

Short Communications

Vestigial teeth in the genus *Scotoecus* (Mammalia: Chiroptera): adapted dental formulae for vespertilionids with vestigial teeth

M. van der Merwe

Department of Zoology & Entomology, University of Pretoria, Pretoria, 0002 Republic of South Africa

Received 3 February 1997; accepted 26 May 1997

Some members of the genus *Scotoecus* Thomas, 1901 have an inconspicuous vestigial tooth which occurs on both sides of the upper jaw between the canine and following premolar. This tooth is regarded as permanent premolar P³ in vestigial form.

The genus *Scotoecus* belongs to the family Vespertilionidae, and has previously been treated as a subgenus of *Nycticeius* (Ellerman, Morrison-Scott & Hayman 1953; Hayman & Hill 1971), but more often as a full genus (Allen 1939; Rosevear 1965; Koopman 1975, 1978; Corbet & Hill 1980; Swanepoel, Smithers & Rautenbach 1980). Ellerman *et al.* (1953) recognized two species: *S. albofuscus*, with pale wings, and *S. hirundo*, with dark wings. Hill (1974), however, suggested that the dark-winged group is comprised of two species, a smaller one, *S. hirundo*, and a larger one, *S. hindei*. In the southern African subregion, the genus *Scotoecus* was recorded only in southern Mozambique (Meester, Rautenbach, Dippenaar & Baker 1986; Skinner & Smithers 1990), and Meester *et al.* (1986) placed it in the subspecies *S. albofuscus woodi*. However in 1995, P.J. Taylor, Curator of Mammals at the Durban Museum (Natural History), collected a specimen of *S. albofuscus woodi* as far south as St Lucia in Kwa-Zulu Natal. The genus *Scotoecus* appears to be unique in that its members exhibit variable dental formulae, with the result that this genus has two dental formulae (Hill 1974). Some individuals retain the minute upper premolars that lie immediately behind the canines, whereas other individuals lack them (Skinner & Smithers 1990). An examination of the upper jaw of four specimens of *S. hindei* collected in Malawi revealed the persistent presence of this minute tooth on both sides between the upper canine and following premolar (Figure 1a). The purpose of the present study was to elucidate the position of these vestigial teeth and to propose an adapted dental formula for this genus, as well as for other vespertilionids where such vestigial teeth exist.

Four skulls of *S. hindei* (the whole collection) from the Transvaal Museum, and one *S. albofuscus woodi* (the only specimen DM4885) from the Durban Museum (Natural History), were examined. Skulls were observed through a dissecting microscope for signs of vestigial teeth (i.e. rudimentary, degenerated teeth of little or no utility, presumably relicts of prominent premolars during ancestral times). Electron micrographs of the four skulls from the Transvaal Museum were taken using a Philips 500 scanning electron

microscope (at 5 kV).

All the *S. hindei* specimens from the Transvaal Museum had a vestigial tooth on both sides between the canine and premolar of the upper jaw. However, there were no vestigial teeth in *S. albofuscus woodi* from the Durban Museum (Natural History). Vestigial teeth are inconspicuous in cleaned skulls and the majority are likely to be non-functional (Figure 1a). The vestigial tooth is minute and wedged between the canine and premolar to the palatal side of the toothrow, where it is largely obscured by the cingulum of the canine and following premolar (Figure 1b). Those vestigial teeth which are covered by the cingulum of the canine and the following premolar are probably completely hidden beneath the gum (gingiva) in the living animal and could thus play no role in mastication. This view is supported by observations on the cusp tip of these teeth, the majority of which are sharp or rounded with no signs of erosion (Figure 1a). In some, however, where the cusp tip is level with the surface of the cingulum of the canine and following premolar (and thus also level with the surface of the gum, or else protruding slightly above it in the living animal) they are subjected to some attrition. In one of the skulls of an older individual (judging by the wear of the teeth) the tips of the vestigial teeth were flat, suggesting attrition (Figure 1c). However, the role that these minute tips of the vestigial teeth can play in mastication cannot be significant.

The presence of an additional premolar in vestigial form in many bats belonging to this genus suggests the following dental formula:

$$I \ 1/3 \ C \ 1/1 \ P \ (1)1/2 \ M \ 3/3 = 30/32 \text{ or}$$

$$\begin{array}{l} \text{Incisors } 1 \ \text{Canines } 1 \ \text{Premolars } (1)1 \ \text{Molars } 3 = 30/32 \\ \text{Incisors } 3 \ \text{Canines } 1 \ \text{Premolars } 2 \ \text{Molars } 3 \end{array}$$

The (1) indicates that an inconspicuous vestigial premolar with no or little utility may or may not be present (either throughout life or else during part of life). The position of this tooth is also indicated, i.e. lying in front of the normal-sized and prominent premolar (P⁴).

Should it be necessary to indicate which teeth have remained in this species from the primitive placental stages to modern times, the dental formula can be expressed as:

$$\begin{array}{l} \text{Incisors } 1,0,0 \ \text{Canines } 1 \ \text{Premolars } 0,0,(3)4 \ \text{Molars } 1,2,3 = 30/32 \\ \text{Incisors } 1,2,3 \ \text{Canines } 1 \ \text{Premolars } 0,0,3,4 \ \text{Molars } 1,2,3 \end{array}$$

Here (3) indicates that an inconspicuous P³ with no or little utility may or may not be present in vestigial form anterior to P⁴.

The vestigial teeth under discussion are so minute that it is doubtful whether they would have been detected if the skulls were not carefully cleaned and examined with the aid of a dissection microscope, or if examined by a person not anticipating the possible presence of such teeth. Rosevear (1965) described the extra upper premolar in the West African genus *Scotoecus* as being minute and tucked away, internal to the toothrow, in an angle between the canine and the posterior premolar. He mentioned that no light-winged species of this genus is known to possess this extra tooth, but that it does occur inconsistently in the dark-winged species. Hill (1974)

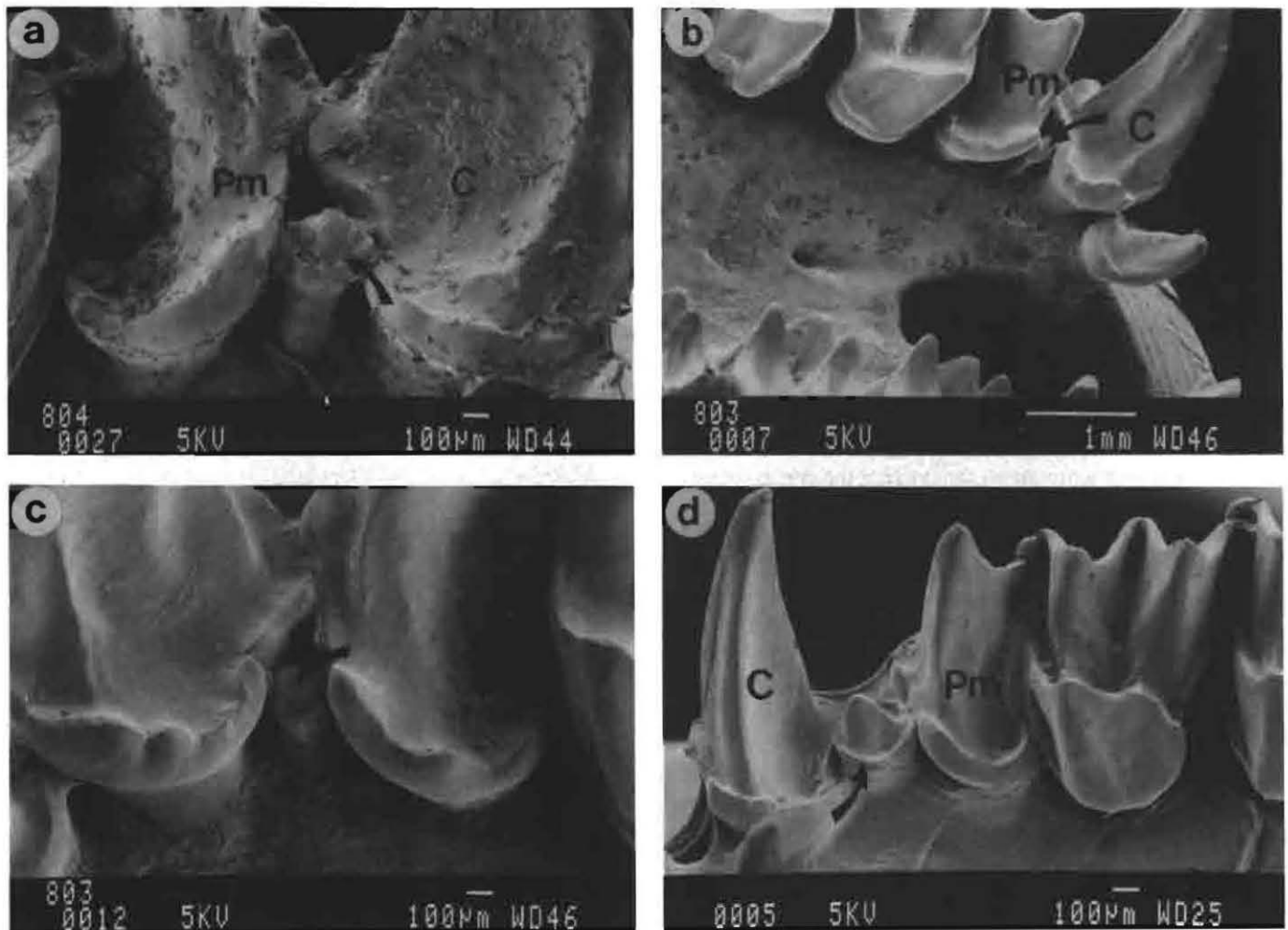


Figure 1a Electron micrograph of the upper jaw of an adult *Scotoecus hindei* showing the minute vestigial premolar (arrow) wedged in between the canine (C) and the following premolar (Pm).

Figure 1b Electron micrograph of the upper jaw of an adult *Scotoecus hindei* showing the minute vestigial tooth (arrow) partly covered by the cingula of the canine (C) and premolar (Pm).

Figure 1c Electron micrograph of the upper jaw of an adult *Scotoecus hindei* showing the flat top (arrow) of the vestigial tooth (probably owing to attrition).

Figure 1d Electron micrograph of the upper jaw of an adult *Pipistrellus nanus* showing the small premolar (arrow) between the canine (C) and following premolar (Pm). In this species, the tip of the small premolar protrudes above the cingula of the canine and premolar.

found this minute upper premolar to be present in 26 specimens of the dark-winged *S. hindei* in the collection of the British Museum (Natural History), although not always on both sides of the jaw. Furthermore, he found this tooth to be absent in all eight *S. albofuscus* specimens examined. The present study, although based on a limited number of specimens, supports Hill's (1974) findings that a vestigial premolar is common in the dark-winged *S. hindei*, but absent in the light-winged *S. albofuscus*.

Rosevear (1965) mentioned that in some species, the minute premolar is loose and gives the impression of being deciduous. This begs the question of whether these are persistent deciduous teeth or whether they represent permanent premolar teeth in vestigial form. It is extremely doubtful that this is a persistent deciduous tooth, however, because earlier studies on a similar tooth in other vespertilionids, *Miniopterus schreibersii natalensis* (Van der Merwe, 1985a), *M. fraterculus* and *M. inflatus* (Van der Merwe, 1985b), have shown a similar tooth to be of vestigial nature, although much

more reduced than in *Scotoecus*. Van der Merwe (1985c) showed that, at least in *M. s. natalensis*, there is a deciduous tooth for each corresponding permanent tooth (except the molars) and that the vestigial teeth are more closely associated with permanent teeth than with deciduous teeth. Deciduous teeth are aligned on the buccal side of the permanent tooththrow (Van der Merwe 1985c), whereas the vestigial teeth are inside the line of the latter (Van der Merwe 1985a,b). The position of these teeth in *Scotoecus* is exactly the same as in *Miniopterus* and there is no reason to suspect that they are deciduous. It was suggested that this tooth in *M. s. natalensis*, *M. fraterculus* and *M. inflatus*, is P² and that the two remaining premolars are P³ and P⁴, respectively. Contrary to the case in vespertilionids, a similar minute anterior premolar in some members of the family Rhinolophidae is again situated external to the tooththrow (Skinner & Smithers 1990). However, whether this is a permanent premolar in vestigial form or a persistent deciduous tooth is uncertain and needs further investigation.

The proposal that this tooth in the vespertilionids might have been a prominent functional premolar, which has become vestigial, is supported by the situation occurring in another vespertilionid, *Pipistrellus nanus*. In this species, the anterior upper premolar (P³) is very small and situated between the canine and posterior premolar (P⁴) (Figure 1d). It is clear that this tooth is in the process of becoming vestigial, because it is very small, with the tip of the cusp just protruding above the cingula of the canine and posterior premolar. However, despite its small size, it is still present in all species examined, and apparently still participates in mastication. It is obvious that in the course of evolutionary time this tooth is gradually being reduced in size and pushed to the inside of the toothrow, with the cingula of the canine and posterior premolar gradually obscuring it from the outside (Figure 1d).

There is a strong argument for revising the dental formulae of species where such minute and inconspicuous vestigial teeth may be present, to eliminate any confusion. Two dental formulae for the same species suggest variability in the number of conspicuous and prominent teeth amongst its members, i.e. teeth that play a significant role during mastication. Because vestigial teeth play no significant role in mastication, they should be indicated as such. Even experienced scientists are not always aware of these vestigial teeth, which may lead to misinterpretation. A classic example is the work of Smithers (1983) and Skinner & Smithers (1990). Smithers (1983) stated that there are two premolars in *Miniopterus* on either side of the upper jaw, and gave the dental formula as $1 \frac{2}{3} C \ 1/1 \ P \ 2/3 \ M \ 3/3 = 36$. However, in the revised edition by Skinner & Smithers (1990), the authors stated that *Miniopterus* has two normal and one vestigial premolar on each side of the upper jaw, and changed the dental formula accordingly to $1 \frac{2}{3} C \ 1/1 \ P \ 3/3 \ M \ 3/3 = 38$. This change was based on the work done by Van der Merwe (1985a,b) who described the presence of this vestigial tooth in some members of the genus *Miniopterus*. This is confusing, especially to scientists not familiar with bat taxonomy, as all members of even the same species do not possess these vestigial teeth. Therefore, to eliminate any possible confusion, the proposed dental formula for *Miniopterus* is:

$$1 \frac{2}{3} C \ 1/1 \ P \ (1) \frac{2}{3} \ M \ 3/3 = 36/38, \text{ or}$$

$$\text{Incisors } 2 \text{ Canines } 1 \text{ Premolars } (1) \frac{2}{3} \text{ Molars } 3 = 36/38$$

$$\text{Incisors } 3 \text{ Canines } 1 \text{ Premolars } 3 \text{ Molars } 3$$

where (1) suggests the possible presence of a third inconspicuous premolar in vestigial form with no or little utility. Its position is also indicated by putting it in parentheses in front of premolar 3 (P³).

To indicate which permanent teeth have remained through evolutionary times, the dental formula can also be expressed as:

$$\text{Incisors } 1,2,0 \text{ Canines } 1 \text{ Premolars } 0,(2),3,4 \text{ Molars } 1,2,3 = 36/38$$

$$\text{Incisors } 1,2,3 \text{ Canines } 1 \text{ Premolars } 0, 2, 3,4 \text{ Molars } 1,2,3$$

where (2) indicates that P² is an inconspicuous vestigial tooth with little or no utility that may or may not be present anterior to P³.

Acknowledgements

I am grateful to the University of Pretoria for financial assistance. A special word of thanks to Mr A.J. Botha of the Unit of Electron Microscopy at the University of Pretoria, who prepared the material and took the electron micrographs. My gratitude is extended to Dr N.C. Bennett and Mr T. Richter for critically reading the manuscript and for the positive suggestions they made.

References

- ALLEN, G.M. 1939. A checklist of African mammals. *Bull. Mus. Comp. Zool. Harv.* 83: 1-763.
- CORBET, G.B. & HILL, J.E. 1980. A world list of mammalian species. British Museum (Natural History) and Cornell University Press, London and Ithaca.
- ELLERMAN, J.R., MORRISON-SCOTT, T.C.S. & HAYMAN, R.W. 1953. Southern African mammals 1758-1951: a reclassification. British Museum (Natural History), London.
- HAYMAN, R.W. & HILL, J.E. 1971. Order Chiroptera. In: The mammals of Africa: an identification manual 2: 1-73, (eds.) J. Meester & H.W. Setzer. Smithsonian Institution Press, Washington D.C.
- HILL, J.E. 1974. A review of *Scotoecus* Thomas, 1901 (Chiroptera: Vespertilionidae). *Bull. Br. Mus. Nat. Hist. (Zool.)* 27: 169-188.
- KOOPMAN, K.F. 1975. Bats of the Sudan. *Bull. Am. Mus. nat. Hist.* 154: 355-443.
- KOOPMAN, K.F. 1978. The genus *Nycticeius* (Vespertilionidae), with special reference to tropical Australia. In *Proc. Fourth Int. Bat Res. Conf.*: 165-171, (eds.) R.J. Olembo, J.B. Castellino & F.A. Mutere. Kenya Literature Bureau, Nairobi.
- MEESTER, J.A.J., RAUTENBACH, I.L., DIPPENAAR, N.J. & BAKER, C.M. 1986. Classification of Southern African Mammals. Transvaal Museum Monograph No. 5, Transvaal Museum, Pretoria.
- ROSEVEAR, D.R. 1965. The bats of west Africa. Trustees of the British Museum (Natural History), London.
- SKINNER, J.D. & SMITHERS, R.H.N. 1990. The mammals of the Southern African subregion. (New edition). University of Pretoria, Pretoria.
- SMITHERS, R.H.N. 1983. The mammals of the southern African subregion. University of Pretoria, Pretoria.
- SWANEPOEL, P., SMITHERS, R.H.N. & RAUTENBACH, I.L. 1980. A checklist and numbering system of the extant mammals of the Southern African subregion. *Ann. Trans. Mus.* 32: 155-196.
- VAN DER MERWE, M. 1985a. The vestigial teeth of *Miniopterus schreibersii natalensis* (Mammalia: Chiroptera). *J. Zool., Lond.* 207: 483-489.
- VAN DER MERWE, M. 1985b. The vestigial teeth of *Miniopterus fraterculus* and *Miniopterus inflatus*. *S. Afr. J. Zool.* 20: 249-252.
- VAN DER MERWE, M. 1985c. Deciduous teeth and their replacement in *Miniopterus schreibersii natalensis*. *S. Afr. J. Zool.* 20: 71-76.