



Fig. 5. Apparatus for the production and detection of acoustic signals in crocodilians. (A) Sagittal section of a crocodilian head showing the position of the palatal valve. (B) Crocodilian outer ear. (C) Structure of the crocodilian middle and inner ear (see text for further details).

Environmental conditions such as temperature also have an effect on vocalization properties. Garrick & Garrick (1978) studied the effect of temperature on the distress calls of 10 spectacled caimans during the first three months post hatching. A temperature increase was accompanied by a linear decrease in both call duration and inter-call interval whereas spectral composition of calls remained unchanged (27 calls were analysed over a temperature range of 12.8–33.0°C). Increased metabolic activity was thus associated with increased call frequency. Above 33°C, emission of vocalizations was apparently impaired by an increased frequency of thermoregulatory gular pulsations.

(2) Detection and localization of sounds

Crocodilians have well-developed auditory capabilities utilized during foraging as well as in communication among individuals.

(a) The crocodilian ear

The crocodilian ear is divided into three regions: the outer, middle and inner ear, and has numerous similarities with

the avian ear (Dooling, Lohr & Dent, 2000). It is located at the same level and just behind the eye, allowing a crocodile to swim with only the ears, eyes and nostrils above the water surface. The anatomical structure of the outer ear is also adapted to an aquatic life: a pair of rostro-caudally oriented muscular flaps ('ear lids'; Saunders *et al.*, 2000) control the opening to the external meatus and protect the tympanic membrane from water entry (Fig. 5B). In the air, the ear lids are relaxed and the tympanic membrane is exposed to the environment (Wever & Vernon, 1957; Saunders *et al.*, 2000; A.L. Vergne, personal observations).

As in other vertebrates, the middle-ear system uses impedance matching to transmit airborne sound into the aqueous medium of the inner ear. The middle-ear apparatus was originally described by Retzius (1884) and Wever (1978) and is reviewed in Saunders *et al.* (2000). The crocodilian and bird middle ear have many structural similarities despite the great variations existing among different families of birds (Henson, 1974; Manley, 1990; Manley & Gleich, 1992; Saunders, 1985; Saunders *et al.*, 2000). The crocodilian middle ear (Fig. 5C) contains a tympanic membrane found on the floor of the external meatus. As in birds, there is a single ossicle, the stapes or