

Equus (Plesippus) simplicidens (Cope), not *Dolichohippus*

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Summary. – Ever since Skinner (1972) compared the extant Grevy's zebra (*Equus grevyi* Oustalet) and the earliest known representative of the genus *Equus* (*E. simplicidens*) for their skulls and teeth and found similarities, *E. simplicidens* has been referred to the subgenus *Dolichohippus* together with *E. grevyi*. The meaningfulness of subgeneric categories in the structurally homogeneous genus *Equus* can be questioned. However, the primitive proportions of the basicranium of *E. simplicidens* do not allow uniting that species and *E. grevyi* within the same subgenus.

Résumé. – Depuis le travail de Skinner (1972), il est classique d'attribuer au même sous-genre (*Dolichohippus*), l'actuel Zèbre de Grévy d'Afrique de l'Est et le plus ancien *Equus* connu d'Amérique du Nord, *Equus simplicidens*. L'étude des proportions basi-crâniennes (distances basion - bord postérieur du vomer et bord postérieur du vomer - bord postérieur du palais) à l'aide de régressions montre que les deux espèces sont très différentes : *E. simplicidens* est beaucoup plus primitif qu'*Equus grevyi*.

INTRODUCTION

Heller (1912) erected a new genus *Dolichohippus* for the East African Grevy's zebra, *E. grevyi*. Skinner (1972) compared the skull and teeth of *E. simplicidens* from the Pliocene of North America with those of *E. grevyi*. He concluded that these species are closely similar and therefore referred also *E. simplicidens* to *Dolichohippus*, which he considered a subgenus of *Equus*. Since then *E. simplicidens* is usually referred to in paleontological texts as *E. (Dolichohippus) simplicidens*, e.g. in Kurtén and Anderson (1980).

Equus simplicidens is considered the earliest common ancestor of *Equus* and fits that position nicely in time, as indicated by mitochondrial DNA studies on the recent *Equus* species (George and Ryder 1986), but is separated from *E. grevyi* by > 1 Ma, by several species branchings, and geographically. Can *E. simplicidens* and *E. grevyi* really be united in a single subgenus ?

Although Skinner (1972) found cranial similarities (most of which are allometrically related to large skull size, however), he did not compare *E. simplicidens* and *E. grevyi* for their basicrania, e.g. for the proportions between the distances palatal rear border to vomer notch (PR-VN) and foramen magnum to vomer notch (FM-VN). This relation, often expressed as Franck's vomer index, is phylogenetically important: lengthening of the distance FM-VN during the evolution of *Equus* is believed to have led to the decrease of the index (Osborn 1912, Gromova 1949).

COMPARISONS

We compared the basicranial proportions of *E. simplicidens*, wild-caught *E. grevyi* and *E. hemionus* Pallas, and of fossil/subfossil true horse (*E. caballus* L. s.l.) (data own and from the literature: Nehring 1884, Hay 1917, Gromova 1949, Belan 1985). We plotted the skulls on the distance palatal rear border to vomer notch (PR-VN) to the distance foramen magnum to vomer notch (FM-VN) (Fig. 1), then fitted a major axis to each sample and compared the four axes for their position using the z-statistic (Miller

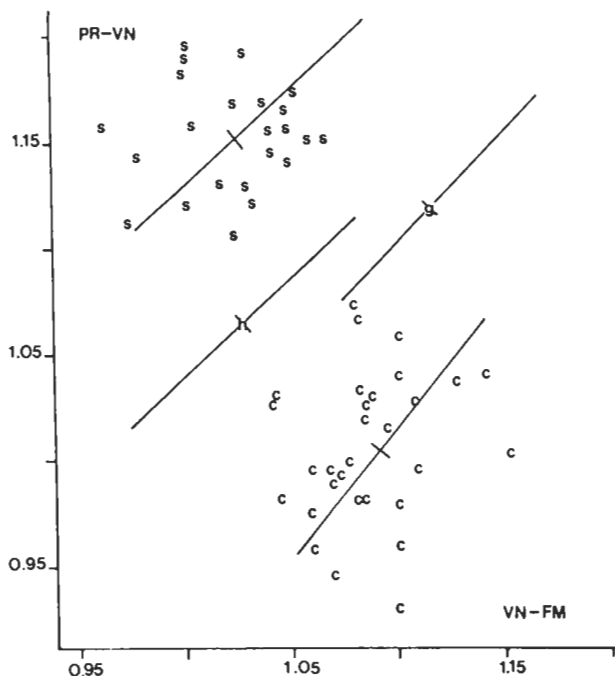


Fig. 1. — Palatal rear border (PR) to vomer notch (VN) logarithmic distance plotted to the logarithmic distance foramen magnum (FM) to vomer notch in fossil *Equus simplicidens*: s (number of specimens $n = 23$) and fossil/subfossil true horse, *E. caballus* s.l.: c ($n = 31$). Major axes fitted to these samples and to recent *E. grevyi*: g ($n = 54$) and *E. hemionus*: h ($n = 25$) samples.

and Khan 1962). The axes differ significantly in position (Table 1). Of the compared species, true horse has PR-VN shorter than FM-VN (Fig. 1 : c). In *E. grevyi* and *E. hemionus* these distances are equal or PR-VN is slightly longer than FM-VN (Fig. 1 : g, h). Of the other extant species, Plains zebra (*E. burchelli* (Gray), including Quagga) resembles the true horse, while the Mountain zebra (*E. zebra* L.) and African ass (*E. asinus* L.) resemble *E. grevyi*. *Equus simplicidens* (including *E. shoshonensis* Gidley, see Skinner 1972), on the other hand, has a long PR-VN in relation to FM-VN. Plotted on PR-VN to FM-VN, skulls of *E. simplicidens* are clearly separated from those of all extant *Equus* (Fig. 1 : s).

TABLE 1. – Comparison of the position of the major axes using the z-statistic (Miller and Khan 1962).

Species compared	z - value	significance
<i>E. simplicidens</i> - <i>E. grevyi</i>	6,58	+
<i>E. simplicidens</i> - <i>E. hemionus</i>	5,41	+
<i>E. simplicidens</i> - <i>E. caballus</i>	10,60	+
<i>E. grevyi</i> - <i>E. hemionus</i>	2,79	+
<i>E. grevyi</i> - <i>E. caballus</i>	8,19	+
<i>E. hemionus</i> - <i>E. caballus</i>	8,77	+

The placement of the skulls of *E. simplicidens* in the plot corresponds to a high vomer index. In *Pliohippus* (*Dinohippus*), considered the generic ancestor of *Equus*, the vomer index is also high (Eisenmann 1980, Fig. 39), thus a high index is primitive. *Equus grevyi* and the other extant species of *Equus*, with lower indices because of relatively longer FM-VN distance, are derived.

The character palatal rear border to vomer notch distance in relation to the distance vomer notch to foramen magnum has undergone evolution during the a. 4 Ma of *Equus* existence : the distance vomer notch to foramen magnum has become relatively longer. The functional significance is unknown.

The true or caballoid horses have the most derived character state, i.e. the relatively longest distance vomer notch to foramen magnum. This they share with the Plains zebra, including the Quagga, shown to be molecularly and morphologically similar to one another (Eisenmann 1980, 1986, Lowenstein and Ryder 1985, Higuchi *et al.* 1987). Already in the middle Pleistocene and possibly earlier (Eisenmann 1992), *E. mauritanicus* Pomel from North Africa, shows the derived basicranial proportions of Plains zebra (Eisenmann 1980, Table 8). On the other hand, *E. scotti* Gidley from the Irvingtonian of North America, dentally an early true horse, has *grevyi*-like basicranial proportions (data own and Gazin 1936, Table 1). Old World stenonid horses (Pliocene-early Pleistocene), with *simplicidens*-like teeth, plotted on their basicranial proportions fall in between *simplicidens* and *grevyi*, or between *grevyi* and *hemionus*.

Skinner (1972) commented on supposedly primitive characters of the limbs in *E. grevyi*, e.g. well-developed ulna and fibula and long splints. Gazin (1936 : 308, 312), however, noted that in *E. simplicidens* ulna and fibula are more reduced than in his comparative material of extant *Equus*, including *E. grevyi*. In all monodactyl horses the lateral metapodials or splints are equally reduced in length relative to the cannon bone (Robb 1936). *Equus simplicidens* and *E. grevyi* have long cannon bones, thus also long splints.

The enamel pattern of the teeth of *E. simplicidens* is primitive : in the uppers the protocone has a short heel and little lingual concavity ; a hypoconal lake often forms with wear. In the lowers a protostylid plication occurs. The shape of the metaconid-metastylid double knot is similar in *E. simplicidens* and the extant zebras, i.e. with a sharply V-shaped entoflexid lingually separating the loops.

CONCLUSIONS

Every extant species of *Equus* has been given its own (sub)generic name(s) ; Grevy's zebra several (see Skinner 1972 for synonyms). This (sub)generic (and accompanying specific) splitting is unnecessary in view of the structural homogeneity of the genus. The extant species form four groups (and probably six species) defined on mitochondrial DNA : the three zebras (heterogeneous for their vomer proportions), the Asiatic and African asses, and the true horse. *Equus simplicidens* with its primitive vomer proportions and teeth stands apart. It cannot be united with Grevy's zebra under a (sub)generic name common for these two species alone. If a subgeneric name be used for *E. simplicidens*, it should be *Plesippus* Matthew (1924).

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