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Feeding Behavior, Mastication, and Tooth Wear in the Western Tarsier (*Tarsius bancanus*)

Nina G. Jablonski[1] **and Robin H. Crompton**[2,3]

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We assessed feeding and masticatory function in western tarsiers, Tarsius bancanus, *from field study, from videotaped recordings of the feeding and chewing behavior of wild-caught animals in temporary captivity, from dissections of the muscles of mastication, and from scanning electron microscopic (SEM) examination of wear features of the teeth. Ingestion of large items of animal prey is made possible by the animal's extremely wide gape. Anterior translation of the knob-like mandibular condyle in the anteroposteriorly elongated mandibular fossa makes possible a gape angle of 60–70°. We observed two means of ingestion of grasshopper prey: ingestion by mastication, in which the postcanine teeth sever and reduce bites of the food as it is thrust into the mouth cavity, and repeated gape-shove sequences, during which the tarsier pushed grasshoppers of large diameter into the anterior part of its mouth and attempted to sever a bite with its anterior teeth. Morsels were successfully severed after three to five such sequences, and reduced quickly, with relatively few powerful, crushing chews. The insect cuticle was not evenly comminuted during mastication. We observed a marked side-to-side grinding component in the normal chewing cycle of* T. bancanus *on videotape and confirmed it by SEM. The main jaw adductors are bulky, long-fibered muscles that can accommodate wide grapes and still generate, at wide degrees of gape, the high occlusal pressures necessary to fracture thick chitinous exoskeletons of the scarabid beetles that form a substantial element of the western tarsier's diet.*

KEY WORDS: tarsier; *Tarsius bancanus*; feeding behavior; mastication; temporomandibular joint; tooth wear; gape.

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[1] Department of Anatomy and Human Biology, University of Western Australia, Nedlands, Perth, Western Australia.

[2] Department of Human Anatomy and Cell Biology, University of Liverpool, P.O. Box 147, Liverpool L69 3BX, UK.

[3] To whom correspondence should be addressed.

INTRODUCTION

Few living primate genera have received more attention than the tarsiers. This attention has not, however, been focused evenly over all aspects of tarsier biology. Before the era of modern field studies, while some earlier research stressed parallels between some adaptations of the tarsier consequent to a habitually upright posture and similar changes in the course of human evolution (Wood-Jones, 1918), later research centered on the origins and ambiguous phyletic position of the tarsier. Since the advent of modern field studies of tarsiers in the 1970s, research into their biology has broadened in scope and now includes studies (Crompton, 1989; Crompton and Andau, 1986, 1987; MacKinnon and MacKinnon, 1980; Musser and Dagosto, 1987; Oxnard *et al.*, 1991; Niemitz, 1984a–d) dealing with various aspects of the distribution, ecology, ranging behavior, and activity patterns of the five species of *Tarsius*.

Studies of the functional anatomy of tarsiers have concentrated mostly on the limbs and trunk, and the mechanics of their highly specialized, vertical clinging and leaping mode of locomotion. Relatively little attention has been paid to tarsiers' method of food procurement and chewing or to the mechanics of their masticatory apparatus, despite the fact that their unusual, highly "carnivorous" dietary habits have been known for some time. Of the few studies that have dealt with the masticatory apparatus of tarsiers, two noteworthy contributions include Fiedler's (1953) classic study of the jaw musculature of insectivores, which included *Tarsius syrichta*, and Maier's (1984) study of dental wear in the same species.

Our study represents an adjunct to field studies of western tarsiers, *Tarsius bancanus*, undertaken by one of us (R.H.C.) in Sepilok Forest Reserve, Sabah, East Malaysia, from 1984 to 1989. In the present study, several further kinds of information have been brought together in order to derive a more comprehensive understanding of feeding behavior and mastication in tarsiers. These include (1) information on head and jaw movements during foraging, initial stages of food processing, and chewing derived from a videotape recording of *T. bancanus* in temporary captivity; (2) preliminary observations on the morphology of the muscles of mastication and temporomandibular joint in two wild-caught specimens of *T. bancanus*; and (3) preliminary information on patterns of dental microwear in the same species based on scanning electron microscopical (SEM) examination of the dentition of one of the specimens.

We intend to pave the way for further studies of the feeding behavior, feeding apparatus, and energetics of tarsiers. Thereby, we hope to illuminate the history of its highly specialized locomotor and feeding adaptations.

MATERIALS AND METHODS

Foraging and feeding behavior were observed in tarsiers under free-ranging conditions in the field, using methods described by Crompton and Andau (1987), and in temporary captivity. It was frequently possible to observe foraging and feeding behavior for periods of ≤2.5 hr at a range of <5 meters, and indeed the subjects would pounce on natural prey as close as 0.5 m. from the observer's feet. We noted all items of food eaten by the tarsiers when they could be identified, and we estimated the size and the manner in which items of food were harvested and ingested. We also observed and videotaped feeding by one adult male and one adult female tarsier that we captured for removal of radiocollars and held in temporary captivity at the headquarters of the Sepilok Forest Reserve. They were kept overnight in a large, airy room in which several limitation saplings had been assembled from large branches to mimic their habitat. Live grasshoppers, identified as a common prey of tarsiers in the wild, were provided *ad libitum* for their consumption. Despite the artificial surroundings, the tarsiers engaged in apparently normal bouts of foraging, feeding, and locomotion. We made recordings via a standard VHS PAL videocamera and portable VCR, giving 50 fields/sec. Illumination for the videotape was via a red-filtered "Q-beam" 200,000-candlepower portable spotlight/floodlight. We analyzed the tape with a Panasonic VHS video editing suite and a Sony Hi-band U-matic editing suite, the latter of which allowed field-by-field analysis. We printed single fields of moving video from a Hi-band U-matic working master tape using a Sony video printer.

One adult male and one adult female tarsier that had been legally captured outside the Sepilok Reserve died of natural causes while awaiting shipment to the U.S. National Zoo, Washington, D.C., and Duke University Primate Center. We dissected them and the teeth of the male were prepared for SEM examination.

We prepared the specimen for SEM as follows. Following gentle maceration of the skull in boiling tap water, we rinsed it under a distilled water drip for 3 days. Then we treated it in acetone dilutions of increasing strength before placing it in a desiccation chamber. After drying, the skull was gold-coated in a sputter coater. We performed all SEM on a JEOL JXA 840 scanning electron microanalyzer. We took stereopairs with a Wild M3 Plan stereomicroscope, equipped with two beam splitters and synchronized 35-mm cameras.

RESULTS

Foraging, Feeding Behavior, and Chewing

Foraging—the active searching for food—accounts for over 60% of the activity of *T. bancanus* at Sepilok (Crompton and Andau, 1986). In an earlier report on the surviving captive animals sent from Sabah, then at the U.S. National Zoo, Washington, D.C., Roberts and Cunningham (1986) claimed that these tarsiers forage primarily above ground level. This finding is artifactual and gives an erroneous impression of the behavior of free-ranging tarsiers. In the wild, Niemitz's (1984c) earlier observations and those of Crompton and Andau (1986) are in complete accord in finding that, overwhelmingly, *T. bancanus* cling onto the vertical trunks of saplings near ground level and survey the ground visually and aurally for prey in the leaf litter. Relatively little prey is taken above ground level. In the "artificially wooded" room in which the videotape was made, the tarsiers clung to available vertical supports and surveyed the floor and other surfaces for grasshoppers (Fig. 1) in exactly the same way. The tarsiers also captured grasshoppers on branches and narrow shelves.

Fig. 1. Female *T. bancanus* foraging in temporary captivity at Sepilok.

R.H.C.'s observations of *T. bancanus* at Sepilok confirm the previous observations of several previous investigators (Davis, 1962; Niemitz, 1984c) that western tarsiers are strictly animalivorous. Davis (1962) reported that relatively large orthopterans (≥ 25 mm in length) formed the bulk of the food items taken by *T. bancanus* at the Sapagaya Forest Reserve. While the diet of *T. bancanus* at Sepilok will form part of a further communication, it is sufficient to note here that scarabid beetles, and orthopteran insects such as crickets, grasshoppers, and forest cockroaches constitute the major fraction of the diet of *T. bancanus* in the wild at Sepilok. However, we also saw free-ranging tarsiers capture and eat moths, spiders, small freshwater crabs, and small vertebrates such as flying frogs, which are generally consumed in their entirety. As reported by Crompton and Andau (1986), tarsiers have voracious appetites and are capable of eating many large prey in one night.

During a typical feeding bout recorded on video (Figs. 2 and 3A–H), a tarsier pounced on and manually seized a grasshopper, with a maximum diameter of 1.5 cm at its cranial end. It quickly transferred the prey to the front of its mouth and held it there sideways as it leapt to a secure branch. This behavior exactly matches that which R.H.C. observed in free-ranging tarsiers. The tarsier repositioned the grasshopper in its hands so that its cranial end faced its mouth, and then took the head into its mouth and held it in the region of the upper canine tooth with no further activity for several seconds.

The tarsier initially ingested the grasshopper via a series of movements, repeated in rapid succession, involving widely opening the mouth, shoving as much of the prey as possible into its oral cavity, and partially closing its jaws. It punctured the exoskeleton with its anterior teeth during the last action. In cases on videotape, the tarsier achieved a maximum gape angle (Herring and Herring, 1974), θ, of between 60 and 70°. During the widest gapes its eyes were partially or completely closed (Fig. 3D). Such gape-shove sequences were repeated, generally three to five times, until a bite of the prey was successfully severed with the animal's stout anterior teeth (Fig. 3H). (We use anterior teeth in preference to "incisors" and "canines," as the homologies of these teeth in tarsiers are not yet determined.) We also observed ingestion by mastication (severing of a morsel by the posterior teeth) during the consumption of more caudal, smaller-diameter portions of the grasshopper (Fig. 4).

Gape-shove sequences involved considerable forward, backward, and sideways movements of the head and trunk. The video recording, supported by R.H.C.'s tactile experience with hand-held tarsiers, suggests that the dorsally directed force of the prey being shoved into the mouth was countered by strong contractions of the tarsier's nuchal flexor musculature—the in-

Fig. 2.

Figs. 2 and 3. A typical gape-shove sequence of a male *T. bancanus* ingesting a grasshopper. Video prints were made from the working videotape at appropriate intervals during the 32-sec (50 fields/sec) sequence. In Fig. 2 the grasshopper is held bimanually against the vertical trunk of sapling, with its head held in the tarsier's mouth in the region of the canine, with no chewing for several seconds.

frahyoid muscles. With its head brought forward by this ventrally directed muscular effort, the tarsier shoved the prey farther into the oral cavity. Again, visual inspection suggests that initiation of jaw closure and puncturing of the exoskeleton with the anterior teeth were accompanied by dorsally directed contractions of the nuchal extensor musculature—the ster-

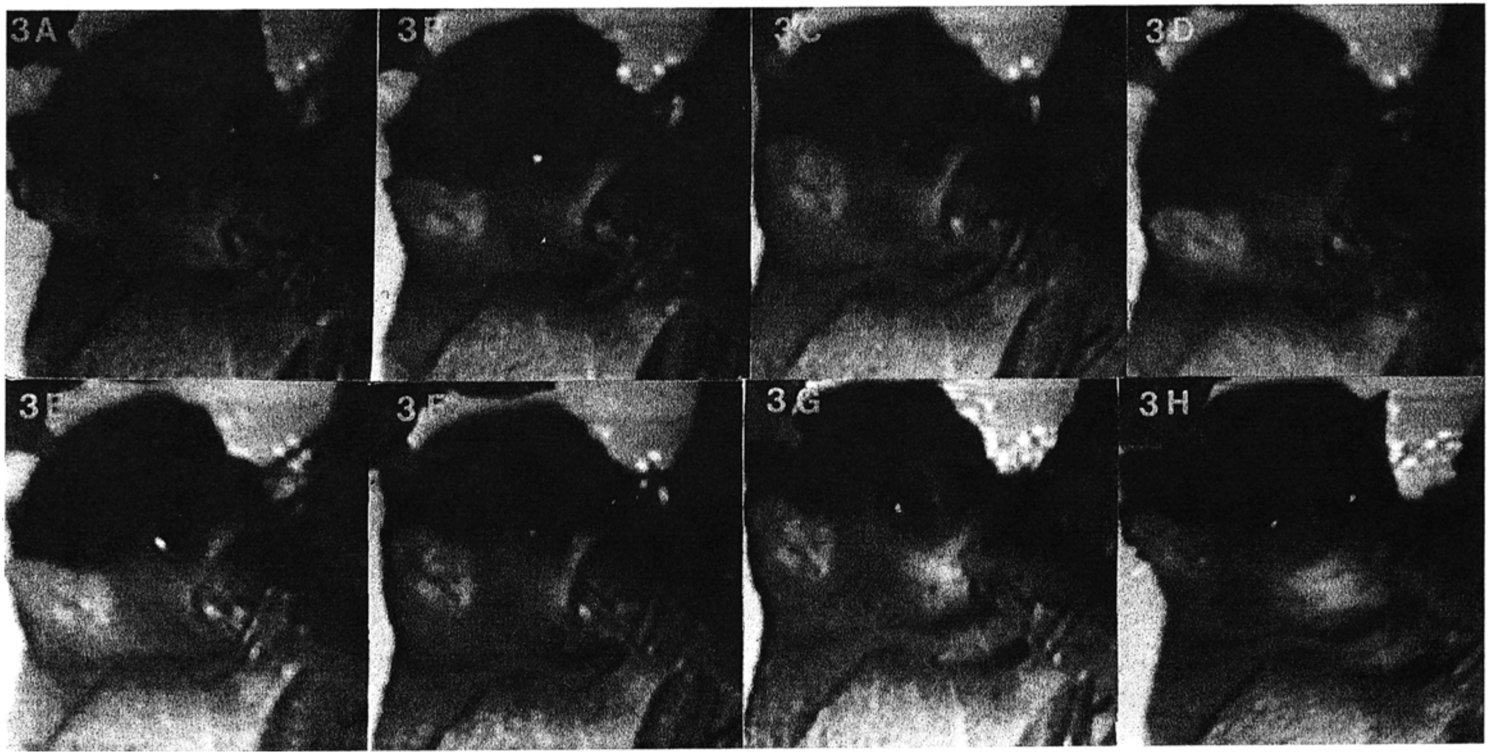


Fig. 3. (A) The tarsier rotates its head slightly as shoving commences. (B) Its jaws close slightly on the grasshopper's head, with its left eye closed and its head rotated farther forward. (C) Its head rotates to face fully forward, its jaws open widely, and it shoves the grasshopper's head farther into its oral cavity. (D) Maximum gape, with eyes closed. (E) Its jaws close down again on the grasshopper's head. (F) After holding the grasshopper stationary for approximately 3 sec, it resumes thrusting. (G) Its jaws close down on the grasshopper's head for the last time. (H) It successfully severes a bite after several smaller gape-shove sequences.

Fig. 4. Ingestion by mastication of a grasshopper by a male *T. bancanus* in temporary captivity. (Videoprint taken from the videotape recording discussed in the text.)

nocleidomastoid and scalenes. Thus, with the prey held firmly in the hands, the jaws began to close and the prey was punctured, while concurrently the head extended in an effort to sever the bite. The tarsier finally tore off a bite by simultaneous, strong side-to-side and dorsally directed movements of the head. We expect that contraction of the nuchal extensor muscles would be accompanied by contraction of the erector spinae muscle and contraction of the nuchal flexor muscles by contraction of the muscles of the abdominal wall.

In nearly all cases, after the tarsier severed a bite, it pulped it for a short time between the premolar and the molar teeth before swallowing. The tongue was visibly active to maintain the position of the bolus between the cheek teeth, as observed by Maier (1984) during the ingestion of a mealworm by captive *T. bancanus*. Because of the rapidity of chewing movements, we could not trace the shape of the masticatory orbit. It was clear, however, that strictly orthal movements of the mandible, i.e., motion in a parasagittal plane, did not occur during puncture-crushing or chewing. Both elastic body parts such as the gut tube and hard items such as the coxae apparently required relatively large lateral components in the chew (simulations using our prepared skull permitted an estimate of 5 mm for the largest displacements). Movements of the mandible during mastication of grasshopper prey could be best described as strong crushing movements during which its exoskeleton is cracked and partially pulped. The bolus did not appear to be uniformly well chewed before being swallowed. The number of chews per swallow varied, depending on the relative amount of exoskeleton ingested in the bite. Because of the difficulty of observing the actual swallow, the number of chewing cycles per swallow could not be consistently counted. The tarsier swallowed bites from near the head and thorax of the grasshopper after 7–9 chews and those from more caudal regions after 10–14 chews. When portions of the grasshopper's gut were exposed by a bite, the tarsier repeatedly pulled and sucked on the gut tube (Fig. 5); it then chewed detached sections of gut only five or six times before swallowing. Portions of the grasshopper, such as the wing covers, composed mostly of chitin and thus not directly digestible, were usually (but not always) discarded. However, R.H.C.'s observations of free-ranging tarsiers indicate that few parts are wasted.

Temporomandibular Joint and Muscles of Mastication

Ingestion of large items of prey is made possible by the tarsier's specialized temporomandibular joint (TMJ) and muscles of mastication. The tarsier's temporomandibular joint is highly reminiscent of that seen in many gnawing rodents (Vaughan, 1974, Jacobs, 1984): the mandibular fossa is an anteroposteriorly elongated trough that receives a knob-like mandibular condyle (Rosenberger, 1985). This morphology provides a stable arrangement for long anterior excursions of the mandible both in tarsiers and in gnawing rodents. In the latter, the groove-like mandibular fossa accommodates the knob-like mandibular condyle as the mandible is translated anteriorly in preparation for incisal gnawing and as it shifts posteriorly in preparation for molar grinding (Turnbull, 1970). However, while the main

Fig. 5. Male *T. bancanus* in temporary captivity pulling and sucking at the gut tube of a grasshopper. (Photograph taken from the videotape recording discussed in the text.)

function of the anteroposteriorly elongated fossa of rodents is to allow incisor–incisor occlusion during gnawing (Jacobs, 1984), in *T. bancanus* it facilitates a wide gape by allowing considerable anterior and inferior translation of the mandibular condyle, so that the ramus of the mandible can be rotated posteriorly for a much greater distance before bony contact with the external auditory meatus. (Rodents such as the beaver, *Castor,* may also use this mechanism for enhancing gape, e.g., for gnawing tree trunks.) When traced from posterior to anterior, the articular surface of the mandibular fossa is inclined downward. ([In Figs. 6A–7B, stereopairs per-

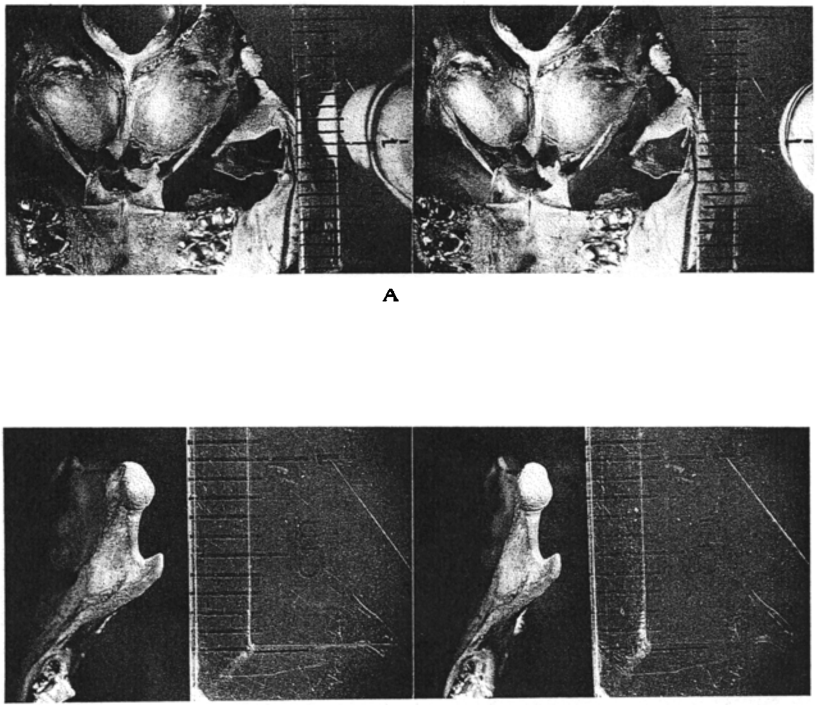


Fig. 6. Stereopairs, showing the bony elements of the temporomandibular joint of a western tarsier. (A) Posterior portion of cranial base on right side showing anteroposteriorly elongated mandibular fossa in *T. bancanus.* (B) Right mandibular condyle in *T. bancanus.*

mit comparison of the fossa and condyle of our prepared specimen with those of a Malabar squirrel, *Ratufa bicolor* (LAH3-86 in the Liverpool departmental collection).] Because we examined specimens preserved under field conditions, detailed examination and manipulation of the soft structures of the TMJ were not possible. Nevertheless, the shape of the fibrous disc was not such as to alter radically the motion path indicated by the bony TMJ. A loose joint capsule permits considerable anteroposterior movement. Very wide gapes are achieved by the anterior and inferior sliding (translation) of the condyle in the mandibular fossa. Gape—the angle through which the jaw can be opened—can be estimated as the angle be-

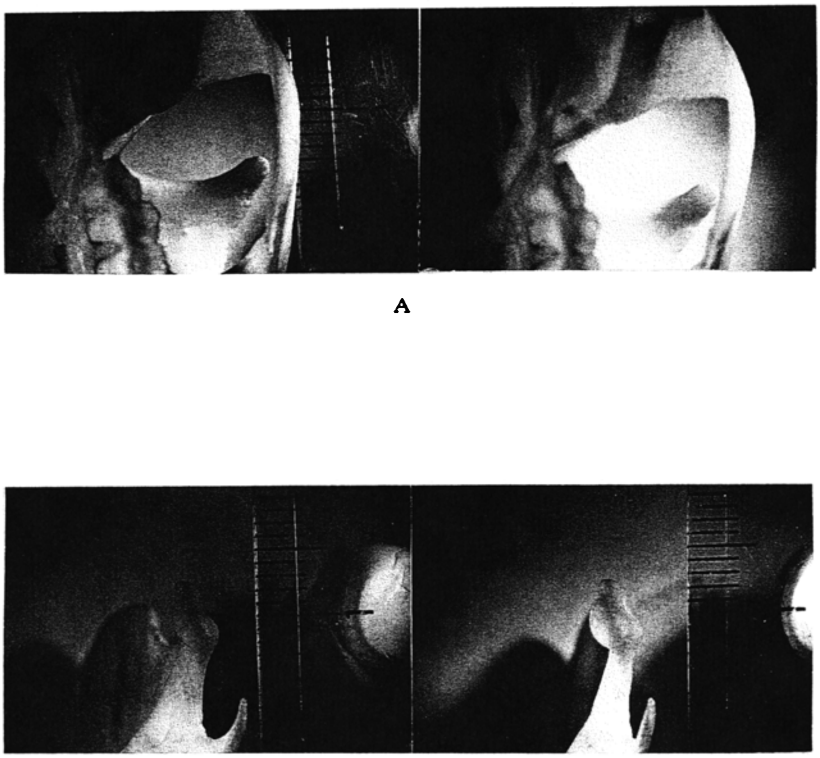


Fig. 7. Stereopairs, showing the bony elements of the temporomandibular joint of the Malabar swuirrel (*Ratufa bicolor*). (A) Posterior portion of cranial base on right side showing anteroposteriorly elongated mandibular fossa. (B) Right mandibular condyle.

tween the occlusal plane of the maxillary and that of the mandibular molar teeth. Figure 8 indicates that a gape of approximately 60–70° is possible in *T. bancanus*. Specimens as large as the 25-g flying frog used in this figure can readily be taken into the oral cavity. The evident sigmoid curvature in the maxillary occlusal plane (Fig. 8) may act to increase the effective gape between the anterior teeth by raising the plane of the anterior maxillary teeth above that of the posterior teeth.

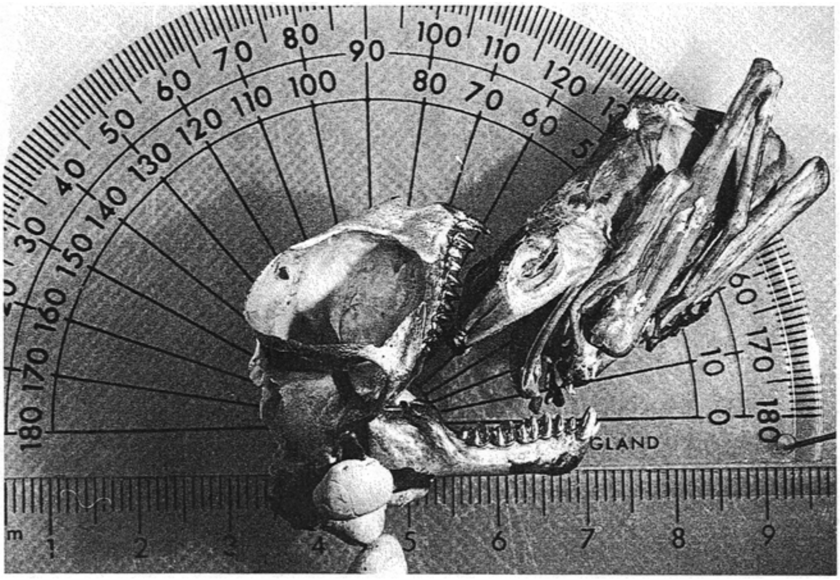
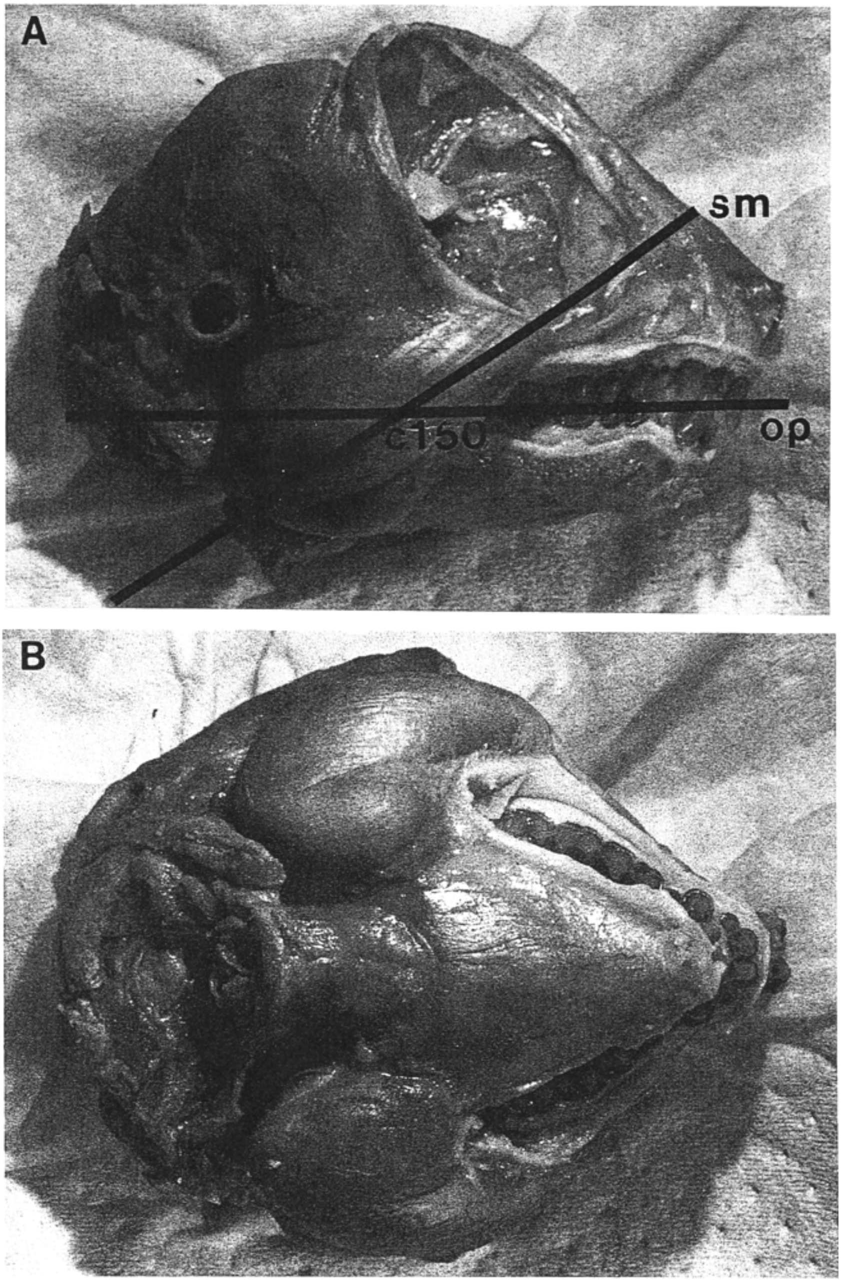


Fig. 8. The skull of a male tarsier, mounted in the position of maximum gape (mandibular condyle at anterior edge of mandibular fossa), showing the gage angle θ, in relation to the body of a 25-g flying frog.

As evidenced in Figs. 9A and B, the muscles of mastication in *T. bancanus* are prominent features of its cranial anatomy. Dissection indicated that the general arrangement and pattern of internal architecture of the muscles of mastication in our specimens agrees qualitatively with the arrangement of those of *T. syrichta* (Fiedler, 1953). Accordingly, we limit our discussion to the factors that affect gape and power.

The muscles of mastication in *T. bancanus* appear to be relatively long-fibered, with simple patterns of internal pinnation and relatively little tendinous content. This is especially true of the superficial masseter, temporalis, medial pterygoid, and zygomaticomandibularis (deep masseter) muscles. The superficial masseter and the superficial portion of the medial pterygoid muscles are oriented obliquely relative to the occlusal plane (see Figs. 9A and B). The most anterior fibers of the superficial masseter muscle, which has a much more rostral extension than the origin of the medial pterygoid muscle does and thus greater action in limiting effective gape, are particularly long and arranged in nearly parallel bundles. The medial pterygoid muscle is somewhat thinner, but its fiber length is comparable with that of the masseter muscle, and they do not differ in the relative


A
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degree of internal pinnation. Again, like the masseter muscle, the fiber length in the medial pterygoid muscle is longest in its anterior and superficial parts.

In the two dissected specimens, the angle subtended by the fibers of the superficial aponeurosis of the superficial masseter muscle and the occlusal plane of the mandibular dentition is approximately 150° (Fig. 9A: the superficial aponeurosis is visible by its sheen). Accordingly, relatively small contractions of the superficial masseter muscle, by moving the mandibular condyle forward over the posterior part of the trough-like, posteroanteriorly downward-sloping mandibular fossa, will bring about initiation of anterior translation of the mandible, in concert with the lateral pterygoid muscle. At a later stage in anterior translation, the superficial masseter muscle will have to relax to allow the lateral pterygoid muscle to complete anterior translation (protrusion) of the mandible. The fibers of the superficial masseter muscle will, in any case, soon come to lie in a more vertical direction, thereby reducing the anterior component of their force vector. However, protrusion is still accompanied by depression of the jaw brought about by the shape of the mandibular fossa.

Species that need to be able to produce a wide gape face problems with the mechanics of their jaw musculature. While the muscles of mastication need to be long enough to accommodate the widest gape, they need to be able to exert power over a wide range of gapes. Up to a point, a stretched muscle contracts more forcefully than a resting one, and pinnate muscles, like those of mastication, have optimal stretch lengths somewhat greater than those of parallel-fibered muscles (Gowitzke and Milner, 1988). However, the physiological limits to stretch are about 1.5 times resting length in parallel-fibered muscles, and this factor is probably reduced to approximately 1.3 to 1.4 in the case of the muscles of mastication in general, on account of their pinnate structure (Herring and Herring, 1974). Further, if the resting length of the muscles of mastication is achieved at jaw positions during or near the occlusal phase of chewing (Herring and Herring, 1974), it follows that wide gapes will tend, at some point, to stretch them beyond the optimum point in their length/tension curve. Beyond this point, their ability to generate tension, and hence occlusal pressure, will decline at wider gapes, unless the elastic tension developed in connective

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Fig. 9. The superficial muscles of mastication of *T. bancanus*. (A) Lateral view, showing the ca. 150° angle subtended by the anterior fibers of the superficial masseter muscle (sm) and the occlusal plane (op). Note especially the large size of the superficial masseter muscle and the orientation of its superficial fibers—the superficial aponeurosis is visible by its sheen. (B) Basal view. Note the large size of the superficial masseter and medial pterygoid muscles. Note also the more rostral origin of the masseter muscle compared with the medial pterygoid muscle.

tissue within the muscle, such as the intermuscular septa, compensates for the loss in active tension. In *T. bancanus,* the low level of pinnation and simplicity of fascial arrangements probably rule out the latter possibility.

Carlson (1977) demonstrated for *Macaca mulatta* that the anterior translation of the mandible that is typical of anthropoid jaws contributes to reduction in the stretch, or maximum excursion, of the superficial masseter muscle. In his model, without anterior translation, maximum producible tension in the superficial masseter muscle falls to 45% of that at resting length full gape; with anterior translation, 80% of the maximum resting-length tension is retained at full gape.

The "stretch factor" of the masseter muscle—its stretched length divided by its unstretched length (Herring and Herring, 1974; Herring, 1975)—is a measure of its excursion. A high excursion for the superficial masseter muscle reduces its capability to exert tension at wide gapes, and a very high stretch factor (between 1.3 and 1.5) indicates that wide gapes may bring an animal's masticatory muscles to a stretch beyond physiologically effective or safe limits or both. Herring (1975) indicated that different species make different adaptive compromises in order to reduce the excursion, or stretch factor, of the superficial masseter muscle. One way to reduce maximum excursion is by changing the muscular geometry to make the "origin—insertion" ratio of the masseter muscle—the ratio between the distance from the center of the TMJ to the most anterior origin of the superficial masseter, and the distance between the center of the TMJ and its most posterior insertion—as different from unity as possible, so that either the origin is much farther from the TMJ than the insertion is or vice versa. Alternatively, or additionally, the stretch factor may be reduced by moving the origin of the masseter muscle dorsally or the insertion posteriorly or both, thus reducing Herring's angle Φ—the angle between these lines when the jaw is closed.

In a single specimen of *T. bancanus*, the origin–insertion ratio for the superficial masseter muscle is 1.64, and the angle Φ is 87°. Another specimen, measured later, did not differ significantly from these values. Using the formula of Herring and Herring (1975), it was possible to examine the relationship between the stretch factor of the superficial masseter muscle and the angle of gape in *T. bancanus*. Table I shows that gape angles of 60°, with a stretch factor of 1.10, or even as much as 70°, with a stretch factor still as little as 1.17, can readily be accommodated in *T. bancanus.* We can compare the origin–insertion ratio and figures with data for other species provided by Herring and Herring (1975). Both the origin–insertion ratio and Φ are at the high end of the range for Primates, but it is the origin–insertion ratio that is notably higher than in other primates, with the exception of *Lemur.* The same applies to a comparison with Rodentia,

Table I. Calculation of the Stretch Factor of the Superficial Masseter of *T. bancanus* at Gape Angles (θ) of 30–90°, for an Origin/Insertion Ratio of 1.64 and a Φ^a of 87°

Stretch factor^b at a gape angle of						
30°	40°	50°	60°	70°	80°	90°
0.88	0.95	1.02	1.10	1.17	1.27	1.37

[a] If a = the distance from the most anterior point of the origin of the superficial masseter to the TMJ and b = the distance between the joint and the insertion of the muscle, then Φ = the angle between them, when the jaw is closed.

[b] The stretch factor (the stretched length of a muscle divided by its unstretched length) was calculated from the equation of Herring and Herring (1974):

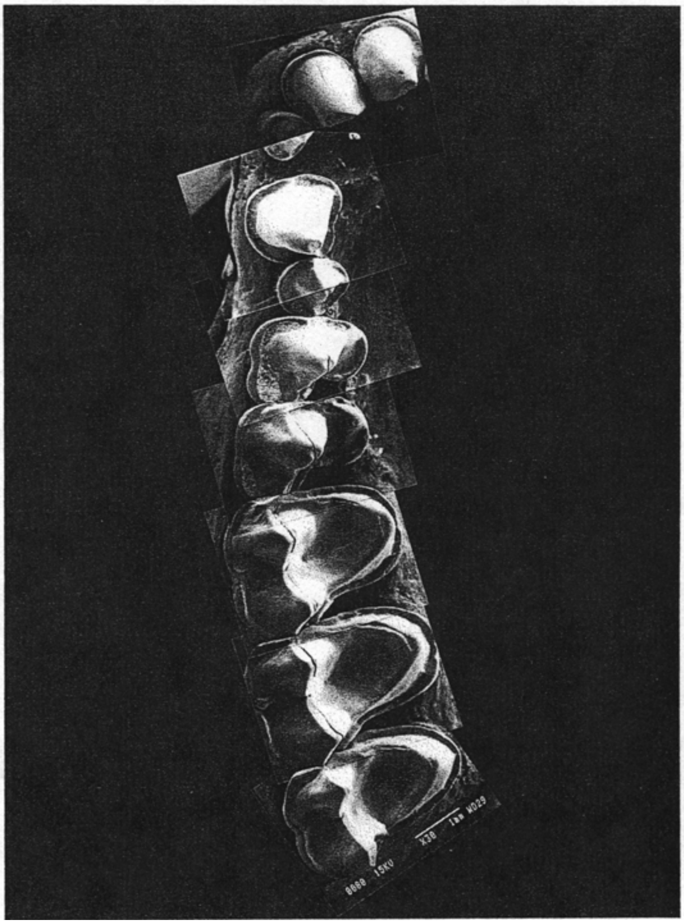
$$\text{stretchfactor}^2 = \frac{[a^2 + b^2 - 2ab\cos(\theta + \Phi)]}{(a^2 + b^2 - 2ab\cos\Phi)}.$$

of which only three genera have higher ratios, Φ, however, is smaller than for most of the rodents measured. All Carnivora had higher values for both measures. The values for *T. bancanus* fall in the midrange of the values for Insectivora. In *T. bancanus,* the high value for the origin–insertion ratio appears to have been achieved primarily by moving the origin of the masseter muscle forward, rather than reducing the depth of the angle of the jaw, since the jaw of *Tarsius* is not unusual among small primates in this respect. According to Herring and Herring (1974), moving the origin of the masseter muscle is the most effective modification for a species with a wide gape, since this actually increases the moment arm of the masseter muscle. However, this change is permitted only because the largest food objects are taken into the anterior portion of the mouth. Recall that only smaller items are ingested in the side or rear of the mouth. This ingestive position has its costs, in that the occlusal force that the muscle can exert, which probably reaches a peak at one-third of the way along the jaw from the temporomandibular joint (Greaves, 1988), will be lower for the anterior dentition. It may well be for this reason that *T. bancanus* appears to work so hard to shove food items as deeply into the mouth as they will go before biting down on them.

It is the length of the fibers of the superficial masseter and medial pterygoid muscles in *T. bancanus* that is the critical factor, permitting them to commence contraction and jaw closing at the wide gape angles that occur during the ingestion of large food items. While, at maximum gape, the superficial masseter muscle is in a disadvantageous position to initiate closure, as soon as closure has been initiated, probably by the action of the posterior temporalis muscle via drawing the coronoid process posteriorly, the relative importance of the superficial masseter muscle will increase with every degree of closure, as Carlson (1997) demonstrated for *Macaca.*

Teeth and Tooth Wear

As is the case with insectivorous mammals in general, the cheek teeth of the tarsier are large relative to its anterior teeth (Maier, 1984) and large relative to its body size (Gingerich and Smith, 1985). The tarsier's retention of a paraconid on the lower molars is considered a primitive feature, but



A

in other structural and functional respects, the dentition of the tarsier has departed significantly from the primitive tribosphenic configuration characteristic of many Insectivora (Figs. 10A and B).

The anterior teeth are stubby and sturdy and are well designed for grasping and impaling large prey (Maier, 1984; Musser and Dagosto, 1987; Schmid, 1983). The tips of the incisors bear numerous pits and deep, nonuniformly oriented striations that are consistent with this usage (Fig. 11). In contrast to the situation reported for *T. pumilis* and *T. spectrum* (Musser

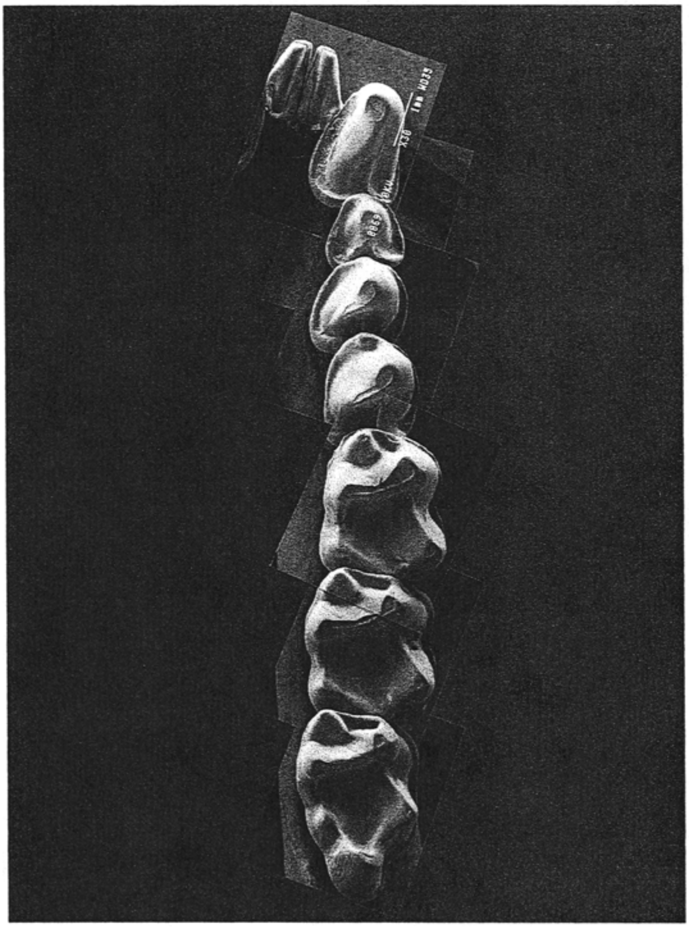


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Fig. 10. Scanning electron micrographs of the (A) maxillary and (B) mandibular dentitions of *T. bancanus*. Original micrographs showed the dentitions enlarged 30 times. Scale bar = 1 mm.

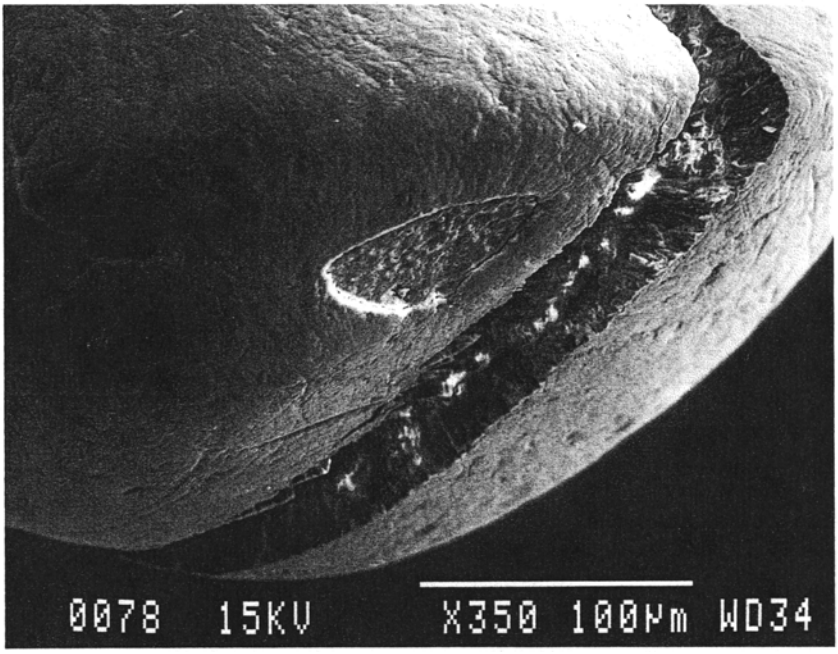
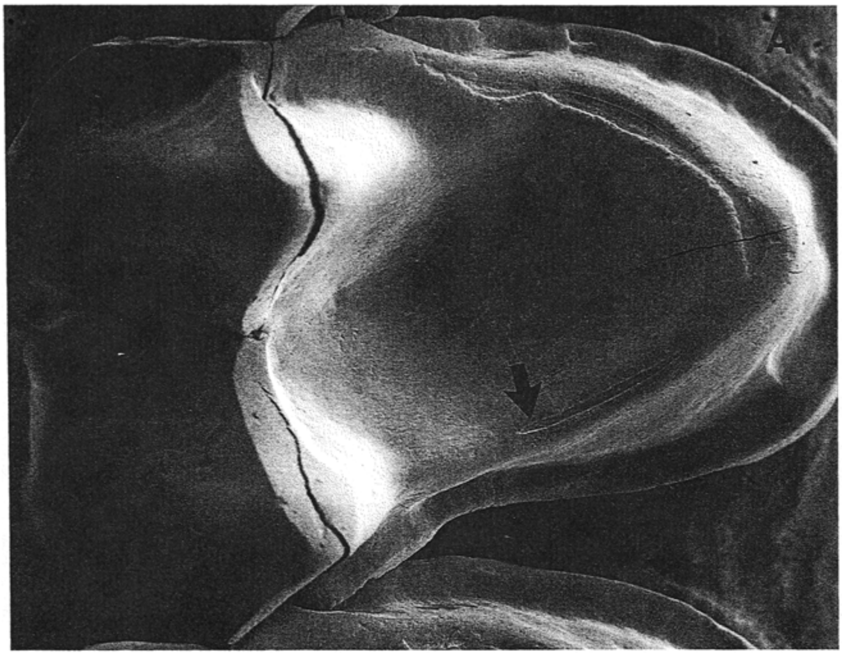


Fig. 11. Tip of the right lower central incisor tooth of a male *T. bancanus* enlarged 350 times. Note the deep pits and grooves on the enamel and dentinal surfaces. The large crack occurred during preparation of the specimen for SEM.

and Dagosto, 1987), no evidence of hair-grooming striations on the lingual ridges of the lower incisors and canines could be detected in our specimen of *T. bancanus*. If, as seems likely from R.H.C.'s observations, prosimian autogrooming is carried out more with the grooming claw(s), and allogrooming more often with the toothcomb, a low level of allogrooming in the more solitary *T. bancanus* (Crompton and Andau, 1987; cf. Niemitz, 1984b), in contrast with more common social grooming in the pair-living *T. spectrum* (MacKinnon and MacKinnon 1980), might partially account for this observation. The molars bear crowns of relatively high relief, but the cusps are low relative to those of Insectivora; the trigon and talonid basins are relatively wide, and distinct tip-crushing as well as grinding surfaces are evident. In most members of the Insectivora, movements of the jaws during chewing are said to be predominantly orthal (sagittal), with a relatively small transverse or Phase II component to the power stroke of the masticatory cycle. The molars of tarsiers however, bear distinctive, Phase II grinding surfaces with transversely or anteromedially oriented striations. Such highly oriented striations can easily be identified on both the upper and the lower molars of *T. bancanus* (Figs. 12A–F). As noted by Maier (1984), these features of wear clearly define a masticatory apparatus that has departed significantly from the scissors-like *en echelon* shearing mechanism that characterizes insectivores with classic tribosphenic dentitions.



12 A

Fig. 12. Selected occlusal surfaces of the molar teeth of a male *T. bancanus* to show tip-crushing, and grinding surfaces. (A) Right M^2 enlarged 30 times (reduced 10% for reproduction). Arrow indicates area of crista obliqua enlarged 450 times in B (where scale bar = 10 μm). Note that the predominant direction of wear striations on the crista obliqua is nearly horizontal. (C) Right M_3 enlarged 30 times with arrows indicating areas of paraconid and hypoconulid enlarged in D–F. (D, E) Tip of paraconid enlarged 250 times (D; scale bar = 100 μm) and 550 times (E; scale bar = 10 μm), showing the nonoriented pits and striations characteristic of a crushing surface. (F) Posterior edge of hypoconulid showing striations in a predominantly anteromedial direction (scale bar = 10 μm).

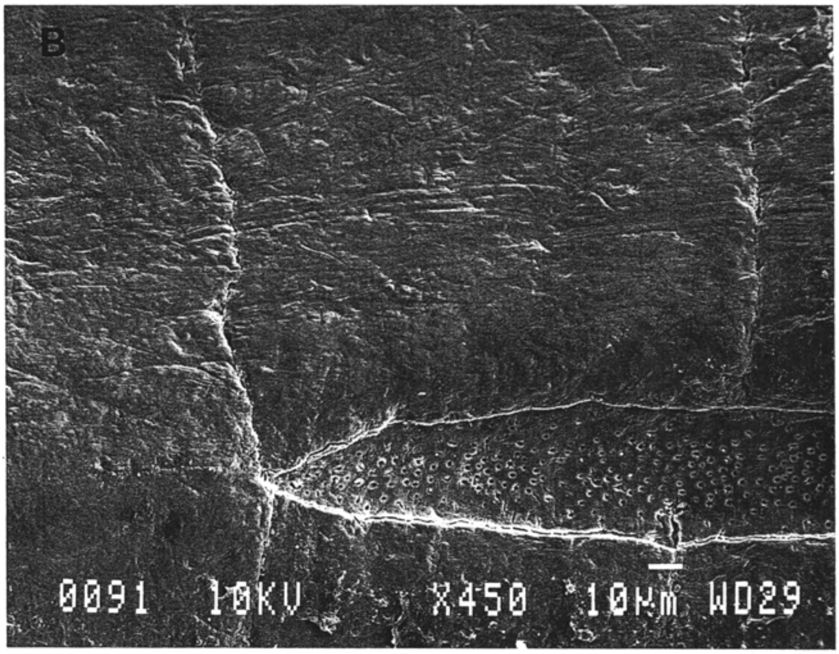


Fig. 12B.

Gastrointestinal Tract, Stomach Contents, and Gut Passage Time

The gut of the male tarsier was removed to examine its structure and stomach contents. The gut of *Tarsius* is simple in both external and internal features. As is evident from Figs. 13A and B, and as reported by Hill (1955), the stomach is piriform, the cecum quite large, and the large intestine relatively short. Specializations for fermentation in the foregut appear to be lacking, and any fermentation is likely to occur in the cecum. Histological examination of the lining of the gut was not possible because of extensive autolysis before the gut was preserved.

Examination of the stomach contents of a specimen that had died in captivity revealed that the grasshopper parts in the stomach were generally small but irregular in shape. The cuticle had not consistently been finely divided by the molar teeth: the particles in the stomach ranged from 1 to 5 mm. The few materials recovered from the cecum were not clearly distinguishable from those in the stomach. It was not possible, for ethical reasons, to carry out extensive tests on gut passage times, since the subjects

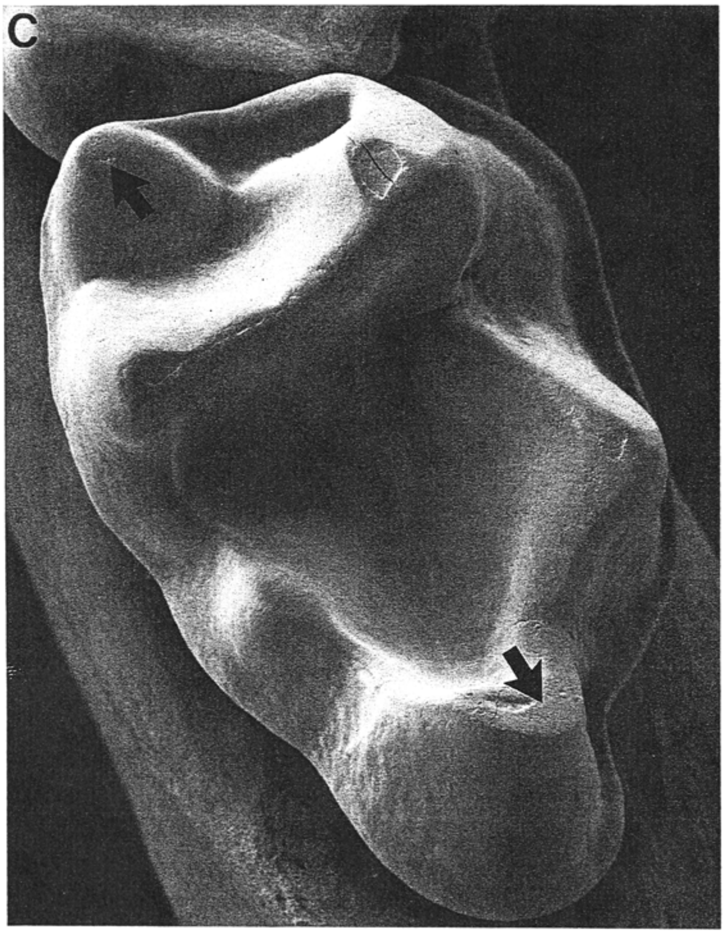


Fig. 12C.

were held only temporarily. However, one tarsier was fed grasshoppers, the thoraxes of which had been opened and filled with biobeads, which are chemically inert, fine-diameter polystyrene beads. Examination of its feces at regular intervals indicated that gut passage times are typically >10 hr. Niemitz (1984c) suggests a figure of 15 hrs, based on nonexperimental observations of an infant, but our estimate is also supported by unpublished studies on captive animals at Duke University Primate Center (P. Wright, personal communication).

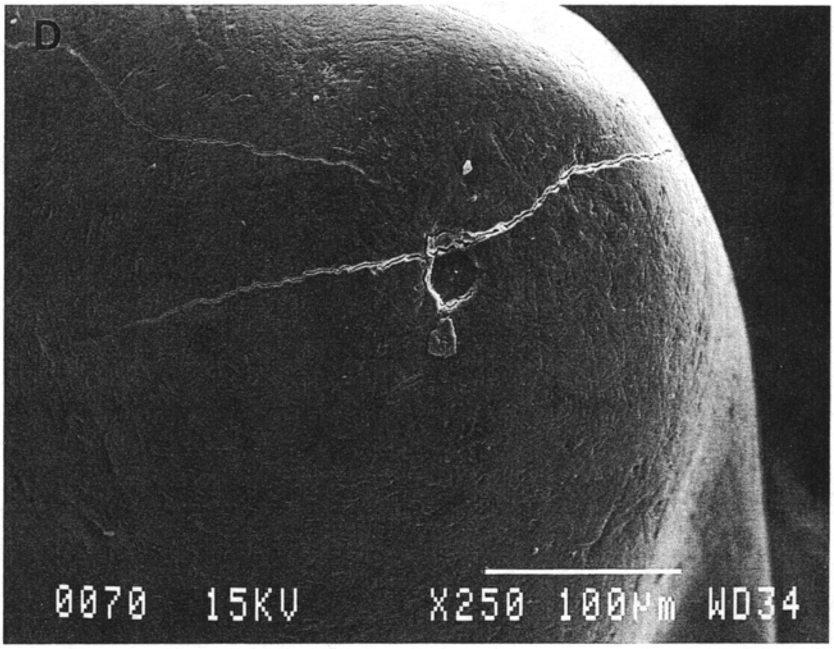


Fig. 12D.

DISCUSSION AND CONCLUSIONS

The masticatory apparatus of tarsiers is highly specialized for acquisition and efficient processing of relatively large animal prey. These specializations are seen in the muscles of mastication, the temporomandibular joint, and the teeth. However, it is important to recognize that the anatomical specializations, rather than being optimal configurations for a single functional requirement, are compromises between a number of competing pressures.

The ability of tarsiers to achieve a wide gape has made it possible for them to capture and ingest items of prey of relatively large diameter. In *T. bancanus*, the bony constraints on gape are minimal. The rounded mandibular condyle can slide easily forward and downward in the elongated and inferiorly inclined mandibular fossa. With regard to the muscles of mastication, Herring and Herring (1974; Herring, 1975) pointed out that a wide gape can be achieved by increasing the length of the muscle fibers of the jaw elevators, by modifying the positions of the origin and insertion of the jaw elevators to reduce the relative distance to be stretched, or by a combination of these means. In the tarsier, both means have been used,

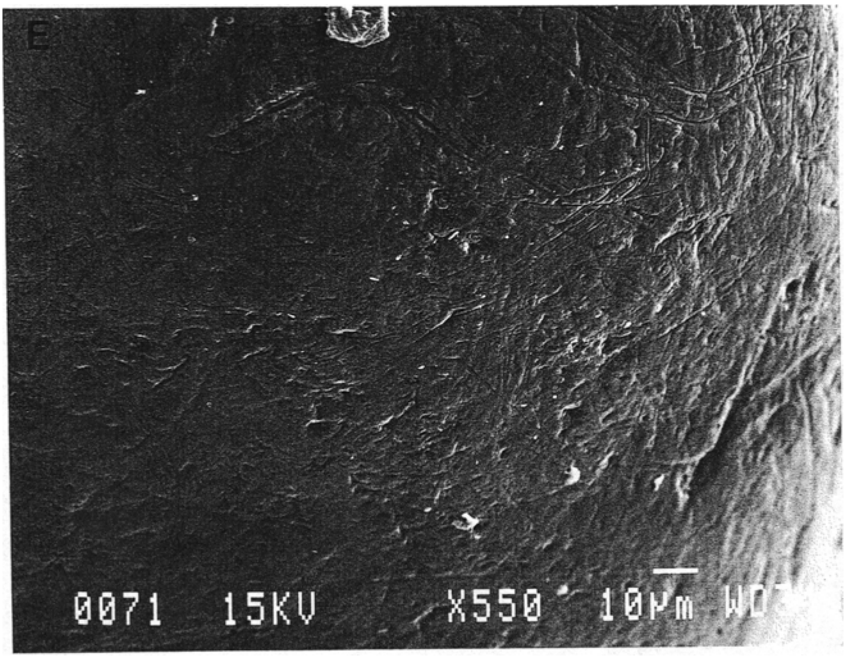


Fig. 12E.

with a rostral migration of the origin of the masseter muscle, but the most marked change appears to have been an increase in the length of the muscle fibers of the jaw elevators. This arrangement, while also conducive to effective contraction at wide gape angles, entails the sacrifice of the potential strength at lower angles of gape that could be given by more complex patterns of internal pinnation (which would necessitate shorter fiber lengths). Lack of complex pinnation also implies sacrifice of the passive tension that could be developed at wide angles of gape by elastic effects in connective tissue.

These mechanical disadvantages appear to have been compensated for almost entirely by a dramatic increase in the relative and absolute size of the muscles of mastication (Figs. 9A and B). While the geometry of the masseter muscle is little different from that of most insectivores, the masseter muscle in *Tarsius* is notably bigger than it is in most Insectivora (Fiedler, 1953).

The compromises that are typical of the functional design of the masticatory system of *T. bancanus* are also apparent in dental morphology. Prey such as frogs, orthopterans, and scarabid beetles present quite different

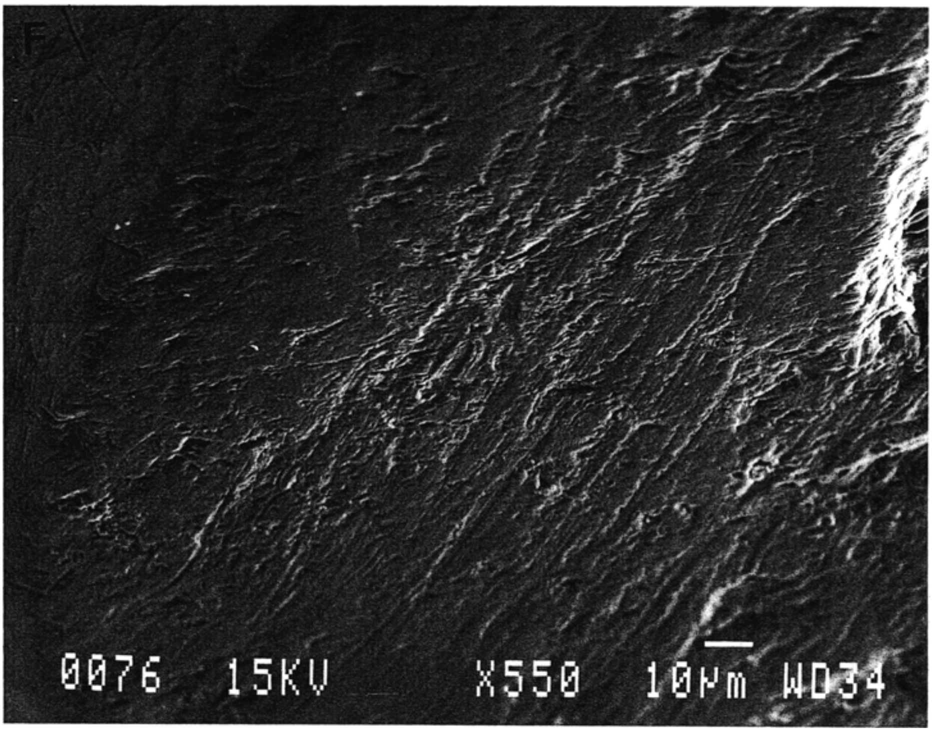


Fig. 12F

mechanical problems during the food reduction process. In general, the cuticle forming the exoskeleton of insects is strong in tension, and quite stiff, with stiffness-for-weight properties similar to those of bone (Wainwright *et al.*, 1982). The cuticle consists of several layers: a nonchitinous epicuticle that consists of a waxy layer, a layer of highly oriented lipid, and a layer of tanned lipoprotein. Below this lies a chitinous procuticle, with a tanned, lamellate outer layer (the exocuticle) and an often untanned inner layer. Alternating fiber directions in the lamellate parts of the cuticle give it the properties of plywood, being equally stiff in several directions in the plane of the cuticle. Tanning or sclerotization involves cross-linking of the protein chains, which increases the stiffness and hardness of the chitin. While the cuticle, as a unit, is an excellent material for resisting bending (Wainwright *et al.*, 1984), the cuticle of orthopterans is much less extensively tanned than that of beetles and, thus, much less stiff and brittle.

Lucas and Luke (1984) argue that high, sharply pointed cusps are best suited to induce failure stress in brittle foods, while soft, tough foods

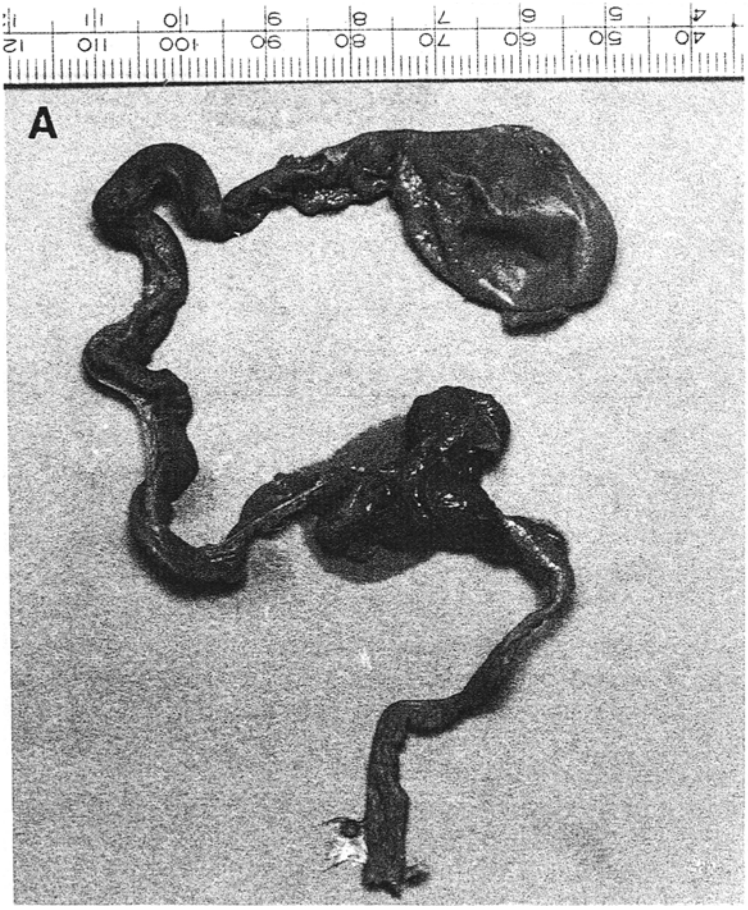


Fig. 13. (A) The stomach and intestines of a male *T. bancanus*, with an enlarged view (B) of the cecum.

are more effectively disrupted by aligned blades. The molar teeth of western tarsiers, while having higher and more pointed relief than the molars of Lorisidae, do not have as sharply pointed cusps as those of many Insectivora do. Accordingly, they would seem to be less than ideally suited to fracture brittle beetle exoskeletons, which could best be achieved by maximizing point forces. Further, they do not possess extensive shearing blades and, thus, would seem to be less effective than the teeth of *Loris tardigradus* are in the disruption of softer, more compliant foodstuffs, such as the lami-

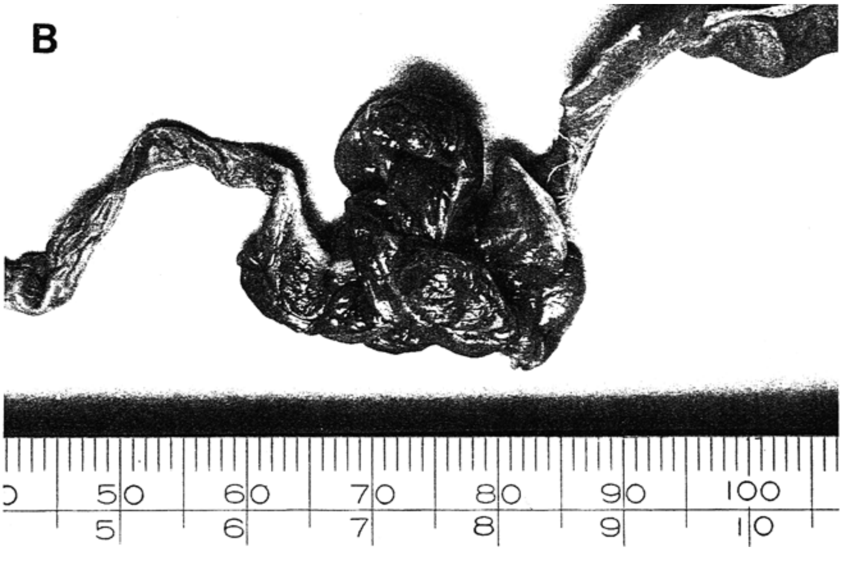


Fig. 13B.

nated, but not highly sclerotized, insect cuticle of grasshoppers and other large orthopterans. However, it is not only the effectiveness of teeth in inducing failure stress in food that has to be considered, but also the ability of the teeth to resist failure.

The jaw of tarsius has a condyle not far elevated above the occlusal plane, partly as a consequence of a substantial lateral flare of the ramus (which is itself related to the breadth of the cranial base of *T. bancanus*). Thus, it is likely that all the molar teeth do not occlude simultaneously (Greaves, 1974), and therefore, the teeth will not always be loaded in a plane normal to the occlusal surface. The robust, but still relatively high-cusped molars of the tarsier may thus, because of a higher polar moment of inertia, be better able to resist bending loads applied to the teeth when biting hard objects—such as beetle cuticle and bone—at oblique angles. Similarly, some increase in robusticity and hence bending strength may be called for because of the increase in Phase II of the power stroke, when lateral forces will be applied to the cusps. Disruption of the softer cuticle of the abdomen of orthopterans may be achieved by grinding, rather than slicing, in a dentition that is a compromise dictated by the catholic, if always animalivorous, diet of the tarsier, in which frog bones as well as insect guts form part of the diet.

We also argue that compromise is apparent in the digestive system itself. According to our own observations and those of Hill (1955), tarsiers have a simple gut. How, then, do we explain their long gut passage times? There can be few possibilities other than that tarsiers maintain a population of microflora in the large cecum and that fragments of cuticle may be retained there for fermentation. Careful trituration of an insect's exoskeleton in the mouth in preparation for chemical breakdown in the gut may not be important when food is abundant. The important factor is that the prey be ingested as quickly as possible and chewed just enough to release the contained viscera and fluids, which are rich in protein and readily digestible carbohydrate. The exoskeletons of orthopteran insects and beetles are fibrous composites composed of chitin and structural proteins. In mechanical terms a beetle or orthopteran can thus be thought of as a juice container with sturdy, laminated sides or, as Lucas and Luke (1984) described them, as fluid-filled sealed tubes. The tarsier's goal in mastication is to break open and pulp the walls of this container sufficiently to expose the contained viscera and energy-rich body fluids. However, when food is less abundant, an ability to make use of the chitin, by digesting the structural charbohydrate to simpler, assimilable sugars, may indeed be important.

Crompton and Andau (1986) pointed out that the energy budget of *T. bancanus* is in delicate balance. Tarsiers have a high energy requirement because of their small bodies and energy-intensive mode of locomotion. Their energy needs are met by ingesting large numbers of large, nutritious prey, which provide the greatest rewards of readily digestible protein and carbohydrate. There are, however, limits to the number of *large* arthropod prey in a given area of forest. Moreover, these large prey are patchily distributed throughout the tarsier's large home range. Further it is now apparent that seasonality and cyclicity in rainfall are more typical features of tropical rain forest than had previously been thought, so temporal as well as spatial patchiness has to be considered. While leaping is not a particularly fast or energy-efficient means of locomotion, in a three-dimensional forest environment, with an uneven forest floor, it has the advantage of allowing a leaping species to avoid detours and even more expensive height change through climbing (Crompton, Sellers, and Günther, 1993). Overall, it may be an efficient way for a small-bodied species to explore a large home range. Further, it has obvious advantages in predator avoidance, when moving very near ground level (Crompton, 1984).

The scaling of energetics and dietary choice (Crompton, 1984) dictates that a small animalivorous species should maximize the size of prey that it can handle, since these bring the largest rewards for success. The relatively high cost of their acquisition is balanced by the relatively higher volume of easily digested soft tissues contained in the bodies of larger prey. Thus tarsiers have, in a sense, evolved into a circular metabolic trap: They must literally eat to leap and leap to eat. Energetic constraints in *Tarsius* appear to have led to an increasing dependence on a high-energy, rapid-turnover diet and, eventually, to a highly specialized type of animalivory, but one that is founded on compromise rather than optimization.

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