsal stripe fades out halfway down the tail, and there are no dark rings around the hooves.

The nasal bones are raised and are longer than in other onagers (Groves 1986, Fig. 1), whilst the teeth are relatively large. Otherwise, the skull, with its concave profile, high-placed orbit, and high crown, resembles that of a small *E. khur*. The metapodials are more elongated than in other species, and the terminal phalanges are shorter.

For skull measurements, see Table 8.3.

**Localities:** Aleppo.

### 8.3.3 Subgenus *Asinus*: true asses

These asses are characterised externally by a long, thin “scruffy” mane, a tufted tail, chestnuts on the forelimbs only, a thin dorsal stripe, usually with traces of stripes on the legs (at least the fetlocks) and a restricted white (or pale) region on the underside. Cranially, it is distinguished by a very long cranium, a short palate, long diastema, and large pterygopalatine fossa, and a squared, upturned occipital crest. The nasal end of the premaxilla is narrow and insinuated into the corner of the narial notch. The external auditory meatus is wide; the orbit is high, rounded, and not anteroposteriorly elongated like other subgenera (except *Hippotigris*). Postcranially, it has a short scapula and very short, narrow distal phalanges. The metacarpus is short compared to the metatarsus. Biischial breadth is high compared to biacetabular breadth, and the height of the pelvic inlet is strongly sexually dimorphic.

Eisenmann (1995) has recently reviewed the palaeontological evidence for the evolution of the genus, and the evidence for extinct early Holocene populations.

***Equus africanus*** Heuglin and Fitzinger 1866: African wild ass

**Description:** All African wild asses tend to be more reddish in summer, greyer in winter, with contrastingly white legs and 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.

For skull measurements, see Table 8.4.

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, in the 1960s by Hufnagel (1965). Eisenmann (1995) discusses whether the name *Equus melkiensis* Bagtache, Hadjouis and Eisenmann 1984 (from the late Pleistocene of Allobroges, Algeria) might apply to this form. In the earliest Holocene, wild asses were also present in northern Arabia (Ducos 1986; Groves 1896); 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.

1. *Equus africanus africanus* Heuglin and Fitzinger 1866: Nubian wild ass

*Asinus africanus* Heuglin and Fitzinger 1866. Ain Saba, Eritrea (fixed by Schlawe 1980).

*Asinus asinus diana* Dollman 1935. Wadi Hafta, Tokar, Red Sea Hills.

**Description:** The ears are longer than other subspecies, measuring 182–245mm; the shoulder height averages 115–121mm; the hooves are narrow, and the breadth of its sole is 69–84% of its height. A dorsal stripe is always present and nearly always complete from mane to tail-tuft. Leg-stripes, where present, are restricted to a few bands at the fetlocks. The skull length is usually less than other subspecies; the diastema is relatively short, and the postorbital constriction well marked. The orbit is high-placed, generally interrupting the dorsal cranial profile in lateral view; the crista facialis extends forward to above the first molar. The nasal process of the premaxilla ends bluntly. There is never a “bridge” between the metaconid and the metastylid in the lower premolars and molars.

As shown by Groves (1986), specimens from the Atbara differ, on average, from those from the Red Sea Hills (Sudan) and Eritrea.

In the Atbara population, the colour is more buffy (reddish-buff in summer, brown-grey in winter); the transverse stripe across the shoulder is thick (15–65mm at spine), well-marked, but usually short (110–150mm long, although it occasionally extends up to 230mm). The diastema is shorter and the occipital crest is narrower. In this population there are never even traces of leg-stripes.

In the Red Sea population, the colour is greyer (reddish-grey in summer, ashy-grey in winter); the shoulder-cross is nearly always thin (12–24mm at the spine) and poorly expressed, and sometimes absent altogether – when present, the length is between 100

and 150mm. The diastema is longer and the occipital crest broader.

These differences are fairly pervasive, and probably reach the 75% rule-of-thumb for subspecific differentiation. I will investigate the problem further to see if a new subspecies ought to be described for the Atbara.

Localities for Nubian wild asses are as follows:

1. <i>E. a. africanus</i> , Atbara population:	N	E
Jalalub (?=Gulalab)	18.15	33.45
Nakheila (South bank of Atbara)	17.25	34.18
Regeb, Atbara		
Ruins of Wadi Safra	16.53	35.49
Kassala	15.24	36.30
“Abyssinia east of the Nile”		
2. <i>E. a. africanus</i> , Red Sea population:		
Plains south of Erkowit	18.49	37.01
Khor Sabbat, Tokar Plain	18.27	37.41
Agahet el Homar	18.08	37.12
Wadi Sharag	17.52	37.57
Wadi Hafta	17.43	37.30
Ain Saba	16.00	38.00
Upper Barca (=Baraka)	15.50	37.20

2. *Equus africanus somaliensis* Noack 1884: Somali wild ass

1884 *Equus somaliensis* Noack. Berbera, Somalia.

1885 *Equus asinus somalicus* Sclater. Based on the same specimens as Noack’s name.

**Description:** As in previous papers, I reiterate my opinion that *Asinus taeniopus* Heuglin (type locality: Little Dobar, south of Berbera) is a cross between a Somali wild ass and a domestic ass. The ears are short, measuring some 187–200mm; the shoulder height is 120–125mm; the hooves are wider, with the breadth of the soles being 89–90% of their height (N.B. taken from only two specimens!). The dorsal stripe is often absent and, when present, is often incomplete and broken at some point along the dorsum. The shoulder-

cross, when present, is 130–200mm long, but only 20mm broad where it crosses the spine. Leg-stripes are present from the hooves to above the carpus and tarsus. Skull length averages greater; the diastema is relatively long, and the postorbital constriction less marked. The orbit is placed well below the cranial dorsal outline; there is a thickened bar of bone behind the orbits, marking the highest point on the profile; the crista facialis extends to the posterior premolar region. The nasal process of the premaxilla is thin and pointed. There is always at least a trace of a “bridge” between the metaconid and the 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 are less marked than those between the two populations of *E. a. africanus*. The more northerly individuals (from Danakil and Djibouti) more frequently have a shoulder-cross and they are less iron-grey; the single available adult skull has a rather narrow occipital crest and only a weakly expressed metaconid-metastylid bridge.

Localities for *E. a. somaliensis* are as follows, with coordinates where known:

	N	E
Assaorta, Plain of Salt		
Assab		
Curub-Bahari, plains near Cayele		
Near Sardo	11.58	41.18
Obock, Djibouti	11.59	43.20
Issituggan valley, south of Bulhar	10.30	44.20
Hekebo Plateau, S.E. of Bulhar		
50 miles from Berbera	10.30	45.30
Bir Kaboba	10.26	42.38
Lafa Rug, between Hargeisa and Berbera	10.00	44.42
Haili, Durhan	10.09	46.14
Las Dureh (Lasdero, Durhan)	10.09	46.00
South of Upper Sheikh	9.56	45.13
Cianno, near Ebili, Awash River		
Road by L. Abiata		

**Table 8.4. Skull measurements of *Equus africanus* (mm).**

	<i>E. a. africanus</i> Atbara	<i>E. a. africanus</i> Red Sea	<i>E. a. somaliensis</i>
<b>Males</b>	5	1	6
Greatest length	515.2 (483–526)	503	520.3 (513–543)
Occiput breadth	56.4 (53–60)	66	63.0 (57–68)
Diastema length	78.6 (74–83)	87	87.2 (85–105)
Postorbital br.	73.4 (71–80)	77	82.2 (75–87)
<b>Females</b>		3–4	7
Greatest length		502.3 (485–528)	517.6 (507–544)
Occiput breadth		59.3 (57–61)	59.7 (53–64)
Diastema length		80.8 (78–92)	89.9 (79–94)
Postorbital br.		66.0 (63–68)	79.1 (74–87)

L. Hertale, east of Addis Abeba	9.55	40.24
Nogal valley, Las Anod, Dodi Plain	8.26	47.19
Wadi Run, upper Nogal	8.30	48.50
Imi, Webi Shebeli	6.28	42.10

### 3. *Equus africanus* subspecies: Saharan wild ass

1966 *Equus asinus africanus sahariensis* Dupuy. Nomen nudum.

**Description:** Best authenticated for Ahaggar, Tibesti, and Fezzan, the (apparently indigenous) wild ass of the Sahara was reconstructed by Groves (1986) as similar to *E. a. africanus*, but smaller and greyer, and with a long, thin shoulder-cross.

#### 8.3.4 Subgenus *Hippotigris*: Mountain zebras

Characterised externally by the long, rather thick upright mane, tufted tail, chestnuts on forelimbs only, small dewlap, and striking black and white stripes (except on venter) that form what has been called a “gridiron” pattern (with short transverse stripes meeting the uppermost of a long, thick, oblique/longitudinal series) on the croup.

Cranially, the occiput is high and raised, the postorbital constriction deep, the muzzle and vomer long, whilst the nasal end of the premaxilla is truncated or rounded, so that the nasal forms the angle of the narial notch. The external auditory meatus is wide and (uniquely) directed horizontally instead of upward and backward. The ventral bar of the orbit, which is high and rounded like that of asses, is slender. Postcranially, the scapula is short; the distal phalanges are short and narrow. The metacarpus is long compared to the metatarsus. The skull is relatively large. The biischial breadth is low compared to the biacetabular breadth, and the height of the pelvic inlet is not strongly sexually dimorphic.

***Equus zebra zebra*** Linnaeus 1758: Cape mountain zebra

1758 *Equus zebra* Linnaeus. Paardeberg (fixed by Roberts 1951)

1822 *Equus montanus* Burchell. “Wagenpadsberg [=Wagenpadskop?], beyond the Snow Mountains” (see Grubb, 1999).

1905 *Equus zebra frederici* Trouessart. Northern Cape

Mountains of Southern Cape.

**Description:** The size is smaller, and black stripes are broader than white interspaces. Groves and Ryder (2000) proposed that the two subspecies could be better treated as

distinct species; they are instantly recognisable externally and some of the skull measurements do not overlap, although sample sizes are small. For example, the occipital crest breadth is 63–71mm in male *zebra*, 74–78mm in male *hartmannae* (n=5 of each); 63–68mm in female *zebra*, 70–86mm in female *hartmannae* (n=3 and 6, respectively). In the present sample, there is a sexual size difference in *zebra* (mean skull length is 516.0mm in males and 530.8mm in females, although  $P>0.05$ ), but not in *hartmannae* (548.0mm and 549.9mm respectively).

Smuts and Penzhorn (1988) claimed that females have a broader occipital crest than males, but this does not hold in my opinion.

***Equus hartmannae*** Matschie 1898: (= *Equus zebra hartmannae*) Hartmann’s zebra

1898 *Equus hartmannae* Matschie. Between Hoanib and Unilab Rivers

1900 *Equus penricei* Thomas. Moninho valley, Angola

1924 *Hippotigris hartmannae matschiei* Zukowsky. Swakopmund, Namibia.

Arid, hilly regions from southern Angola formerly to north-western Cape.

The size is much larger, and the black stripes are narrower than the white interspaces.

#### 8.3.5 Subgenus *Quagga*: Plains zebras

Externally, the mane varies from long, thick, and neat to shorter, thinner, and even absent altogether; the tail is tufted and chestnuts exist on the forelimbs only; striping varies from dark brown and white on the 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.

Postorbital constriction is relatively narrow, the vomer is long, the diastema long, the teeth relatively small, and the occiput extremely raised. The narial notch is less deep than other subgenera. The interorbital part of the frontal bone is strongly convex. The bizygomatic width generally exceeds that of the biorbital. The nasal end of the premaxilla is narrow and insinuated into the corner of the narial notch. The premaxilla, unlike other subgenera, curves downward below the level of the alveolar line of the cheekteeth. The tuber maxillae extends back, hiding the pterygopalatine fossa in ventral view, like *Hemionus* and unlike other subgenera. The foramen magnum is a uniquely rectangular shape. The metapodials are somewhat lengthened. The metacarpus is long compared to the metatarsus. The distal phalanges are less reduced than in *Hippotigris*. The biischial breadth is low compared to the biacetabular breadth; the height of the pelvic inlet is not strongly sexually dimorphic.

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 the subgenus *Quagga* is unlike any other subgenus.

***Equus quagga* Gmelin 1788: (= *Equus burchellii*) Plains zebras**

The true Quagga (*E. q. quagga*) lived west of the Drakensberg and south of the Vaal-Orange system. The

available museum material was fully discussed by Rau (1974, 1978), who showed that there was no sharp division between it and *burchellii*, to the extent that some specimens (especially the Mainz female and another specimen in Mainz, the type of *paucistriatus* Hilzheimer) are difficult to allocate; they are surely correctly placed in the same species. The physical barriers between the two are, however, sufficient to make a 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

**Table 8.5. Distinguishing characters of living subspecies of *Equus quagga* (measurements in mm).**

	<i>burchellii</i>		<i>zambeziensis</i>		<i>crawshayi</i>	<i>boehmi</i>		
	Zulu	Etosha	SE Afr	Angola	WZam.	all	EAFr	NW
<b>Skull: Male</b>								
Mean	518.3	530.5	531.2	535.1	-	522.2	501.3	527.2
s.d.	19.14	11.88	11.56	15.98	-	13.31	16.09	14.92
n	6	6	16	7	-	20	64	13
Range	500–552	508–542	509–548	504–553	-	489–545	450–548	498–540
<b>Skull: Fem.</b>								
Mean	513.5	524.5	525.1	545.8	522.0	520.3	496.4	517.4
s.d.	23.05	13.77	17.47	12.37	12.83	12.51	16.85	9.56
n	6	4	10	4	4	10	47	5
Range	476–540	516–545	500–557	530–559	510–540	500–534	466–547	511–534
<b>Belly stripes</b>								
3–4	5	23	36	4	7	-	25	3
5	-	-	2	-	1	13	3	-
>5	-	-	-	-	-	15	-	-
<b>Body colour</b>								
ochery	2	8	5	1	2	-	-	-
off-wh	2	6	25	3	2	10	7	-
white	-	-	-	-	4	18	27	3
<b>Shad stripes</b>								
++	5	10	2	-	-	-	-	-
+	1	21	27	3	1	-	3	-
±	-	4	23	2	2	1	13	-
-	-	-	6	1	5	29	36	4
<b>Leg stripes</b>								
—	-	5	1	-	-	-	-	-
-	5	10	2	-	-	-	-	-
±	6	14	15	-	-	-	-	-
+	1	3	24	5	-	-	-	-
++	-	-	3	1	7	28	52	4
<b>Infun.</b>								
pres.	1	2	3	1	-	1	1	-
cup	-	-	6	6	1	10	15	-
abs.	-	-	1	-	-	7	11	4
<b>Abbreviations:</b>								
Skull: greatest skull length. Belly stripes: number of stripes making contact with median ventral line between elbow and “saddle”								
Shadow stripes: ++ broad, approaching prominence of main stripes								
+								
less well expressed but still noticeable								
±								
vaguely expressed								
-								
absent								
Leg stripes: — none; stripes barely reaching even to haunch								
-								
none, but stripes do cover haunch								
±								
a few stripes above carpus and tarsus								
+								
stripes present, broken, below carpus and tarsus								
++								
stripes complete to hooves								
Infun: presence of infundibulum on I <sub>1,2</sub>								

to 528mm in length, and so average smaller than other subspecies apart from *boehmi*.

For skull measurements and other distinguishing characters of the surviving subspecies of *E. quagga*, see Table 8.5.

1. *Equus quagga burchellii* Gray 1824: (= *Equus burchellii burchellii*, *Equus burchellii chapmani*, *Equus burchellii antiquorum*) Burchell's zebra

1824 *Asinus burchelli* Gray. Little Klibbolikhoni Fontein (=Modder River, Northern Cape at 27°33'S, 23°33'E, according to Skead, 1980).

1841 *Hippotigris antiquorum* Hamilton Smith. Molopo (Mafeking district), Northern Cape (see Grubb 1999).

1841 *Hippotigris isabellinus* Hamilton Smith. Apparently based unknowingly on the same specimen as *antiquorum* (Grubb 1999)

1865 *Equus chapmani* Layard. Between Zambezi and Botletle Rivers, Botswana (=about 30 miles east of the south-flowing loop of the Boteti River, according to Grubb, 1999)

1897 *Equus burchellii wahlbergi* Pocock, 1897. Kwazulu-Natal

1897 *Equus burchellii selousi* Pocock. Manyami valley, Zimbabwe

1897 *Equus burchellii transvaalensis* Ewart. Northern former Transvaal

1912 *Equus (Hippotigris) kaufmanni* Matschie. Caprivi Peak.

1924 *Hippotigris chapmani kaokensis* Zukowsky. Kaokoveld, Namibia

**Description:** Their size is large. Three or four stripes (very rarely two or five) meet (or sometimes 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. The colour is ochery or off-white, but never pure white. The shadow stripes are usually well marked, and the leg stripes are absent or poor, and almost never complete to hooves. The infundibulum on the lower incisors is better expressed than in other subspecies. The mane is well developed.

This subspecies exists (or existed) throughout southern Africa, from Kwazulu-Natal north to the Zambezi, but not it seems in Mozambique, except for the southernmost part; published photos of zebras from Gorongosa, for example, are clear *crawshayi*. Populations in Zimbabwe and former Transvaal average palest, being offwhite, more rarely ochery, with less strikingly marked shadow stripes and more complete leg stripes than other populations. Those from Kwazulu-Natal and northern Namibia (Etosha and Kaokoveld) average more ochery with

stronger shadow-stripes and fewer leg-stripes; as a whole, these two populations, though geographically separate, strongly resemble each other, although shadow stripes are stronger in Kwazulu-Natal and leg stripes are less developed in Namibia, where the haunch itself may even be unstriped. The Kwazulu-Natal population averages smaller than the other two.

Some may prefer to regard these three populations as distinct subspecies from each and from *burchellii*, in which case the prior names are *chapmani* (Zimbabwe/Transvaal), *wahlbergi* (Kwazulu-Natal) and *kaokensis* (Etosha/Kaokoveld), though the name *burchellii* probably takes precedence over *wahlbergi* (see below). But the overlap in characters is so great that many specimens could not be correctly identified; overlap is least in leg-striping (Table 8.5).

Rau (1978) has pointed out how little evidence there is for "the extinct true Burchell's Zebra"; the distinguishing feature from extant forms (that is, the failure of the flank stripes to meet the median ventral line at all) is sometimes seen in Kwazulu zebras, as well as in the type (from the Kuruman district), and in a zoo specimen known only to have been from Botswana. There is as little evidence that such a feature typified the zebras from the Free State and that it was confined to them.

2. *Equus quagga crawshayi* de Winton 1896: (*Equus burchellii crawshayi*) Crawshay's zebra

1897 *Equus burchellii crawshayi* de Winton. Henga, Malawi

1899 *Equus (Hippotigris) foai* Prazak and Trouessart. Mozambique, opposite Tete

1906 *Equus annectens* Rothschild. Fort Jameson, Zambia.

**Description:** The size is large. Stripes are numerous and narrow; always at least five stripes (often six to eight) meet the median ventral line between the elbow and the "saddle" stripe. The body tone is white or off-white. There are almost never even traces of shadow-stripes, and leg stripes are complete to hooves.

This is the subspecies from east of the Luangwa, as far north-east as the Tendaguru district, south-eastern Tanzania; but it also occurs south of the Zambezi in Mozambique as far as the Gorongosa district.

3. *Equus quagga zambeziensis* Prazak 1898: (= *Equus burchellii zambeziensis*) Upper Zambezi zebra

1898 *Equus burchellii zambeziensis* Prazak. Barotse, Upper Zambezi.

**Description:** The size is large and stripes are broad, of which only three or four meet the median ventral line between the elbow and the “saddle” stripe. Colour varies from ochery through off-white to white. Shadow-stripes vary from fairly prominent to absent. Leg stripes are usually complete, or nearly so.

Externally, this subspecies most resembles *E. q. boehmi*, but is separated from it by *E. b. crawshayi*. Angolan and western Zambian populations differ somewhat. The Angolan population averages larger and more ochery, with better shadow-stripes and more broken leg-stripes; in other words, it somewhat approaches *E. q. burchellii*, although it is the Zimbabwe/Transvaal population that it resembles, and is strikingly different from the nearby Namibian population.

4. *Equus quagga boehmi* Matschie 1892: (= *Equus burchellii boehmi*) Grant's zebra

1892 *Equus boehmi* Matschie. Pangani River, Tanzania

1896 *Equus burchellii granti* de Winton. Thika, upper Tana River, Kenya

1902 *Hippotigris chapmanni jallae* Camerano. Southern Ethiopia?

1906 *Hippotigris muansae* Matschie. Mwanza, N.W. Tanzania

1911 *Equus quagga* var. *goldfinchi* Ridgeway. Rift valley, Kenya

1914 *Equus quagga cunninghamei* Heller. Archer's Post, north-east Kenya

1922 *Equus borensis* Lönnberg. Bor, south-east Sudan

1959 *Zebra burchelli isabella* Ziccardi. Lower Juba, Somalia

**Description:** The size is small, and the stripes are few and broad – rarely more than three or four meet the median ventral line between elbow and “saddle” stripe. The colour is generally pure white. Shadow-stripes are usually absent, but sometimes are vaguely expressed. Leg stripes are always complete to the hooves. The infundibulum is generally absent.

The northerly populations of this subspecies have high frequencies of manelessness. From Mt Kenya, north-west via Lake Baringo to Karamojong and the south-eastern Sudan, manes are, in three-quarters of individuals, either sparse and tufty or completely absent; inadequate evidence suggests that the situation is the same north-east of Mt Kenya (the type of *granti*, from the upper Tana River, is maneless) to the Juba River in Somalia, where the character is apparently fixed.

In these same populations, the ears are either very vaguely striped or completely white. A maneless, white-eared zebra brought from “Abyssinia” to the Emperor Jahangir's court in Delhi is depicted in a Mughal

painting of 1621, now in the Victoria and Albert Museum, London.

There might be grounds for recognising a distinct subspecies with these two characters, except that another character, size, separates the north-eastern and north-western populations. The north-eastern zebras average small like other *boehmi* or even smaller (mean skull length 496.2 in both sexes, n=6 males and six females), while the north-western ones are large, like the more southerly subspecies (Table 8.5).

### 8.3.6 Subgenus *Dolichohippus*: Grévy's zebras

Externally, it has a long thick upright mane, a tufted tail, chestnuts (very small) on the forelimbs only; there are short erect black hairs along the dorsal stripe; narrow, almost dazzling, black and white stripes occur over the whole body except venter and croup, and there is a complex triradial pattern on croup.

Cranially, the occiput is high and raised; the postorbital constriction is deep; the muzzle is long; the vomer is long. The nasal end of the premaxilla is rounded and wedged into the nasal. The scapula is lengthened. The metapodials are somewhat lengthened. The metacarpus is long compared to the metatarsus. The distal phalanges are small. The skull is very elongated, exceeding the cervical spine in length unlike other subgenera. The biischial breadth is low compared to the biacetabular breadth; the height of the pelvic inlet is not strongly sexually dimorphic.

#### *Equus grevyi* Oustalet 1882: Grévy's zebra

Provisionally, two subspecies can be recognised, based entirely on size, although they need to be tested on larger samples. There appears to be no sexual dimorphism in size in the species, so values for the two sexes can be combined; moreover, maximum size seems to be achieved by the time the second molars have erupted.

##### 1. *Equus grevyi grevyi* Oustalet 1882

1882 *Equus grevyi* Oustalet. Galla country, Ethiopia

1898? *Equus faurei* Matschie. Lake Rudolf (now Turkana), Ethiopia (the name ‘*faurei*’ is not definitely a synonym of *E. g. grevyi*).

1902 *Equus grevyi berberensis* Pocock. Ogadain, northern Somalia.

The greatest skull length recorded was 587.1mm (529–615mm; n=8).

**Localities:** Arussi; Webi River, 8°N, 41°E; Harrar; Diredawa; Northern Frontier District, Kenya. These all lie in the Somali Arid zone.

## 2. *Equus grevyi* subspecies

Greatest skull length was 624.0mm (608–639mm; n=7).

**Localities:** Meru; Guaso Nyiro; Longaya Water.

Three specimens from Archer's Post average 602.3mm (596–608mm), and five from Isiolo average 590.0mm (554–621mm). These are therefore intermediate, though closer, to the arid zone form.

## 8.4 References

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