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Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates

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Qualitative observations suggest that grazing ungulates have relatively broader muzzles than browsing ones, and that grazers have incisors that are all of a similar size, as opposed to the large central and smaller lateral incisors seen in browsers. These differences may be correlated respectively with the need for grazing ungulates to maintain a large daily intake, or for browsing ungulates to forage selectively in a stand of vegetation. Quantitative examination of relative muzzle width and incisor width ratio in 95 species of living ungulates, correlated with seven different types of dietary preferences, substantiated these observations, although phylogenetic history may exhert a strong influence on morphological proportions. For example, equids have relatively narrower muzzles than grazing ruminants despite their less selective mode of feeding. The narrowest relative muzzle widths are not found in regular browsers, but in high level browsers and in mixed feeders in open habitats. Incisor width ratio can distinguish grazers from browsers, but can not be used to discriminate mixed feeders from other feeding types, and grazers appear to have incisors that are relatively broader overall than those of other dietary types, in correlation with their relatively broader muzzles.

KEY WORDS:—Cranial morphology – ungulates – dietary preferences.

CONTENTS

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INTRODUCTION

Numerous workers in ungulate ecology have commented on the relationship between the type of diet in ungulate mammals and the shape of the muzzle and the form of the anterior dentition (e.g. Bell, 1969, 1970; Gwynne & Bell, 1968; Jarman, 1974; Owen-Smith, 1982). Owen-Smith (1982) remarked that a relatively narrow muzzle is likely to be important in ungulates that feed selectively, taking grass leaves or dicotyledonous material at ground level in a tall stand of vegetation, or nutritious foliage from within a woody plant canopy, enabling them to pick out certain plants or plant parts from within a tall stand of vegetation. This is because ungulates need to ingest large amounts of food per day, and are time-limited in their selection of appropriate items of herbage (see Owen-Smith & Novellie, 1982). In contrast, a broad muzzle would be preferable for a less selective grazer feeding in short grass, as such morphology would enable the animal to take large bites, and hence maintain a high rate of intake. A high rate of intake is important for a grazer, as grass is usually of a lower nutritional value (higher fibre content) than dicotyledonous browse material. Owen-Smith (1982, 1985) made the subjective observation that the muzzles of selective feeders such as the kudu (*Tragelaphus strepciceros*) and the impala (*Aepyceros melampus*) are particularly narrow, the muzzle of the short-grass feeding wildebeest (*Connochaetes taurinus*) is broad, whereas the muzzles of the tall grass grazing topi (*Damaliscus lunatus*) and the fresh grass grazing waterbuck (*Kobus ellipsiprymnus*) appear to be intermediate in width.

Other observations bear out this suggestion that the ability of certain ungulates to feed selectively may be critical to their foraging efficiency. Allden & Whittaker (1970) report that the intake of grazing sheep, which resemble the impala in their selection of a mixture of grass and browse material in open habitats (Hofmann, 1985), is related more to the plant height than to herbage productivity. Nge'the & Box (1976) report observations of goats and eland feeding in an *Acacia* community. The goats were able to insert their narrow muzzles through the spines and to obtain a greater proportion of pure leaf material, whereas the eland placed their larger muzzles over the entire twig, thus ingesting a much coarser diet. Both absolute and relative muzzle width in ungulates may probably bear an important relationship to the selectivity of the species' feeding.

Comments have also been made about the relative size and shape of the anterior dentition in ungulates of different dietary habits. Bell (1969) notes that in grazing ruminants the lower incisors tend to project forwards in a spatulate-like fashion (the upper incisors are missing in all extant ruminant artiodactyls), whereas in browsers they are inserted in a more upright position, with a cupped appearance. Boué (1970) noted a similar correlation, and also provided qualitative data to show that in grazing ruminants the width of the central lower incisor (I_1) tends to be fairly similar to the width of the lower canine (which is incisiform in ruminant artiodactyls, and forms part of the lower incisor row), whereas in browsing ruminants the central incisors are much broader relative to the canine and the lateral incisors.

This paper presents a quantitative test of these hypotheses, evidence for which has previously been derived primarily from qualitative observations (though see Bell, 1969). The hypotheses are as follows:

1. In ungulate species, the relative width of the muzzle is related to the degree of selectivity in the diet. The expectation is that grazers would have a relatively broader muzzle than browsers or mixed (intermediate) feeders, and that within grazers short-grass grazers would have relatively broader muzzles than tall-grass grazers.

2. In ungulate species, the relative size of the central incisor to the lateral incisor is related to dietary type. The expectation is that grazing ungulates possess incisors that are more or less of similar size, while browsing ungulates possess central incisors (I_1) that are considerably broader than the lateral incisors (I_3). (In all ruminants, the third incisors are of similar size and morphology to the incisiform lower canine.)

METHODS

Measurements were taken on 95 species of living ungulates, from the Orders Perissodactyla, Artiodactyla and Hyracoidea (see Appendix for list of species measured, and documentation of sample size.) The following measurements were taken: 1. muzzle width, measured at the junction of the maxillary and premaxillary bones (maximum outer distance); 2. palatal width, measured between the lingual face of the upper second molars (at the level of the protocone); 3. incisor width, measured on the first and third lower incisors as the maximum width along the anterior occlusal surface.

The third lower canine was measured here, in preference to Boué's measurement of the lower canine, to allow direct comparison between ruminant artiodactyls and those ungulates that do not possess an incisiform lower canine, such as camelids, perissodactyls and hyracoids. All measurements were taken on mature, but not excessively aged, animals. That is, on animals with fully-erupted permanent dentitions, but in which the dental wear was not excessive (where no more than 30% of the occlusal enamel on the second molars had been worn away to reveal the underlying dentine). No zoo specimens were included in the data set. Figure 1 illustrates the sites measurement of muzzle and palatal width.

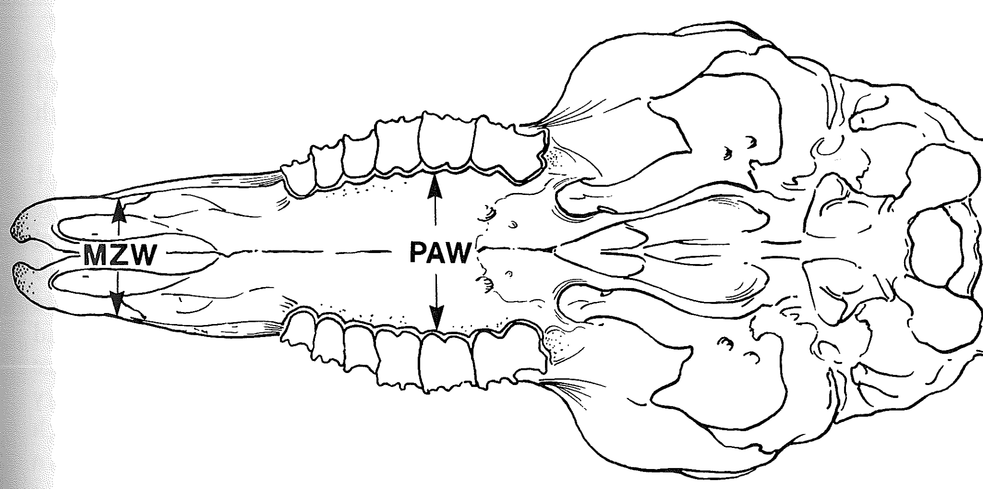

Figure 1. Palatal view of sheep skull (*Ovis* sp.), to illustrate measurements taken. MZW = Muzzle width, PAW = palatal width.

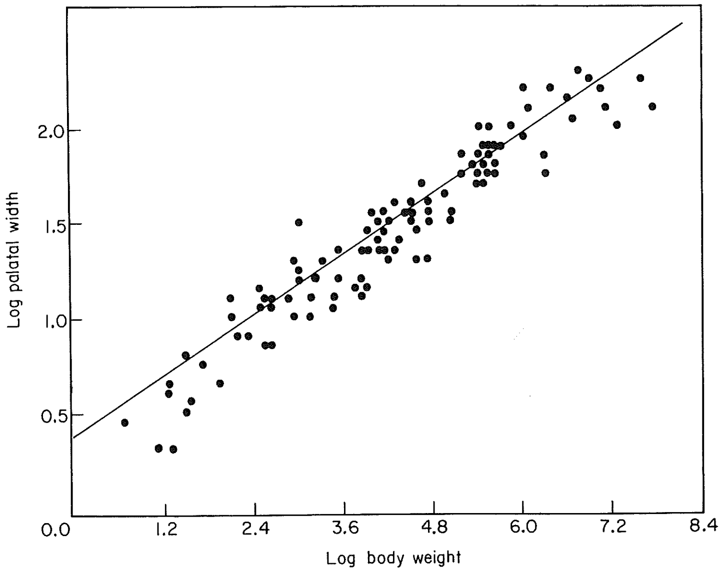

Figure 2. Plot of log palatal width against log body weight (all ungulates, excluding suines).

The ratios used in the analyses were obtained in the following manner. Relative muzzle width ratio was calculated for each species as the mean palatal width divided by the mean muzzle width. Large relative muzzle widths represent animals with relatively narrow muzzles. Palatal width correlates strongly with body weight ($r^2=0.92$: see Fig. 2), while muzzle width is less strongly correlated ($r^2=0.87$). The scatter of the points around the regression line is random with respect to the dietary categories of the taxa, as evidenced by a pairwise comparison of the means of the residuals, using a parametric t test. It may be the case that palatal width represents a measure of the rate at which food can be orally processed and swallowed once ingested, which would be reflected in the high correlation with body weight. Relative muzzle width represents the ratio of the intake aperture of the mouth to the total body size, and may reflect the ratio between intake ability and rate of food processing. Incisor width ratio was calculated as the mean first lower incisor width divided by the mean third lower incisor width. Large values represent animals with small lateral incisors relative to the central ones: see Appendix.

Hypsodonty index, used to separate species points along the y axis in Figs 1 and 3, is a measure of the molar crown height of the species, calculated as the third lower molar height (measured on the outside of the tooth from the tip of the protoconid to the base of the crown), divided by the length of the second lower molar (measured along the labial occlusal surface of the tooth). These measurements were taken only on young animals, in which the third molar had erupted, but in which there was little or no wear apparent on this tooth (see Appendix). These hypsodonty indices should be taken as preliminary measurements, and are used in this paper only to rank species in relation to each other. In animals with high crowned teeth, the position of the base of the crown was estimated by feeling for the junction between the crown and the root of the tooth within the body of the mandible. This measurement is adequate for the

purposes of this paper, as there is a consistancy of measurements taken in this way between different individuals of the same species, and close similarity exists between values estimated in this way and actual measurements of tooth crown height that were obtained in the occasional cases of isolated individual molars or animals with broken jaws. A more precise investigation of tooth crown height in ungulates, using X-rays photographs, is in preparation (Janis, in press).

Specimens were measured at the following institutions: British Museum (Natural History), London, England; Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.; National Museum of Kenya, Nairobi, Kenya; Museum of Cape Town University, Cape Town, South Africa; and Transvaal Museum, Pretoria, South Africa. The data presented here represent, in most instances, all the individuals of a suitable age stage that were available for measurement at these institutions.

The dietary categories were determined in part following Hofmann & Stewart (1972), the differences between their categories and ours reflecting in part the fact that we looked at a wider variety of species than the African bovids that they considered. Dietary information was derived from a variety of published sources: (Lamprey, 1963; Field, 1972; Schaller, 1967, 1977: Talbot & Talbot, 1962; Stewart & Stewart, 1970; Field, 1972; Whitehead, 1972; Haltenorth & Diller, 1977; Hansen & Clark, 1977; Olsen & Hansen, 1977; Owen-Smith, 1982; Walker, 1983).

Grazing ungulates were defined as those taking at least 90% of their year-round diet as grass. Fresh grass grazers were defined as those grazers which habitually reside in areas near water, feeding on tall stands of near-water vegetation (as opposed to the definition of Hofmann & Stewart of grazers dependent on water). Mixed feeders were defined as those species which took between 10 and 90% of grass in their diet. No attempt was made to classify these animals on the basis of percentage of grass taken, as this feeding category represents a distinct morphological category in terms of the stomach anatomy, despite the breadth of the categorization (Hofmann & Stewart, 1972). Instead the category was subdivided into open habitat animals, feeding primarily in tall stands of vegetation in open savanna, prairie or arid desert habitats; and closed habitat animals, those feeding in woodland, forest or ecotonal habitats.

Browsers were defined as those species taking $>90\%$ of their diet as dicotyledonous material. Browsing ungulates were further subdivided into 'regular' browsers, taking a mixture of leaves, shrubs, herbs and succulent items; 'succulent browers', taking very little leaf material and concentrating mainly on fruit and buds (our category is more restricted than the equivalent of the "fruit and dicot foliage selectors" of Hofmann & Stewart); and 'high level browsers' which feed almost exclusively on tree leaves, eating items at or above their own head level in preference to lower level shrubs or herbs (no equivalent category exists in the classification of Hofmann & Stewart).

We are aware that these categories, and the assignation of species to particular categories, may be open to some dispute, and regard them as being open to future revision and adjustment, but we do not consider that the occasional misplaced or problematical species would effect the conclusions of this paper. The appendix lists the species measured, including the number of individuals measured, the assigned dietary category, and the means and standard deviations for all the observations.

RESULTS

Relative muzzle width in relation to dietary type

Figure 3 plots the species means for relative muzzle width against the means of the hypsodonty indices. As a general trend grazers and fresh grass grazers have relatively broad muzzles, whereas the muzzles of the browsers are more narrow. The narrowest relative muzzle width belongs to the dik-dik (*Madoqua kirki*). Although mixed feeders in open habitats show a diversity of relative muzzle widths, they tend to have narrow muzzles. Those species in this dietary category which possess relative muzzle widths of less than 1.2 primarily represent species which have an abberant dietary type for their tribe, which otherwise consist of grazers. They include the African buffalo (*Syncerus caffer*) and the zebu (*Bos indicus*) in the Bovini, Hunter's hartebeest (*Damaliscus hunteri*) in the Alcelaphini, and the mountain reedbuck (*Redunca fulvorufula*) in the Reduncini.

The other taxonomic groupings of ungulates (perissodactyls and hyracoids) show a similar relation of relative muzzle width to dietary type as selenodont artiodactyls, i.e. ruminant and camelid artiodactyls. (Suoid artiodactyls were not examined in this paper.) Among the artiodactyls camelids have relatively broad muzzles for mixed feeders in open habitats, and the equids have relatively narrow muzzles in comparison to artiodactyl grazers. Among the rhino, the data are biased by the inclusion of the Indian rhinos, which retain some of the incisors and so have relatively broad muzzles irrespective of feeding type. In contrast, the African rhinos have lost all their incisors. However, the grazing African white rhino (*Ceratotherium simum*) has a considerably broader muzzle

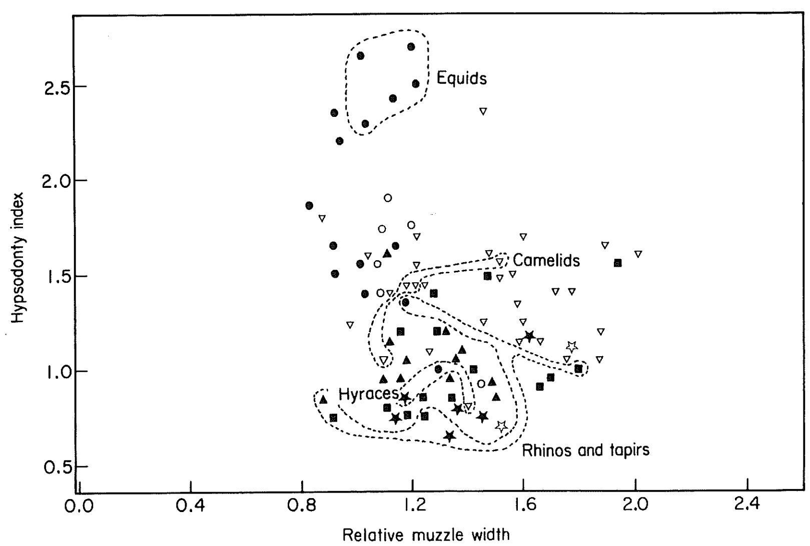

Figure 3. Plot of relative muzzle width against hypsodonty index. (Encircled points show distribution of non-ruminant taxa in this plot. Separate lines encircle values for equids, camelids, hyraces and rhinos plus tapirs, see notation on figure.) ● = Grazers, ○ = fresh grass grazers, ▽ = mixed feeders (open habitat), ▲ = mixed feeders (closed habitat), ■ = browsers, ☆ = selective browsers, ★ = high level browsers.

than the African browsing black rhino (*Diceros bicornis*). Thus although the plot in Fig. 3 demonstrates a general correlation of relative muzzle width with dietary type, both within ruminant artiodactyls and across a greater diversity of ungulate taxonomic groups, it also illustrates the fact that the phylogenetic history of the species concerned may impose morphological constraints on the degree of plasticity in cranial design. For our quantitative examination of this relationship we looked only at selenodont artiodactyls, which represent the majority of species in the total study, in order to avoid this problem of phylogenetic constraint. However, it is of interest to note that perissodactyls and hyracoids also fit this general pattern, even if the absolute values of relative muzzle widths may differ between ungulate taxonomic groups.

Table 1 shows the means and standard deviations of the relative muzzle widths (for selenodont artiodactyls only, with equids considered separately) between the different dietary categories. The grazer and browser categories were considered both as the narrow categories previously defined (although succulent browsers were included with regular browsers because of the small sample size of three species), and as broader categories, with regular and fresh grass grazers lumped together, and regular, succulent and high-level browsers lumped together.

Table 2 shows the results of a multiple pairwise comparison of the distribution of the means of the relative muzzle widths among dietary categories (taken from Table 1) using Wilcoxon's rank sum test. Grazers (taken both as regular grazers alone, or as the lumped categories of regular and fresh grass grazers) were distinguishable, at at least the $P = 0.05$, from all other dietary categories by the possession of a relatively broader muzzle. Fresh grass grazers have a relatively narrower muzzle than regular grazers, but cannot be distinguished from any other category except mixed feeders in open habitats. (However, the small sample size of fresh grass grazers may contribute to the difficulty in distinguishing them from other dietary types.)

The strongest distinction is between all grazers and mixed feeders in open habitats ($P = 0.0001$), or between grazers and browsers when all browsers are considered together ($P < 0.001$). The distinction is not so strong when the

TABLE 1. Relative muzzle widths in selenodont artiodactyls of different feeding types (equids considered as a separate grazing category)

No. of species	Dietary type	Mean	S.D.
8	G	1.04	0.098
13	G+F	1.01	0.11
5	F	0.895	0.040
6	G (equids only)	0.882	0.085
11	W	0.81	0.08
17	B+S	0.77	0.26
22	B+H+S	0.76	0.23
29	M	0.72	0.16
5	H	0.72	1.00

Key for dietary types: G = dry grass grazer; F = fresh grass grazer; M = mixed feeder in open habitat; W = mixed feeder in closed habitat; B = unspecialized browser; S = selective browser; H = high level browser.

TABLE 2. Table of probability differences in mean relative muzzle widths in selenodont artiodactyls

	G+F	G	F	W	B+S	B+S+H	M	H	Equids
G+F		—	—	0.0128	0.002	0.0005	0.0001	0.01	N.E.
G			0.045	N.E.	N.E.	N.E.	N.E.	N.E.	0.041
F		*		—	—	—	0.033	—	N.E.
W					—	—	0.024	—	N.E.
B+S	**					—	—	—	N.E.
B+S+H	***						—	—	N.E.
M	***		*	*				—	N.E.
H	**								N.E.
Equids	N.E.	*	N.E.	N.E.	N.E.	N.E.	N.E.	N.E.	N.E.

Key to dietary types as for Table 1.
N.E. = Not examined.
*** $P < 0.001$; ** $P < 0.01$; * $P < 0.01$.

grazers are considered in separate categories with the browsers in the two different browsing categories, but the reduction in the level of confidence may be the result of the smaller sample sizes used in this comparison. There is a weakly significant difference ($P < 0.05$) between grazers and the mixed feeders in closed habitats, and between mixed feeders of different habitat types. It is not possible to distinguish any category of browser from any type of mixed feeder, or to distinguish between the two different categories of browsers. Thus grazers can be strongly distinguished from feeding types by virtue of a relatively broader muzzle, but it is not possible to distinguish other feeding types from each other with a high degree of confidence, although the narrowest muzzles usually belong to mixed feeders open habitats.

A surprising feature of these results is that the grazing antelopes that are specialists in tall grass habitats, (i.e. the topi, *Damaliscus lunatus*, and the hartebeest, *Alcelaphus buselaphus cokii*), do not appear to have relatively narrower muzzles than the short grass grazing wildebeest species (genus *Connochaetes*). Nor do the less selective equids have broader muzzles than the ruminant grazers. In fact, the reverse is true, in contrast with the expected condition (see Owen-Smith, 1982), as the mean relative muzzle width is significantly different from that of regular grazing ruminants ($P < 0.05$) (see Table 2). These results appear to contradict subjective observations of living animals, as hartebeest especially appear to have long thin faces in comparison with wildebeest.

In order to be sure that these apparent results were not a consquence of certain genera possessing relatively narrower palates, and thus biasing the relative muzzle width ratios, we calculated relative muzzle width for these problematical species in a different fashion. Work in preparation has shown that log lower molar row length bears a slightly better correlation with log body weight ($r^2 = 0.94$) than does log palatal width ($r^2 = 0.91$). We divided the means for both muzzle width and palatal width by lower molar row length, obtaining relative figures for these means unbiased by body mass, or by differences in relative palatal widths. We also recalculated the relative muzzle width ratio using these new relative values for muzzle and palatal width (see Table 3). Both measures of relative muzzle width are similar between different species, suggesting that species differences in palatal width were not a factor in obtaining the orginal conclusions. We conclude that the relative muzzle width

TABLE 3. Alternative calculation of relative muzzle/palatal width ratios, and calculations of relative jaw length, for alcelaphine (bovid) species and for equid species. (See appendix for sample sizes and variance)

Species	MZW	PAW	MRL	MZW/MRL	PAL/MRL	MJL/MRL
Alcelaphus buselaphus	5.57	5.17	6.82	0.82	0.76	5.79
Aepyceros melampus	3.11	3.80	5.65	0.55	0.67	4.20
Connochaetes gnou	6.19	5.18	7.38	0.84	0.70	3.71
Connochaetus taurinus	6.32	5.97	7.92	0.80	0.75	5.66
Damaliscus hunteri	4.62	4.56	6.81	0.68	0.67	4.32
Damaliscus lunatus	5.30	4.82	6.75	0.79	0.71	5.67
Damaliscus dorcus	4.35	3.98	5.63	0.77	0.71	5.40
Equus burchelli	6.50	6.65	7.74	0.84	0.86	5.43
Equus greyvi	5.88	7.15	8.75	0.67	0.82	5.43
Equus zebra	6.48	6.57	7.86	0.82	0.84	5.95

Key: MZW = mean absolute muzzle width (for species); PAW = mean absolute palatal width; MRL = mean absolute molar row length; MZW/MRL = relative muzzle width (i.e. relative to molar row length); PAW/MRL = relative palatal width; MJL/MRL = relative jaw length (mean jaw length divided by mean molar row length).

of these alcelaphine bovid species is indeed similar, and greater than that observed in equids.

The hartebeest and the topi have absolutely narrower muzzles than the wildebeest, but this difference appears to be related to the smaller body size. The illusion of a longer thinner muzzle in these species is probably created by their somewhat greater relative jaw length (see Table 3). However, a narrow muzzle relative to body size *is* a feature of those *mixed* feeders that graze in tall strands of grass, most notably members of the bovid tribes Gazellini, Neotragini and Rupicaprini, and is also notable in Table 3 in the impala, *Aepyceros melampus*. Fresh grass grazers (members of the bovid tribe Reduncini and Pere David's deer, *Elaphurus davidianus*) have weakly significantly narrower muzzles ($P < 0.05$) than the regular grazers in the tribe Alcelaphini (see Table 2). However, the relative muzzle widths of the tall grass regular grazers in the tribe Hippotragini are comparable to the reduncine fresh grass grazers.

A further way of looking at this data set is to plot the mean muzzle width against mean palatal width for the range of species (bearing in mind that palatal width is better correlated with body weight than is muzzle width, $r^2 = 0.92$ as opposed to $r^2 = 0.87$, and in the case of muzzle width the distribution of the points around the regression line is not random with respect to dietary category.) Plots were generated for both normal and log values of the muzzle and palatal width means. Both plots showed a straight line relationship, with similar r^2 values (0.88 for normal values; 0.91 for log values) and similar mean square error values (0.015 for both), so we used the normal value plot in order to retain the maximum amount of the original information.

This plot (see Fig. 4) shows that selenodont artiodactyl grazers (both regular and fresh grass grazers) consistently fall above the regression line (although equids do not), meaning that for any given palatal width the muzzle width is broader than would be expected. In contrast, at small body sizes (i.e. small values for palatal width), mixed feeders in open habitats tend to lie below the regression line, and at larger body sizes this also holds for the high level browsers.

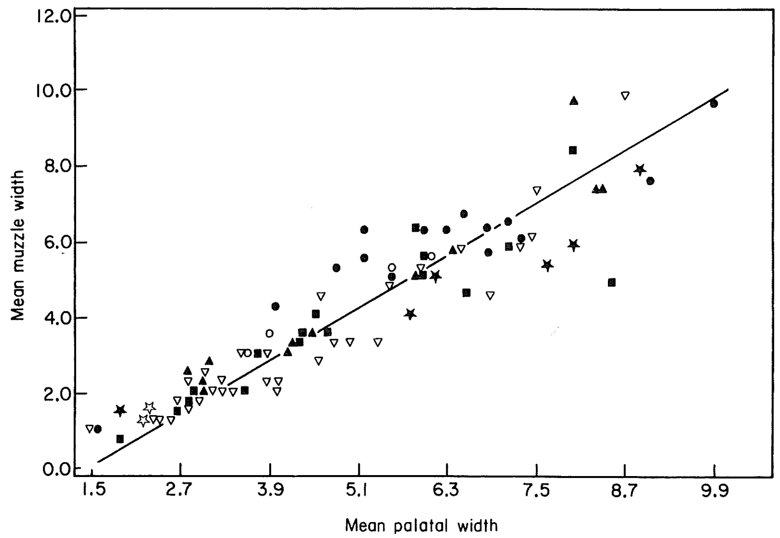

Figure 4. Plot of mean muzzle width against mean palatal width. Key as for Fig. 1. (All ungulate species are included on this plot, but the regression line is calculated for selenodont artiodactyls only: see text for explanation.)

The distribution of the residuals about the regression line was examined for selenodont artiodactyls in each dietary category, using a non-parametric signed rank test, and only the regular grazers' residuals differed significantly from a random distribution about zero. A pairwise comparison of the means of the residuals was also made, comparing the different dietary categories (for selenodont artiodactyls only), by means of a parametric comparison using a *t* test (see Table 4).

In this comparison, high level browsers can be distinguished from every other dietary category, having a narrower muzzle than would be expected for a given value of palatal width, even though the means of the residuals do not differ significantly from random. Grazers can similarly be distinguished, by virtue of their relatively broad muzzles, from every dietary category except fresh grass grazers and succulent browsers. None of the other dietary categories could be distinguished from each other by this method of comparison.

TABLE 4. Comparison of differences between means of residuals around regression line for muzzle/palatal width for different dietary types among selenodont artiodactyls

	G	F	W	B	S	M	H
G		0.42	0.77	1.28	0.42	0.84	1.51
F			0.34	0.37	0.01	0.41	1.08
W	*			0.04	0.42	0.08	0.67
B	*				0.37	0.04	0.71
S						0.42	1.09
M	*						0.67
H	*	*	*	*	*	*	

Key to dietary types as for Table 1.
* $P < 0.05$.

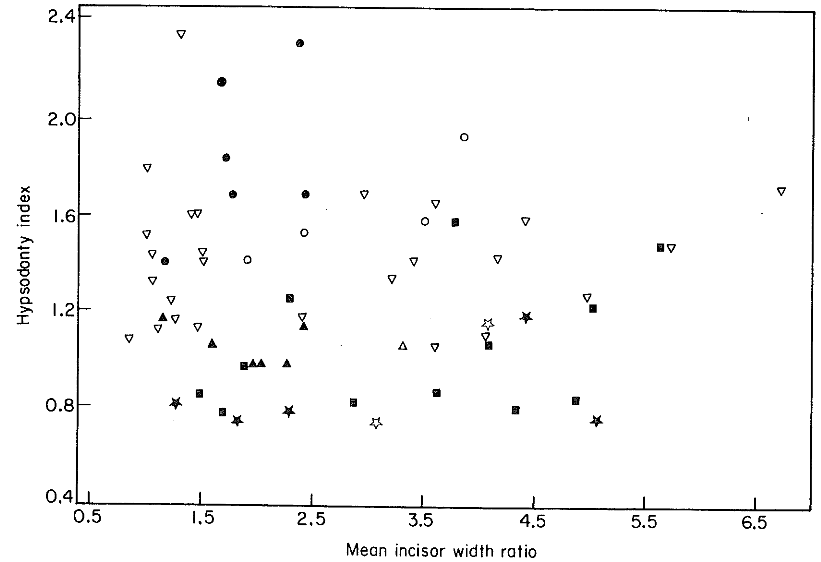

Figure 5. Plot of mean incisor width ratio against hypsodonty index. Key as for Fig. 1.

Relative incisor width in relation to dietary type

Figure 5 shows the plot of incisor width ratio for artiodactyls (mean first incisor width divided by mean third incisor width) against hypsodonty index. Sample sizes for incisor width ratios were considerably smaller than those for muzzle/palatal width ratios (see Appendix), due to the frequent occurrence of damage to the anterior part of the jaw in specimens in museum collections. The plot shows a great deal of scatter, especially among the mixed feeders in open habitats, which have the relatively smallest ratio (*Camelus dromedarius*) and the relatively largest ratio (*Antidorcas marsupialis*). However, grazers do have a relatively small ratio (i.e. incisors that are more nearly equal in size), whereas browsers of all types tend to have larger ratios. The means of the incisor widths ratios of grazing and browsing selenodont artiodactyls were significantly different ($P < 0.05$ in a Wilcoxon test; see Table 5). Given the apparent spread of the data points for the mixed feeding categories, we did not investigate the differences between other dietary types.

Relative incisor width was also examined by plotting the log values of the widths of the central and lateral incisors against log body weight (see Figs 6 & 7). For these plots, the dietary types were combined as previously detailed into three categories of grazers, intermediate feeders and browsers. A pairwise comparison was made in each case of the means of the residuals for the dietary

TABLE 5. Comparison of incisor width ratios (IWR) between grazing and browsing selenodont artiodactyls

No. of species	Dietary type	IWR Mean	S.D.
7	Grazers	1.91	1.36
21	Browsers	3.20	0.480

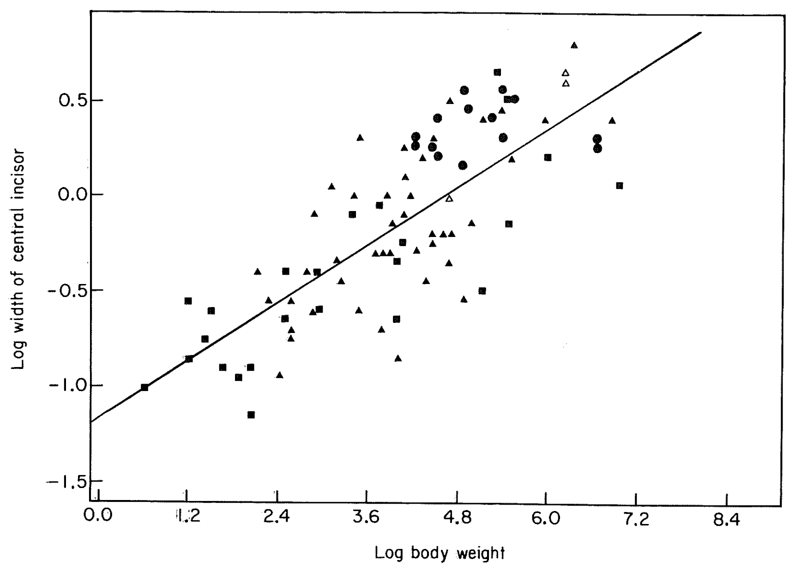

Figure 6. Plot of log width of central incisor against log weight (selenodont artiodactyls only). ● = Grazers, ▲ = intermediate feeders (ruminants), △ = intermediate feeders (camelids), ■ = browsers.

categories by means of a parametric comparison using a t test. In the case of the central incisor, grazers had significantly wider incisors than both browsers ($P < 0.01$) and intermediate feeders ($P < 0.05$). In the case of the lateral incisor, intermediate feeders had significantly wider incisors than browsers ($P < 0.05$). (Camelids, all intermediate feeders, had particularly high values for the width of the lateral incisor.)

These results imply that, while grazers have more subequal incisors than

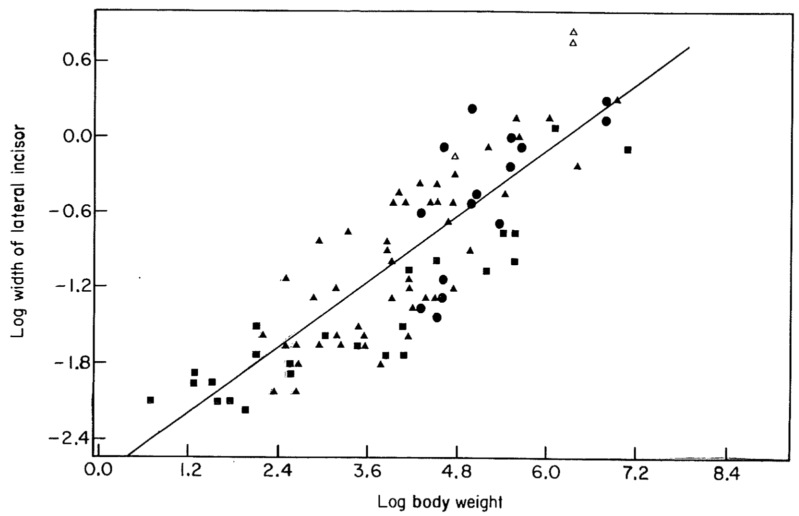

Figure 7. Plot of log width of lateral incisor against log body weight (selenodont artiodactyls only). Key as for Fig. 6.

browsers, all the incisors are relatively broad in comparison with other feeding types, resulting in an overall broader incisor row. This would correlate with the broader muzzle observed in grazers. The more subequal incisor row of many intermediate feeders in comparison with browsers (especially that of camelids, which were cited by Boué (1970) as an example of a typically 'grazing' type of incisor row), appears to be achieved by a relative widening of the lateral incisors, but with less overall broadening of the total incisor row. This would correlate with the relatively narrow muzzle observed in intermediate feeders.

DISCUSSION

Relative muzzle width in ungulates is indeed correlated with dietary category, and more selective feeders tend to have relatively narrower muzzles. Grazers, the least selective feeders, have a mean relative muzzle width that is significantly broader than that of all other feeding categories. Within grazing species, fresh grass grazers and certain types of tall grass grazers (members of the bovid tribe Hippotragini) have a narrower muzzle than that of other grazing artiodactyls. Even though grazing equids are less selective than grazing ruminant artiodactyls (Bell, 1969, 1970), they have a slightly narrower relative width, which indicates that phylogenetic history may affect the absolute value of morphometric proportions, and that caution should be exercised when comparing animals of different taxonomic groupings.

Within selenodont artiodactyls, mixed feeders in open habitats and high level browsers possess the narrowest muzzles. Animals in both types of feeding categories need to be highly selective; the mixed feeders to select grass leaves and low level dicotyledonous material from within a tall stand of vegetation, and the high level browsers to strip leaves off twigs or branches. (This is in contrast to the feeding strategy of regular browsers, which are more prone to consume entire portions of herbaceous shrubs.) Mixed feeders in open habitats have relatively narrower muzzles than mixed feeders in closed habitats, on the basis of mean relative muzzle width ratios, and high browsers can be distinguished from other dietary categories by the distribution of residuals around the regression line of mean muzzle width plotted against mean palatal width. The difference in statistically distinguishing these feeding categories by all tests employed is probably related to the wide diversity of muzzle widths among the mixed feeders, and to the small sample size of the high level browsers.

Relative incisor width varies widely among selenodont artiodactyls, especially among species in the mixed feeding categories. However, it is possible to distinguish between the incisor width ratio of grazers (which tend to have relatively equal sized incisors) and those of browsers (which have central incisors that are broader than the lateral ones). These incisor differences are probably related to the different functional uses of the anterior dentition: for cropping grass swards in the grazers, or for selectively picking off individual leaves from twigs in the browsers. However, this simple ratio conceals the fact that all the incisors in grazers are relatively broad, in correlation with the broader muzzle.

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APPENDIX

List of species measured, and mean values for each measurement with sample size for each species in parenthesis. RMW = relative muzzle width (palatal width/muzzle width); IWR = incisor width ratio (I_1 width/I_3 width): HI = hypsodonty index (M_3 height/M_2 length).

Species	Diet	Muzzle width		Palatal width		RMW	1st Incisor width		3rd Incisor width		IWR	HI
		Mean	S.D.	Mean	S.D.		Mean	S.D.	Mean	S.D.		
ORDER HYRACOIDEA												
Dendrohyrax dorsalis	H	1.40(7)	0.13	1.63(7)	0.13	1.16						0.85(1)
Heterohyrax johnstoni	M	0.97(8)	0.07	1.36(8)	0.06	1.41						0.79(2)
Procavia capensis	G	1.07(4)	0.09	1.40(4)	0.18	1.30						1.02(4)
ORDER PERISSODACTYLA												
Family Equidae												
Equus burchelli	G	6.50(4)	0.28	6.65(4)	0.12	1.02						2.22(1)
Equus grevyi	G	5.88(6)	0.37	7.15(6)	0.36	1.22						2.48(1)
Equus hemionus	G	5.67(5)	0.10	6.77(5)	0.30	1.19						2.69(1)
Equus kiang	G	6.05(5)	0.16	6.72(5)	0.26	1.11						2.63(1)
Equus przewalski	G	6.24(2)	0.33	7.05(2)	1.06	1.13						2.42(1)
Equus zebra	G	6.48(9)	0.38	6.57(9)	0.34	1.01						2.67(2)
Family Rhinocerotidae												
Ceratotherium simum	G	7.41(3)	0.68	8.80(4)	0.08	1.19						1.33(3)
Dicerorhinus sumatrensis	B	6.18(2)	0.39	7.30(2)	0.43	1.18						0.76(1)
Diceros bicornis	B	4.81(4)	0.66	8.68(5)	0.77	1.81						1.01(6)
Rhinoceros sondaicus	B	8.30(1)	—	7.80(1)	—	0.94						0.60(1)
Rhinoceros unicornis	W	9.62(4)	1.23	8.52(4)	1.03	0.89						0.58(2)
Family Tapiriidae												
Tapirus indicus	H	4.96(2)	0.06	6.24(2)	0.23	1.26						0.54(1)
Tapirus terrestris	H	4.17(5)	0.16	5.60(5)	0.16	1.34						0.65(1)
ORDER ARTIODACTYLA												
Family Antilocapridae												
Antilocapra americana	M	3.22(11)	0.29	4.73(11)	0.26	1.47	0.84(7)	0.10	0.65(7)	0.05	1.29	2.36(2)

Appendix *continued*

Species	Diet	Muzzle width Mean	Muzzle width s.d.	Palatal width Mean	Palatal width s.d.	RMW	1st Incisor width Mean	1st Incisor width s.d.	3rd Incisor width Mean	3rd Incisor width s.d.	IWR	HI
Family Bovidae												
Alcelaphini												
Aepyceros melampus	M	3.11(8)	0.33	3.80(9)	0.25	1.22	1.25(8)	0.11	0.29(8)	0.06	4.38	1.57(2)
Alcelaphus buselaphus	G	5.57(18)	0.32	5.17(18)	0.38	0.93	1.48(8)	0.25	0.62(7)	0.07	2.38	1.66(3)
Connochaetes gnou	G	6.19(3)	0.40	5.18(4)	0.54	0.84	1.69(3)	0.19	0.98(2)	0.40	1.72	1.84(3)
Connochaetes taurinus	G	6.32(18)	0.42	5.97(19)	0.44	0.95	1.71(8)	0.34	1.04(9)	0.18	1.65	2.16(6)
Damaliscus dorcas	G	4.35(10)	0.27	3.98(11)	0.33	0.91	1.25(9)	0.21	0.52(8)	0.08	3.60	1.51(5)
Damaliscus hunteri	M	4.62(7)	0.19	4.56(7)	0.13	0.99	1.15(4)	0.21	0.60(3)	0.05	1.92	1.19(1)
Damaliscus lunatus	G	5.50(10)	0.19	4.82(10)	0.13	0.91	1.63(5)	0.07	0.70(4)	0.08	2.33	2.33(1)
Boselaphini												
Boselaphus tragocamelus	W	4.97(6)	0.37	5.83(7)	0.48	1.17	1.34(2)	0.12	0.84(2)	0.21	1.60	1.03(3)
Tetracerus quadricornis	W	2.16(9)	0.08	2.99(11)	0.22	1.38	0.69(4)	0.13	0.28(4)	0.02	2.42	1.12(4)
Bovini												
Bison bison	G	9.61(9)	0.96	9.92(9)	0.65	1.03	1.30(5)	0.18	1.15(15)	0.15	1.13	1.42(2)
Bison bonasus	W	7.26(1)	—	8.40(1)	—	1.16						1.59(2)
Bos gaurus	M	7.29(2)	1.72	7.53(2)	0.11	1.03	1.60(1)	—	1.16(1)	—	1.38	1.59(1)
Syncerus caffer	M	9.85(10)	1.21	8.70(10)	0.56	0.88	1.42(2)	0.07	1.40(2)	0.22	0.99	1.79(1)
Caprini												
Capra ibex	M	1.98(2)	0.03	3.99(2)	0.14	2.02	0.52(2)	0.13	0.36(2)	0.04	1.46	1.60(1)
Ovis canadensis	M	2.15(4)	0.28	4.95(4)	1.25	1.57	0.78(2)	0.04	0.74(2)	0.05	1.05	1.34(2)
Pseudois nayaur	M	2.54(1)	—	3.88(1)	—	1.53						1.76
Cephalophini												
Cephalophus monticola	S	1.21(8)	0.04	2.16(8)	0.12	1.77	0.43(4)	0.09	0.11(4)	0.01	4.05	1.12(5)
Cephalophus silvicultor	B	3.56(5)	0.35	4.65(5)	0.29	1.31	0.76(6)	0.06	0.33(6)	0.07	2.29	1.22(3)
Silvicapra grimmia	B	1.96(2)	0.16	2.99(2)	0.13	1.53						1.45(3)
Gazellini												
Ammodorcas clarkei	H	1.74(3)	0.32	2.82(3)	0.05	1.62	0.98(3)	0.16	0.22(3)	0.05	4.39	1.17(1)
Antidorcas marsupialis	M	2.04(11)	0.21	3.26(11)	0.16	1.60	1.41(11)	0.11	0.21(11)	0.10	6.69	1.69(5)
Gazella granti	M	2.28(5)	0.21	3.95(7)	1.00	1.73	1.21(5)	0.07	0.29(5)	0.02	4.13	1.41(1)
Gazella thomsoni	M	1.63(21)	0.11	2.91(21)	0.16	1.79	1.00(21)	0.12	0.30(21)	0.43	3.38	1.41(8)
Litocranius walleri	H	2.05(15)	0.28	2.91(15)	0.22	1.42	0.92(8)	0.07	0.18(10)	0.01	5.04	0.72(2)
Hippotragini												
Hippotragus equinus	G	6.15(1)	—	6.30(1)	—	1.02						1.54(1)
Hippotragus niger	G	4.89(7)	0.61	5.55(10)	0.36	1.14	1.33(3)	0.24	0.75(3)	0.04	1.77	1.67(2)
Oryx gazella	M	5.28(6)	0.27	5.91(7)	0.34	1.12	1.40(3)	0.11	0.95(3)	0.04	1.48	1.41(5)
ORDER ARTIODACTYLA												
Family Bovidae												
Neotragini												
Dorcatragus megalotis	M	1.22(3)	0.12	2.32(3)	0.13	1.90	0.72(1)	—	0.20(1)	—	3.60	1.65(1)
Madoqua kirki	B	0.78(3)	0.11	1.91(3)	0.10	2.45	0.44(3)	0.02	0.15(3)	0.01	2.85	0.79(1)
Nesotragus moschatus	B	1.14(6)	0.12	2.20(7)	0.06	1.93	0.47(6)	0.03	0.12(5)	0.03	3.75	1.56(1)
Orebia orebi	M	2.63(9)	0.12	3.57(10)	0.17	1.48	0.91(9)	0.06	0.29(7)	0.33	3.17	1.58(3)
Oreotragus oreotragus	M	2.77(2)	0.11	3.56(5)	0.24	1.88	0.47(3)	0.12	0.20(3)	0.06	2.41	1.18(1)
Raphicerus campestris	M	1.37(13)	0.09	2.42(14)	0.15	1.76	0.67(11)	0.16	0.19(11)	0.13	3.59	1.05(6)
Raphicerus melanotis	M	1.36(9)	0.06	2.57(9)	0.21	1.87	0.62(4)	0.10	0.15(4)	0.05	4.03	1.07(6)
Reduncini												
Kobus ellipsiprymnus	F	5.18(13)	0.80	5.55(14)	0.26	1.07	1.31(3)	0.17	0.34(2)	0.08	3.48	1.54(1)
Kobus kob	F	3.26(2)	0.59	3.72(2)	0.12	1.14						1.75(1)
Kobus lechwe	F	3.52(4)	0.41	3.92(4)	0.50	1.12	1.86(3)	0.25	0.53(3)	0.06	3.84	1.91(1)
Pelea capreolus	M	2.12(3)	0.21	3.10(5)	0.21	1.46	0.80(2)	0.09	0.16(2)	0.00	4.97	1.25(1)
Redunca arundinum	F	3.04(13)	0.30	3.62(14)	0.17	1.19						1.75(2)
Redunca fulvorufula	M	2.48(13)	0.17	3.04(14)	0.22	1.22	1.14(4)	0.16	0.20(4)	0.04	5.71	1.46(4)
Rupicaprini												
Budorcas taxicolor	M	5.79(4)	1.05	7.28(6)	0.56	1.26	1.27(2)	0.04	1.15(3)	0.05	1.10	1.12(1)
Capricornis sumatrensis	M	3.19(4)	0.20	5.29(4)	0.32	1.66	0.83(3)	0.07	0.57(3)	0.12	1.46	1.14(1)
Nemorhaedus goral	M	2.36(7)	0.22	3.79(7)	0.20	1.61	0.62(6)	0.12	0.49(6)	0.04	1.27	1.15(1)
Oreamus americanus	M	2.88(6)	0.41	4.49(8)	0.34	1.56	0.77(4)	0.14	0.75(3)	0.03	1.02	1.52(3)
Ovibos moschatus	M	4.79(1)	—	6.90(1)	—	1.47	0.75(1)	—	0.83(1)	—	0.90	1.29(1)
Rupicapra rupicapra	M	2.12(5)	0.16	3.38(5)	0.20	1.60	0.50(4)	0.07	0.42(4)	0.07	1.21	1.25(2)
Tragelaphini												
Taurotragus oryx	M	6.13(10)	0.98	7.45(10)	1.14	1.33	2.03(8)	0.30	0.68(8)	0.16	2.97	1.68(1)
Tragelaphus angasi	W	3.40(8)	0.35	4.45(11)	0.33	1.31	1.49(4)	0.21	0.30(7)	0.14	4.93	1.22(1)
Tragelaphus buxtoni	B	4.60(2)	0.88	6.52(3)	0.26	1.42	1.50(2)	0.28	0.37(1)	—	4.05	1.02(2)
Tragelaphus euryceros	B	5.73(6)	0.45	7.11(7)	0.48	1.24	1.91(2)	0.04	0.45(2)	0.06	4.28	0.75(1)
Tragelaphus imberbis	B	4.00(5)	0.59	4.49(5)	0.35	1.22	1.50(4)	0.21	0.31(4)	0.01	4.85	0.79(2)
Tragelaphus scriptus	B	2.93(9)	0.44	3.73(12)	0.20	1.28	1.15(15)	0.08	0.21(16)	0.05	5.59	1.42(1)
Tragelaphus strepsiceros	B	5.07(10)	1.58	5.93(12)	0.56	1.17	1.68(8)	0.11	0.34(8)	0.06	4.99	1.19(1)

Appendix *continued*

Species	Diet	Muzzle width Mean	Muzzle width S.D.	Palatal width Mean	Palatal width S.D.	RMW	1st Incisor width Mean	1st Incisor width S.D.	3rd Incisor width Mean	3rd Incisor width S.D.	IWR	HI
Family Camelidae												
Camelus bactrianus	M	5.81(3)	0.84	6.44(3)	1.15	1.12	1.78(3)	0.41	2.16(3)	0.30	0.83	1.07(2)
Camelus dromedarius	M	4.83(2)	1.31	5.50(2)	0.42	1.14	1.34(1)	—	1.68(1)	—	0.80	0.83(1)
Lama guanicoe	M	2.95(4)	0.27	3.40(4)	0.23	1.19	0.97(4)	0.11	0.91(4)	0.13	1.06	1.45(2)
Lama pacos	M	2.18(1)	—	3.20(1)	—	1.47	0.80(1)	—	0.32(1)	—	2.50	1.56(1)
Vicugna vicugna	M	2.06(6)	0.27	3.49(6)	0.32	1.25	0.78(6)	0.06	0.52(6)	0.11	1.50	1.43(3)
Family Cervidae												
Alces alces	H	5.84(7)	0.69	8.02(7)	0.54	1.37	1.27(3)	0.06	1.03(3)	0.05	1.23	0.80(3)
Blastocerus dichotomus	M	3.18(2)	0.16	4.49(2)	0.41	1.42						0.90(1)
Capreolus capreolus	W	2.68(2)	0.56	3.93(2)	0.38	1.47						0.90(1)
Cervus canadensis	W	5.73(1)	—	6.35(1)	—	1.11	1.29(2)	0.23	0.67(2)	0.08	1.93	0.96(2)
Cervus nippon	W	2.99(4)	0.91	4.09(4)	0.13	1.37	0.88(4)	0.11	0.27(4)	0.04	3.30	1.03(2)
Elaphurus davidianus	F	5.57(6)	0.31	6.10(6)	0.48	1.10	1.34(6)	0.14	0.70(6)	0.71	1.92	1.39(3)
Hippocamelus bisculus	W	3.17(2)	0.24	4.23(3)	0.53	1.33	0.73(3)	0.09	0.32(3)	0.12	2.27	0.96(1)
Hydropotes inermis	W	2.66(7)	0.23	3.06(7)	0.27	1.15	0.38(3)	0.03	0.19(3)	0.01	2.00	0.96(1)
Mazama mazama americana	B	2.06(4)	0.11	3.49(4)	0.30	1.69	0.63(4)	0.06	0.20(4)	0.02	3.14	0.75(1)
Moschus moschiferus	W	2.48(6)	0.07	2.80(6)	0.08	1.12	0.38(4)	0.03	0.32(4)	0.03	1.17	1.16(2)
Muntiacus reevesi	W	2.03(1)	—	2.99(1)	—	1.47	0.60(1)	—	0.17(1)	—	3.53	0.76(1)
Odocoileus hemionus	B	3.55(1)	—	4.37(1)	—	1.23	0.72(1)	—	0.50(1)	—	1.44	0.84(1)
Odocoileus virginianus	B	3.17(16)	0.34	4.25(16)	0.39	1.34	0.64(11)	0.10	0.18(11)	0.03	3.58	0.83(4)
Pudu pudu	B	1.57(3)	0.10	2.66(3)	0.22	1.69	0.38(3)	0.08	0.21(3)	0.02	1.83	0.96(1)
Rangifer caribou	B	6.30(6)	1.13	5.82(6)	0.94	0.92	0.60(2)	0.04	0.36(2)	0.01	1.65	0.76(1)
Rangifer tarandus	B	5.46(4)	0.19	5.99(4)	0.15	1.10	0.60(3)	0.04	0.35(3)	0.03	1.71	0.59(1)
Family Giraffidae												
Giraffa camelopardalis	H	7.87(3)	1.81	8.95(7)	0.62	1.14	1.84(1)	—	0.82(1)	—	2.24	0.75(2)
Okapia johnstoni	H	5.21(4)	0.75	7.64(5)	0.33	1.47	0.91(2)	0.04	0.51(2)	0.01	1.81	0.74(3)
Family Tragulidae												
Hyemoschus aquaticus	S	1.48(3)	0.03	2.26(6)	0.06	1.53	0.56(5)	0.03	0.18(5)	0.10	3.07	0.71(2)
Tragulus javanicus	S	1.19(1)	—	1.53(1)	—	1.29						0.79(1)

Key to dietary symbols (see text for further explanation): G = dry grass grazer; F = fresh grass grazer; M = mixed feeder in open habitat; W = mixed feeder in closed habitat; B = unspecialized browser; S = selective browser; H = high level browser.

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Wing-scales of *Pseudoleptocerus chirindensis* Kimmins (Trichoptera: Leptoceridae)

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The African species *Pseudoleptocerus chirindensis* belongs to a small group of Trichoptera most unusual in having scaly wings. Electron microscope studies reveal 13 structurally distinct kinds of cuticular process on the wings, including several types of squamiform and hair-like macrotrichia. These are described in detail and their possible functions inferred. The optical properties of the scales forming the colour pattern of the forewings are related to ultrastructural elements including diffraction and thin film interference systems. Trichopteran scale structure is compared with that of the Lepidoptera, the sister-group in the Amphiesmenoptera. Differences are found and it is tentatively concluded that wing-scales have evolved independently in the two orders.

KEY WORDS:—Trichoptera – Leptoceridae – *Pseudoleptocerus* – *Ceraclea* – Lepidoptera – Amphiesmenoptera – ultrastructure – functional morphology – wing-scales – interference colours.

CONTENTS

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