



Short communication

Bullate stapedes in some phalangeriform marsupials

By M. R. SÁNCHEZ-VILLAGRA and SIRPA NUMMELA

Zoologisches Institut, Universität Tübingen, Tübingen, Germany and
Department of Ecology and Systematics, University of Helsinki, Finland.

Receipt of Ms. 06. 10. 2000

Acceptance of Ms. 12. 12. 2000

Key words: Marsupialia, possums, ossicles, stapes, ear

Stapes form varies considerably among mammals and has been a disputed topic in morphology-based mammalian systematics (NOVACEK and WYSS 1986; ROSE and EMRY 1993; GAUDIN et al. 1996). One particular specialization that has received recent attention (WILKINS et al. 1999) is the bullate form of the stapes' footplate. A bullate stapes possesses 'a highly convex hollow footplate that protrudes into the vestibule of the inner ear' (WILKINS et al. 1999), instead of being flat or nearly flat like in most mammals. This situation was first reported by HYRTL (1845) for the common ring-tailed possum *Pseudocheirus peregrinus* (= '*Phalangista cooki*', Petauridae, Marsupialia). Subsequent to this work, other authors have described this anatomical specialization in several phylogenetically distant eutherian mammals (DORAN 1878; SEGALL 1971; BURDA et al. 1992; WILKINS et al. 1999 and references therein). Contrary to the statements of WILKINS et al. (1999), *P. peregrinus* is not the only marsupial showing a bullate stapes. SEGALL (1971) reported (but did not illustrate) this for the feathertail glider, *Acrobates pygmaeus* (Acrobatidae, Diprotodontia).

During the course of our studies on the evolution of ear ossicles in marsupials, we examined the stapes in more than 70 specimens representing 26 species in eight

'families'. In all cases the stapedial footplate was flat and not bullate, with the following three exceptions (Fig. 1): the brush-tailed opossum, *Trichosurus vulpecula* (n = 13); the grey cuscus, *Phalanger orientalis* (n = 2); and the spotted cuscus, *Spilocuscus maculatus* (n = 1). Of these three taxa, *T. vulpecula* shows this feature most marked, followed by *S. maculatus*. In *T. vulpecula*, the depth of the footplate equals that of the crural portion of the stapes, while in the other two taxa the proportion is smaller.

Some other marsupial taxa in addition to those mentioned above have a somewhat bullate stapes. SEGALL (1971: 34) reported that in *Petaurus norfolcensis* 'the vestibular surface of the plate is only slightly convex.' FLEISCHER (1973: 142) noted in his description of the stapes of *Petaurus breviceps* that '...seine Basis ist geringfügig ins Vestibulum vorgewölbt.' The condition in these species of *Petaurus* approximates that described here for *Phalanger orientalis*, as confirmed by examination of a specimen of *Petaurus breviceps* (SM-64418). Several eutherians have a convex footplate that approximates the bullate condition, e.g. *Sus* and *Cynocephalus* (DORAN 1878; ROSE and EMRY 1993). These cases illustrate well the fact that the definition of a bullate stapes is to some extent a matter of evaluation.



Fig. 1. Stapes of left) *Trichosurus vulpecula* (WM-pers.coll.) center) *Phalanger orientalis* (SM-54981) and right) *Spilocuscus maculatus* (SM-5610). Scale = 0.5 mm.

All the marsupial taxa for which a bullate stapes is reported here and elsewhere are phylogenetically close and taxonomically ordered within the Phalangeriformes (KIRSCH et al. 1997). The stapedes of other members of this group were studied by SEGALL (1971), including *Pseudocheirus herbertensis*, *Petauroides volans*, and *Dactylopsila trivirgata*, and in no case did this author mention any peculiarity in their stapes. Plotting the distribution of bullate stapedes in the phylogenetic tree of Phalangeriformes based on DNA-hybridization studies by KIRSCH et al. (1997), it is obvious that the bullate condition (at least in its marked form) has either evolved independently in several taxa, or has been lost independently if present in the last common ancestor of *Acrobates* and the other Phalangeriformes.

In addition to the adult macerated skulls, we examined histologically prepared specimens of several South American and Australasian marsupial taxa. Most species are represented by pouch-young, in some cases complete developmental series were examined (for a complete list, see SÁNCHEZ-VILLAGRA 2001). Among the species showing bullate stapes as adults, *T. vulpecula* was represented by two specimens.

An early pouch-young of *Trichosurus vulpecula* shows already a prominently outbulging footplate of the stapes that protrudes into the inner ear (Fig. 2), a condition that persists in the adult. Of all other taxa examined, only an early pouch-young of the eastern quoll, *Dasyurus viverrinus* also shows this condition. Adults of this species, as well as other adults of the Dasyuromorpha (ARCHER 1976) do not show this feature. For comparison, a pouch-young of *Perameles* sp. with the plesiomorphic marsupial condition of the stapes' footplate is shown in figure 2. In the specimens illustrated, the ear ossicles are in a blastemous, pre-cartilaginous stage. Much remodeling and growth takes place in the ear ossicles between these stages and adulthood.

The eutherians showing the most pronounced bullate stapes are rodents belonging to the Heteromyidae and Geomyidae, with highly derived middle ears and specialized to low-frequency hearing. Of all marsupials possessing bullate stapedes, only for *Trichosurus vulpecula* there has been an (electrophysiological) audiogram published (GATES and AITKIN 1982). Even though *T. vulpecula* does not have similar hearing abilities to those of the desert rodents mentioned above, an interesting departure from the few other marsupials (phylogenetically

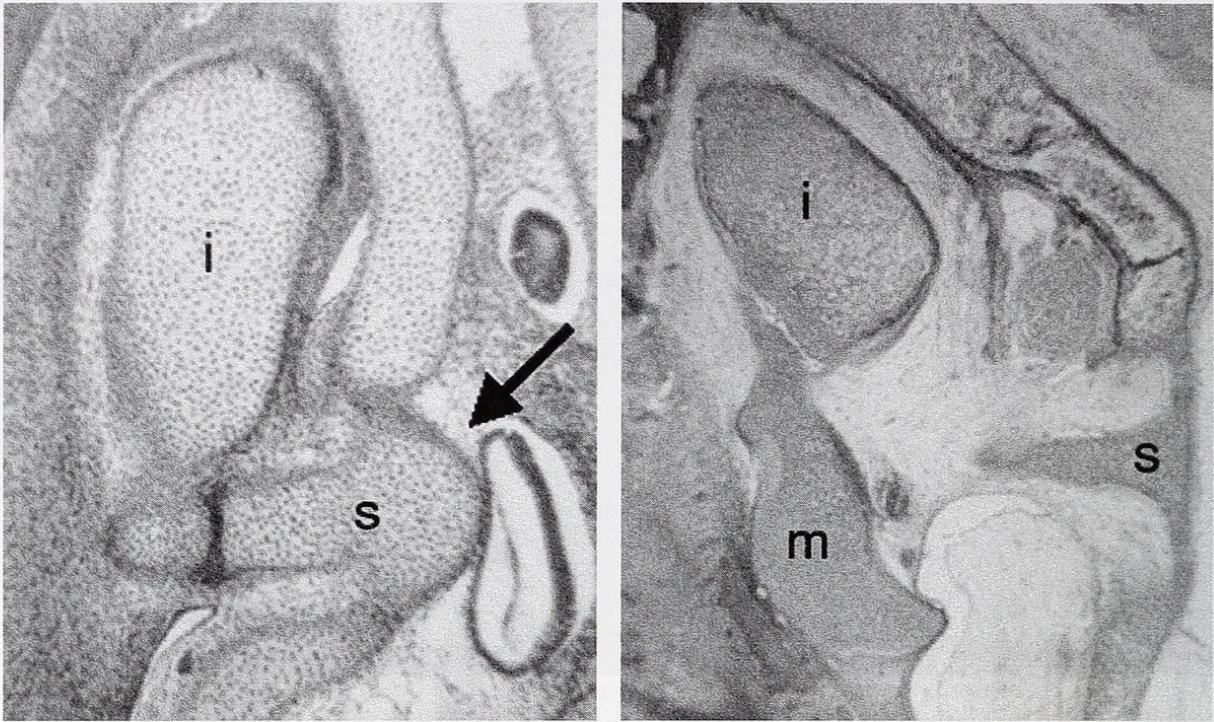


Fig. 2. Cross sections of a portion of the right middle ear of left) *Trichosurus vulpecula* (ZSH, HL = 7.5 mm) and right) *Perameles* sp. (ZSH, HL = 17.5 mm). m = malleus, i = incus, s = stapes. The arrow indicates the bullate condition of the stapes. Not to scale.

and ecologically disparate) for which audiograms are available can be noticed. As pointed out by ATKIN (1995), *T. vulpecula* is more sensitive over a wide range to low frequencies than the other marsupials.

Based on the distribution of the bullate stapes among mammals, it appears that there is no obvious correlation between the possession of a bullate stapes and any particular habit or ecology. A wide size-range is represented by the marsupial species showing a bullate stapes, from the 10–17 g *Acrobates* to the much larger *Trichosurus* reaching around 4.5 kg (NOWAK 1999). They include mostly arboreal species, omnivorous-herbivores and predominantly nectar-eaters (HUME 1999).

In summary, we report here the presence of a singular specialization of the stapes in three marsupial taxa. Based on the study of pouch-youngs of one of them, we observe that this feature appears relatively early in ontogeny. A bullate stapes represents either an autapomorphy of Phalangeriformes lost independently in several members of this monophylum, or characterizes several clades within this group of diprotodontian marsupials.

Acknowledgements

Osteological specimens reported in this study are deposited in the Senckenberg Museum, Frankfurt (SM) or belong to WOLFGANG MAIER's personal collection (WM). Histological specimens belong to the Lehrstuhl für Spezielle Zoologie, Zoologisches Institut, in Tübingen (ZSH). We thank the following persons and institutions for allowing us to examine collections under their care: G. STORCH (SM), A. FORSTÉN (Zoological Museum, Helsinki), S. B. McLAREN and J. R. WIBLE (Carnegie Museum), J. A. W. KIRSCH (University of Wisconsin), K. K. SMITH and A. VAN NIEVELT (Duke University, Durham), and W. MAIER (Tübingen). We thank R. BRITZ for his help with photographic equipment and procedures, W. MAIER (Tübingen), T. REUTER and S. HEMILÄ (Helsinki) for their support, and W. MAIER and an anonymous reviewer for their helpful criticisms to the manuscript. Ella and Georg Ehrnrooth Foundation, and Oskar Öflund Foundation supported SN. A research travel grant from DFG supported MRSV.

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Authors' addresses:

MARCELO R. SÁNCHEZ-VILLAGRA, Spezielle Zoologie, Zoologisches Institut, Universität Tübingen, Auf der Morgenstelle 28, D-72076 Tübingen, Germany
(e-mail: marcelo.sanchez@uni-tuebingen.de);
SIRPA NUMMELA, Department of Ecology and Systematics, University of Helsinki, P.O. Box 17, FIN-00014, Helsinki, Finland.



Sánchez-Villagra, Marcelo R. and Nummela, Sirpa. 2001. "Bullate stapedes in some phalangeriform marsupials." *Zeitschrift für Säugetierkunde : im Auftrage der Deutschen Gesellschaft für Säugetierkunde e.V* 66, 174–177.

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