J. Anat. (1984), **138**, 2, pp. 217–225
With 3 *figures*
Printed in Great Britain

The structure of the vomeronasal organ and nasopalatine ducts in *Aotus trivirgatus* and some other primate species*

A. J. HUNTER, D. FLEMING AND A. F. DIXSON
*Department of Reproduction, Institute of Zoology, Zoological Society of London, Regents Park, London NW*1

(*Accepted* 16 *June* 1983)

INTRODUCTION

The vomeronasal organ was first fully described by Jacobson (1811), although its presence had been noted by Ruysch (1703). Since its discovery, the occurrence and structure of the organ has been well documented in many species (Allison, 1953; Negus, 1956; Cooper & Bhatnagar, 1976; Vaccarezza, Sepich & Tramezzani, 1981). The vomeronasal organ is a bilateral, symmetrical structure encapsulated by cartilage. It lies at the base of the nasal septum and, in most mammals, opens anteriorly into the nasopalatine canal via the vomeronasal duct.

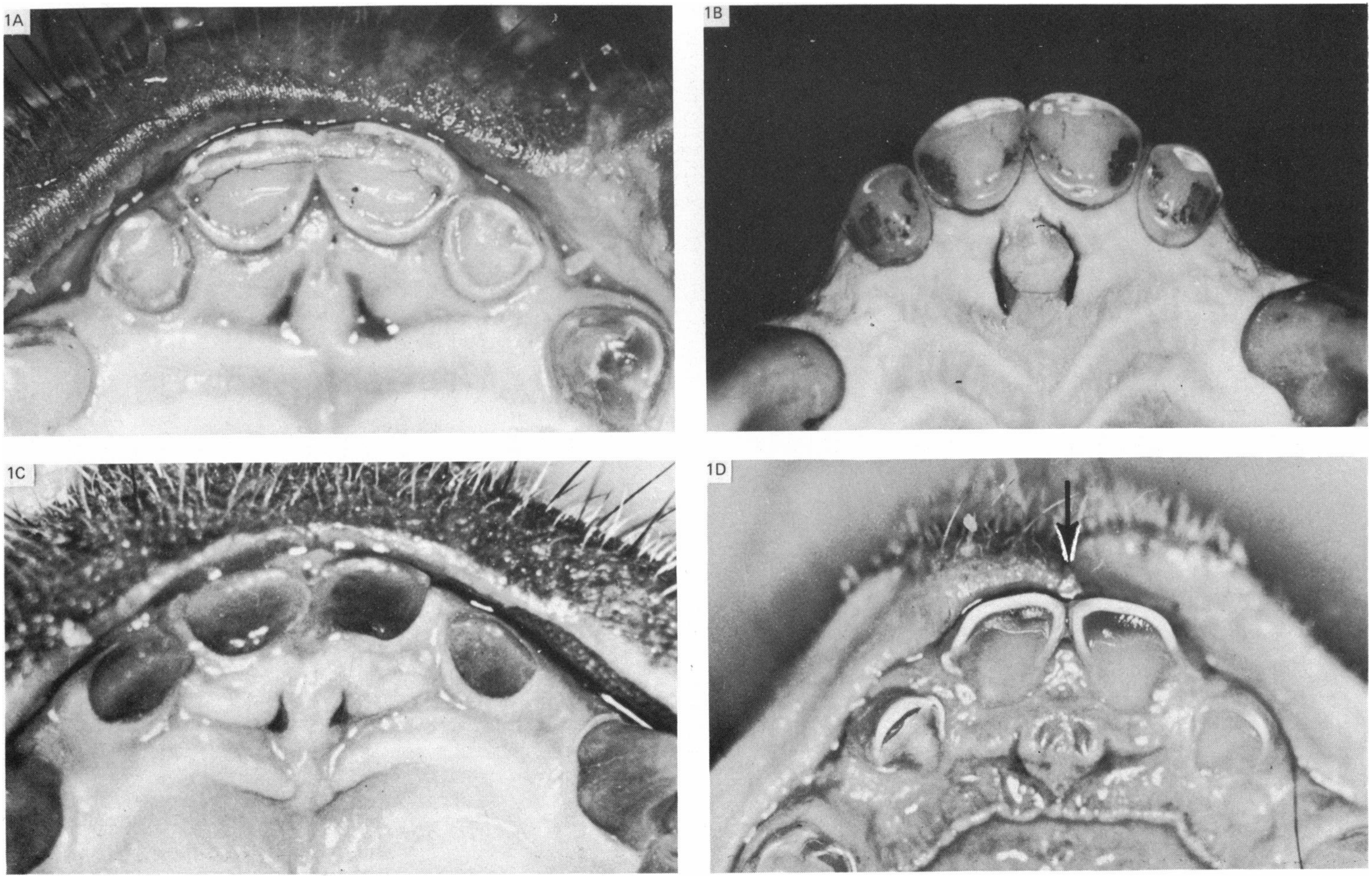
Detailed studies of the structure of the vomeronasal organ have only been carried out in a few primate species: the mouse lemur, *Microcebus murinus* (Schilling, 1970); the tarsier, *Tarsius bancanus borneanus* (Starck, 1975); the bushbaby, *Galago senegalensis* (Eloff, 1951), *Galago demidovii* and the squirrel monkey, *Samiri sciureus* (Maier, 1980). Frets (1912) studied the organ in the fetuses of a number of Platyrrhine and Catarrhine species, but in only one adult specimen of *Cebus hypoleucus*. He concludes that the organ is well developed only in Platyrrhine primates. Similar results were obtained by Jordan (1972) and Loo (1974), with the organ being present in the slow loris, lemur and capuchin monkey but absent in the gibbon and various macaque species, although in many studies it is not clear whether fetal or adult material has been used (e.g. Loo, 1974; Starck, 1975).

Further, Martin (1973) states that nasopalatine ducts and a functional vomeronasal organ are present only in Strepsirrhine primates. Eisenberg (1977) proposes that, whereas Callitrichid primates have a vomeronasal organ, it is lacking in other New World species (family Cebidae). In Catarrhine primates and man, there is a general consensus that the organ is conspicuous only during fetal development, although it can persist into adulthood in a very rudimentary form (Roper-Hall, 1945; Eloff, 1951; Jordan, 1972).

The aim of the present study has been to describe the structure of the vomeronasal organ in adults of three New World species: the owl monkey (*Aotus*); the spider monkey (*Ateles*) and the saddle-backed tamarin (*Saguinus*). One adult of a prosimian species, the angwantibo (*Arctocebus*), has also been studied for comparative purposes.

---

* Reprint requests to Dr A. J. Hunter, Department of Pharmacology, Glaxo Group Research Ltd, Greenford, Middlesex UB6 0HE


1A
1B
1C
1D

MATERIALS AND METHODS

The palate and rhinarium of one adult specimen of each of the following species were examined externally: *Aotus trivirgatus griseimembra; A. t. bolivensis*; *Saguinus fuscicollis; Callithrix jacchus* and *Ateles geoffroyi*. Histological studies were carried out on a total of five specimens of *Aotus* and on one specimen from each of the following primate species: *Saguinus fuscicollis*, *Ateles geoffroyi* and *Arctocebus calabarensis*. Specimens had been preserved in 10% buffered formol saline. From each head the frontal portion of the upper jaw was removed, including the palate and the nasal fossa as far as the cribriform plate. Attached skin and muscle tissue were removed from these specimens, apart from the skin around the upper lip. The canines were cut away as much as possible to facilitate the decalcification process. Sections were then decalcified for periods of between three and five months, depending on the weight of the tissue, in a solution of 5–10% EDTA in a phosphate buffer.

When decalcification was well advanced, the tissue was trimmed down to smaller pieces for embedding. A double embedding technique was used and wax sections were stained either with Martius scarlet–blue or with Luxol fast blue–Cresyl fast violet.

From one *Aotus*, the vomeronasal organ and its associated cartilages were dissected out. They were then embedded, mounted and sectioned as described above.

RESULTS

External examination

The rhinarium was smooth in all specimens examined, there being no median cleft or furrow present as has been described for the strepsirhine condition. However, in the single specimen of *Callithrix* examined, a short median furrow was found in the external surface of the upper lip (arrowed in Fig. 1). This furrow did not split the upper lip, but disappeared on reaching the glabrous margin of the lip. In all New World specimens examined, the upper lip was not tethered to the gum, as in the Prosimians, and thereby appeared to be fully involved in facial expression. On or just above the first palatal ridge, a pair of incisive ducts, or foramina, opened into the oral cavity (Fig. 1). The shape of these ducts differed between species but appeared to be fairly constant between individuals. In the two subspecies of *Aotus*, the separation of the foramina was approximately the same, although their shape was slightly different (Fig. 1 A, B). The papillae palatinae were also similar in structure. The openings of the ducts were approximately 3 mm apart in the specimen of *Ateles* and appeared more elongated and narrow than those of the other species. The papillae palatinae of *Callithrix* were very distinctive, overhanging the incisive openings slightly (Fig. 1 D).

Histological examination

Aotus

Frontal sections were taken from two animals. The papillae palatinae did not have any specialised cartilages associated with them, but the lamina transversalis anterior was well developed and joined, but did not fuse with, the septum nasi. The nasopalatine ducts were kidney shaped in transverse section and curved outwards. The

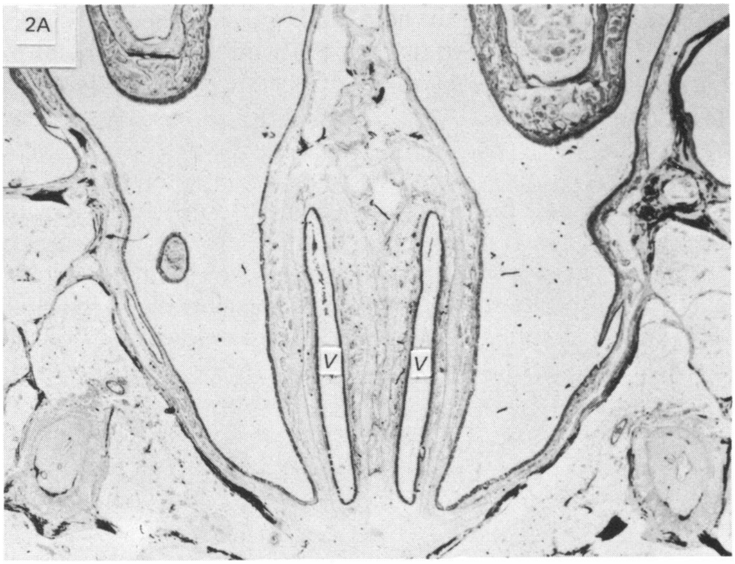
Fig. 1 (A–D). The palatal opening of the nasopalatine ducts in *Aotus*. *Callithrix* and *Ateles*. A, *Aotus trivirgatus*; B, *Ateles geoffroyi*; C, *Saguinus fuscicollis*; D, *Callithrix jacchus*. Note the furrow in the upper lip (arrowed in D) together with the highly developed papillae palatinae in *Callithrix*. *V*. vomeronasal organ.

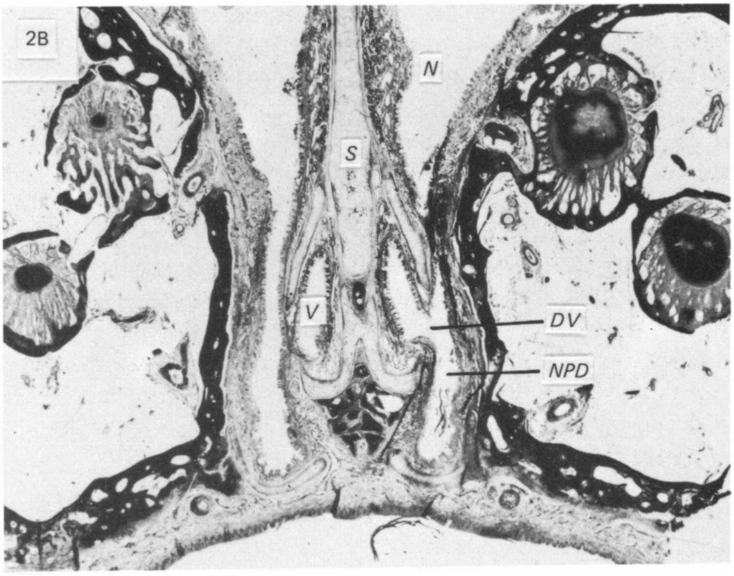
ducts were patent, i.e. they joined the nasal and oral cavities with no occlusion along their length. They did not appear to travel directly upwards towards the nasal cavity, but first bent backwards slightly, and then travelled upwards to join the nasal cavity. The short ductus vomeronasalis joined the nasopalatine canal just below its point of fusion with the nasal cavity (Fig. 2B), thereby connecting the organ to both oral and nasal cavities. The vomeronasal organ lay just beside the margin of the septum nasi and at the base of the nasal cavity. It was almost completely enclosed by the paraseptal cartilage. The two anterior paraseptal cartilages were fused together ventrally, while the dorsal segments were separate and neither cartilage was joined to the septum nasi. The ductus vomeronasalis passed between these two parts of the paraseptal cartilage (Fig. 2B). A large vein lay just below the septum and the organ itself was well vascularised. The premaxillary bone and the cartilaga palatina were also visible. The organ was oval in cross section, and decreased in size at the posterior end. The paraseptal cartilage also began to decrease in size, although it terminated a little way beyond the posterior margin of the vomeronasal organ. The vomeral bone became visible towards the posterior region of the organ, and approached, but did not fuse with, the paraseptal cartilage. Figure 2C shows a longitudinal section through the organ. Two *Aotus* nasal regions sectioned in this way revealed a small amount of cartilage associated with the nasopalatine canals; alar cartilage in the anterior nasal region was also visible. The nasopalatine canals had a roughly triangular shape and the paraseptal cartilage gradually appeared at the apex of the duct. The vomeronasal organ was almost completely surrounded by cartilage (Fig. 2C). The organ itself was cigar shaped and its size varied considerably between individuals. The mean lengths for three animals were approximately 3·3 mm, 3·3 mm and 1·7 mm and the respective widths were 0·33 mm, 0·28 mm and 0·25 mm. The animal with the smallest vomeronasal organ was a female which had apparently died of old age. The other two organs measured were from an adult male and an adult female. In two further female specimens the organs were much shorter in length, 1·6 mm and 2·00 mm respectively. However, no further male specimens were available to investigate possible sex differences in the size of the vomeronasal organ. The vomeronasal epithelium was similar in appearance to the sensory epithelium of the nasal cavity. The epithelium was columnar but its cells were more closely packed and elongated than in the mucous epithelium lining the nasopalatine ducts.

Other species examined

In all species examined (*Arctocebus*, *Saguinus* and *Ateles*) the nasopalatine ducts were patent. In *Saguinus* and *Arctocebus* the structure of the vomeronasal organ and associated cartilages was similar to that found in *Aotus* (Fig. 3). In both species the vomeronasal duct joined the nasopalatine canal just below its point of fusion with the nasal cavity. An extremely elaborate turbinate system was present in *Arctocebus* compared with the New World primates examined. The vomeronasal epithelium in *Arctocebus* appeared to have two components – a high, sensory epithelium on the

Fig. 2 (A–C). The vomeronasal organ in *Aotus*. (A) A longitudinal section. (B) Fusion of the vomeronasal duct and nasopalatine duct. On the left side of the picture the organ is separated from the nasopalatine duct, which has opened into the nasal cavity. On the right side the vomeronasal duct joins the vomeronasal organ and the nasopalatine duct. (C) Sagittal section of the vomeronasal organ which was dissected out with its associated cartilage prior to sectioning. *S*, septum; *N*, nasal cavity; *NPD*, nasopalatine duct; *V*, vomeronasal organ; *DV*, vomeronasal duct.


2A
V
V


2B
N
S
V
DV
NPD


2C
V

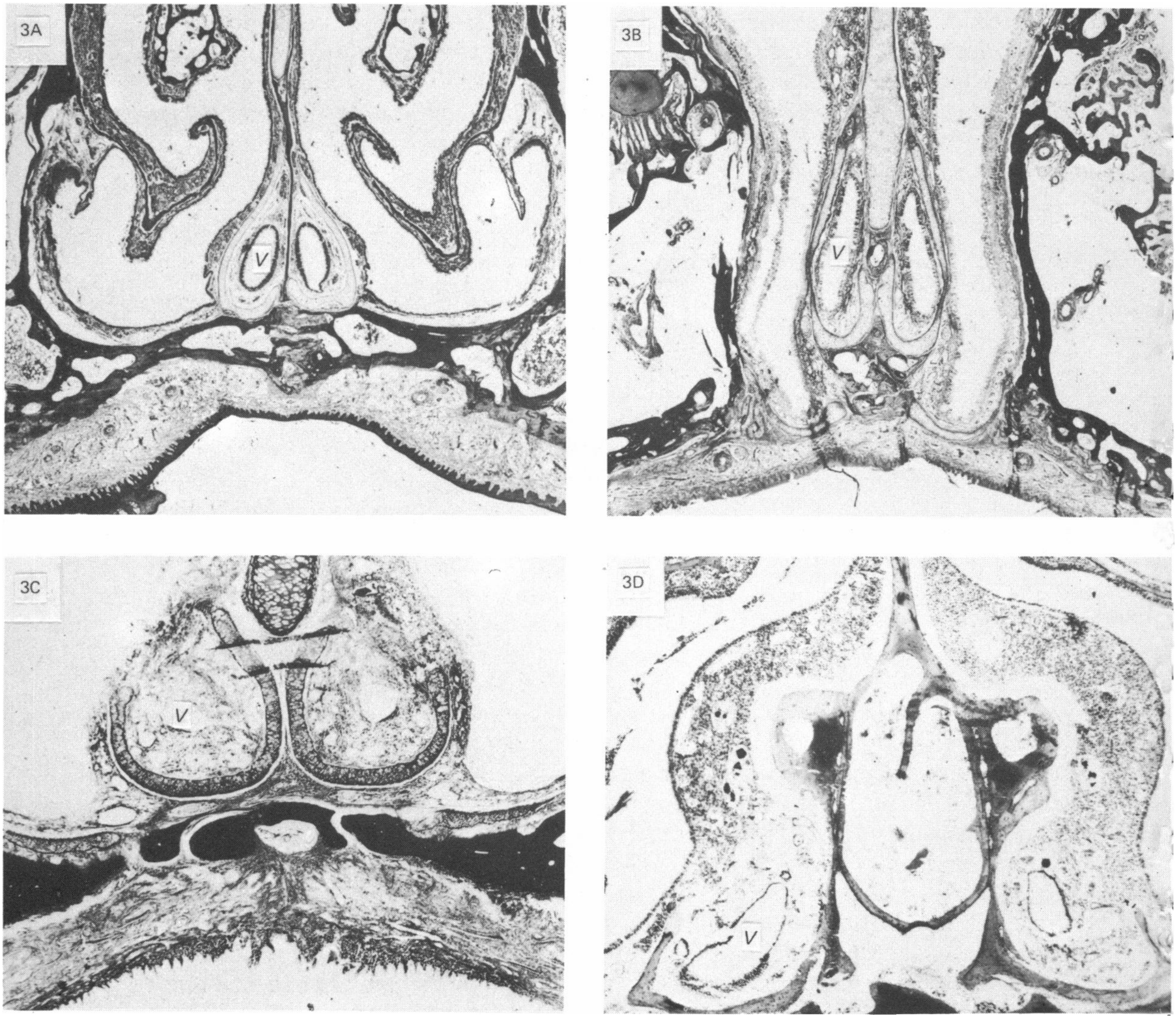


Fig. 3 (A–D). Frontal sections of the vomeronasal organs of (A) *Saguinus fuscicollis*; (B) *Aotus trivirgatus*; (C) *Ateles geoffroyi*; (D) *Arctocebus calabarensis*. *V*, vomeronasal organ.

ventral surface and a low, non-sensory epithelium on the dorsal surface. As only frontal sections were taken, no accurate measurement of length could be obtained but the width of the organ in *Saguinus* was 0·33 mm and in *Ateles* the maximum width was 0·66 mm. The organ in *Ateles* was partially surrounded by paraseptal cartilage along its length (Fig. 3C) and the epithelium lining the organ was similar to that lining the nasopalatine ducts, being thinner and less close packed than in the other three species examined.

DISCUSSION

External examination of the rhinarium and upper lip of the New World species investigated in the present study shows that there is no furrow, or sulcus, to join the rhinarium to the sulcus papillae palatinae, as exists in prosimian primates (Schilling, 1970; Hofer, 1977). It has been suggested that such a furrow enables substances to be brought into contact with the vomeronasal organ (Verberne, 1976). Contrary to Martin's (1973) assertion, a patent nasopalatine duct and a vomeronasal organ are present in all the specimens examined. Although Eisenberg (1977) states that a functional vomeronasal organ is present in the Callitrichidae but not in the Cebidae, many other studies have shown the presence of patent nasopalatine ducts and vomeronasal organs in both orders: *Cebus* (Jordan, 1972); *Callicebus*, *Samiri* and *Allouatta* (Maier, 1980; Stark, 1975); *Callithrix jacchus*, *Saguinus fuscicollis illigneri* and *S. f. nigrifrons* (Wysocki & Epple, unpublished data cited in Wysocki, 1979). The present study confirms some of these observations and enlarges upon them.

The structure of the organ in *Aotus* and *Saguinus* is essentially similar to that described in other New World primates (Jordan, 1972; Maier, 1980). The appearance of the vomeronasal epithelium in *Ateles* is different from that present in *Aotus* and *Saguinus*, resembling the mucosal epithelium lining the nasopalatine duct. It is possible that the epithelium was distorted during the prolonged decalcification needed for the large *Ateles* tissue specimens. Only in *Arctocebus* is there an obvious definition between a high sensory epithelium and a low, non-sensory epithelium in the organ, as described by Schilling (1970) in *Microcebus murinus*.

The vomeronasal organ in *Microcebus murinus*, a prosimian about one tenth of the weight of an *Aotus* monkey, was approximately 3 mm long (Schilling, 1970). Thus, compared to that of *Microcebus*, the relative size of the organ in *Aotus* is small. In *Saimiri*, whose body weight is comparable with that of *Aotus*, the organ is still only 5 mm long (Maier, 1980). Additionally, there is a large individual variation in the size of the organ in *Aotus* (range 1·6 to 3·3 mm). This variation is too large to be accounted for simply by differences in body dimensions. It could be argued that the percentage of sensory epithelium as compared with non-sensory epithelium is a better predictor of functional status than the relative size of the organ. However, detailed studies of this nature have been carried out only on *Microcebus* (Schilling, 1970). It remains to be seen whether a similar individual variation exists for other Platyrrhine species but such variations, coupled with the relatively small size of the organ in *Aotus*, makes it unlikely that the vomeronasal organ plays a crucial role in olfactory communication in the owl monkey.

In rodents, the vomeronasal organ plays an integrative role in the control of reproduction (Bellringer, Pratt & Keverne, 1980; Reynolds & Keverne, 1979; Wysocki, 1979) and there has been some speculation as to the possible role of the organ in mediating reproductive processes in primates. If a reduction of the olfactory apparatus is a characteristic of more highly evolved primates (Napier, 1977), then it might be expected that the vomeronasal organ would be less well developed in *Ateles* than in other Platyrrhines. *Ateles* is a highly specialised animal and exhibits other modifications, for example, reduction of the thumb and absence of the penile bone. It is therefore not surprising that the male spider monkey examined here did not possess an organ which appeared functional. The importance of chemical communication in the reproductive biology of spider monkeys, Callitrichids and other New World primates has been stressed in some studies (Klein, 1971; Epple, 1974, 1976) but it is possible that the effects observed are mediated principally by the main olfactory system.

Against this argument must be set the fact that several New World species possess distinct accessory olfactory bulbs (Stephan & Andy, 1969) and, further, that absence of an accessory olfactory bulb does not necessarily indicate absence of a vomeronasal organ (Cooper & Bhatnagar, 1976). Many Callitrichids exhibit licking and tongue-flicking displays which regularly precede copulation (Abbott & Hearn, 1978; Moynihan, 1970) and these displays may serve to bring chemical substances into contact with the organ. The occurrence of 'Flehmen', a display which has been linked to vomeronasal function (Estes, 1972; Ladewig & Hart, 1980) has also been reported for several primate species: *Lemur catta* (Bailey, 1978; Evans & Goy, 1968) and *Saguinus fuscicollis* (Epple, personal communication).

The conclusion of Maier (1980) that the Platyrrhini possess a vomeronasal organ that is still functional but reduced, compared to the prosimians, is supported by the present study. Although the function of the organ in primates remains unclear, it is unlikely to play a crucial role in mediating reproductive processes in the Platyrrhini, although it could be retained for other (social) signalling purposes.

SUMMARY

A vomeronasal organ and patent nasopalatine ducts were found in adult specimens of *Aotus trivirgatus*, *Arctocebus calabarensis*, *Ateles geoffroyi* and *Saguinus fuscicollis*. The vomeronasal complex appeared to be functional except in *Ateles*. However, the relative size of the organ in the Platyrrhini is much reduced compared to that in prosimians. The possible role of the organ in mediating neuroendocrine processes in primates is discussed.

The authors would like to thank Dr Bill Holt for his advice on histological techniques. This work was supported by a grant from the MRC and the Wellcome Trust (UK).

REFERENCES

ABBOTT, D. & HEARN, J. P. (1978). Physical hormonal and behavioural aspects of sexual development in the marmoset monkey, *Callithrix jacchus*. *Journal of Reproduction and Fertility* **53**, 155–166.

ALLISON, E. D. (1953). Morphology of the olfactory system in the vertebrates. *Biological Reviews* **28**, 195–244.

BAILEY, K. (1978). Flehmen in the ring-tailed lemur (*Lemur catta*). *Behaviour* **65**, 309–319.

BELLRINGER, J. F., PRATT, H. P. M. & KEVERNE, E. B. (1980). Involvement of the vomeronasal organ and prolactin in pheromonal induction of delayed implantation in mice. *Journal of Reproduction and Fertility* **59**, 223–228.

COOPER, J. G. & BHATNAGAR, K. P. (1976). Comparative anatomy of the vomeronasal complex in bats. *Journal of Anatomy* **122**, 571–600.

EISENBERG, J. F. (1977). Comparative ecology and reproduction in New World monkeys. In *The Biology and Conservation of the Callitrichidae* (ed. D. Kleiman), pp. 13–22. Washington, D.C.: Smithsonian Institution Press.

Eloff, F. C. (1951). On the organ of Jacobson and the nasal floor cartilage in the chondrocranium of *Galago senegalensis*. *Proceedings of the Zoological Society of London* **121**, 651–655.

Epple, G. (1974). Olfactory communication in South American primates. *Annals of the New York Academy of Sciences* **237**, 261–278.

Epple, G. (1976). Chemical communication and reproductive processes in non-human primates. In *Mammalian Olfaction, Reproductive Processes and Behaviour* (ed. R. L. Doty), pp. 257–282. New York: Academic Press.

Estes, R. D. (1972). The role of the vomeronasal organ in mammalian reproduction. *Mammalia* **36**, 315-341.

Evans, C. S. & Goy, R. W. (1968). Social behaviour and reproductive cycles in captive ring-tailed lemurs. *Journal of Zoology* **156**, 181–197.

Frets, G. P. (1912). On the Jacobson's organ in primates. *Proceedings of Section of Sciences, Akademie Wetenschappen Amsterdam* **15**, 184–185.

Hofer, H. O. (1977). The anatomical relations of the ductus vomeronasalis and the occurrence of taste buds in the papilla palatine of *Nycticebus coucang* (Primates, Prosimiae) with remarks on Strepsirrhinism. *Gegenbaurs morphologisches Jahrbuch* **123**, 836–856.

Jacobson, L. L. (1811). Description anatomique d'un organe observé dans les mammifères. *Annales du Muséum national d'histoire naturelle de Paris* **18**, 412-424.

Jordan, J. (1972). The vomeronasal organ (of Jacobson) in primates. *Folia morphologica* **31**, 418–432.

Klein, L. L. (1971). Observations on copulation and seasonal reproduction of 2 species of Spider monkey (*Ateles belzebuth* and *Ateles geoffroyi*). *Folia primatologia* **15**, 233–248.

Ladewig, J. & Hart, B. L. (1980). Flehmen and vomeronasal organ function in male goats. *Physiology and Behaviour* **24**, 1067-1071.

Loo, S. K. (1974). Comparative study of the histology of the nasal fossa in 4 primates. *Folia primatologia* **21**, 290–303.

Maier, W. (1980). Nasa. structures in Old and New World primates. In *Evolutionary Biology of the New World Monkeys and Continental Drift* (ed. R. L. Ciochon & A. B. Chiarelli), pp. 219–241. New York: Plenum Press.

Martin, R. D. (1973). Comparative anatomy and primate systematics. *Symposia of the Zoological Society of London* **33**, 301-337.

Moynihan, M. (1970). Some behaviour patterns of platyrrhine monkeys. I. *Saguinus geoffroyi* and some other tamarins. *Smithsonian Miscellaneous Contributions to Zoology* **28**, 1–68.

Napier, J. R. (1977). *Primates and Their Adaptations. Carolina Biology Readers* **83**. Oxford University Press.

Negus, V. (1956). The organ of Jacobson. *Journal of Anatomy* **90**, 515–519.

Reynolds, J. & Keverne, E. B. (1979). The accessory olfactory system and its role in the pheromonally mediated suppression of oestrus in grouped mice. *Journal of Reproduction and Fertility* **57**, 31–35.

Roper-Hall, H. T. (1945). Jacobson's organ. *Proceedings of The Royal Society of Medicine* **38**, *Section on Odontology* 1–10.

Ruysch, F. (1703). *Thesaurus Anatomicus III*. Amstelod.

Schilling, A. (1970). L'organe de Jacobson du lemurien malgache, *Microcebus murinus* (Miller, 1977). *Mémoires du Muséum national d'histoire naturelle*, Série A **61** (4), 203–280.

Starck, D. (1975). The development of the chondrocranium in primates. In *Phylogeny of the Primates* (ed. W. P. Luckett & F. S. Szalzay), pp. 127–155. New York: Plenum Press.

Stephan, H. & Andy, D. J. (1969). Quantitative comparative neuroanatomy of the primates: An attempt at a phylogenetic interpretation. *Annals of the New York Academy of Sciences* **167**, 370–387.

Vaccarezza, O. L., Sepich, L. N. & Tramezzani, J. H. (1981). The vomeronasal organ of the rat. *Journal of Anatomy* **132**, 167–185.

Verberne, G. (1976). Chemocommunication among domestic cats, mediated by the olfactory and vomeronasal senses. II. The relation between the function of Jacobson's organ (vomeronasal organ) and Flehmen behaviour. *Zeitschrift für Tierpsychologie* **42**, 113–128.

Wysocki, C. J. (1979). Neurobehavioural evidence for the involvement of the vomeronasal organ in mammalian reproduction. *Neuroscience and Behavioural Reviews* **3**, (4), 301-341.