

MORPHOLOGICAL ADAPTATIONS OF THE MUZZLE AND ANTERIOR DENTITION OF THE LESSER MOUSEDDEER, *TRAGULUS JAVANICUS* (OSBECK), IN RELATION TO ITS DIETARY PREFERENCES

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SUMMARY

The skulls and mandibles of seven (2 males, 5 females) adult lesser mouseddeer (*Tragulus javanicus*) were subjected to various morphometrical analysis, in order to determine adaptations to dietary preferences. The muzzle is narrow (10.4 ± 0.5 mm) and elongated, with a relative muzzle width of 1.44 units. These features of the muzzle enable *T. javanicus* to select succulent, nutritious plant material among the more matured, high fibrous foliage. The central incisor is the largest of the incisors, and possesses a broad crown (2.9 ± 0.3 mm), and narrow neck. The two lateral incisors are relatively narrow, sickle shaped, and possess sharp crowns (0.3 ± 0.1 mm). The lower canine is incisiform, chisel shaped and incorporated into the lower incisor arcade. The incisor width ratio of 8.06 units, is higher than that reported for other ruminant artiodactyles. It is suggested that such dental specialization is an adaptation suitable for nibbling and cutting soft ripe fruit. The incisors are upright and cupped with an incisor insertion angle of 47.8 ± 2.9 degrees. We suggest that this is an adaptation to dig into soft ripe fruit pulp. The morphology of the muzzle and anterior dentition of *T. javanicus* exhibit an adaptation to select a diet consisting of succulent, highly nutritious plant material, typical for a selective browser.

Keywords: Muzzle, dentition, diet, *Tragulus javanicus*.

INTRODUCTION

Several studies on ungulate ecology have revealed a correlation between dietary preference and craniomorphological specialization (e.g. Gwyne and Bell, 1968; Bell, 1969, 1970; Boue, 1970; Jarman, 1974; Vidyadaran *et al.*, 1981; Owen-Smith, 1982; Janis and Ehrhardt 1988; Spenser, 1995). Janis and Ehrhardt (1988) correlated relative muzzle width to the degree of diet selectivity, and suggested that grazers have relatively broader muzzles compared to browsers and mixed feeders. A narrow muzzle is essential in ungulates that feed selectively, allowing them to pick out certain plant parts (e.g. dicotyledonous material or other nutritious foliage) at ground level in a tall stand of vegetation (Owen-Smith, 1982). A relatively broader muzzle, however, is important to a less selective grazer feeding on short grass, enabling it to take large bites, hence maintaining a high rate of intake to fulfill its nutritional requirements, as grass is usually high in fiber and low in nutritional content (Janis and Ehrhardt, 1988).

Studies on ungulate dental morphology have also indicated adaptations to diet selectivity. Vidyadaran *et*

al. (1981), noted that in *T. javanicus* the shape of the incisors and premolars indicate a type of dentition suited to a diet of succulent grasses and vegetables, fruits, roots and tubers. The angle of insertion of the lower incisors also reflects the degree of diet selectivity in ungulates. Grazing ruminants have been shown to possess forward projecting, spatula like, lower incisors, compared to the more upright, cupped lower incisors of browsers (Bell, 1969). Studies by Boue (1970) suggest that, in grazing ruminants the crown width of the central incisors tends to be fairly similar to that of the lower canines and lateral incisors, whereas in browsers the central incisors are relatively broader.

In order to investigate further the correlation between craniomorphological specialization and dietary preference, we performed morphometrical analysis on various cranial structures of the lesser mouseddeer (*T. javanicus*), a small, primitive, ruminant artiodactyl, widespread throughout lowland forest of South East Asia (Medway, 1978; Payne and Francis, 1985). Several authors have suggested that this tragulid feeds on succulent plant material including fallen fruits on the forest floor, leaf shoots and fungi (Lekagul and McNeely, 1977; Medway, 1978; Vidyadaran *et al.*

1981; Payne and Francis, 1985). Janis and Ehrhardt (1988) have attempted to categorise *T. javanicus* as a selective browser, but conclusions were drawn based on analysis of only one specimen.

This study reports morphometrical findings on the muzzle and anterior dentition of captive *T. javanicus*, and suggests the functional adaptation of these structures in relation to its dietary preferences. It further strengthens knowledge on the dental morphology of this tragulid, as reported by Vidyadaran *et al.* (1981), and investigates the dietary class of *T. javanicus* proposed by Janis and Ehrhardt (1988), in order to place this animal in a more accurate position among the other ungulates (namely artiodactyl browsers), with regard to dietary preference.

MATERIALS AND METHODS

The skulls and mandibles of seven adult *T. javanicus* (2 males and 5 females) that had died in captivity, were obtained from the Anatomy Museum, Faculty of Veterinary Medicine and Animal Science, Universiti Putra Malaysia. All the animals had fully erupted permanent dentition. Linear measurements of the skulls and mandibles were recorded using vernier calipers to the nearest 0.1 mm. These measurements

(illustrated in Figure 1), together with the calculated ratios, were adapted from Janis and Ehrhardt (1988). They include :

- Muzzle width (mzw) - measured at the junction of the maxillary and premaxillary bones (maximum outer distance).
- Palate width (paw) - measured between the lingual surfaces of the upper second molars (at the level of the protocone).
- Incisor width (iw) - measured on the first and third mandibular incisors (maximum width along the crown).
- Incisor insertion angle (ia) - the angle between the first mandibular incisor and the horizontal plane of the mandible.

These measurements were then used to calculate two parameters that we used to relate to diet selectivity and specialization, namely :

- Relative muzzle width (rmw) - the mean palate width divided by mean muzzle width.
- Incisor width ratio (iwr) - the mean width of the first lower incisor divided by the mean width of the third lower incisor.

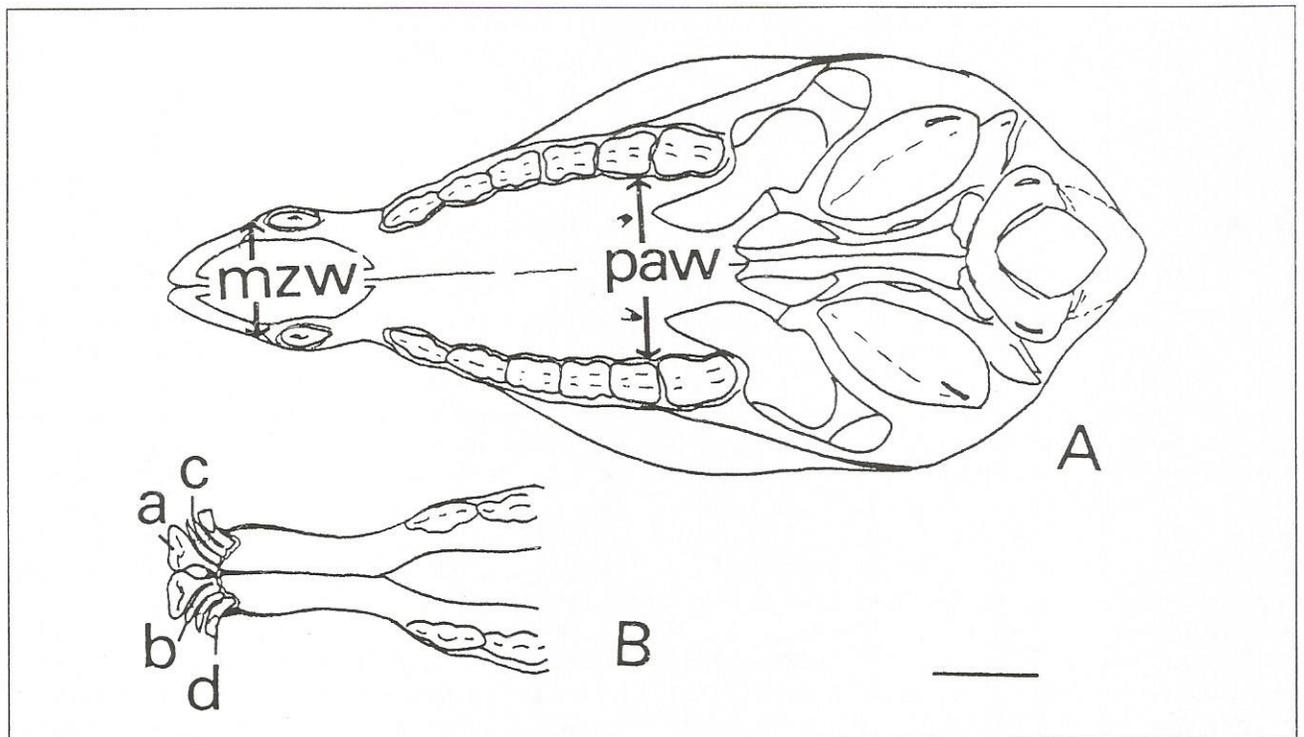


Figure 1. (A) Ventral view of the skull of *T. javanicus* illustrating measurements for palate width (paw) and muzzle width (mzw). (B) Dorsal view of the anterior portion of the mandible *T. javanicus*. The first incisors (a) are unique, in that, they possess rather broad crowns and narrow cylindrical necks. The second (b) and third incisors (c) are narrow, pointed and curve posteriorly, as to accommodate the broad crowns of the first incisors. The atypical canine teeth (d) are incisiform and incorporated into the row of incisors. Scale bar represents 10 mm.

In order to facilitate comparison with previously published information, the definitions of dietary classes correspond to those coined by Janis and Ehrhardt (1988). They include :

- Grazers consume at least 90% grass as year round diet.
- Mixed feeders consume between 10 to 90% grass as year round diet.
- Browsers consume more than 90% of dicotyledonous material as year round diet.

Browsers were further defined as: unspecialised browsers - taking a mixture of leaves, shrubs, herbs and succulent items; selective browsers - taking very little fibrous material and concentrating mainly on succulents, fruits and buds; high level browsers - feed almost exclusively on tree leaves, eating items at or above their own head level in preference to lower shrubs or herbs.

RESULTS

The linear measurements of the muzzle and dentition of *Tragulus javanicus* are given in Table 1. The muzzle of *T. javanicus* is relatively narrow (10.4 ± 0.5 mm) and elongated, leading posteriorly to a broader palate (15.0 ± 0.8 mm). Due to the large orbitals, the muzzle appears narrower than the calculated relative muzzle width ($rmw = 1.44$). The narrow muzzle and pointed premaxilla, carries a dental pad, which is comparable (but not as prominent) to that of other ruminants.

Table 1. Linear measurements of the muzzle and dentition of adult *T. javanicus* (2 males, 5 females).

| Parameters | Measurements (mm) | | |
|--------------|-------------------|------|-------------|
| | mean | SD | range |
| mzw | 10.37 | 0.49 | 9.4 - 10.8 |
| paw | 14.97 | 0.74 | 13.7 - 15.8 |
| iw (1) | 2.90 | 0.28 | 2.5 - 3.4 |
| iw (3) | 0.36 | 0.05 | 0.3 - 0.4 |
| ia (degrees) | 47.79 | 2.89 | 45.0 - 52.5 |

mzw - muzzle width

paw - palate width

iw(1) - crown width of first incisor

iw(3) - crown width of third incisor

ia - incisor insertion angle

cupped-like, with an incisor insertion angle of 47.8 ± 2.9 degrees in reference to the horizontal plane of the mandible. The second and third incisors however, are relatively narrow, sickle shaped and possess sharp crowns (0.3 ± 0.1 mm). They appear to curve posteriorly, so as to accommodate the broad crown of the first incisor. The incisor width ratio was calculated as 8.06 units. While the lower central incisors occlude with the anterior tip of the premaxilla, the lateral incisors (and incisiform canines) appear to protrude away from the lateral borders of the premaxilla. This is due to the differences in the relative curvatures of the premaxilla and the lower incisor arcade. The premaxilla appears to be more pointed, with an acute curvature, whilst the lower incisor arcade has a broader curvature (due to the broad crowns of the central incisors).

The lower canines are reduced to incisiform, chisel shaped teeth, incorporated into the row of lower incisors. The lower canine tooth possess a broader body and apex compared to the second and third incisors and its overall appearance is atypical of canine teeth. The lower incisor arcade (including the lower canines) is separated from the first lower premolar by a wide maxillary diastema.

DISCUSSION

Relative muzzle width in relation to dietary preference

In ungulates, the relative width of the muzzle is related to the degree of diet selectivity (Owen-Smith, 1982; Janis and Ehrhardt, 1988). Grazers tend to possess relatively broader muzzles compared to mixed feeders and browsers. Nge'the and Box (1976) supported this argument with observations on goats and elands feeding on *Acacia*. The goats with their narrow muzzles, were able to obtain a larger proportion of pure leaf material by inserting their muzzles through the spines of the plant community, compared to the elands that possess a broader muzzle.

Among the browsers, high level browsers tend to possess narrower muzzles compared to selective and unspecialised browsers (Janis and Ehrhardt, 1988). Despite the varying body sizes among artiodactyls, it is interesting to note that muzzle shape is fairly independent of body size. Browsers as large as *Giraffa camelopardalis* and as small as *Madoqua saltiana* have pointed muzzles, while grazers as large as *Bison bison* and as small as *Ourebia ourebi* have broader muzzles (Solounias and Moelleken, 1993). This information may enable us to rule out the possibility that the relatively narrow muzzle of *T. javanicus* is due to its small body size and not indicative of dietary preferences. The value for relative muzzle width of *T. javanicus* is lower compared to other selective browsers like *Cephalopus monticola* and *Hyemoschus aquaticus* but greater than values for high level

The dental formula of *T. javanicus* is 0/3 1/1 3/3 3/3. The first incisor is the largest of the incisors, and possess a rather broad crown (2.9 ± 0.3 mm) with a

Giraffa camelopardalis (Janis and Ehrhardt, 1988). In this respect, *T. javanicus* is intermediate between the two classes of browsers mentioned. We suggest that since this tragulid has not been observed to feed above its head level (as exhibited by high level browsers), its relative muzzle width value may indicate that it is a selective browser, using its narrow muzzle to feed on selected, nutritious plant material, that would provide an adequate source of energy to maintain its high metabolic rate. As suggested by Solounias and Moelleken (1993), a pointed narrow muzzle is conducive to greater selectivity when browsing, acting as forceps to collect browse items that are normally distributed in a dispersed fashion. Our dietary classification of *T. javanicus*, based on its relative muzzle width, corresponds with that proposed by Janis and Ehrhardt (1988). Although Bodmer (1990) classifies *T. javanicus* as a frugivore, we believe that this dietary class may not be comprehensive as fruits may not be readily available year round, and this would necessitate the mousedeer to increase its foraging activities. We suggest that the narrow muzzle is an adaptation to a diet which includes succulent young leaves, shoots, and ripe fruits which it is able to select among the more matured, high fibrous foliage. In this respect, the narrow muzzle of *T. javanicus* may indicate a morphological adaptation that is not suited for efficient cropping at base of grasses at ground level as in other grazing artiodactyles. As this tragulid relies on a nutritious diet to provide for, and maintain its high metabolic rate, a narrow muzzle allows it to perform selectivity with greater precision. In addition to this, succulent diets may provide a good source of energy, which the mousedeer would certainly rely upon in order to attempt quick movements to avoid predators.

Evidence of selective, concentrate feeding in this animal has also surfaced from studies of its digestive system (Kay *et al.*, 1980; Vidyadaran *et al.*, 1982, 1994; Langler, 1988; Richardson *et al.*, 1988; Hofmann, 1989; Agungpriyono *et al.*, 1992; Hawa, 1995). Vidyadaran *et al.* (1994), reported that the parotid and mandibular glands of *T. javanicus* are relatively large, and further supported suggestions by Hofmann (1989), that large amounts of salivary secretion may be an important feature in concentrate feeders, for protection against tannins and to reduce retention time and increase rumen by-pass.

Incisor width ratio in relation to dietary preference

Incisor width ratios (iwr) have also been employed as an indicator of diet selectivity (Boue, 1970; Janis and Ehrhardt, 1988). It has been shown quantitatively by these authors that in browsing ruminants, the central incisors are much broader relative to the lateral incisors and canines (which is incisiform), whereas in grazing ruminants, the width of the central incisors tend to be fairly similar to the width of the lateral incisors and canines. The incisor

width ratio of *T. javanicus* is the highest (iwr = 8.06) compared to values for all other browsing ruminants reported by Janis and Ehrhardt (1988).

The marked difference in crown width of the first and third incisors accounts for the high incisor width ratio, supporting the argument that this tragulid is a specialised browser. Such an adaptation may be suitable for nibbling and cutting soft fruit. Moreover, the design of the central incisors does not resemble that of grazing artiodactyles, which possess incisors that are more suited to cut into coarse, fibrous plant material.

Incisor insertion angle in relation to dietary preference

Studies on the lower anterior dentition of ruminants by Bell (1969) and Boue (1970), indicate that grazers have incisors that tend to project forward in a spatulate-like fashion, whereas in browsers they are inserted in a more upright position, with a cupped appearance. In this respect, we propose that the cupped, upright incisors of *T. javanicus* may be an adaptation, to assist in nibbling off selected young leaves and shoots, or digging into ripe, succulent fruit pulp and not to cut into grass, leaves or other coarse material. This supports observations on the feeding habits of this animal in captivity, where it is not known to consume grass (Vidyadaran *et al.*, 1981), but prefers succulent vegetables such as kangkong (*Impomea aquatica* and *Impomea reptans*), long beans (*Vigna sesquipedalis*), sweet potatoes and ripe fruits.

The unique occlusal pattern of the premaxilla and lower incisor arcade, is such, that a gap is created between the lateral premaxilla and the lateral incisors. This may enable the mousedeer to grip selected vegetation, trap it between the incisors and premaxilla, and effectively pull it for browsing. This feature may be comparable to that reported for other browsers, namely, the giraffe (*Giraffa camelopardalis*) and okapi (*Okapi johnstoni*), where the incisors protrude anterior to the premaxilla (Solounias and Moelleken, 1993). In grazers, the premaxilla always occludes with the apices of the lower incisors (Solounias and Moelleken, 1993), to facilitate efficient cropping of grass.

CONCLUSION

The present findings confirm earlier reports that relative muzzle width, incisor width ratio and incisor insertion angle, in ungulates, correlate with dietary preference. More selective feeders (browsers), tend to possess relatively narrower muzzles, with higher incisor width ratios and more upright lower incisors. Based on these craniomorphological characteristics, *T. javanicus* exhibits a specialization to enable it to efficiently select a diet consisting of highly nutritious plant material with low fiber content, typical for a selective browser.

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RINGKASAN

PENYESUAIAN MORFOLOGI MUZEL DAN PENGGIGIAN ANTERIOR DALAM KANCIL TRAGULUS JAVANICUS (OSBECK), DALAM PERKAITAN DENGAN PILIHAN DIET

Tengkorak dan mandibel daripada tujuh (2 jantan, 5 betina) kancil dewasa (*Tragulus javanicus*) telah dikenakan pelbagai analisis morfometrik untuk menentukan penyesuaian kepada pilihan diet. Muzel di dapati sempit, (10.4 ± 0.5 mm) dan memanjang, dengan kelebaran muzel bandingan 1.44 unit. Ciri muzel ini membenarkan *T. javanicus* untuk memilih bahan tumbuhan sukulen berzat di antara daun matang bergentian tinggi. Kacip tengah adalah yang terbesar daripada gigi kacip, dan mempunyai korona lebar (2.9 ± 0.3 mm), dan leher ramping. Dua kacip lateral agak sempit, berbentuk sabit, dan mempunyai korona tajam (0.3 ± 0.1 mm). Taring bawah ialah insisiform, berbentuk pahat dan tergabung dengan arked kacip bawah.

Nisbah lebar kacip 8.06 unit adalah lebih tinggi daripada yang dilaporkan untuk artiodaktil ruminan lain. Adalah disarankan yang pengkhususan gigi seperti ini merupakan penyesuaian yang baik untuk mengunggis dan memotong buah-buahan masak lembut. Kacipnya tegak dan tertekup dengan sudut sisipan kacip 47.8 ± 2.9 darjah. Kami menyarankan ini adalah suatu penyesuaian untuk membenam ke dalam pulpa buah-buahan masak lembut. Morfologi muzel dan penggigian anterior T. javanicus menunjukkan suatu penyesuaian untuk memilih diet yang terdiri daripada bahan tumbuhan sukulen berzat tinggi, tipikal untuk sesuatu peragut memilih