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Indices in equid systematics and phylogeny

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Certain measurements on the equid skull, teeth, and limbs which are often used for calculating indices (ratios) considered taxonomically or phylogenetically significant are analysed in bivariate plots. The aim of the work is to investigate whether or not such indices are valid as used.

A major axis was fitted to the logs of the respective measurements plotted and the slope and position of the axes in different taxa were compared. Indices are considered unreliable, because: 1) an index may change progressively, simply due to allometric growth (i.e. due to shifts in size along a single growth axis); 2) different taxa may differ in the position of their growth axes (i.e. in the initial growth relationships of the dimensions analysed). Both alternatives occur in the analyses in this paper. Indices do not show which are the growth relationships between the measurements used for their calculation, and should therefore be avoided. The growth relationships between two measurements are best analysed in plots.

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1. Introduction

Indices (=ratios, calculated as measurement A / measurement B) are often given in descriptions of cranial and limb bone material, as they are believed to reflect the shape of the bone independently of size. Indices are believed to be useful for taxonomic characterization, comparison, and phylogenetic evaluation (Gromova 1952, Sondaar 1968, Alberdi 1974, Sen, Sondaar & Staesche 1978, Staesche & Sondaar 1979, Eisenmann 1980). Kurtén (1954) critically reviewed the use of indices in taxonomy. He maintains that indices are unreliable for taxonomic characterization when growth of the dimensions used for their calculation is allometric and when size differences are great. This is because:

1) Indices may progressively increase or decrease simply due to increase in size. Two samples pertaining to animals simply differing in size (i.e. in their placement along a common growth axis) may differ in their indices. An increase or decrease in an index may be due to allometric growth (i.e. with increase in size one of the dimensions used for calculating the index increases faster than the other). The relationship between the two dimensions x and y is expressed by the allometry formula $y=bx^k$. The rate of growth is expressed by the slope (k) of the growth axis fitted to the data in a bivariate scattergram.

2) Two samples may roughly lie along a common growth axis, but may differ in the slope of the axis fitted separately to each sample. With increase in size this would result in an initial similarity in proportions changing into dissimilarity, or an initial dissimilarity in proportions changing into similarity.

3) Two samples may differ in the position of their growth axes (i.e. in proportions unrelated to size). In this case the initial relationship between the two dimensions is different in the samples. This is expressed by the means M_x and M_y, and by b (= the value of y when x=0).

In a recent review of fossil and recent *Equus,* Eisenmann (1980) calculated indices from various mean measurements on the skull and upper cheek teeth. She then used data derived from the indices for taxonomic characterization and phyletic evaluation of species. Sen, Sondaar & Staesche (1978) introduced a keel index to help evaluate the phylogenetic and stratigraphic position of a fossil horse. In an attempt to study whether indices are valid as used by Eisenmann (1980) and Sen, Sondaar & Staesche (1978), I plotted the logarithms of the dimensions used for calculating the respective indiced in bivariate scattergrams (Figs. 1-7). A reduced major axis was fitted to each data scatter. The materials used are shown in Table 1.

Table 1. Data (published and own) used in the analyses. (AMNH= American Museum of Natural History, New York; GI= Geological Institute of the Academy of Sciences, Moscow; HL= Hessisches Landesmuseum, Darmstadt; ISEZ= Institute of Systematic & Experimental Zoology, Kracow; MZ= Musei Ziemi, Warsaw; NM= National Museum, Prague; NMu= Naturhistorisches Museum, Mainz; PIN= Paleontological Museum of the Academy of Sciences, Moscow; ZMH= Zoological Museum, Helsinki)

Skulls

Equus caballus — Published: Franck 1875, Nehring 1884, Merriam 1913, Hay 1913, Hay 1915, Brinkmann 1919-20, Hanko 1936, Hooijer 1949, Gromova 1949. — Own: 7 recent skulls (ZMH), 14 subrecent-fossil skulls (HL, NMu, MZ, ISEZ).
E. przewalski — Published: Nehring 1884, Hay 1913, Hay 1915, v.Reichenau 1915, Motohashi 1930, Hooijer 1949. — Own: 1 skull (ZMH), 2 skulls (NM).
E. asinus — Published: Nehring 1884, Brinkmann 1919-20, Motohashi 1930, Hooijer 1949. — Own: 1 skull (ZMH).
E. heinonus (+ *E. kiang*) — Published: Nehring 1884, Hay 1915, Motohashi 1930, Hooijer 1949, Antonius 1951. — Own: 1 skull (ZMH).
E. zebra — Published: Nehring 1884, Hay 1915, Gromova 1949, Hooijer 1949, Antonius 1951.
E. quagga (several subsp.) — Published: Hay 1915, Motohashi 1930, Hooijer 1949, Gromova 1949, Antonius 1951. — Own: 2 skulls (ZMH).
E. grevyi — Published: Hay 1915, Gromova 1949, Hooijer 1949, Antonius 1951.
Hipparion (several species) — Material in various museums and institutes.

Limbs

Mesohippus spp. (AMNH).
Miohippus spp (AMNH).
Anchitherium spp. (AMNH).
"*Kalobatippus*" spp. (AMNH); synonym of *Anchitherium.*
Hyrohippus spp. (AMNH).
Parahippus spp. (AMNH).
"*Desmatippus*" spp. (AMNH); synonym of *Parahippus.*
Merychippus spp. (AMNH).
"*Griphippus*" spp. (AMNH); synonym of *Pseudhipparion.*
Hipparion spp. (AMNH, ZMH, PIN, GI).
Astrohippus spp. (AMNH).
"*Dinohippus*" spp. (including "D." interpolatus) (AMNH); probably synonym of *Pliohippus.*
Equus spp. (including *E. mosbachensis*) (AMNH, ZMH, GI, NMu).

My data are chiefly borrowed from the litterature. I also used my own data on recent/subfossil/fossil *Equus* s.l. in the Zoological Museum, Helsinki; National Museum, Prague; Hessisches Landesmuseum, Darmstadt; Naturhistorisches Museum, Mainz; Academy of Sciences and Musei Ziemi, Warsaw, and Institute of Systematic and Experimental Zoology, Krakow (Table 1). My cordial thanks go to the keepers of the numerous collections seen.

2. Comparisons

2.1. Crania

For comparison, I plotted some of the measurements on species of Old World *Hipparion.* The *Hipparion* skulls are less well preserved than those of *Equus* s.l. Certain amendments had to be made in the choice of measurements so as to secure a maximum number of measureable specimens. For example, I evaluated the position of the orbit (=facial length) in relation to the basal length of the skull in *Equus* and *Hipparion* using Gromova's measurement no. 7 (originally according to Tscherski 1892) (i.e. the distance $I^{1\text{-}1}$- anterior rim of the orbit; Gromova 1952, table 1), in addition to using Nehring's (1884) facial length (i.e. $I^{1\text{-}1}$-posterior rim of the orbit). I measured frontal width between the supraorbital foramina (originally according to Franck 1875), in addition to Nehring's (1884) frontal width at the posterior rims of the orbits. Only adult skulls were used.

Table 2. Coefficients of allometry (*k*) and correlation (*r*) and their significance of $r \neq 1$ by 1-sided test, significance of $r \neq 0$ according to table; significance level denoted by asterisks: $P < 0.05$*. <0.01**, <0.001***)

	N	*k*	*r*
Skulls			
Muzzle l./palatal l.			
Equus s.l.	47	1.33**	0.84***
Hipparion s.l.	80	1.229***	0.905***
Muzzle l./ basal l.			
Equus s.l.	46	1.57***	0.808***
Hipparion s.l.	36	1.27**	0.91***
Postorbital w./basal l.			
Equus hemionus	37	1.11	0.426**
E. przewalski	20	1.02	0.86***
E. caballus	62	0.74***	0.91***
E. quagga	51	0.806*	0.28*
E. grevyi	18	0.714*	0.16
E. asinus	31	0.879*	0.91***
E. zebra	25	0.889*	0.347
Width at supraorbital foramina/basal l.			
Equus s.l.	30	1.036	0.817***
Hipparion s.l.	16	0.905	0.766***
Facial l.to postorbita/basal l.			
Equus s.l.	62	0.978	0.988***
Hipparion s.l.	12	1.10	0.98***
Facial l. to preorbita/basal l.			
Equus s.l.	35	1.067	0.928***
Hipparion s.l.	34	1.13*	0.96***
Muzzle br/ muzzle l.			
Equus s.l.	43	0.71**	0.637***
Hipparion s.l.	77	1.11	0.58***
Limbs			
Diameter medial condyle/diameter sagittal keel			
pad-footed tridactyl			
MC III	25	1.08***	0.955***
MT III	25	1.02	0.99***
tip-toed tridactyl			
MC III	76	0.93***	0.99***
MT III	75	0.928***	0.996***
monodactyl (early forms)			
MC III	23	0.89	0.949***
MT III	46	0.79***	0.936***
monodactyl (late forms)			
MC III	70	1.05	0.93***
MT III	59	1.016	0.946***
Diameter sagittal keel/distal articular breadth			
Equus mosbachensis			
MC III	21	1.438*	0.818***
MT III	22	0.708	0.75***
"*Dinohippus*" *interpolatus*			
MC III	22	0.92	0.878***
MT III	25	0.89	0.599**
Hipparion (Concud)			
MC III	26	1.176	0.671***
MT III	25	0.699*	0.614***
Hipparion (Taraklia)			
MC III	24	0.856	0.689***
MT III	25	1.106	0.586**
Hipparion (Pavlodar)			
MC III	25	0.832	0.731***
MT III	25	0.647**	0.326

2.2. Muzzle length

Eisenmann (1980: 67–69, fig. 35) calculated a muzzle length index as 100× muzzle length/palatal length, and plotted the mean index to mean basal length of the skull. In her opinion the index shows a progressive increase in *Equus* s.l. with time.

In my material of chiefly recent *Equus*, muzzle length (I^{1-1}- P^{2-2}) plotted to palatal length (I^{1-1}-choanae) grows by positive allometry: with increase in size of the skull, muzzle length increases relatively faster than palatal length (Table 2). An index y/x calculated on the basis of these dimensions would increase (see also Eisenmann 1980: 49). In Eisenmann's fig. 35 this is evident in the distribution of the indices on recent *Equus*.

The growth pattern of the muzzle is confirmed by analysing the relative growth of muzzle length plotted against the basal length of the skull (Fig. 1). Growth is positively allometric in this case too (Table 2).

In both comparisons correlation between the dimensions is high, probably spuriously so because muzzle length is part of both palatal and basal length. I pooled the various species of *Equus*, since the spread of the observations inside the single species *Equus caballus* L. is as great as inside the total material. However, certain species may have a relatively long muzzle (e.g. *E. quagga* Gmelin, including *E. burchelli* (Gray)), others a relatively short muzzle, falling above and below the common growth axis, respectively. Such cases should be investigated by separately analysing taxonomically homogeneous samples and by comparing them for position and slope of their axes. This was not done here because of lack of data.

In Old World *Hipparion* muzzle length plotted against palatal length and basal length (Fig. 1) of the skull, respectively, also grows by positive allometry (Table 2). The spread of the observations around the common growth axis is negligible and there is no clear difference between different species in relative length of the muzzle. However, *Hipparion* differs significantly from *Equus* s.l. in having a longer muzzle at a corresponding palatal length or basal length, i.e. *Hipparion* and *Equus* differ in the position of their growth axes (Table 3). There is no difference in the slope of the axes.

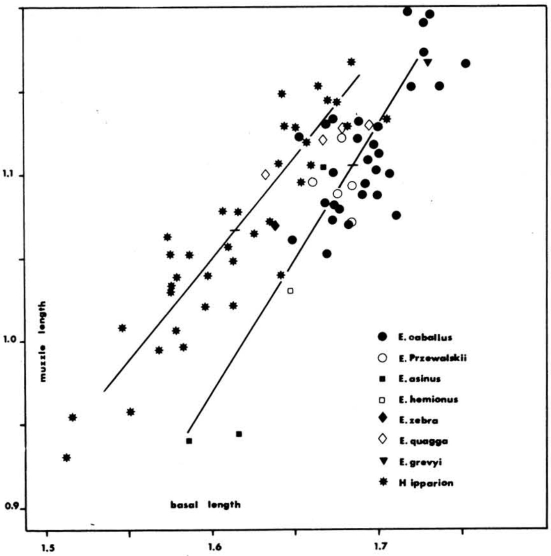

Fig. 1. Muzzle length (I^{1-1}-P^{2-2}) plotted against basal length of the skull in species of *Equus* and in *Hipparion* spp. (log. data). Growth axes fitted to data on *Equus* spp. and *Hipparion* spp.

Table 3. Comparison of the slope (d_k) and position (t) of growth axes (2-sided tests).

	N/N	d_k	t
Skulls			
Equus s.l.-*Hipparion* s.l.			
muzzle l./palatal l.	47/80	0.85	4.108***
muzzle l./basal l.	46/36	1.819*	5.22***
supraorbit.w./basal l.	30/16	0.716	8.69***
postorb.facial l./basal l.	62/12	2.14*	4.15*
preorb.facial l./basal l.	35/34	0.07	3.62***
muzzle br./muzzle l.	43/77	2.597**	5.84***
Limbs			
Diameter medial condyle/diameter sagittal keel			
pad-footed–tip-toed			
MC III	25/76	5.23***	5.898***
MT III	25/75	1.79	3.198***
pad-footed–monodactyl (early forms)			
MC III	25/23	2.08*	4.45***
MT III	25/46	1.17	5.24***
pad-footed–monodactyl (late forms)			
MC III	25/70	0.72	7.06***
MT III	25/59	0.22	6.93***
tip-toed–monodactyl (early forms)			
MC III	76/23	0.32	1.92
MT III	75/46	0.16	1.39
tip-toed–monodactyl (late forms)			
MC III	76/70	2.48*	3.12***
MT III	75/59	0.77	2.07*
Diameter sagittal keel/distal articular breadth			
Concud–*E. mosbachensis*			
MC III	26/21	0.96	2.66**
MT III	25/22	0.05	5.01***
Concud – "*Dinohippus*" *interpolatus*			
MC III	26/22	1.15	6.59***
MT III	25/25	1.04	14.26***
Concud–Taraklia			
MC III	26/24	1.39	3.56***
MT III	25/25	1.87	3.33**
Concud–Pavlodar			
MC III	26/25	1.63	2.83**
MT III	25/25	0.31	4.55***
Taraklia–Pavlodar			
MC III	24/25	0.13	4.18***
MT III	25/25	2.00*	4.07***
E. mosbachensis–"*Dinohippus*"*interpolatus*			
MC III	21/22	1.81	6.49***
MT III	22/25	0.94	3.39**

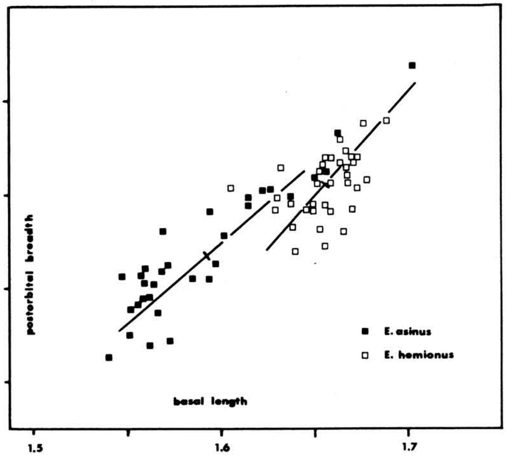

Fig. 2. Postorbital frontal width plotted against basal length of the skull in *Equus asinus* and *E. hemionus* (log. data). A growth axis has been fitted separately to each species.

2.3. Frontal width

Eisenmann (1980: 69–70, fig. 36) calculated a frontal index as 100 × Nehring's frontal width/ basal length of the skull. She then plotted the index against mean basal length. Although Eisenmann (p. 69) distinguishes three stages in her diagram, she does not believe that the frontal index has evolutionary significance.

In plotted frontal width at the posterior rims of the orbits against basal length (Figs. 2–4). Three main groups of recent *Equus* emerge:

1) *Equus asinus* L. and *E. hemionus* Pall., which have a broad forehead (Fig. 2);

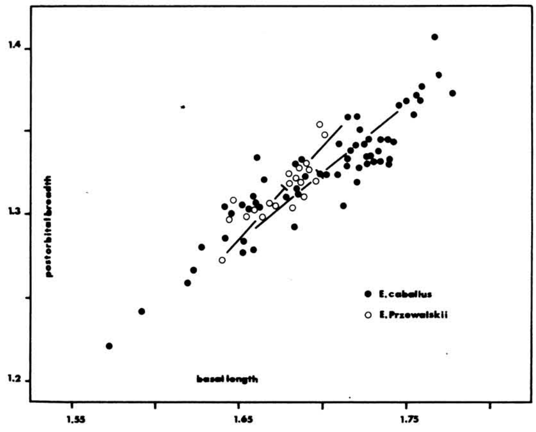

Fig. 3. Postorbital frontal width plotted against basal length of the skull in *Equus caballus* and *E. przewalski* (log. data). A growth axis has been fitted to each species.

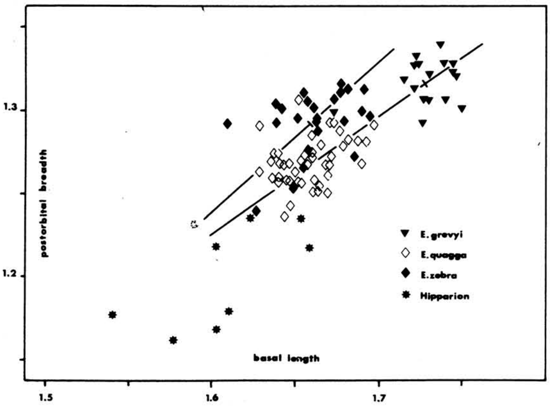

Fig. 4. Postorbital frontal width plotted against basal length of the skull in *Equus grevyi*, *E. quagga*, *E. zebra*, and *Hipparion* spp. (log. data). A growth axis has been fitted to the data on *E. zebra* and *E. grevyi*.

2) *E. quagga* and *E. grevyi* Oust., which have a narrow forehead (Fig. 4);

3) and *E. caballus*, *E. przewalski* Polj., and *E. zebra* L., which are intermediate (Figs. 3 and 4).

Some observations of *Hipparion* (Gromova 1952; table 1) as plotted in the diagrams, show that in this genus the forehead is even narrower than in *E. quagga* and *E. grevyi* (Fig. 4).

Relative growth does not differ significantly from isometry in *E. homionus* and *E. przewalski*, but is negatively allometric in *E. caballus*, *E. quagga*, *E. grevyi*, *E. asinus*, and *E. zebra* (Table 2). In these species the forehead becomes relatively narrower with increasing size of the skull and an index y/x would decrease (see also Eisenmann 1980: 48). The greatest difference between the samples is in the position of the growth axes, i.e. in the proportions of the skull independent of size. When compared for heterogeneity of covariances (Bonnier & Tedin 1940: 142–155), the species samples are seen to differ significantly in the inclination of their growth axes ($v^2 = 4.816$, *df* 6, 230, $P<0.001$). The sample means are also more strongly spread around their own regression axis then they are expected to do simply by chance if drawn from the same population ($v^2 = 42.81$, *df* 5, 236, $P<0.001$).

I also plotted frontal width, measured between the supraorbital foramina, against basal length of the skull. In *Equus* s.l. growth is isometric (Table 2), i.e. with increase in size the two dimensions grow together without any change in proportions. There is little spread of the observations around the common growth axis, but certain species may have a relatively broad forehead and fall above the axis (e.g. *E. przewalski*), while others have a relatively narrow forehead and fall beneath it (e.g. *E. quagga* and *E. grevyi*). In Old World *Hipparion* frontal width measured between the supraorbital foramina in comparison with the basal length of the skull grows isometrically (Table 2). The difference between *Equus* sl. and *Hipparion* in the slope of the growth axes is not significant, but *Hipparion* does differ from *Equus* in that the forehead is narrower at a corresponding skull length, i.e. there is a significant difference in the position of the axes (Table 3).

2.4. The position of the orbits

To determine the relative position of the orbits, Eisenmann (1980: 72–73, fig. 38) calculated an index as 100 × cranial length/Nehring's facial length. She then plotted this index against the basal length of the skull. Eisenmann interprets fig. 38 as showing that the smaller the skull, the more anterior the orbit (i.e. the larger the skull the longer the face) but she refrains from interpreting the index phylogenetically.

Reeve & Murray (1942) plotted the logarithm for these measurements for monodactyl and tridactyl horses. In the adult monodactyl forms growth is isometric. The dense clustering of the observations around the growth axis indicates that in the relative length of the face there are no differences between the different species used in the analysis (Reeve & Murray 1942: fig. 1). A few observations on *Hipparion* (Gromova 1952; table 1 and own data) show a relatively longer cranial part compared to facial part in *Hipparion* than in *Equus* s.l.

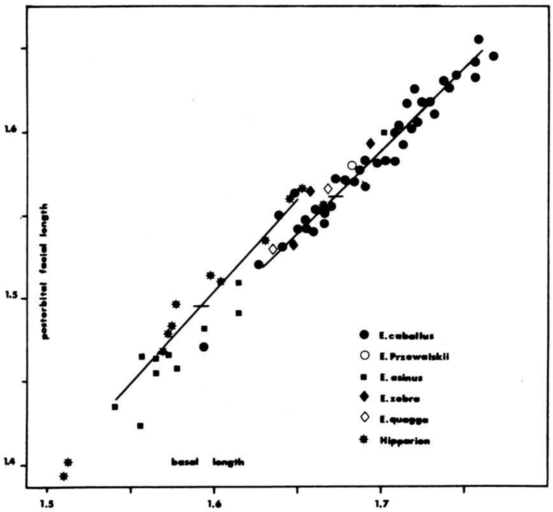

Fig. 5. Postorbital facial length (I^1- posterior rim of orbit) plotted against basal length of skull in species of *Equus* and in *Hipparion* spp. (log. data). Growth axes fitted to *Equus* spp. and *Hipparion* spp.

I plotted Nehring's facial length ($I^{1-\bar{1}}$-posterior rim of orbit) against the basal length of the skull (Fig. 5). In *Equus*, growth is isometric (Table 2), which conforms to Reeve & Murray's (1942) results on adult monodactyl horses. There are no differences between different species of *Equus*: all the observations cluster tightly around the common growth axis and correlation is very high (Table 2).

In *Hipparion*, growth is also isometric (Table 2) and correlation very high. The slope of the growth axes of *Equus* and *Hipparion* is not or is barely significantly different, but the axes differ in position (Table 3), the face in *Hipparion* being longer at a corresponding basal length (Fig. 5).

I also plotted Tscherski's (1892) "preorbital" facial length (I^{1-1}- anterior rim of orbit) against the basal length of the skull (see also Robb 1935). As in the preceding analysis, growth in *Equus* is isometric (Table 2), but certain species may differ in the position and/or slope of their growth axes and should be separately analysed. Such species are *E. hemionus* (+ *E. kiang* Moorcr.) and *E. zebra*, which may have a relatively short preorbital face and fall beneath the common growth axis. This is contrary to Eisenmann's observations (1980: 49, 72). In *Hipparion* the orbit is placed farther back (i.e. the face is longer), at a corresponding basal length, than in *Equus*. Since growth of these measurements in *Hipparion* is positively allometric (Table 2), the orbit tends to be situated increasingly farther back the larger the skull. The difference in position of the growth axes is significant, but there is no difference in their slope (Table 3).

2.5. Muzzle breadth

Eisenmann (1980: 74–75, fig. 40) calculated an index as 100 × muzzle breadth/ muzzle length, and plotted the index against the basal length of the skull. She is of the opinion that in the phylogeny of *Equus* the muzzle changed progressivey in relative breadth.

In *Equus* muzzle breadth plotted against muzzle length (I^{1-1}- P^{2-2}) grows by negative allometry (Table 2), the muzzle becoming relatively narrower with increasing length, as also pointed out by Eisenmann (1980: 49, 74). There is a considerable spread of the observations around the common growth axis, but none of the species seems to have a relatively broader or narrower muzzle than any other. In the sample of *E. przewalski* alone, the spread of observations is almost as great as in the total sample.

Most *Hipparion* species in my sample have a relatively narrow muzzle, and growth is isometric (Table 2). *Hipparion schlosseri* Antonius from Samos Q1, Q4, and Q6 has a broad muzzle for its muzzle length. It is not included in the analysis of *Hipparion*. *Hipparion* differs from *Equus* in both the slope and the position of the growth axes (Table 3).

The initial proportions of the skull consistently differ between species of *Equus* and *Hipparion*, the skull of the latter being narrower with a longer face. In *Hipparion* facial length in relation to basal skull length is greater than in *Equus*, although shorter in relation to cranial length. This is probably due to the occipital crest reaching farther posterior in relation to the foramen magnum in *Hipparion* than in *Equus*. Within the genus *Hipparion* growth relationships of the various dimensions vary little among local forms, contrary to the genus *Equus*, in which several different growth patterns occur. In most cases *Hipparion* and *Equus*, as well as species of *Equus*, are significantly different in their initial proportions. This cannot be judged on the basis of indices, however, but has to tested statistically.

2.6. Teeth

Relative length of the protocone

A relatively long protocone of the upper cheek teeth is considered advanced in the equids. The implications are that the protocone increased progressively in length during phylogeny (e.g. Eisenmann 1980: 138). The possibility that protoconal length is correlated with tooth length has not been considered.

In analysed Musil's (1968: tables 3 & 4) measurements on P^{3-4} and M^{1-2} of *E. germanicus* Nehr. from Ehringsdorf. Within these samples protoconal length is positively correlated with tooth length (linear data, measured at the wear surface): P^{3-4} all wear stages: $N = 68$, $r = 0.38$, $P = 0.01-0.001$; P^{3-4} wear stage 2 only: $N = 29$, $r = 0.54$, $P = 0.01-0.001$; M^{1-2} all wear stages: $N = 68$, $r = 0.47$, $P < 0.001$; M^{1-2} wear stage 2 only: $N = 30$, $r = 0.51$, $P = 0.01-0.001$.

To investigate whether or not the protocone is correlated with tooth length between samples, too, I plotted Eisenmann's (1980: tables 38-47, 56-59, 61, 63-68) measurements on mean protoconal length to mean length of P^{3-4} and M^{1-2} respectively (linear data, measured at the wear surface) in 10 recent and 11 Pleistocene forms of *Equus*. The means for *E. stenonis* Cocchi (tables 56-58) fall to the right in the scattegram, the means for recent asinines (tables 42-45) and caballines (tables 46-47) to the left, and the zebrines (tables 38-41) are roughly intermediate. These groups differ in the initial length of their protocone relative to tooth length, the stenonid horses having a shorter protocone in relation to tooth length than the asinines and caballines. There is a gradual shift from one group to the next, with intermediate forms spanning the gaps. Within each group mean protoconal length appears to be positively correlated with mean tooth length. I analysed this by plotting mean protoconal length against mean tooth length for P^{3-4} and M^{1-2} in 10 recent and 1 Pleistocene form of *Equus* (Eisenmann 1980: tables 38-47, 59). The mean length of the protocone is positively correlated with tooth length: P^{3-4}: $N = 11$, $r = 0.87$, $P < 0.0001$; M^{1-2}: $N = 11$, $r = 0.90$, $P < 0.001$. This indicates that:

1) Within samples, as well as between them, the length of the protocone is dependent on tooth length, both probably ultimately functionally dependent on the absolute size of the animal, its energy requirements, etc.

2) The recent forms of *Equus* do not fall into clearly defined groups on the basis of the relative length of the protocone: the observed deviations from the common growth axis being no larger than deviations due to sampling error.

I further analysed 28 local samples of Old World *Hipparion* for between sample correlation by plotting mean protoconal length (P^{3-4} and M^{1-2} combined) against mean length og M^{1-2} (measured at the base of the crown). The measurements (linear data) are positively highly correlated: $N = 28$, $r = 0.89$, $P < 0.001$. There is no grouping of different forms of *Hipparion*: all the samples analysed cluster around the common growth axis.

In *Equus*, as well as in *Hipparion*, protoconal length, both within single samples and between samples, is positively correlated with the length of the teeth. Relative growth of the two measurements, both within samples and between sample means, is isometric or positively allometric for log data, and an index calculated on these dimensions (= protoconal index of Eisenmann 1980) would remain unaltered or increase, or growth is isometric or negatively allometric for linear data. It is chiefly the anterior part of the protocone (the heel) which increases in length, both in single samples and between samples. I plotted Musil's (1968: table 3 & 4) data on the anterior and posterior lengths of the protocone in P^{3-4} and M^{1-2}, respectively (wear stage 2 only) against the length of the tooth. Only anterior protoconal length is positively correlated with tooth length (P^{3-4}: $N = 29$, $r = 0.48$, $P = 0.01$; M^{1-2}: $N = 31$, $r = 0.39$, $P = 0.05-0.04$). The correlation is not significant for posterior length of the protocone plotted against tooth length. An increase in heel length is also evident between samples: in the stenonid horses the heel is absent or weak, but is well developed in the modern horses, especially in the large caballine forms.

2.7. Limbs

The keel index

Sen, Sondaar & Staesche (1978) introduced a "keel index" to help evaluate the phylogenetic position of a fossil horse. The keel index is calculated as the antero-posterior diameter of the sagittal keel/minimal diameter of the medial condyle, both of the distal articular surface of the cannon bone (MC III and MT III). The sagittal keel is believed to have increased progressively in relative diameter during the phylogeny of the horses, so as to increasingly firmly hold the fetlock joint and prevent lateral dislocation (Gromova 1952, Sondaar 1968). If a horse's position in the phylogeny could be evaluated on the basis of the relative diameter of the sagittal keel of the metapodials, this character would be useful as a stratigraphic marker.

I measured the diameter of the medial condyle and of the sagittal keel in fossil horses of the subfamilies Anchitheriinae, characterized as pad-footed tridactyl, and Equinae, characterized as tip-toed tridactyl and monodactyl, respectively (see Camp & Smith 1942, Sondaar 1968, for terminology), then plotted the diameter of the medial condyle against that of the sagittal keel separately for MC III and MT III (Table 1, Figs. 6 & 7).

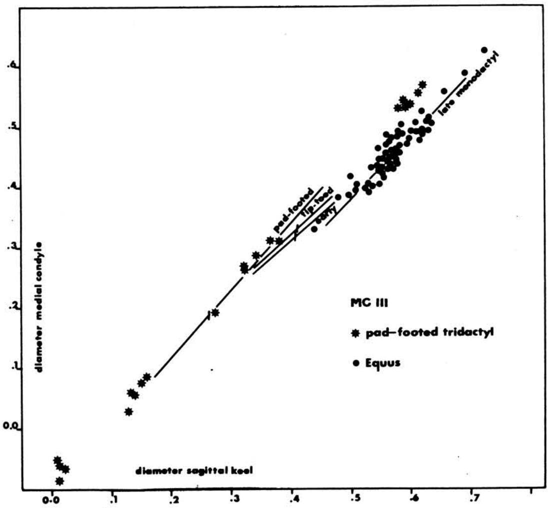

Fig. 6. Diameter of medial condyle plotted against diameter of sagittal keel in MC III of pad-footed tridactyl, tip-toed tridactyl, and monodactyl horses (log. data). A growth axis has been fitted to each category.

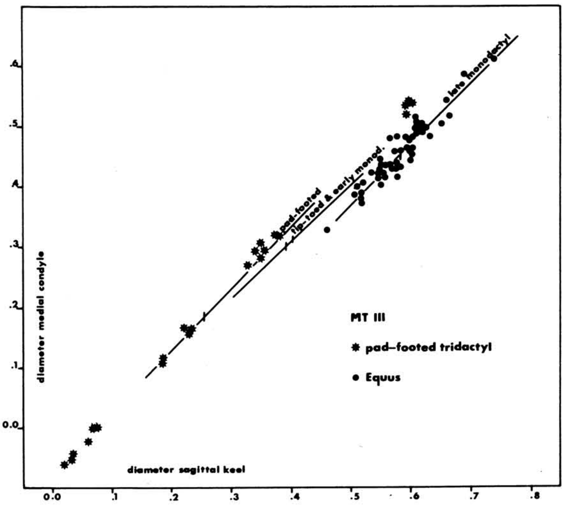

Fig. 7. Diameter of medial condyle plotted against diameter of sagittal keel in MT III of pad-footed tridactyl, tip-toed tridactyl, and monodactyl horses (log. data). A growth axis has been fitted to each category.

Pad-footed tridactyl horses

In the pad-footed tridactyl horses the relative growth of the distal dimensions of MT III is isometric, relative growth in MC III is positively allometric (Table 2). Compared with the tiptoed tridactyl and monodactyl horses there is a significant difference in the position of the growth axes, the relative diamter of the sagittal keel being less in the pad-footed tridactyl than in those froms (Table 4).

Tip-toed tridactyl horses

In the tip-toed tridactyl horses relative growth is negatively allometric (Table 2), the diameter of the sagittal keel increasing relatively faster than that of the medial condyle with increase in overall size. The keel index should thus progressively increase. The mean relative diameter of the keel is significantly greater than in the pad-footed tridactyl forms, but significantly less than in some of the monodactyl forms, i.e. there is a difference in the position of the growth axes (Table 4).

Monodactyl horses

Growth is negatively allometric in early monodactyl horses ("*Dinohippus*" and *Astrohippus*), but isometric in *Equus* s.l. (Table 2). The samples of early and late monodactyl horses differ neither in the slope, nor in the position of their growth axes (Table 4), i.e. between early and late monodactyl horses there is no significant difference in the relative diameter of the sagittal keel.

There is no significant difference in the relative diameter of the keel between the early monodactyl and the tip-toed tridactyl forms (Table 4). In *Equus* s.l. the keel is significantly relatively greater than in the tip-toed forms (Table 4), but since relative growth of the diameter of the sagittal keel is faster in the tip-toed forms than in *Equus* s.l., in very large representatives of the former the diameter of the keel would, in fact, surpass that in the latter.

The correlation between the two dimensions is very high, but probably spuriously so because both dimensions measure the same thing (viz. distal antero-posterior diameter). To avoid this error I measured cannon-bone distal breadth and keel diameter in some large samples of *Hipparion* (localities Pavlodar, Taraklia, and Concud), a sample of *"Dinohippus" interpolatus* Cope (Sand Clay Flats, Oklahoma), and of *Equus mosbachensis* Reich. (Mosbach). A keel index (keel diameter/distal metapodial breadth) shows lower mean values in the monodactyl "*Dinohippus*" and *Equus* than in the tridactyl hipparions, probably because of metapodial distal flattening in the monodactyl forms (see also Forstén 1973). In a scattergram this difference appears as a difference in the position of the growth axes, which is particularly clear between *Hipparion* from Concud and "*Dinohippus*" of the same size. The difference in the position of the growth axes is statistically significant (Table 3). The hipparions are almost indentical with regards to the mean index, but differ significantly in the position of their growth axes (Table 3). Relative growth is not significantly different from isometry in 6 cases, and is allometric in 4 cases (Table 2).

A keel index should not be used for taxonomic or phylogenetic purposes. There was no gradual progressive shift in keel proportions during the phylogeny of the equids, but shifts in proportions were probably rather correlated with the size, weight, and foot adaptation of the animals in question. The cannon-bone became flattened in the monodactyl horses, accompanied in the late forms by a shift in the initial proportions of the sagittal keel and medial condyle. These changes may have had functional significance.

3. Discussion

I have analysed the relative growth of certain dimensions of the equid skull, upper cheek teeth, and limbs, which are often used for calculating indices. Such indices are believed to be taxonomically and/or phylogenetically significant. The aim of this study has been to investigate whether, with increase in absolute size, such indices realiably express the relationships between the dimensions used for their calculation, and whether they are as useful for evaluating relationships and evolutionary trends as they are believed to be.

Differences in proportions independent of size are best detected in scattergrams, where they appear as differences in the position of the growth axes fitted to samples. Transposition of the growth axes shows shifts in the initial proportions of dimensions, and may reflect phylogenetic and/or functional differences between samples or groups of samples. Such differences should be tested for significance by comparing the position of the growth axes. On the other hand, differences in the inclination of individual growth axes may, with shifts in absolute size, result in an initial similarity in proportions which changes into dissimilarity, or an initial dissimilarity which changes into similarity.

In many cases a single growth axis, when extended proximally and distally, picks up the data of several samples differing from each other only in size. Growth in most cases is either positively or negatively allometric (i.e. with increase in absolute size one of the dimensions plotted grows relatively faster than the other). An index calculated on these dimensions would indicate a progressive change in proportions. In fact relative growth remains the same throughout, and the change in the index simply reflects the shift in absolute size along the common growth axis. Such a progressive change in the index does not show phylogenetic progression and cannot be used as a measure of the phyletic position of a taxon.

Differences in proportions appear in plots as differences in the position and/or slope of growth axes fitted to samples. Indices, although easy to calculate and simple to handle, are unreliable, because they do not show how the compared samples differ: whether in the position and/or in the slope of their individual growth axes, or simply in absolute size along a single growth axis. All three alternatives occur in the analyses in this paper: in *Equus* the analysed species seem to fall along a single growth axis when compared for the relative position of the orbits (Reeve & Murray 1942), relative facial length, muzzle breadth, and distal metapodial dimensions. Species of *Equus* fall along different growth axes (which may also differ in slope) when compared for relative muzzle length, frontal width, and (for recent and fossil forms) protoconal length. In *Hipparion* the species analysed seem to fall along a single growth axis for all measurements compared, except for relative muzzle breadth and keel diameter relative to metapodial distal breadth.

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