Deciduous teeth and their replacement in *Miniopterus schreibersii natalensis*

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The sequence of replacement of the deciduous teeth by permanent teeth in *Miniopterus schreibersii natalensis* is described. A table showing the changes in tooth characteristics from birth until seven weeks of age is given.
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Die volgorde van melktandvervanging deur permanente tande in *Miniopterus schreibersii natalensis* word beskryf. 'n Tabel wat die veranderinge in tandkenmerke vanaf geboorte tot en met die sewende week na geboorte beskryf, word gegee.
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Miniopterus schreibersii natalensis, widely distributed in South Africa (Hayman & Hill 1971), are among the most abundant cavern-dwelling bats in the Transvaal. Seasonal migrations take place annually between the Transvaal Highveld where the bats overwinter and the bushveld where maternity colonies are formed (Van der Merwe 1975). During spring and summer thousands of females congregate at the maternity caves where the young are born from November to early December. Various methods have been used to establish reliable age criteria in bats during the postnatal growth period.

Davis, Barbour & Hassell (1968) banded newborn *Eptesicus fuscus* and recorded weight and forearm lengths at 3-day intervals throughout the growth period. O'Farrel & Studier (1973) found postnatal weight, forearm length, wingspan and fifth-finger length to be good criteria for estimating age to about 21 days post-partum in *Myotis thysanodes*. Apart from parameters such as body weights and forearm lengths, commonly used during these studies, other criteria used have been the epiphyses of the metacarpals and phalanges either alone or in conjunction with the former. Measurements of the epiphyseal cartilages and gap between the fourth metacarpal-phalangeal joint have been used for *Eptesicus fuscus* and *Myotis lucifugus* (Burnett & Kunz 1982; Kunz & Anthony 1982) and fusion of the epiphyses has been used for *Pipistrellus pipistrellus* (Stebbings 1968). Other criteria such as eye lens weight and tooth characteristics have also been used to age some species. Perry & Herreid (1969) used toothwear and eye lens weight in *Tadarida brasiliensis mexicana* as a criterion while tooth characteristics including tooth eruption have been used in *Hypsignathus monstrosus* (Bradbury 1977) and *Epomophorus wahlbergi* (Sowler 1980). The purpose of the present paper is to provide information on the sequence of tooth replacement in *Miniopterus schreibersii natalensis* and variations that may occur.

Methods

Tooth replacement and eruption were studied on neonates and juveniles collected on various dates during the postnatal period at Sandspruit Cave No. I, Rooiberg (24°37′S/27°40′E) and Peppercorn's Cave, Makapansgat (24°08′S/29°12′E). These caves, situated in the Transvaal bushveld, were visited at weekly intervals from October 1974 to February 1975. Because the females were found to be sensitive to disturbance in the maternity chambers the maternity caves were, after the first few visits, only entered after the females had left the caves on their foraging flights. The duration of observing the juveniles in the maternity chambers was also kept as short as possible. On these visits the general appearance of the juvenile clusters was checked to see if there was an increase in number and what percentage was naked, pigmented or covered with juvenile fur. On each visit a representative sample of juveniles was taken at random for comparative purposes. In order to obtain juveniles with known ages 100 neonates were banded at Sandspruit Cave No. I at the beginning of this study. The intention was to collect some of these banded juveniles at intervals and examine them at known ages. This technique proved to be a failure as will be discussed later. Another technique whereby a sample (average 5) of the oldest and therefore most advanced juveniles was collected on each visit was then used. These juveniles would then represent those that had been born at the beginning of the parturition period. This was done by noting their size, pigmentation and condition of their fur. Because it was known when the parturition period was initiated, their ages could be calculated. All these juveniles were preserved in AFA (i.e. a mixture of 95% ethyl alcohol, 40% formalin, glacial acetic acid and distilled water in the relation of 3:1:1:5 respectively). Because they were stored for a prolonged period in AFA, it is believed that the acetic acid present decalcified the minute teeth making them soft, transparent and easily breakable. Furthermore, because of their small tooth size the skulls of those used for tooth replacement studies were not cleaned. The head was severed from the body and the lower jaw separated from the upper jaw. The tongue was removed and jaws examined with a dissecting microscope. Because the deciduous teeth are so small and difficult to see, and especially because of problems encountered in identifying the various deciduous premolars, serial sections were cut at 25 µm of both the upper and lower jaws of four juvenile bats between the ages of one and seven days. These sections were coloured with Carazzi's haematoxylin and mounted in series on microscope slides. Erupted teeth in the present study were those where the cusps of a tooth were pushed well through the gums i.e. protruding well above the flesh covering the jawbones. The tooth nomenclature used in the present study largely follows Miller (1907).

Results

At birth all the deciduous teeth have not erupted, only the incisors and canines being evident. Except for the incisors in the lower jaw these teeth are sharp and bent backwards. This is an important adaptation making it possible for the neonate to cling effectively to one of the female's teats directly after birth. The incisors of the lower jaw each have three rather flat cusps that are visible above the surface of the gums, much the same as in the permanent stage (Figure 1). Both deciduous and permanent incisors of the upper jaw have a rather sharp cusp protruding well above the surface (Figure 1). The total number of deciduous teeth in a juvenile *M. s. natalensis* is 22 with the dental formula as follows: $i\frac{2}{3}\ c\frac{1}{1}\ p\frac{2}{2}$ (Figure 2). A feature is that the deciduous premolars actually never erupt completely to become established teeth but are replaced by the permanent premolars before doing so, being pressed bucally out of the gums. The total number of permanent teeth in adult *M. s. natalensis* is 36 with the dental formula as follows: $I\frac{2}{3}\ C\frac{1}{1}\ P\frac{2}{3}\ M\frac{3}{3}$ (Figures 1 & 2).

Tooth replacement starts in the lower jaw and is completed prior to that of the upper jaw. At about one-and-half weeks of age deciduous incisor i_3 in the lower jaw is shed, followed shortly by i_1. About a week later permanent incisor I_3 starts erupting followed shortly afterwards by I_1. At two-and-half weeks of age I_3 and I_1 may be well established. Deciduous incisor i_2 is only replaced at about four weeks of age. All the

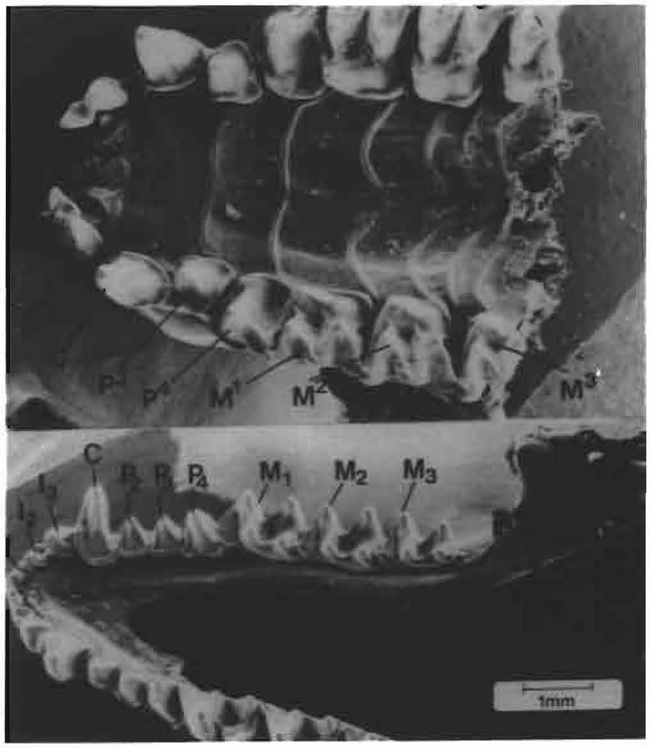

Figure 1 Permanent teeth of the upper and lower jaw of an adult *Miniopterus schreibersii natalensis*.

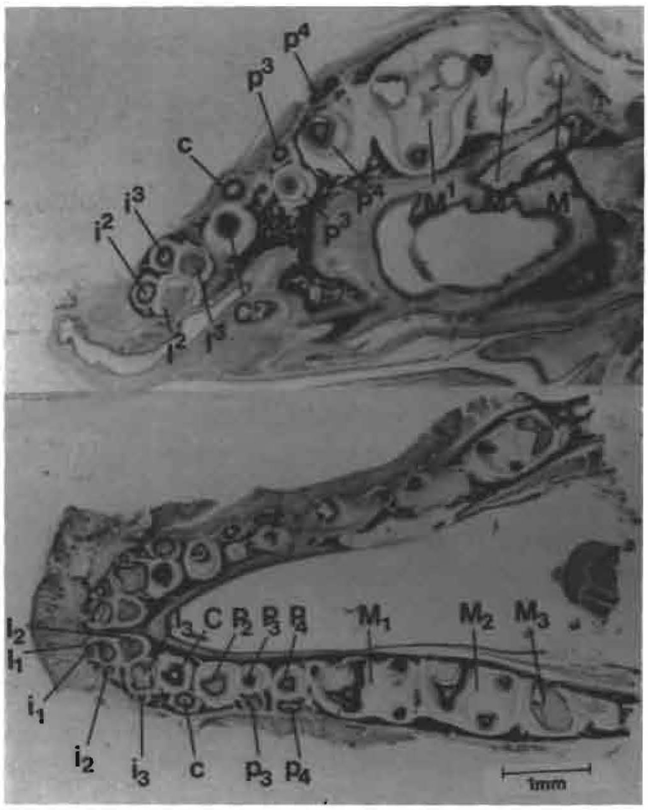

Figure 2 Permanent and deciduous teeth of the upper and lower jaw of a juvenile *Miniopterus schreibersii natalensis*.

deciduous teeth in the lower jaw are replaced by about 5 weeks of age.

Although some variation occurs, and some teeth are replaced more or less simultaneously, the general sequence in which the deciduous teeth of the lower jaw are replaced is as follows:

$i_3\ i_1\ c_1\ i_2\ p_4\ p_3$

Replacement of the deciduous teeth in the upper jaw starts at about two-and-half weeks when the permanent canines start erupting. At three-and-half weeks, deciduous p^4 is replaced and the permanent canines and premolars P^4 may be exposed above the gumline. By the end of six weeks of age, replacement may be completed. After seven weeks of age no deciduous teeth were found, and the incisors, canines and premolars were well exposed, with the cusps of the molars all above the surface of the gums. Although variation occurred, the sequence in which the deciduous teeth of the upper jaw are replaced is as follows: p^4 p^3 i^2 i^3 c^1. Table 1 summarizes tooth replacement in representative juveniles collected at various estimated ages. The legend used in the table was devised in such a way that individual teeth can be recognized. Therefore, the codes used in the legend illustrating the condition of the individual teeth, by reason of their

Table 1 Tooth replacement in a few representative juvenile *M. s. natalensis* at various ages also showing variation that occurs

Estimated age	Physical appearance	Deciduous teeth	Permanent teeth
Up to 1 day	Umbilical cord plus placenta	$i\frac{\vert\vert}{\vert\vert\vert}\ c\frac{\vert}{\vert}\ pm\frac{--}{--}$	
		$i\frac{\vert\vert}{\vert\vert\vert}\ c\frac{\vert}{\vert}\ pm\frac{--}{--}$	
1 Week	Naked with only slight pigmentation on the rostrum	$i\frac{\vert\vert}{\vert\vert\vert}\ c\frac{\vert}{\vert}\ pm\frac{--}{--}$	
		$i\frac{\vert\vert}{\vert\vert\vert}\ c\frac{\vert}{\vert}\ pm\frac{--}{--}$	
$2\frac{1}{2}$ Weeks	Dorsal surface of arms, legs and tail starts darkening	$i\frac{\vert\vert}{+\vert+}\ c\frac{\vert}{\vert}\ pm\frac{--}{--}$	$I\frac{--}{--\circ}\ C\frac{-}{-}\ PM\frac{--}{---}\ M\frac{---}{---}$
		$i\frac{\vert\vert}{+\vert+}\ c\frac{\vert}{\vert}\ pm\frac{--}{--}$	$I\frac{--}{\bullet-\circ}\ C\frac{-}{-}\ PM\frac{--}{---}\ M\frac{---}{---}$
		$i\frac{\vert\vert}{+\vert+}\ c\frac{\vert}{+}\ pm\frac{\bullet+}{\bullet\bullet}$	$I\frac{--}{\circ-\vert}\ C\frac{\circ}{\circ}\ PM\frac{--}{\circ\bullet\bullet}\ M\frac{---}{---}$
$3\frac{1}{2}$ Weeks	Patagium and uro-patagium starts darkening	$i\frac{\vert\vert}{+\vert+}\ c\frac{\vert}{\vert}\ pm\frac{\bullet\bullet}{\circ\circ}$	$I\frac{--}{\vert-\vert}\ C\frac{\bullet}{\bullet}\ PM\frac{-\bullet}{\bullet-\bullet}\ M\frac{\bullet--}{\bullet--}$
		$i\frac{\vert\vert}{+\vert+}\ c\frac{\vert}{\vert}\ pm\frac{\bullet\bullet}{\circ\circ}$	$I\frac{--}{\vert-\vert}\ C\frac{\bullet}{\bullet}\ PM\frac{-\bullet}{\bullet-\bullet}\ M\frac{\bullet--}{\bullet--}$
		$i\frac{\vert\vert}{+\vert+}\ c\frac{\vert}{\vert}\ pm\frac{\bullet+}{\circ\circ}$	$I\frac{\bullet-}{\vert-\vert}\ C\frac{\circ}{\circ}\ PM\frac{-\bullet}{\circ\bullet\bullet}\ M\frac{\bullet--}{\bullet--}$
		$i\frac{\vert\vert}{+\vert+}\ c\frac{\vert}{+}\ pm\frac{\circ+}{++}$	$I\frac{\circ\bullet}{\vert-\vert}\ C\frac{\circ}{\circ}\ PM\frac{\bullet\circ}{\circ\bullet\bullet}\ M\frac{\bullet--}{\bullet--}$
$4\frac{1}{2}$ Weeks	Patagium and uro-patagium fully pigmented	$i\frac{\vert\vert}{+++}\ c\frac{\vert}{+}\ pm\frac{\circ+}{\circ\circ}$	$I\frac{\circ\bullet}{\vert\bullet\vert}\ C\frac{\circ}{\circ}\ PM\frac{\bullet\bullet}{\circ\bullet\bullet}\ M\frac{\bullet\bullet\bullet}{\bullet\bullet\bullet}$
		$i\frac{\vert\vert}{+++}\ c\frac{\vert}{+}\ pm\frac{\circ+}{++}$	$I\frac{\circ\bullet}{\vert\bullet\vert}\ C\frac{\circ}{\circ}\ PM\frac{\bullet\bullet}{\circ\bullet\bullet}\ M\frac{\bullet\bullet\bullet}{\bullet\bullet\bullet}$
$5\frac{1}{2}$ Weeks	Body fully pigmented and covered with short continuous hair	$i\frac{\vert\vert}{+++}\ c\frac{\vert}{+}\ pm\frac{\circ+}{++}$	$I\frac{\circ\bullet}{\vert\vert\vert}\ C\frac{\vert}{\vert}\ PM\frac{\circ\circ}{\circ\circ\circ}\ M\frac{\bullet\bullet\bullet}{\circ\bullet\bullet}$
		$i\frac{+\vert}{+++}\ c\frac{\vert}{+}\ pm\frac{++}{+\circ}$	$I\frac{\vert\bullet}{\vert\circ\vert}\ C\frac{\vert}{\vert}\ PM\frac{\bullet\bullet}{\bullet\bullet\bullet}\ M\frac{\bullet\bullet\bullet}{\circ\bullet\bullet}$
		$i\frac{++}{+++}\ c\frac{+}{+}\ p\frac{++}{++}$	$I\frac{\vert\circ}{\vert\vert\vert}\ C\frac{\vert}{\vert}\ P\frac{\circ\circ}{\circ\circ\circ}\ M\frac{\circ\circ\bullet}{\circ\circ\circ}$
7 Weeks	Body covered with a thick dark pelage		$I\frac{\vert\vert}{\vert\vert\vert}\ C\frac{\vert}{\vert}\ PM\frac{\circ\vert}{\vert\vert\vert}\ M\frac{\circ\circ\bullet}{\circ\circ\circ}$
			$I\frac{\vert\vert}{\vert\vert\vert}\ C\frac{\vert}{\vert}\ PM\frac{\circ\vert}{\vert\vert\vert}\ M\frac{\circ\circ\bullet}{\circ\circ\circ}$
			$I\frac{\vert\vert}{\vert\vert\vert}\ C\frac{\vert}{\vert}\ PM\frac{\circ\vert}{\vert\vert\vert}\ M\frac{\circ\circ\bullet}{\circ\circ\circ}$
			$I\frac{\vert\vert}{\vert\vert\vert}\ C\frac{\vert}{\vert}\ PM\frac{\circ\vert}{\vert\vert\vert}\ M\frac{\circ\circ\bullet}{\circ\circ\circ}$

$\vert$ = Tooth erupted (well established)
$\circ$ = Cusp/s well through gum
$\bullet$ = Cusp/s just above or just below surface
$-$ = Cusp/s still well underneath surface of gum
$+$ = Tooth gone

position in the legend, refer to one of the following teeth:

Deciduous teeth: $\mathrm{i}\frac{23}{123}\ \mathrm{c}\frac{1}{1}\ \mathrm{p}\frac{34}{34} = 22$

Permanent teeth: $\mathrm{I}\frac{23}{123}\ \mathrm{C}\frac{1}{1}\ \mathrm{P}\frac{34}{234}\ \mathrm{M}\frac{123}{123} = 36$

Discussion

The typical complete dentition of higher mammals is a set of 44 teeth expressed by the formula $\frac{123.}{123.}\ \frac{1.}{1.}\ \frac{1234567}{1234567}$ for the one half of the upper and lower jaw (Miller 1907) which then can be expressed as $\mathrm{I}\frac{123}{123}\ \mathrm{C}\frac{1}{1}\ \mathrm{P}\frac{1234}{1234}\ \mathrm{M}\frac{123}{123}$ to make a clearer distinction between the different types of teeth and their positions. *M. s. natalensis* has 36 teeth indicating the loss of 8 teeth from the ancestral mammalian condition. Miller (1907) indicates the teeth that are lost in *M. schreibersii* in the one half of the upper and lower jaw with the following dental formula:

$$\frac{-23.}{1\,23.}\ \frac{1.}{1.}\ \frac{-2-4567}{-2\,3\,4567}$$

Therefore, in *M. s. natalensis* the permanent dentition should be represented as follows with reference to the ancestral mammalian condition: $\mathrm{I}\frac{-23}{1\,23}\ \mathrm{C}\frac{1}{1}\ \mathrm{P}\frac{-2-4}{-2\,3\,4}\ \mathrm{M}\frac{123}{123}$. However, owing to the presence of a vestigial premolar in the upper jaw, similar to the one described for the European *M. schreibersii* by Mein & Tupinier (1977 — to be discussed elsewhere), the permanent dentition of *M. s. natalensis* in the present study is represented as follows:

$$\mathrm{I}\frac{-23}{123}\ \mathrm{C}\frac{1}{1}\ \mathrm{P}\frac{--34}{-\,2\,34}\ \mathrm{M}\frac{123}{123}$$

Amongst the Chiroptera the maximum number of teeth, both permanent and deciduous to be found, occurs amongst members of the genus *Myotis* (Miller 1907) which totals 38 permanent teeth and 22 deciduous teeth in *M. lucifugus* (Fenton 1970). Although *M. s. natalensis* has two less permanent teeth (36) it has a similar number of deciduous teeth (22). Because of a consistent error with the deciduous premolars of *M. s. natalensis* during my Ph. D. studies the number of deciduous teeth was wrongly given as 24 instead of 22 (Van der Merwe 1977).

Sowler (1980) working on tooth eruption in known age specimens of *Epomophorus wahlbergi* expressed some doubt about the accuracy of age determination in the wild using age criteria developed from caged animals. She feels that examination of wild recaptured juveniles will be necessary to validate the use of such data. This is true in that changes occurring with age in caged animals will not necessarily reflect those occurring under natural conditions exactly. It is not always known or appreciated what influences unnatural conditions (such as captivity) may have on the growth and development of young. However, it is believed that data obtained from captive animals may in many respects give a more accurate account of the situation occurring in the wild than by observing them directly in their natural surroundings. This may very well be one of the drawbacks in the present study. At present it is still not possible to keep and breed *M. s. natalensis* successfully in captivity and therefore all observations must be made in their natural surroundings. There is thus no way in which the accuracy of such observations can be correlated with a control group in captivity. The problem as was found during the present study, is also magnified by the vast numbers of juveniles occurring in many clusters, some being inaccessible.

All the juveniles are born over a 4 – 5 week period, the peak of parturition occurring within 14 days at the end of November and the beginning of December (Van der Merwe 1978). Total numbers of juveniles per breeding season exceeded 100 000 at Sandspruit Cave No. 1 and 50 000 at Peppercorn's Cave respectively (Van der Merwe 1973, 1978). The most successful manner in which juveniles with known ages can be collected amongst such vast numbers of juveniles is by banding a number of them and then recapturing some at specific intervals. Although 100 neonates were banded at the beginning of this study none were ever found again. The most acceptable reason for the 'loss of banded juveniles' is that the bands slipped from their small and thin forearms as a result of normal interactions between them and their mothers or between them and other juveniles in the tightly packed juvenile clusters.

Collecting a few of the oldest possible juveniles on each visit (to represent those born first) proved to be the best alternative though it had its hazards. During the first two weeks of the parturition period it is not difficult finding the oldest bats as numbers are still low and clusters few. Older juveniles showing sings of pigmentation are conspicuous amongst unpigmented neonates and they also tend to concentrate at the perimeter of clusters or even to form separate clusters. However, as numbers increase to thousands with clusters of pigmented and fur-covered juveniles scattered all over the ceiling, identification becomes increasingly difficult, especially as these juveniles hang tightly packed together with only their heads protruding (Van der Merwe 1978). With increasing age they also become more active, move around, mix with other clusters or even form new clusters, some in inaccessible places. In the absolute dark of the interior of the caves with only weak headlamps, identification of the oldest juveniles becomes extremely difficult. In view of these problems there is a slight concern that the ages of juveniles might have been over-estimated owing to the possibility that not always the oldest juveniles were collected on a visit. Furthermore, when comparing postnatal development of *M. s. natalensis* with that of other vespertilionids it appears to be much slower thus adding to the concern. Some vespertilionids can already fly at an age of approximately three weeks. O'Farrell & Studier (1973) recorded flight in young *Myotis thysanodes* at 16,5 days of age and 14 – 15 days in *M. lucifugus*. Kunz (1973) recorded three weeks for *M. velifer* and Davis *et al.* (1968) three weeks for *Eptesicus fuscus*. At roughly three weeks of age *M. s. natalensis* only starts showing signs of pigmentation (Table 1). However, Dwyer (1963) has similarly found slow postnatal development in *M. s. blepotis* in north-eastern New South Wales and states that they remain virtually naked and pale for three weeks and can only fly 'blindly' at six weeks of age and from the ground at the seventh week. The age at which flight is initiated in *M. s. natalensis* young has never been determined although it is expected that it is similar to that of *M. s. blepotis*. This assumption is based on the fact that there is an apparent drop in body mass when bats become volant for the first time. This decrease may be caused by the loss of body fats after young have become volant (Short 1961) and weight loss under natural conditions may be accounted for by a combination of factors related to the weaning period and early flight activity which includes reduced milk consumption, expenditure of accumulated fats and inefficient insect capture (Kunz 1973). In *M. s. natalensis*, weight loss or stabilization was found at six weeks in both caves (Van der Merwe 1978), which may indicate initiation of first flight corresponding with Dwyer's (1963) observations for *M. s. blepotis*. At this age some of the juveniles had lost all their deciduous teeth with most of the permanent teeth well established (Table 1) indicating that solid food could be taken. In view of these facts it is clear that postnatal development in *M. s. natalensis* is slower than in other vespertilionids so far investigated and that the replacement of deciduous teeth is only complete at around six weeks of age (Table 1).

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