OSMOREGULATION IN CROCODILIANS

By LAURENCE E. TAPLIN

Queensland National Parks and Wildlife Service, Marlow St., Pallarenda,
Queensland, 4810, Australia

CONTENTS

1. INTRODUCTION

The crocodilians are an ancient group of morphologically conservative archosaurians which have long played a role in human culture. Yet remarkably, it has been only in the last two decades that concerted efforts have been made to understand some of the details of their biology. In the case of osmoregulatory studies, these studies have led to new and controversial interpretations of the evolutionary origins of the modern species. Specifically, it has been postulated that some or all of the extant species of true crocodiles (Suborder Eusuchia, Family Crocodylidae, Subfamily Crocodylinae) are derived from marine rather than fresh-water ancestors. The alligatorids (Suborder Eusuchia, Family Alligatoridae), in contrast, are regarded as a fundamentally fresh-water stock showing significant and far-reaching differences in various aspects of their osmoregulatory physiology from the Crocodylinae.

These postulates have their origins in detailed studies of osmoregulation in estuarine/marine and fresh-water crocodilians and independent studies of molecular evolution in the group. Critical evaluation of these ideas depends on a clear understanding of both the issues and the uncertainties inherent in the work done so far. This review focusses on the physiology of crocodilians as inhabitants of both fresh and saline waters, concentrating on those elements which will contribute most to debate about marine origins among the Eusuchia. Its primary aim is to draw attention to the need for basic information on most of the living species before their worldwide decline removes all possibility of answering some fascinating questions in vertebrate evolution.

2. ENVIRONMENT AND OSMOREGULATORY STRATEGIES

2.1. *Crocodilians as inhabitants of fresh and saline waters*

The extant crocodilians utilize a wide array of aquatic habitats from the open sea to small spring-fed pools at the very sources of inland streams. The majority inhabit fresh waters but one or two species are found characteristically in coastal, saline waters. It is not widely recognized that many 'fresh-water' species also occur more or less commonly in saline habitats (Table 1) and clearly have some ability to tolerate salt water. There has been little systematic study of these salt-water populations and only rarely is the published information adequate to assess the physiological strategies they have adopted. Few accounts give details of ambient salinities, temperatures, habitat descriptions, numbers and size classes of crocodilians, or assessments of the rarity or otherwise of the occurrence of a particular species in salt water. This information is directly relevant to current efforts to understand the evolution and zoogeography of the group (Section 6). To collect appropriate data, we need to understand something of the nature of the estuarine environment and the osmoregulatory strategies available to crocodilians.

2.2. *The estuarine environment of crocodilians*

Unlike the marine turtles and sea snakes, none of the extant crocodilians can be considered truly marine in habits. Even the sea-going Estuarine Crocodile, *Crocodylus porosus*, is principally an inhabitant of estuaries and rivers rather than the open ocean. We tend, therefore, to think of the salt-water crocodilians as 'estuarine' rather than 'marine', and allow the term 'estuarine' to imply a less osmotically stressful

Table 1. *Recorded observations of the occurrence of crocodilians in fresh and saline habitats*

Data from Neill (1971), Groombridge (1982) and other sources as indicated.

Family Crocodylidae	Notes	
Crocodylus acutus	Principally coastal waters and brackish estuaries. Also inland fresh water	King et al. (1982); Kushlan (1982); Gaby et al. [(1985)
C. cataphractus	Mainly freshwater in rainforests but also brackish coastal lagoons and mangrove swamps	Lang (1919); Villiers (1958); Brazaitis (1973); Pooley (1980)
C. intermedius	Virtually restricted to inland fresh water. Some records from Trinidad attributed to 'passive migration', probably during floods	Medem (1976, 1981 b)
C. johnstoni	Primarily inland fresh water. Not uncommon in saline waters, even as small animals in high salinities	Messel et al. (1979 85); Taplin et al. (1985)
C. moreletii	Primarily coastal fresh waters but occasionally brackish water. Occasional adults found in sea water along coast	Brazaitis (1973); M. Lazcano-Barrero (in litt.)
C. niloticus	Fresh and saline waters of inland and coast Africa. Common in estuaries and mangrove swamps. Common in the hypersaline St Lucia Estuary Lake	Villiers (1958); Pooley (1971)
C. n. novae-guineae	Primarily inland fresh water. Also brackish water of the Fly and Sepik river deltas. Not found on offshore islands	Downes (1971); Whitaker (1980); Cox (1984)
C. n. mindorensis	Primarily inland fresh water but no reliable information	Ross (1984)
C. palustris	Largely fresh water. The Sri Lankan subspecies is not uncommon in salt pan lagoons	Derinayagala (1933); Whitaker & Whitaker (1978)
C. porosus	Common in coastal fresh, brackish and highly saline waters. Hatchlings tolerant of very high salinities	Messel et al. (1979–85); Taplin (1984a); Grigg et al. (1986)
C. rhombifer	Primarily fresh water swamps. Collected from salt-water lagoons of northern Cuba	Varona (1966); Guggisberg (1972)
C. siamensis	Apparently restricted to fresh water. No reports from saline waters	Brazaitis (1973)
Osteolaemus t. tetraspis	Primarily in fresh water streams and ponds in rainforest. Apparently not uncommon in mangrove swamps	Pooley (1980)
Osteolaemus t. osborni	Apparently restricted to inland fresh water.	
Subfamily Tomistominae		
Tomistoma schlegelii	Apparently restricted to fresh waters	
Family Alligatoridae		
Alligator mississippiensis	Primarily fresh waters. Also common in brackish waters of low salinity. May be killed by exposure to hyperosmotic salt water during storm surges	Joanen & McNease (1972); McNease & Joanen (1978); Birkhead & Bennett (1981)
A sinensis	Apparently restricted to fresh waters	Huang (1982)

Table 1. (cont.)

Caiman crocodilus	Primarily fresh waters. Subspecies C. c. crocodilus and C. c. fuscus not uncommon in brackish and salt water and known from offshore islands. C. c. apaporiensis restricted to fresh water. C. c. jacare reported to avoid salt waters	Alvarez del Toro (1975); Varona (1976); S. Gorzula (in litt.); Medem (1981 a, b)
Ca. latirostris	Primarily fresh waters. Not uncommon in coastal salt waters	Brazaitis (1973); Brazaitis cit. Groombridge (1982); Medem (1981 b)
Melanosuchus niger	Apparently restricted to fresh waters	Medem (1981 a, b)
Palaeosuchus palpebrosus	Apparently restricted to fresh water. Found close to the coast in places suggesting some tolerance of salt water	Medem (1981 a, b)
P. trigonatus	As for P. palpebrosus	Medem (1981 a, b)
Family Gavialidae		
Gavialis gangeticus	Apparently restricted to fresh waters. Reputedly occurred historically in a brackish coastal lagoon	Singh & Bustard (1982); Whitaker & Basu (1983); R. Whitaker (pers. comm.)

environment intermediate (geographically and physiologically) between the open sea and fresh water. While this may be appropriate for some estuaries, it is an oversimplification which obscures some important physiological issues.

An estuary may be defined as '...a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage' (Cameron & Pritchard, 1963). This definition is appropriate for the many estuaries in areas where run-off exceeds evaporation and fresh-water influx continues throughout the year – the 'positive estuaries' of Pritchard (1952). In the wet–dry tropics, however, there are many 'negative estuaries' in which evaporation greatly exceeds run-off for much of the year and hypersaline conditions (salinities $> 35 \%_0$) are the norm during the dry season. In these estuaries both the saline and thermal environments can be far more severe than in the open sea. Furthermore, both hypersaline and brackish water arms can be found within the confines of a single estuary (e.g. Messel et al., 1979–81; Grigg, 1981; Taplin, 1984a).

Consideration of the habitat preferences and physiological capabilities of crocodilians and other aquatic reptiles in estuaries requires some means of classifying the different salinity regimes into physiologically meaningful categories. Many different schemes have been proposed (Hedgpeth, 1957) but none has achieved universal acceptance. None of the early classificatory schemes described by Hedgpeth (1957) are of particular value for consideration of aquatic reptiles, as their boundaries are not related in any obvious way to the physiological problems faced by the animals. Grigg (1981) proposed a four-tiered classification based on the physiological characteristics of C. porosus, subsequently modified by Taplin (1984a) to accommodate hypersaline waters. The resulting five-tiered classification is as follows:

SAL 1 – fresh water, whether tidal or non-tidal;

SAL 2 – some marine influence, but throughout the tidal cycle water salinity never exceeds the osmotic concentration of the plasma;

SAL 3 – tidal salinity fluctuations are such that the osmotic concentration of the water fluctuates alternately above and below that of the plasma;

SAL 4 – water salinity at a higher osmoticity than the plasma at all stages of the tidal cycle but never greater than 35 ‰;

SAL 5 – water salinity $> 35 \%_0$ at all stages of the tidal cycle.

The actual salinity used to define fresh water was not specified in the earlier papers but the upper limit of 0·5 ‰ for coastal fresh waters suggested by Bayly (1967) is appropriate. Grigg's classification is based primarily on two fundamental physiological characteristics of C. porosus:

(i) It is an osmoregulator, maintaining its plasma osmotic pressure within narrow limits across a wide range of salinity.

(ii) It is physiologically incapable of excreting urine more concentrated than its plasma and is therefore likely to adopt different osmoregulatory strategies in hypoosmotic and hyperosmotic water.

The definition of SAL 1 and 5 salinity categories recognizes the extreme conditions at the ends of the salinity spectrum where specialized physiological mechanisms may come into play or salinity may become a limiting factor preventing permanent colonization of estuarine habitats.

These salinity categories provide a convenient basis for the description of salinity regimes for all crocodilians. Nonetheless, the categories convey only part of the information necessary to assess the physiological significance of occurrences of crocodilians in salt water. Factors such as regular rainfall or the presence of fresh-water springs can allow crocodilians to thrive in environments which would otherwise impose severe osmotic stress. Any investigation of the ecology of crocodilians in salt water should take account of such factors and provide as complete a description of the physiography of the study area as possible. Detailed descriptive data will provide clues to the locations of 'natural experiments' where tests of the osmoregulatory abilities of various species are possible. The progression from simple survey data to the analysis of physiology in the field is illustrated by the study of C. johnstoni in salt water in Australia (Taplin, Grigg & Beard, 1985). The location of a particular group of animals is not always readily assigned to a single salinity category. Stenohaline fresh-water crocodilians are easily accommodated in SAL 1. Euryhaline estuarine crocodilians may experience conditions from SAL 1–5 over the course of a year, or even a few days if they are very mobile. Even sedentary individuals can be exposed to SAL 2, 3 and 4 conditions at least twice a day as the tide ebbs and flows (Grigg, 1981). Analysis of osmoregulation in estuaries is correspondingly difficult. However, by considering the problems for each salinity category in turn, a view of the whole can be constructed.

2.3. Strategies of osmoregulation

Regardless of which end of the salinity spectrum they inhabit, crocodilians share with all aquatic animals two fundamental problems of osmoregulation: reduction of diffusive leaks of water and electrolytes across permeable surfaces and regulation of active fluxes of ions and water through osmoregulatory effector organs such as the kidneys, cloaca,

skin and gut. The basic difference between living in hyper- or hypo-osmotic salt water lies in the reversal of direction of the diffusive leaks and the necessity to bring effector organs into play in one medium which may have little or no role in the other. The osmoregulatory strategies open to aquatic reptiles can be separated into those which minimize diffusive leaks and those which compensate for temporary imbalances by active uptake or extrusion of electrolytes and water: the 'evasive' and 'compensatory' strategies of Kirschner (1979). Evasive strategies may be physiological – changing the composition of extracellular fluid or the diffusional permeability of the integument; or behavioural – selecting specific food items or microhabitats. Compensatory strategies include drinking, active uptake of salts, urination, and excretion through salt glands. Before moving on to a review of these individual elements of the salt- and water-balance equation, it is necessary to examine the influence of one other major factor of particular relevance to crocodilians – body size.

2.4. Size as a dominating factor in crocodilian osmoregulation

While the importance of size and the scaling of physiological variables has long been recognized, the literature of crocodilian osmoregulation has not always revealed a clear distinction between the physiological problems of small and large crocodiles. Adult $C.$ $porosus$ are the largest of the living reptiles, growing to a length of at least 7 m and a weight of several tonnes. Even small mature animals of 3·5–4·5 m length and a weight of perhaps 300–500 kg are 5000–10000-fold heavier than hatchlings. This enormous disparity between hatchlings and adults demands that their physiological problems are considered separately. It may be feasible for an adult or subadult crocodile to survive prolonged exposure to salt water because of the insulation afforded by its small surface area:mass ratio (Dunson, 1976). A hatchling under similar conditions will not have remotely the same degree of insulation and must adopt quantitatively or qualitatively different evasive or compensatory strategies to maintain the same degree of osmoregulation. For example, unfed $C.$ $porosus$ in sea water dehydrate and become hypernatraemic, largely through integumental exchanges of sodium and water. A hatchling of 100 g body weight (BW) can survive unfed in sea water (SW) for about 21 days, compared with roughly 4 months for a 10 kg juvenile (Taplin, 1985). Clearly, adult crocodiles should be capable of tolerating many months of exposure to sea water, even if they lack compensatory mechanisms. To understand the osmoregulatory capabilities of any of the crocodilians it will be essential to concentrate attention on the smallest size classes. Capabilities found in newly hatched (neonatal) and hatchling crocodilians are likely to be found in adults. The converse is not necessarily true.

3. THE PATTERNS OF OSMOREGULATION

3.1. Composition of the extracellular fluid

All crocodilians studied to date, from both fresh and salt water, maintain their plasma osmolality in the range 280–340 mOsm/kg, with Na and Cl as the principal osmolytes (Table 2). Interspecific variability is small. There may be some tendency for crocodilians from SAL 1 conditions to have lower plasma Na concentrations than animals from saline waters but any trend is obscured by some low values in newly hatched $C.$ $acutus$ and some high values in SAL 1 animals from farms. Detailed data on intraspecific variability of plasma composition with salinity is available for only three

Table 2. *Mean plasma composition, total body water (TBW) and exchangeable sodium (ExNa) determinations from crocodilians under a variety of salinity conditions. (Note that in some instances the number of samples for particular analyses differs from the total number of animals sampled.)*

	No. animals	Age or body weight (kg)	TBW (ml/100 g)	ExNa (mmol/kg)	Plasma osmolality (mOsm/kg)	Plasma Na (mmol/l)	Plasma K (mmol/l)	Plasma Cl (mmol/l)	Salinity category	Conditions	References
Family Crocodylidae											
Subfamily Crocodylinae											
Crocodylus acutus	1	—				149	70	117	SAL 1(?)	Fresh water	Dill & Edwards (1931)
	7	1–4	729		294				SAL 1	Fresh water	Schmidt-Nielsen & Skadhauge (1967)
	2	27–44						—		Fresh water, lab	Thorson (1968)
	6	0·05–0·07				129		—	SAL 1	Freshly captured	Evans & Ellis (1977)
	4	0·1–1·77				157		—	SAL 4	Freshly captured	Ellis (1981 a)
	2	2·0–4·08				138		—	SAL 4	Freshly captured	
	30	Adult				169	48	115	SAL 4	Freshly captured	
	5	1–16 days			321	137	4·2	115	SAL 1	Fresh water, lab	Dunson (1982)
	5	10 days			334	110	5·7	113	SAL 4 or 5	Fresh water, lab	
	2	180–300 days			337	157	8·3	123	SAL 4	Fresh water, lab	
C. cataphractus	1	0·66	794						SAL 1(?)	Fresh water, lab(?)	Taplin (unpubl. obs.)
C. johnstoni	8	45			299	146	2·8		SAL 1	Fresh water, farm	Taplin (unpubl. obs.)
	19	10–200	734	391	262	142	3·5	114	SAL 4	Freshly captured	Taplin (unpubl. obs.)
C. niloticus	20	0·7–3·7	721	537	292	143	4·8	105	SAL 4	Freshly captured	Taplin et al.
	4	2·2–3·4	721	563	280	151		121	SAL 4	Freshly captured	(1985) and unpubl. obs.
C. palustris	16	0·1–0·8							SAL 1	Fresh water, lab	Thorson (1968)
C. porosus	44	0·1–7·1	734	479	300	150	4·9	114	SAL 1	Fresh captured	Taplin (unpubl. obs.)
	14	1·5–7·2			186	143	3·9	113	SAL 4	Freshly captured	Taplin and Loveridge (1988)
	22	0·1–0·7			108	154		117	SAL 5	Freshly captured	
	11	0·3–0·4				141	4·4		SAL 1	Freshly captured	Taplin (1984a)
	7	0·2–0·3				159	4·1	123	SAL 4	Freshly captured	Taplin & Loveridge (1988)
						157	4·8		SAL 5		
	14	0·6*	811						SAL 1	Freshly captured	Taplin (1984a)
	20	0·6*	757						SAL 2	Freshly captured	
	25	0·6*	769						SAL 3	Freshly captured	
	10*	0·6*	789			196	4·7	121	SAL 5	Freshly captured	
	19	0·8–10			307	135*	3·5	116	SAL 2	Freshly captured	
	19	0·8–10			395	133*	3·3	117	SAL 3	Freshly captured	
	24*	0·8–10			392	139*	3·8	114	SAL 5	Freshly captured	
Family Alligatoridae											
Alligator mississippiensis	8	0·7–0·8	793*		284	136	6·4	88	SAL 1	Fresh water, lab(?)	Rosenblatt (1936)
	8	50–105	729			141	3·8	112	SAL 1	Fresh water, lab(?)	Coulson & Hernandez (1964)
	2	N/A								Fresh water, lab	Thorson (1968)
Caiman crocodilus	10–31	0·03–0·07			326	170		123	SAL 1	Freshly captured	Thorson (1968)
	40	8 × 0·4			392	134		115	SAL 1	Fresh water, lab	Ellis & Evans (1982a)
	8	0·04–0·15			286	139		107	SAL 1	Fresh water, lab	Lauren (1985)
Family Gavialidae											
Gavialis gangeticus	7	0·3–4·1	730			134			SAL 1	Fresh water, lab	Bentley & Schmidt-Nielsen (1965)
	3	4·3–9·0			288	158	10·7	106	SAL 1	Fresh water, farm	Thorson (1968)
									SAL 1	Fresh water, farm	Taplin (unpubl. obs.)

Variability between groups of individuals was considerable, ranging from 110–177 mmol/l. * Dunson notes that climatic conditions in the region at the time of capture were such that access to low salinity water was possible. * Mean values quoted do not reflect the significant trend to lower plasma concentration with increasing salinity. * N = 4. † TBW and ExNa values are for hypothetical 'average' crocodiles calculated by analysis of covariance. * Sample numbers lower than for some animals. * These Na values believed to be underestimates due to a systematic calibration error. Based on analysis of fresh captured in India and should be treated with caution. * High values may be due to difficulties in feeding cold storage in farm. § Value based on a somewhat dubious analytical technique. † Summer. § Winter.

species – C. acutus, C. johnstoni, and C. porosus. The most complete data are those for C. porosus which is a remarkably euryhaline osmoregulator, able to maintain essentially constant plasma electrolyte concentrations in salinities of 0–64 ‰ (Grigg, 1981; Taplin, 1984a; Grigg et al., 1986). Laboratory reared C. porosus have plasma Na levels more comparable with other fresh water crocodilians than with wild-caught C. porosus from seasonally fresh water (Table 2). No data are available yet for SAL 1 C. porosus from permanent fresh water habitats inland.

Data for C. acutus from coastal Florida are less extensive and no clear pattern of composition as a function of salinity is apparent. It does seem that crocodiles of 180 days and older maintain the major plasma electrolytes at levels comparable with other crocodilians. However, young animals have been found with very low plasma Na concentrations (Dunson, 1982) perhaps reflecting some perturbation of Na balance in these smallest animals. Similar low Na concentrations in the range 110–120 mmol/l appear to be characteristic of late-term embryos and freshly hatched C. porosus also (pers. obs.). It is not yet clear whether these low concentrations reflect in any way on the ability of newly hatched C. acutus or C. porosus to osmoregulate in salt water. It has been suggested that young C. acutus avoid osmotically stressful environments, seeking out relatively sheltered microhabitats in lower salinity water (Dunson, 1982). The Australian Freshwater Crocodile, C. johnstoni, is largely restricted to fresh waters. However, isolated individuals and one or two small populations can be found in salt waters, sometimes in highly saline conditions (e.g. a 1 m animal caught in 43 ‰ salt water on the Albert River in Queensland – unpubl. obs.). In at least one of these salt-water populations, C. johnstoni is capable of fairly precise osmoregulation between 0 and 24 ‰ salt (Taplin, Grigg & Beard, 1985), showing a trend to slightly lower plasma osmolarity and Na concentration with increasing salinity. The data for other species are too sparse to allow any firm conclusions.

3.2. Total body water and exchangeable Na pools

The available data on total body water (TBW) and exchangeable Na pools (ExNa) allow few firm conclusions about variation as a function of salinity (Table 2). Data on intraspecific variation of sodium and water pools as a function of salinity are available only for C. porosus and C. johnstoni. C. porosus maintains essentially constant levels of weight-specific TBW across the salinity spectrum while ExNa actually declines with increasing salinity (Taplin, 1984a). C. johnstoni from fresh and saline water similarly hold TBW more or less constant but crocodiles from salt-water populations tend to have higher ExNa than their fresh-water counterparts (Taplin et al., 1985 and unpubl. obs.).

Interspecific comparisons of TBW and ExNa are fraught with difficulty because of the marked allometric scaling of both variables. The problems are well illustrated by data for C. porosus and C. johnstoni (Taplin, 1984a and unpubl. obs), (Fig. 1). Equations of the curves are given by the following relationships:

Total body water (TBW) – C. porosus $= 1{\cdot}03\ \mathrm{SVL}^{-0{\cdot}05}$,
                                – C. johnstoni $= 1{\cdot}39\ \mathrm{SVL}^{-0{\cdot}11}$,
Exchangeable Na (ExNa) – C. porosus $= 0{\cdot}17\ \mathrm{SVL}^{-0{\cdot}18}$,
                                – C. johnstoni $= 0{\cdot}41\ \mathrm{SVL}^{-0{\cdot}33}$,
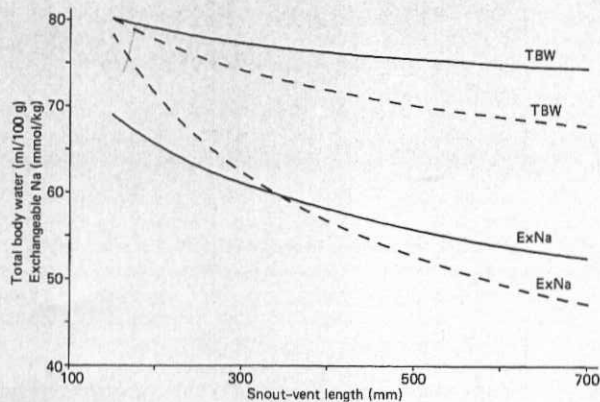where TBW is expressed in ml/100 g, ExNa in mmol/kg and SVL = snout–vent length

Fig. 1. Weight-specific sodium and water pools in C. porosus (——) and C. johnstoni (----) as a function of body size. Curves are derived from empirically determined relationships of total body water, exchangeable Na pool and body weight with length (Taplin, 1984a and unpubl. obs.).

(mm). All slopes in the above relationships are significantly different from one another at the 95 % confidence level.

It is evident from Fig. 1 that comparing levels of TBW or ExNa in the two species depends on selecting appropriately sized animals for comparison. Do we compare animals of the same length or of the same body weight? Regardless of which we select, the result of the comparison will depend very largely on whether we choose to compare large animals or small ones. Analysis of covariance, as used by Taplin (1984a) and Taplin, Grigg & Beard (1985) for intraspecific comparisons, is inapplicable because of the significantly different slopes of the ln TBW/ln SVL and ln ExNa/ln SVL equations (see above).

Obviously there is a need for caution in attributing interspecific differences in body fluid partitioning, such as Thorson (1968) described, to factors other than differences in body form or construction. Dunson & Heatwole (1986) have addressed this problem recently in turtles, in which the proportion of shell to soft tissue can vary enormously with size. Their data indicate that total body Na expressed as a function of dry mass is relatively constant across a range of body size and that the ratio of exchangeable to total Na varies inversely with body size in at least two species. That ExNa scales allometrically with dry mass in C. porosus and C. johnstoni can be shown simply from allometric equations for BW, TBW and ExNa as a function of snout–vent length (Taplin, 1984a). The scaling of all three variables is well described by a simple allometric relationship, $Y = aL^b$, where Y is expressed in μmol or g, L is snout–vent length, and a and b are constants. If we let

$$\mathrm{ExNa}\ (\mu\mathrm{mol}) = a_1\,L^{b_1},$$
$$\mathrm{TBW}\ (\mathrm{g})\quad = a_2\,L^{b_2},$$
$$\mathrm{BW}\ (\mathrm{g})\quad = a_3\,L^{b_3},$$

Dry weight (d. wt) of the body is then given by the difference between BW and TBW:

$$d. \ wt \ (g) = a_3 L^{b_3} - a_2 L^{b_2},$$

and weight-specific ExNa by

$$ExNa \ (\mu mol/g \ d. \ wt) = \frac{a_1 L^{b_1}}{(a_3 L^{b_3} - a_2 L^{b_2})}.$$

Clearly, the only condition under which d. wt-specific ExNa is independent of body size is when $b_1 = b_2 = b_3$, giving $ExNa = a_1/(a_3 - a_2) = $ constant. As b_1, b_2, and b_3 are known to be significantly different from one another in both *C. porosus* and *C. johnstoni*, d. wt-specific ExNa must scale allometrically with body size. That the influence of body size is significant is demonstrated by empirical values for *C. porosus* and *C. johnstoni* of 150 and 700 mm snout-vent length calculated from known relationships (Taplin, 1984 a). The values for *C. porosus* are 0·33 and 0·21 $\mu mol/g$ d. wt respectively in animals of 154 and 8060 g BW respectively. Comparable values for *C. johnstoni* are 0·33 and 0·16 $\mu mol/g.d.$ wt at body weights of 147 and 5800 g respectively. Thus a comparison of hatchlings would suggest similar exchangeable Na pools while a comparison of subadults would reveal a 52 % difference in ExNa. The result is much the same if the comparison is made between animals of similar body weight (8060 g) rather than similar SVL. ExNa is 0·21 $\mu mol/g$ d. wt in *C. porosus* and 0·14 $\mu mol/g$ d. wt in *C. johnstoni*. It would be valuable to extend Dunson and Heatwoles' analyses to consideration of the scaling of total body Na and various other body fluid compartments in crocodilians, where a large size range of animals is readily available. This might be possible if carcasses of commercially harvested species are available for analysis.

4. THE MECHANISMS OF OSMOREGULATION

4.1. *Accumulation of osmolytes*

In none of the crocodilians which have been studied is there any indication that the composition of the extracellular fluid is actively altered by accumulating osmolytes so as to lower the gradients favouring water loss or Na gain across the skin. The accumulation of osmotically active Na, Cl, urea or trimethylamineoxide in the plasma is seen in myxinid hagfish (Robertson, 1963), elasmobranchs (Pang *et al.*, 1977), the coelacanth (Griffith *et al.*, 1974), and the estuarine terrapin, *Malaclemys terrapin* (Gilles-Baillien, 1970; Cowan, 1985). In the case of *Malaclemys*, retention of Na, Cl and urea in the plasma can increase plasma osmolality by 40–50 % and has the potential to reduce osmotic water loss by about 22 % if the osmotic permeability of the integument (P_{osm}) remains constant. In contrast, plasma osmolarity, Na and Cl are more or less invariant in *C. porosus* across all salinities encountered (Table 2) and plasma urea occurs at only trace levels (1–2 mmol/l), contributing little to total plasma osmolality. The absence of urea retention in crocodilians may reflect a lack of urea cycle enzymes (Khalil & Haggag, 1960). However, Grigg (1981) found significant levels of urea in the cloacal urine of *C. porosus* from SAL 4 habitats suggesting that this species at least may have a functional ureogenic system. The seemingly unlikely possibility of urea formation through bacterial degradation of urates in the cloaca could be tested by analyses of ureteral urine.

While there is no evidence to suggest that crocodilians actively accumulate osmolytes to reduce osmotic and ionic gradients across the skin, many species are tolerant of considerable shifts in plasma composition in response to experimental manipulations (Bentley & Schmidt-Nielsen, 1965; Evans & Ellis, 1977; Taplin, 1982, 1985, unpubl. obs.; Lauren, 1985; Taplin & Loveridge, submitted). There is nothing to suggest that these changes in plasma composition are adaptive or play any part in minimizing diffusive exchanges of sodium and water. On the contrary, they appear to be pathological consequences of an inability to osmoregulate under the experimental conditions imposed and lead inevitably to death if the conditions are not changed.

4.2. *Diffusional permeability to salts and water*

Crocodilians, like other aquatic reptiles, have an integument which is impermeable to water in comparison with fish and amphibians (Bentley & Schmidt-Nielsen, 1965; Schmidt-Nielsen, 1969; Dunson, 1979). Hence they experience far lower gross rates of water turnover than fish. This is well illustrated by the observation that *C. porosus* in fresh water has an effective half-life for water turnover of 6·6 days, corresponding to the exchange of 0·4 % of its total body water per hour (Taplin, 1982). Fresh-water fish typically exchange from 6–186 % of their TBW per hour (Evans, 1979). In both cases the vast majority of the exchange is integumental (Taplin, 1982; Kirschner, 1979). While integumental permeability to water may be low in crocodilians, it is still an order of magnitude or more higher than in typical terrestrial reptiles (Bentley & Schmidt-Nielsen, 1966; Schmidt-Nielsen, 1969), suggesting that there may be selective advantages for estuarine/marine crocodilians in reducing permeability and minimizing water losses across the skin. In fact it will be seen later that integumental water loss and Na uptake constitute major osmoregulatory problems for *C. porosus* in sea water. Changes in permeability might be effected by changes in the structure of the skin itself, alteration of peripheral blood flow or a reduction in the surface area exposed. It is convenient to consider separately the rather scant data on evaporative water losses in air, integumental water exchange in water, and integumental Na exchange in water.

(a) *Evaporative water losses*

Measurements of diffusional water losses from crocodilians in air are few (Table 3). Differences of methodology and experimental conditions make interspecific comparisons difficult and very few data sets allow the cutaneous component of water loss to be separated from respiratory and excretory losses. Nevertheless, in addition to the predictable influences of body size, temperature and humidity on evaporative losses, there is a strong indication that the alligatorids, *Alligator* and *Caiman*, suffer water losses about an order of magnitude higher than crocodylines of similar size. Cutaneous water loss accounts for 87 % of the total loss in *Ca. crocodilus* (Bentley & Schmidt-Nielson, 1966) and from 10–75 % of the total in *C. niloticus* (Cloudsley-Thompson, 1969). The data available are suggestive of adaptive changes in integumental water permeability on an evolutionary time scale but provide no information about short-term responses to changes in hydration status.

(b) Integumental water exchange in fresh and salt water

Very few determinations have been made of either diffusional or osmotic water exchange across the crocodilian integument in water. There is presently no evidence of short-term changes in the diffusional water permeability (P_d) of the crocodilian integument in shifting from fresh to salt water, but data are available only for *C. porosus*. Taplin (1982, 1985) measured gross tritiated water effluxes of unfed *C. porosus* as 368 μl/100 g.h in fresh water and 302 μl/100 g.h in sea water, of which 85 and 91 % respectively represented integumental exchange. Information on net osmotic flux across the integument is available for *Caiman crocodilus* in fresh water and 33 ‰ NaCl at 23 °C (Bentley & Schmidt-Nielsen, 1965) and for *C. porosus* in fresh water and sea water at 25 °C (Taplin, 1982, 1984b). P_{osm} in *Caiman* is 0·08 μl/100 cm².h.mOsm in 33 ‰ NaCl and 0·37 μl/100 cm².h.mOsm in fresh water. Comparable values for *C. porosus* are 0·014 and 0·017 respectively. Two points are of interest here. Firstly, the data point to a marked shift of P_{osm} in *Caiman* but not in *C. porosus*. Secondly, the alligatorid has an integumental permeability about an order of magnitude greater than the crocodyline, paralleling the situation for evaporative water loss (Table 3). Once again, methodological differences might account for some of the difference in measured fluxes. However, the similar patterns for P_d in air and P_{osm} in water are worthy of further investigation.

(c) Integumental Na exchange in fresh and salt water

The skin of most aquatic reptiles has a very low overall permeability to Na. Measurements of Na flux across crocodilian skin are few (Table 4) and allow few conclusions. The post-cephalic integument of *C. porosus* is only slightly permeable in vivo. However, the cephalic integument is far more permeable and accounts for a substantial fraction of the total Na exchange in sea water for this species (Taplin, 1985). Ellis & Evans (1984) similarly found that the cephalic integument was substantially more permeable to sodium than the post-cephalic region in *Alligator mississippiensis* (Table 4). The ten-fold difference in integumental flux from *C. porosus* in fresh water relative to that in sea water (1·7 vs. 11·9 μmol/100 cm².h) is suggestive of a change in P_{Na} given that the Na concentration gradient is only two-fold smaller. However, the data are not adequate to draw firm conclusions and the adaptive value of a higher P_{Na} in sea water must be questioned, given that 50 % of the net water loss from unfed *C. porosus* in sea water is attributable to the excretion of excess Na taken up across the integument (Taplin, 1985). In vivo data for *C. acutus* (Table 4) have been questioned because of doubts about the validity of comparing Na fluxes in restrained and unrestrained crocodiles to determine integumental components of exchange (Dunson, 1979). Dunson has recommended in vitro measurements on isolated skin or keratin flakes to determine whether the skin is entirely impermeable or has a small but finite permeability. Isolated flakes of keratin from *C. acutus* proved effectively impermeable to Na (Dunson, 1982). However, it is arguable whether extrapolation from isolated pieces of shed keratin to the entire integument in vivo is more precise or reliable than carefully controlled assessments of permeability by flux partitioning in the living animal. Furthermore, the Na permeabilities measured in vivo (Table 4) are of the same order as in vitro measurements from the estuarine snakes, *Cerberus rhynchops* (1·00

Table 3. *Rates of evaporative water loss (mg/kg.h) from crocodilians under various experimental conditions*

Relative humidity (%)...		0	0	0	0	0	5	25	27	46	75	96·5	References
Temperature (°C)...	Body weight (g)	20	23	25	30	35	25	23	38	38	30	30	
Species													
Crocodylus acutus	81–84	—	—	—	—	—	—	—	—	—	—	600	Dunson (1982)
	326	—	—	—	517	—	—	—	—	—	263	113	Dunson (1982)
	995	—	—	—	288	—	—	—	—	—	—	—	Dunson (1982)
	1544	—	—	—	196	—	—	—	—	—	—	—	Dunson (1982)
Crocodylus niloticus	3200–4700	65	—	79	104	130	—	—	—	—	—	—	Brown & Loveridge (1981)
	71–97	—	—	—	—	—	1842	—	—	—	—	—	Cloudsley-Thompson (1960)
Alligator mississippiensis	668	—	—	—	—	—	—	8333	—	5208	—	—	Bogert & Cowles (1947)
Caiman crocodilus	$\bar{X} = 60$	—	—	—	—	—	—	5542	—	—	—	—	Bentley & Schmidt-Nielsen (1965)
	124	3205	—	—	—	—	—	—	—	—	—	—	Bentley & Schmidt-Nielsen (1966)

Table 4. *Estimates of whole-body and integumental sodium effluxes from crocodilians*

Estimates are based on unidirectional effluxes of ^{22}Na except for *Caiman crocodilus* based on net Na loss in distilled water.

	Body weight (g)	Whole body (μmol/ 100 g.h)	Post-cephalic integument (μmol/ 100 cm^2.h)	Cephalic and post-cephalic integument (μmol/ 100 cm^2.h)	Reference
Fresh water					
Crocodylus porosus	330–680	2·4	—	1·7	Taplin (1982)
	136–204	3·0	—	—	Taplin (1985)
Crocodylus acutus	54–68	1·9	0·12	—	Evans & Ellis (1977)
Crocodylus johnstoni	46–51	2·4	—	—	Taplin (unpubl. obs.)
Alligator mississippiensis	0·03–0·07	3·9	0·7	1·1	Ellis & Evans (1984)
Distilled Water					
Caiman crocodilus	$\bar{X} = 70$	—	—	1·2	Bentley & Schmidt-Nielsen (1965)
9 ‰ Salt water					
Crocodylus acutus	54–68 (restrained)	16·5	1·6	—	Evans & Ellis (1977)
	54–68 (free-swimming)	5·6	—	—	Evans & Ellis (1977)
Sea water					
Crocodylus porosus	250	19·0	1·5	11·9*	Taplin (1985)
Crocodylus acutus	84–413	2·3	—	—	Dunson (1982)

* Based on the cephalic integument making up 25 % of the whole (Dunson, 1982). The area of the cephalic integument is in reality considerably greater when the buccal region is included but appropriate data are unavailable.

μmol/100 cm^2.h) and *Nerodia fasciata clarkii* (3·4 μmol/100 cm^2.h) (Dunson, 1978) and from several hydrophid sea snakes (1·3–12·9 μmol/100 cm^2.h – these measured against a larger concentration gradient from distilled water to 1 M-NaCl (Dunson & Stokes, 1983). The weight of evidence at present points to *C. porosus* and *C. acutus* having an integument of low but finite permeability to Na.

Only two measurements have been made of Na efflux in alligatorids. Bentley & Schmidt-Nielsen (1965) measured the net integumental Na efflux of *Caiman crocodilus* in distilled water. This should approximate the unidirectional efflux measured with ^{22}Na. Net efflux over the first few hours averaged 1·2 μmol/100 cm^2.h in *Caiman*, essentially the same as the 1·6 μmol/100 cm^2.h measured in *A. mississippiensis* by Ellis & Evans (1984). Both values are close to results for *C. porosus* in fresh water (Table 4). This result contrasts with the apparent differences in diffusional and osmotic water permeabilities of the alligatorid and crocodyline integuments and appears contrary to the very close relationship between P_d and P_{Na} observed in a variety of shed skins from hydrophid sea snakes (Stokes & Dunson, 1982). Little can be concluded but the need for more detailed comparative studies.

Table 5. *Literature records of burrowing (B), hibernation (H), and aestivation (A) in the Crocodylia*

Data from Neill (1971), Guggisberg (1972), Brazaitis (1973), Medem (1981 a, b) and other sources as indicated.

	B	H	A	References
Family Crocodylidae				
Subfamily Crocodylinae				
Crocodylus acutus	Y	—	Y	
C. cataphractus		Not recorded		
C. intermedius	Y	—	Y	Medem (1976)
C. jonstoni	Y	—	Probable	Taplin (unpubl. obs.)
C. moreletii	Y	—	Y	Alvarez del Toro (1975)
C. niloticus	Y	Y	Y	Pooley (1962)
C. n. novae-guineae		Not recorded		
C. n. mindorensis		Not recorded		
C. palustris	Y	—	Y	Whitaker & Whitaker (1978)
C. porosus	Y	—	Y	
C. siamensis		Not recorded		
Osteolaemus tetraspis	Y	—	—	Villiers (1958)
Subfamily Tomistominae				
Tomistoma schlegelii	Y	—	—	Groombridge (1982)
Family Alligatoridae				
Alligator mississippiensis	Y	Y	Y	
A. sinensis	Y	Y	—	Huang (1978)
Caiman crocodilus	Y	—	Y	
Ca. latirostris	Y	Y	—	
Melanosuchus niger	Y	—	Y	Plotkin et al. (1983)
Palaeosuchus palpebrosus	Y	—	N	
P. trigonatus	Y	—	N	
Family Gavialidae				
Gavialis gangeticus		Not recorded		

4.3. Behavioural osmoregulation

Crocodilians faced with osmotically adverse conditions have several behavioural options open to them which may reduce osmotic stress. When adverse conditions are localized, movement to more favourable areas may be feasible. If opportunity for movement is restricted then selection of more favourable microhabitats may be important, extending in some instances to active burrowing and aestivation. The distinction between local shifts to favourable microhabitats and longer movements to completely new environments is somewhat hazy. Nor is it clear that contractions in the range of local populations experiencing periods of drought should be considered primarily as osmoregulatory responses, though physiology obviously plays an important role. In this section I will limit the discussion to the localized responses of selecting favourable microhabitats and burrowing/aestivation. Two other behavioural strategies, selective drinking and selective feeding – both aimed at maximizing net uptake of osmotically-free water, are considered separately in sections 4·5 and 5·3 respectively.

Most crocodilians are known to burrow and several tropical and subtropical species are thought to aestivate (Table 5). The term 'aestivation' is poorly defined but is generally taken to mean dormancy or inactivity accompanied by some physiological

adjustment (Gregory, 1982). Very few physiological studies have been made of aestivating reptiles. Fresh water turtles, *Kinosternon flavescens*, burrow into soil when drought affects their waterholes and show some reduction in pulmonary gas exchange which may also reduce water loss (Seidel, 1978). Dehydration can be severe in these turtles, leading to a three-fold increase in plasma electrolyte concentrations, but is undoubtedly lower than would be experienced without burrowing. No comparable studies have been made of burrowing crocodilians so it is unclear whether they can truly be considered to aestivate. Some of the descriptions from the literature suggest that crocodiles might burrow into drying mud and become effectively encapsulated like dormant turtles (Guggisberg, 1972). It seems likely, however, that in the majority of cases the animals simply retreat to relatively cool, moist caverns or burrows, open to the air, and thereby minimize evaporative water losses while waiting for more favourable conditions.

Behavioural avoidance of highly saline water by hatchling *C. acutus* in Florida Bay has been rather better documented (Dunson, 1982; Mazotti & Dunson, 1984; Mazotti *et al.*, 1986). Hatchling *C. acutus* on exposed shore lines seek out microhabitats during the day which offer protection from wave action, direct sun and high temperatures and also from Na uptake in highly saline water. Furthermore, rainfall is frequent in the post-hatching period so small *C. acutus*, at their most vulnerable size in relation to osmoregulation, should be able to locate more favourable fresh or brackish water habitats. These types of behavioural avoidance are considered to play an important role in the survival of small *C. acutus* in highly saline habitats. Similar studies in northern Australia provide no evidence for a similar strategy in *C. porosus* (Grigg *et al.*, 1980; Grigg, 1981; Taplin, 1984 a, 1985). In contrast to Florida, many coastal rivers of northern Australia receive virtually no rainfall during the winter post-hatching period. *C. porosus* hatchlings of 140 g BW and upwards are able to osmoregulate in salinities from fresh water to over 60 ‰ salt without access to fresh drinking water (Grigg *et al.*, 1980; Taplin, 1984 a). No evidence has been found to suggest that *C. porosus* has major difficulties in osmoregulating in high salinities or seeks to avoid exposure to them. However, the physiology of freshly hatched (neonatal) *C. porosus* has not been investigated. In the majority of cases, neonates emerge into fresh or brackish waters during the late wet season and are unlikely to experience very high salinities. However, nests are occasionally constructed alongside hypersaline creeks and hatch sufficiently late in the dry season for neonates to experience SAL 4 or SAL 5 conditions. Investigation of these 'natural experiments' or of nests translocated into such environments would provide invaluable data on the physiological abilities of neonates.

While both burrowing and avoidance of hyperosmotic salt water may remove animals temporarily from osmotically adverse conditions, in neither case is it clear that the behaviour is *primarily* a response to osmotic stress. Reduced activity during droughts may reduce risks of overheating (Voight & Johnson, 1976) or minimize energy expenditure during times of low food availability. Burrows and retreats are not used only during droughts. *C. johnstoni* is found commonly in burrows, even in areas of permanent, spring-fed streams (C.J. Limpus, pers. comm.). Low water levels and resultant high population densities may lead to increased agonistic interactions. Retreat into burrows may be necessary for survival of subordinate individuals. Selection of sheltered microhabitats by young *C. acutus* (Dunson, 1982) may likewise be primarily a response to factors other than osmotic stress.

4.4 *The urinary system*

The extensive literature on the urinary physiology of reptiles in general has been reviewed many times from various perspectives (LeBrie, 1972; Dantzler & Holmes, 1974; Bentley, 1976; Dantzler, 1976; Skadhauge, 1977, 1978; Minnich, 1979, 1982; Dantzler, 1980; Shoemaker & Nagy, 1977). This review will confine itself to those aspects of crocodilian urinary function particularly relevant to the problems of osmoregulation in different habitats.

(a) *The urinary system in fresh water, SAL 1*

Crocodilians, as hyperosmotic osmoregulators in fresh water, face the dual problems of excreting excess water and nitrogenous wastes while minimizing losses of essential solutes, particularly Na. Urinary excretion is regulated by the secretory and absorptive activities of the kidney and cloaca, acting in concert. That the crocodilians are capable of minimizing urinary electrolyte losses in fresh water is apparent from the low concentrations of Na, K and Cl in the cloacal fluid of unfed animals (Table 6) relative to their plasma levels (Table 2). It is notable that these three electrolytes typically contribute only a fraction of the overall osmotic pressure of the excreted urine, much of the balance consisting of NH_4 and HCO_3 in solution (Coulson & Hernandez, 1964, 1970, 1983; Schmidt-Nielsen & Skadhauge, 1967; Grigg, 1981). Gross Na losses in cloacal urine are correspondingly low. Rates of spontaneous urination in SAL 1 have been determined for four species and are similar in magnitude. Unfed *C. porosus* in fresh water void some 50 μl/100 g.h of cloacal urine with a Na content of 0.24 μmol (Taplin, 1982). *C. johnstoni* loses 68 μmol/100 g.h containing 0.22 μmol Na (Taplin, unpubl. obs.), while fasted *A. mississippiensis* average 71 μl/100 g.h containing 0.25 μmol Na (Coulson & Hernandez, 1964). A higher value for *A. mississippiensis* of 156 μl/100 g.h was determined by Ellis & Evans (1984). This high value may be attributable in part to the cloacal cannulation used in the experiment. Bentley & Schmidt-Nielsen (1965) found extremely high urination rates of 350 μl/100 g.h in cannulated *Caiman crocodilus*. No data on rates of spontaneous urination are available for this species.

The cloaca appears to play a major part in determining the composition of voided urine. The kidney itself appears to have only a limited ability to regulate the composition of ureteral urine. In the few Crocodylinae studied to date, neither glomerular filtration rate (GFR) nor urinary osmolal U/P ratios are affected greatly by salt loading or dehydration (Schmidt-Nielsen and Skadhauge 1967; Schmidt-Nielsen & Davis, 1968). Furthermore, the electrolyte composition of the ureteral urine of *C. acutus* varies remarkably little under water loads, NaCl loads or dehydration, and always includes high concentrations of Na (Schmidt-Nielsen & Skadhauge, 1967). In contrast, both GFR and water reabsorption from the distal tubule are highly responsive to salt and water balance status in other fresh water reptiles such as the turtle, *Pseudemys scripta*, and the snake, *Nerodia sipedon*, (Dantzler, 1976, 1980). No determinations of ureteral urine composition have been recorded from any alligatorid.

The role of the cloaca in modifying ureteral urine through reabsorption of Na, Cl and water was demonstrated clearly by Bentley & Schmidt-Nielsen (1965) and Schmidt-Nielsen & Skadhauge (1967). The low concentration of Na characteristic of excreted urine in *C. acutus* and *Ca. crocodilus* is brought about by reabsorption of Na from the ureteral urine during its storage in the cloaca (Schmidt-Nielsen & Skadhauge, 1967).

Table 6. *Cloacal fluid composition of wild-caught and captive crocodilians under various salinity regimes and experimental conditions*

	Conditions	Salinity category	Osmolality (mOsm/kg)	Osmolal U/P	[Na] (mmol/l)	[K] (mmol/l)	[Cl] (mmol/l)	[NH₄] (mmol/l)	References
Crocodylus acutus	Unfed, lab, water load	1	251	0·86	59	27	17	118	Schmidt-Nielsen & Skadhauge (1967)
	Unfed, lab, water load	1	184	0·66	—	—	10	59	
	Unfed, lab, NaCl load	1	310	0·91	38	35	77	74	
	Unfed, lab, dehydrated	1	217	0·70	21	40	36	54	
	Wild, 20–43 ‰	4	279	0·84	17	15	77	—	Dunson (1982)
	Fed ?, lab, FW	1	—	—	17	29	—	—	Ellis (1981 a)
	Fed, lab, SW	4	—	—	5	45	—	—	
	Unfed, lab, 37 ‰ — 62 days	4	—	—	4	—	—	—	
C. porosus	Wild	1	252	0·82	79	22	—	98	Grigg (1981)
	Wild	2	256	0·84	—	27	9·1	83	
	Wild	3	257	0·86	—	33	97	86	
	Wild	4	277	0·92	98	88	6·9	41	
	Wild	4	196	0·65	39	56	48	—	Taplin (1982, 1985)
	Unfed, lab, SW - 10 days	4	386	0·93	50	22	17	—	Taplin (unpubl. obs.)
	Fed ?, lab, FW	1	—	—	40	68	—	—	
	Fed ?, lab, SW	4	—	—	2	28	—	—	
C. johnstoni	Wild	1	191	0·65	44	52	9·6	—	Dunson (1982)
	Wild	1	175	0·60	46	64	37	—	Grigg et al. (unpubl. obs.)
C. niloticus	Unfed, lab, FW	1	147	0·53	0·9	42	<5	—	Taplin & Loveridge (1988)
	Unfed, lab, SW - 5·5 days	4	209	0·78	10	67	29	—	
C. palustris	Fed, farm, FW	1	—	—	5·8	1·1	—	—	Taplin (unpubl. obs.)
	Unfed, lab, FW	1	203	0·72	35	76	2·9	—	Coulson & Hernandez (1964)
Alligator mississippiensis	Fed, lab, FW, pre-experimental	1	245	0·85	16	15	7·8	—	Lauren (1985)
	Fed, lab, FW - 4 weeks	1	251	0·99	50	20	8·8	—	
	Unfed, lab, FW	1	180	0·60	3·8	4·4	<1	96	Ellis & Evans (1984)
	Fed, lab, 5 ‰ - 4 weeks	2	247	0·97	79	4·8	16·9	—	Lauren (1985)
	Fed, lab, 20 ‰ - 4 weeks	4	387	0·94	150	54	26	—	
Gavialis gangeticus	Fed, farm, FW	1	—	—	11	12	—	—	Taplin (unpubl. obs.)

For these reabsorptive processes to be adaptive for fresh water animals, the uptake should presumably be hyperosmotic, suggesting that some hormonally-mediated limitation of cloacal water permeability is likely (see below). Cloacal Na reabsorption may not occur in the alligator, though no comparative analyses of ureteral and cloacal urine are available. Coulson & Hernandez (1964, 1970) noted that the cloacal urine of alligators contains only a fraction of the Na filtered through the glomeruli. Some Na reabsorption in the distal tubule is linked to secretion of NH_3 into the tubular fluid, but the vast majority of the reabsorption takes place independently of this NH_4/Na exchange (Coulson & Hernandez, 1959). They concluded that much of the additional reabsorption was taking place in the proximal tubules, as the Na concentration of cloacal urine varied little with its time of storage in the cloaca (Coulson & Hernandez, 1983). This apparent contrast between *Alligator* and *Crocodylus* may be related to differences in their capacity for extrarenal salt excretion (Section 4·7).

While the cloaca of crocodilians is capable of Na resorption against a substantial osmotic gradient, there is no evidence of active uptake of Na from fresh water by irrigation of the cloaca as reported for the fresh water turtle, *Pseudemys scripta* (Dunson, 1967). No tests of this mode of uptake in crocodilians have been reported.

(b) The urinary system in saline water, SAL 4

The only information available on urinary excretion from crocodilians in hyperosmotic salt water derives from analyses of cloacal urine (Table 6). Urine osmotic pressures and U/P ratios in wild-caught, presumably feeding, Crocodylidae are only marginally higher than in fresh-water animals but K and Cl tend to make up a greater proportion of the osmolytes. Significantly, Na is rarely over 10–20 mmol/l in SAL 4 crocodiles. In keeping with the higher contributions of K and Cl, urine NH_4 and HCO_3 in *C. porosus* fall to 50 % or less of their SAL 1 levels (Grigg, 1981).

The urine of *C. porosus* from SAL 4 habitats is not a significant route for Na excretion (Taplin, 1985). Even in unfed crocodiles, dehydrated in sea water, urine Na remains remarkably low in the face of near lethal rises in plasma Na and a trebling of mean K concentration in cloacal urine (Table 6) (Taplin, unpubl. obs.). Ellis (1981 a) similarly found no change in cloacal fluid Na levels in a *C. acutus* held unfed in sea water for 2 months. However, this animal was sufficiently large that dehydration over that time was minimal. *C. niloticus*, another crocodilian found commonly in highly saline water (SAL 4 and 5), shows a similar response to *C. porosus* on acute exposure to SW (Taplin & Loveridge, 1988). Cloacal fluid Na levels increased only slightly compared with the very large increase in K. No data are available on characteristic rates of urination from crocodilians in SAL 4 habitats. Unfed *C. porosus* in sea water become virtually anuric when unfed (Taplin, 1985). No estimates of urinary electrolyte or water losses in actively feeding crocodiles are available.

The urine solids of crocodylines play a significant role in excretion of divalent cations and K but carry little Na. Grigg (1981) found virtually no Na in cloacal fluid solids of *C. porosus* from any salinity category (SAL 1–SAL 4). Detectable but low concentrations (7–43 μmol/g d. wt) were found in solids from *C. porosus* and *C. acutus* in SAL 4 (Dunson, 1982; Taplin, 1985). Even in freshly captured *C. porosus* from SAL 4 with very low Na in the liquid fraction of cloacal fluid, urates account for only 18 % of the total Na content and 30 % of the total K content of cloacal urine (Taplin,

1985). In these animals urinary K concentrations are an order of magnitude higher than Na in both liquid and solid fractions.

The only data on alligatorids in hyperosmotic salt water come from fed animals held in various salinities in the laboratory (Lauren, 1985). After 4 weeks in 20 ‰ salt water, the cloacal fluid of *Alligator* had very high osmolality and K and remarkably high Na relative to fresh water controls (Table 6). Na U/P levels in these alligators reached 0·82, compared with 0·11–0·39 in fresh-water controls (Lauren, 1985) and maximum levels of about 0·1 in *C. porosus* from any salinity (Taplin, unpubl. obs.). This marked difference between *Alligator* and the various Crocodylidae may relate to differences in their extra-renal salt excreting ability (Section 4·7).

No direct information is available on cloacal function in crocodilians from salt water. The low cloacal fluid Na levels in Crocodylidae from SAL 4 are very suggestive of cloacal Na reabsorption, given the high levels of Na in ureteral urine of normally hydrated, salt loaded or dehydrated *C. acutus* (Schmidt-Nielsen & Skadhauge, 1967). Grigg (1981) remarked on the change in appearance of cloacal urine from a clear fluid in SAL 1 to a more mucous, solids-rich fluid in SAL 4. In some instances cloacal urine •in SAL 4 is voided as a moist loosely compacted solid with virtually no free liquid. Taplin (1985) noted a similar phenomenon in relation to faecal matter of *C. porosus* from SAL 4. Faeces collected from crocodiles held overnight in sea water contained 25 % less water than those from freshly captured animals and were transformed from a liquid paste to hard pellets. Resorption of water may well follow active uptake of Na in the cloaca or rectum. There is some radiographic evidence to suggest refluxing of urine from the cloaca into the rectum in *C. porosus* (Grigg, unpubl. obs.).

(c) The urinary system in brackish water, SAL 2 and 3

The only data on urine composition and renal/cloacal function of crocodilians in brackish water are those of Grigg (1981) based on cloacal urine samples from wild *C. porosus* and of Lauren (1985) on captive *A. mississippiensis* (Table 6). Electrolyte concentrations in *C. porosus* from SAL 2 and 3 are comparable to those in SAL 1 and 4. Urine K is similar in SAL 1, 2 and 3 but increases significantly in SAL 4 in both solid and liquid fractions (Grigg, 1981 and Table 6). A complementary pattern is seen in urinary nitrogen and bicarbonate excretion with a marked shift from ammonotely to uricotely between SAL 3 and SAL 4 (Grigg, 1981). The data suggest a distinct shift in osmoregulatory strategy when *C. porosus* has no access to hypo-osmotic salt water for at least part of the tidal cycle. This shift may be related to the drinking behaviour of crocodilians (Section 4.5).

The data for *Alligator* are less extensive but show interesting parallels and contrasts with the data for *C. porosus* (Table 6). The most significant shifts in urine composition of feeding alligators exposed to fresh water, 5, 10, 15 and 20 ‰ salt water occur between 5 and 10 ‰. Urinary K, Cl and uric acid all increase substantially between these salinities (Lauren, 1985). Urine Na on the other hand shows its greatest increase between fresh water and 5 ‰ but rises to much higher levels at all salinities than have been reported for any of the Crocodylidae.

4.5. *Drinking*

(a) *Drinking in fresh water, SAL 1*

The question of whether fresh water crocodilians replenish evaporative and excretory water losses by drinking or absorption of water through the skin has been open to dispute until recently. Cott (1961) suggested that basking Nile Crocodiles might absorb water through the integument of their tails. Bentley & Schmidt-Nielsen (1965) concluded that *Caiman crocodilus* absorbs 70 % of its net water uptake in fresh water through its skin. However, Diefenbach (1973) questioned the validity of their phenol-red technique used to determine rates of drinking. Cloudsley-Thompson (1968, 1969) and Diefenbach (1973) concluded that integumental water uptake was negligible in *C. niloticus*. However, neither of these studies incorporated adequate controls over respiratory water loss and so were open to question.

Taplin (1982, 1984 b) established that *C. porosus* does drink substantial amounts of fresh water (in the order of 12 ml/kg . day when free-swimming and 5 ml/kg.day when restrained) and absorbs only a relatively small amount through its post-cephalic integument. The only other crocodilians in which drinking of fresh water has been demonstrated to date are *C. johnstoni* (Taplin, Grigg & Beard, unpubl. obs.) and *C. acutus* (Mazotti & Dunson, 1984). It seems likely that all of the crocodilians drink more or less copious amounts of fresh water. Nevertheless, other crocodilians may yet be found to absorb significant amounts of water through their skin. Drinking rates in the fresh water turtles, *Trionyx spiniferus* and *Chrysemys picta*, differ by an order of magnitude, reflecting markedly different integumentary water permeabilities (Bentley & Schmidt-Nielsen, 1970; Taplin, 1984 b). It is quite possible that the integument of *Caiman crocodilus* has a higher osmotic water permeability than *C. porosus* or *C. niloticus*, thus accounting for a smaller contribution of drinking to net water influx. Data on evaporative water loss from crocodilians support this possibility (Section 4.2).

(b) *Drinking in saline water, SAL 4*

C. porosus will not drink sea water even when dehydrated to a stage where death is imminent (Taplin, 1984 b, 1985). It is believed dependent for osmoregulation in SAL 4 or 5 habitats on access to adequate food supplies or, in the absence of food, on periodic access to fresh or brackish drinking water. *C. porosus* is regarded as a facultative drinker of hypo-osmotic water, even at small sizes when it is most vulnerable to water loss (Grigg *et al.*, 1980; Taplin, 1984 a, 1985). The numerous observations of *C. porosus* drinking fresh water from pools or hoses in farms and zoos (Taplin, 1984 b, pers. obs.) are not inconsistent with this view. The field data point unequivocally to the ability of hatchlings to survive and grow in sea water without access to drinking water. *C. porosus* is thought to drink hypo-osmotic salt water but no direct tests have been performed. Grigg (1981) argued from changes in urinary nitrogen excretion that *C. porosus* in SAL 3 drinks brackish water on low tides. This hypothesis has received some confirmation from work of Mazotti & Dunson (1984) on *C. acutus* in simulated SAL 3 conditions. *C. acutus* does not drink sea water but, after dehydrating to 85–90 % of initial BW, will readily drink fresh water and hypoosmotic salt water. None of the animals tested drank at 35 or 27 ‰ and only a few drank at salinities of 12–18 ‰. The alligatorid *Ca. crocodilus* appears unable to discriminate salt from fresh water and suffers severe hypernatraemia after drinking salt water (Bentley & Schmidt-Nielsen, 1965).
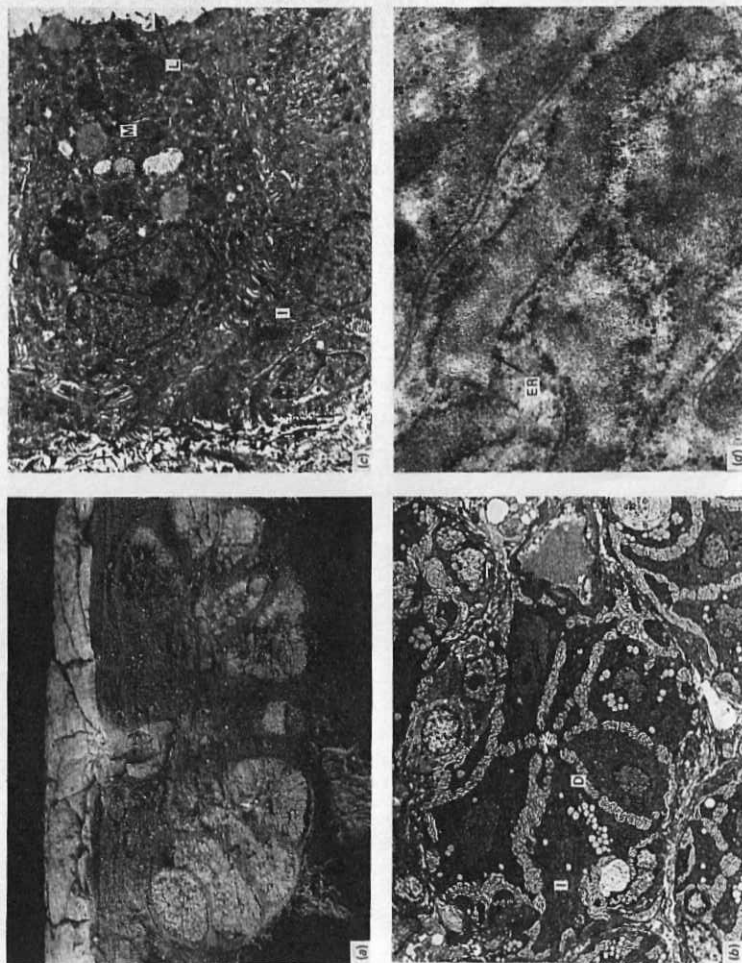
glands (Owen, 1866; Ferdinand, 1884; Rose, 1893; Reese, 1915, 1925; Taguchi, 1920). Their ultrastructure in *C. porosus* shows clearly their similarity to the salt glands of other reptiles, with the characteristically complex interdigitations of lateral cell membranes, expanded intercellular spaces, abundant mitochondria, and extensive network of blood vessels and unmyelinated nerve fibres (Fig. 2b).

Salt glands have now been found in all of the Crocodylinae examined to date; 7 of the 12 living species in all, including the unusual dwarf crocodile, *Osteolaemus tetraspis* (Taplin, Grigg & Beard, 1985). In all of these species, the glands were found capable of secreting hyperosmotic NaCl, often at high rates, despite the fact that many of the individuals tested had never been exposed to salt water (Table 7). In contrast, the two Alligatoridae examined to date appear to lack the complex, highly lobulated glands of high secretory capacity. Their glands are smaller and more numerous than those of the Crocodylinae and contain relatively small numbers of loosely aggregated secretory tubules with much wider lumina than those of *C. porosus* (Reese, 1915, 1925; Taguchi, 1920; Taplin *et al.* 1982; Taplin, 1982, unpubl. obs.). The glands appear incapable of the high rates of hyperosmotic salt secretion seen among the Crocodylinae (Table 7 and Taplin *et al.*, 1982). Electron micrographs of principal secretory cells in *Alligator* reveal marked differences from those of *C. porosus*, including a preponderance of rough endoplasmic reticulum, Golgi bodies swollen with secretory products, abundant electron-dense and more translucent secretory droplets and a smaller number of mitochondria than in *C. porosus* (Fig. 2c, d) (Taplin, 1982). Among the other crocodilians, the gharial, *Gavialis*, has only a few, very small and relatively simple glands along the anterior margin of the tongue (Taplin, 1982, unpubl. obs.). These appear to have minimal secretory capacity (Table 7) and are unlikely to play any significant role in salt excretion. The South American alligatorid, *Paleosuchus trigonatus* reportedly lacks prominent lingual glands (G. C. Grigg and W. E. Magnusson, pers. comm.) and is probably similar to *Alligator* and *Ca. crocodilus*. *Tomistoma*, on the other hand, has prominent lingual glands with large excretory pores similar to those in *Crocodylus* species (Taplin, unpubl. obs.). No opportunity has arisen to assess the secretory characteristics of *Tomistoma*, so they may not be salt glands.

The number of lingual glands is very variable, both within and between species (Table 8). *Alligator* has many small glands while the Crocodylinae tend to have smaller numbers of very prominent glands. There is no obvious basis for the apparent division of the genus *Crocodylus* into species such as *C. porosus* and *C. johnstoni* with small numbers of glands and those such as *C. palustris* and *C. cataphractus* with considerably

Fig. 2. Lingual glands of crocodilians. (a) Vertical section through a single lingual gland of *C. porosus* showing the compound, lobulated structure and the large excretory pore opening to the surface of the tongue (× 30). (b) Electron micrograph of a principal secretory tubule from a lingual gland of *C. porosus*. The minute central duct (D) is lined with microvilli. Grossly expanded intercellular spaces, extensively interdigitated lateral cell membranes and abundant mitochondria are features common to all reptilian salt glands. (c, d) Principal tubular cells from lingual glands of *Alligator mississipiensis* from fresh water. The cells are more rectangular than those of *C. porosus* and border a much wider tubular lumen (L). The cells have luminal microvilli and strongly interdigitated lateral membranes but the intercellular spaces are not dilated. Mucous secretory droplets fill the cytoplasm which is packed with rough endoplasmic reticulum (ER) enclosing secretory products. (Scale bar 2 μm). Fig. 1a reproduced with permission from Taplin & Grigg (1981).

Table 7. *Lingual gland secretory characteristics of various crocodilians representing three major families of the suborder Eusuchia*

Note that all of these animals were either freshly captured from fresh water, raised in fresh water in zoos or farms, or had been held for some months in fresh water after capture. Values expressed as mean ±s.e. N is the number of animals sampled. From Taplin et al. (1982). Reproduced with permission of Surrey Beatty and Sons.

	Body weight (kg)	Max. Na secretion rate (μmol/100 g$^{0.7}$.h)	Max. [Na] (mmol/l)	Mean [Na] (mmol/l)	Max. [K] (mmol/l)	Mean [K] (mmol/l)	N	History
Crocodylus porosus	12.7±6.6 (3.6–32)	449±188	510±100	477±113	155±1.8	140±1.8	4	Recent capture from fresh water
C. johnstoni	6±1.10 (3.6–8.1)	64±5.6	386±21	365±13	103±0.8	91±0.8	4	Recent capture from fresh water
C. acutus	5±0.8 (3.6–6.2)	471±179	499±61	454±90	124±14	117±16	4	Held some months in fresh water
C. palustris	4.8±1.2 (2.3–7.1)	396±83	740±65	518±28	157±13	109±14	4	Raised in fresh water
C. cataphractus	45	282	637	398	137	8.5	1	Held several years in fresh water
C. niloticus	0.2±0.1 (0.12–0.22)	357±22	—	—	—	—	2	Raised in fresh water
Osteolaemus tetraspis	130	41.6	545	463	150	124	1	Held several years in fresh water
Alligator mississippiensis	3.6±0.2 (3.0–4.0)	3.0±1.5	186*	183*	—	—	4	Recently captured or held some months in fresh water
Caiman crocodilus		No collectable secretions					3	Held some months in fresh water
Gavialis gangeticus	64±13	1.0±0.5	—	—	—	—	3	Raised in fresh water

* Samples from one animal only.

Table 8. *Numbers of lingual gland pores opening to the surface of the tongue in various crocodilians*

N = number of animals examined. Taken from Taplin et al. (1982). Reproduced with permission of Surrey Beatty and Sons.

	N	$\bar{X}$ ±s.e.	Range
Family Crocodylidae			
Subfamily Crocodylinae			
Crocodylus porosus (Australia)	12	29±1	22–35
C. porosus (Thailand)	4	27±1	26–28
C. johnstoni	4	23±1	20–26
C. niloticus	12	45±3	30–64
C. siamensis	8	62±6	34–83
C. palustris	11	58±3	47–78
C. cataphractus	1	93	—
C. acutus		No hard data but similar to C. porosus	
C. moreletii*	9	33±0.4	32–34
Osteolaemus tetraspis	1	13	—
Subfamily Tomistominae			
Tomistoma schlegelii	1	39	—
Family Alligatoridae			
Alligator mississippiensis	4	Some hundreds	
Family Gavialidae			
Gavialis gangeticus	8	26±2	22–36

* M. Lazcano-Barrero, pers. comm.

more. Gland number appears not to correlate either intra- or inter-specifically with the secretory capacity of the lingual glands. Nor is there evidence of ontogenetic changes in the number of lingual glands (Taplin, 1982, unpubl. obs.). The inverse weight-dependence of secretory capacity in *C. porosus* (Taplin, 1985) probably reflects allometric changes in the overall glandular mass relative to body size.

Only in *C. porosus* has the role of the lingual glands in osmoregulation been quantified. The glands play a major role in maintenance of sodium balance in sea water, accounting for over 90 % of the Na excreted by unfed animals (Taplin, 1985), and having the capacity to excrete the entire Na load encountered by actively feeding crocodiles in the wild (Grigg et al., 1986). The secretions consist almost entirely of Na, K and Cl at concentrations 3·5–5·5 times their plasma levels (Taplin & Grigg, 1981). Both the concentration and the rate of secretion are a function of body size (Taplin, 1985). Weight specific secretory rates are highest in hatchlings in which Na influxes from feeding and integumental uptake can be expected to be highest. This allometry is an important consideration in intra- or inter-specific comparisons of salt gland function; secretory rate, expressed in the commonly used units of μmol/100 g.h, is four times higher in a 100 g hatchling than in a 10 kg juvenile.

The osmoregulatory significance of the salt glands in the only other predominantly salt water crocodilian, *C. acutus*, is not so clear. Secretory rates and concentrations in animals acclimated to fresh water are almost identical to those in *C. porosus* (Table 7).
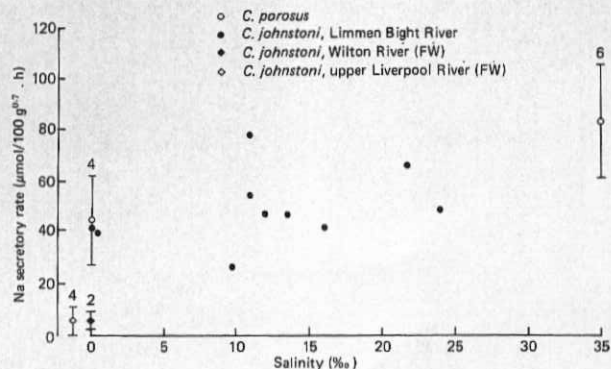
Fig. 3. Sodium secretion rate from methacholine-stimulated lingual glands of *C. johnstoni* and *C. porosus* from estuarine and permanent fresh-water habitats. Secretory rate scales with body weight$^{0.7}$ in *C. porosus* (Taplin, 1985); *C. johnstoni* from both fresh water (SAL 1) and saline water (SAL 2–4) on the Limmen Bight River have similar secretory rates, markedly higher than *C. johnstoni* from inland fresh-water habitats. (Reproduced with permission of Surrey Beatty and Sons from Taplin, Grigg & Beard (1985).

For *C. acutus*, however, the data from field and laboratory studies do not presently support a significant secretory role for the glands in sea water. While *C. acutus* has similar plasma and urine characteristics to *C. porosus* (Section 3.1), indicative of low urinary Na output, measured rates of gross Na efflux in sea water are only about one tenth of those in *C. porosus* and more comparable with effluxes from fresh-water reptiles (Evans & Ellis, 1977; Taplin, 1982, 1985; Dunson, 1982). The low efflux rates are difficult to reconcile with actively functioning lingual salt glands. It should be noted, however, that no tests of Na efflux or salt gland function appear to have been carried out on *C. acutus* freshly captured from SAL 4 habitats in the field. The animals used have all been of more or less uncertain geographic origin, purchased from crocodile farms (Evans & Ellis, 1977; Dunson, 1982). In contrast, definitive experiments on *C. porosus* were carried out within days of capture on animals freshly taken from intensively studied populations in SAL 4 habitats (Taplin, 1982, 1985).

C. johnstoni is the only other crocodilian for which there is any evidence regarding the role of the lingual glands in maintaining Na balance. *C. johnstoni* from inland fresh water habitats have lingual glands of very low secretory capacity (Table 7). Animals from a small salt water population (SAL 1–4) produced secretions as concentrated as *C. porosus* from SAL 4 and at rates 8 times higher than *C. johnstoni* from inland fresh water (Fig. 3) (Taplin *et al.*, 1985). There was no evidence of severe Na or water imbalance in salt water and urinary Na concentrations were low (Grigg, Taplin & Beard, unpubl. obs.). No quantitative Na and water budgets are available for these animals but there can be little doubt that the lingual glands play an important role in osmoregulation.

Little evidence is available regarding changes in the size, structure or function of the lingual glands with ambient salinity. *C. porosus* from seasonally fresh water (SAL 1)
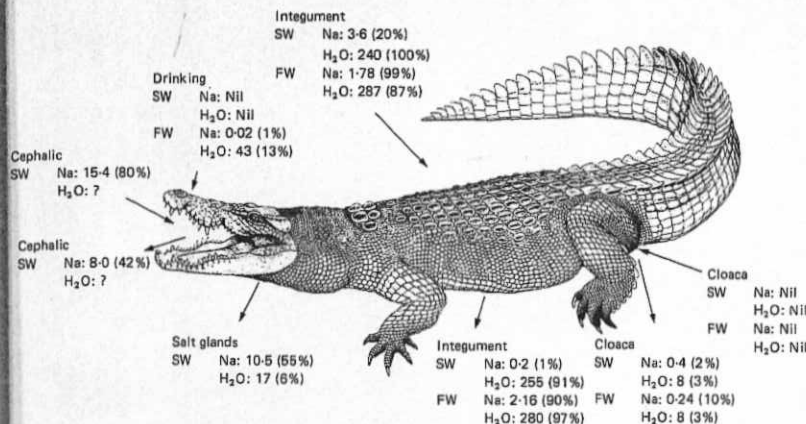
Fig. 4. Sodium and water budgets of a fasted *C. porosus* of nominal 250 g body weight in sea water and in fresh water at 25 °C. Sodium and water fluxes are expressed in units of $\mu mol/100$ g.h and $\mu l/100$ g.h respectively and as percentages of the total flux. Integumental exchange accounts for major fractions of both sodium and water fluxes. In sea water, much of the exchange appears to take place across cephalic epithelia. The lingual salt glands excrete some 55 % of the total sodium efflux and over 95 % of the combined renal/cloacal and extrarenal excretion. In fresh water, cephalic and lingual gland contributions to the low sodium fluxes have not been separated from integumental exchange. Reproduced with permission from Taplin (1985).

have size-adjusted secretory rates about 50 % of those in SAL 4 conditions (Taplin *et al.*, 1985), suggesting some de-differentiation of the gland in fresh water. There is no evidence to suggest, however, that the glands of Crocodylinae will regress to the condition seen in *Alligator* or, conversely, that alligatorid lingual glands are capable of massive acclimatory change to become functional salt glands in saline water. Nevertheless, a comparative study of the lingual glands of both *Alligator* and *Ca. crocodilus* from fresh and saline (preferably SAL 4) habitats would be invaluable in determining the extent of glandular differentiation possible in the Alligatoridae.

5. SYNTHESIS

The consideration of salt glands concludes the assessments of the separate elements of osmoregulation. These are now brought together to develop a more integrated view of osmoregulation in fresh and saline waters.

5.1. *Osmoregulation in salt water*

(a) SAL 4

The only crocodilian for which a detailed sodium and water budget has been constructed is *C. porosus* (Taplin, 1985). As this is the most detailed information available on any crocodilian and among the most detailed for any aquatic reptile, it serves as a useful model against which the data for other species can be compared.
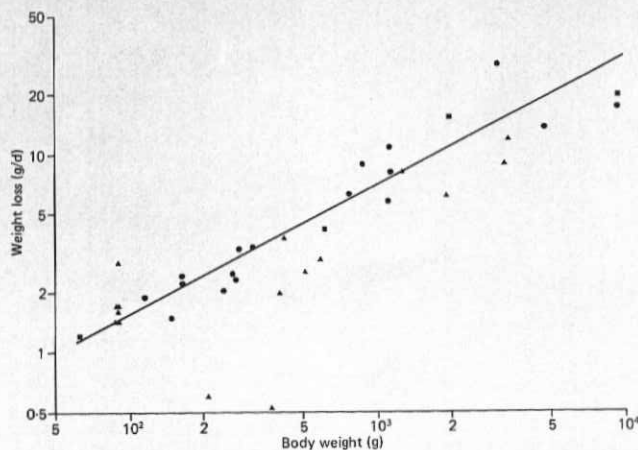
Fig. 5. Rates of weight loss in sea water in *C. porosus* at 25 °C (after Taplin, 1985 – ●) and *C. acutus* at 30 °C (after Mazotti & Dunson, 1984 – ▲; and Ellis, 1981 – ■). The majority of the weight loss is attributable to water loss. The regression line plotted for *C. porosus* is given by; Weight loss (g/d) = 0·085 × Body weight (g)$^{0·631}$, the rate of loss scaling with surface area. There is little to suggest markedly different rates of loss between the two species or any marked difference between hatchlings and larger crocodiles which is not simply a function of scaling of water loss with surface area.

The unfed Estuarine Crocodile in sea water is in Na balance but not in water balance (Fig. 4). Na is gained across the cephalic and post-cephalic integument but not significantly via the cloaca. It is excreted almost entirely by the lingual glands; urinary and faecal losses account for only 2 % of the total exchange. Water is exchanged primarily across the integument. None is gained by drinking and very little is lost by urination. Net water loss in sea water is substantial and markedly weight-dependent (Fig. 5). Water loss is split roughly 50:50 between direct integumental losses and losses in salt gland secretion necessary to excrete the net integumental Na uptake. Continued water loss leads inexorably to dehydration, increasing plasma Na concentrations and eventual death when about 30 % of the TBW has been lost.

Homeostasis of *C. porosus* in SAL 4 conditions is achieved normally by feeding; the crocodile is a facultative but not an obligate drinker of fresh water under natural conditions (Grigg *et al.*, 1980; Taplin, 1984*a*, *b*). There is some question as to the ability of freshly hatched crocodiles of 70–100 g BW to osmoregulate in SAL 4 conditions. However, hatchlings as small as 140 g BW are tolerant of salinities in excess of 60 ‰ (Taplin, 1984a) so it seems likely that smaller crocodiles might be equally competent in lower salinities. This possibility should be tested on one of the relatively few nests laid down in hypersaline (SAL 5) river systems. Hatchlings from such nests are likely to emerge into high salinities during the early dry season in areas where hypo-osmotic drinking water is unavailable.

Table 9. *Unidirectional sodium flux rates from crocodilians in fresh and saline water*

	Conditions*	Na efflux ($\mu mol/100$ g.h)	Na influx ($\mu mol/100$ g.h)	Reference
Crocodylus porosus	FW	3·0	2·1	Taplin (1985)
	SW	19·0	18·8	
C. acutus	FW	2·5	—	Evans & Ellis (1977)
	SW (25 %)	5·6	—	
	SW	0·8–3·8	11·3	Mazotti & Dunson (1984)
	SW	2·3	11·5	Dunson (1982)
C. johnstoni	FW	2·4	—	Taplin (1982 and unpubl. obs.)
Alligator	FW	3·9	—	Ellis & Evans (1984)
mississippiensis	SW	—	10·8	Mazotti & Dunson (1984)

* FW, fresh water; SW, sea water.

The data for *C. acutus* in SAL 4 conditions are less detailed than those for *C. porosus* but show numerous parallels and some contrasts. Plasma electrolyte concentrations in *C. acutus* are, overall, similar to those of *C. porosus*, except in the case of some newly hatched animals with low plasma Na levels (Table 2). Concentrations of Na and K in the cloacal urine of freshly caught SAL 4 animals are very similar to those of *C. porosus* (Table 6), as are the Na and K contents of urine solids (Dunson, 1982). Gross rates of water loss in the two species are quite similar given the differences in experimental conditions (Fig. 5). Three of the data points for *C. acutus* appear anomalously low or high for reasons that are not clear. There is little in the data to suggest that newly hatched *C. acutus* are fundamentally different from larger animals in ways that are not simply the result of isometric scaling of water loss with surface area. Weight losses in the smallest *C. acutus* tested lie very close to the extrapolated line for *C. porosus*, apart from a single animal showing inordinately high loss. Taplin (1985) showed that net water loss in *C. porosus* scales with BW$^{0·63}$, the same exponent as for surface area (Dunson, 1982). Unidirectional water effluxes from hatchling *C. acutus* (260–520 g BW) in sea water are of the same order as efflux from *C. porosus* (Mazotti & Dunson, 1984; Taplin, 1985). In addition to these similarities, the concentration and secretory rate of lingual glands secretions in *C. acutus* from fresh water are essentially identical to those of *C. porosus* from fresh water (Table 7) (Taplin *et al.*, 1982). No tests have been made of the secretory rate of lingual glands in *C. acutus* from SAL 4 conditions, but the glands of *C. porosus* show a two-fold increase in secretory capacity in SAL 4 relative to SAL 1 (Fig. 3) (Taplin *et al.*, 1985).

Only in the case of unidirectional Na fluxes are there substantial differences in the reported physiological characteristics of *C. acutus* and *C. porosus*. Na efflux rates measured from *C. acutus* in sea water are an order of magnitude lower than those in *C. porosus* and more comparable with efflux rates in crocodilians from fresh water (Table 9). Na influx rates are an order of magnitude higher in *C. acutus* and, incidentally, *A. mississippiensis* than in *C. porosus* (Mazotti & Dunson, 1984). The data showing exceedingly low efflux rates in *C. acutus* in sea water and a large excess of Na influx over efflux have been used to argue the case for a significant difference in osmoregulatory strategy between *C. porosus* and *C. acutus*. The latter is thought to lack functional salt glands and to rely primarily on behavioural avoidance of highly saline water or

osmotically stressful environments, on drinking fresh or brackish water and on rapid growth to a size at which osmoregulatory problems are minimized (Dunson, 1982; Mazotti & Dunson, 1984; Mazotti et al., 1986). However, there are some problems in interpretation of the C. acutus data which have not been addressed previously.

Firstly, the determinations of Na effluxes in sea water have all been carried out on animals of more or less indeterminate origin, purchased from farms where they were doubtless reared in fresh water. It would be unwise to dismiss the possibility of significant differences in Na efflux or lingual gland secretory capacity between captive fresh-water animals and free-living SAL 4 animals, or between different natural populations of the one species. Indeed, evidence from salt- and fresh-water populations of C. johnstoni (Taplin et al., 1985; Taplin, unpubl. obs.) suggests that physiological differences between populations can be substantial. This caution applies also to the evidence that C. acutus is unable to maintain body weight when fed in sea water unless brackish water is available (Dunson, 1982; Mazotti & Dunson, 1984).

Secondly, the high values for Na influx in C. acutus and Alligator may be more a reflection of the technique used than of the normal state of affairs in these animals. Taplin (1982, 1985) applied similar techniques to determination of Na influx in C. porosus and found extraordinarily high influx rates of 43 μmol/100 g.h over 115 h in sea water. The high influxes were attributed to inadvertent swallowing of sea water by the animals during periodic removal and return to the experimental chambers. That the data in no way reflect the usual condition of C. porosus is apparent from the close balancing of influx and efflux in free-swimming crocodiles (determined by measuring efflux, influx and net flux simultaneously in a single experiment) and the lack of any evidence of severe disturbance of Na balance which cannot be accounted for by water loss alone (Taplin, 1985).

Thirdly, the hypothesis that rapid growth to a more salt tolerant size is a critical specialization of C. acutus to life in salt water (Mazotti & Dunson, 1984) is interesting but should not be accepted uncritically. The data available are simply inadequate to test the hypothesis. Growth rates in the field are subject to many influences, none of which has been controlled for in the comparisons referred to by Mazotti (1983) and Mazotti et al. (1986). The contention that the relatively low growth rates in C. porosus reported by Grigg et al. (1980) are indicative of substantial stress in high salinities takes no account of seasonal influences on growth rates which may be quite independent of salinity. The problem of determining the influence of salinity on condition from field data for C. porosus is addressed in detail by Taplin (1984a).

(b) SAL 2 and 3

The osmoregulatory strategies employed by crocodiles with permanent or periodic access to hypoosmotic salt water appear to be more similar to those of SAL 1 animals than SAL 4 animals. There have been virtually no quantitative measurements of the various components of sodium and water budgets in SAL 2 and 3 habitats. Qualitative evidence suggests that drinking of hypoosmotic salt water and subsequent excretion of Na by renal or extra-renal routes contributes substantially to water balance. The opportunity to osmoregulate by drinking apparently reduces water balance problems markedly; evidenced by the persistence of NH_4 as the dominant nitrogenous excretory product from SAL 1–3 conditions (Grigg, 1981). The urinary system appears to play

Table 10. Effective half-lives for ^{22}Na efflux from aquatic reptiles in fresh water. Cited as mean ± standard error (N) or as ranges

	Body weight (g)	Half-life (days)	Reference
Crocodylus porosus	330–682	75 ± 16 (5)	Taplin (1982)
C. acutus	54–68	50 ± 11 (6)	Evans & Ellis (1977)
C. johnstoni	46–51	72 ± 10 (3)	Taplin (unpubl. obs.)
Alligator mississippiensis	32–72	42 ± 6 (16)	Ellis & Evans (1984)
Trionyx spiniferus	17–29	179 ± 22 (6)	Dunson (1979)
Pseudemys scripta	72	200–540	Dunson (1967)
Caretta caretta	Hatchlings	240–1110	Evans (1973)
Chelonia mydas	25–100	48 ± 7 (33)	Kooistra & Evans (1976)

a major role in Na and K excretion in alligators in hypoosmotic salt water. Extra-renal excretion of Na and renal excretion of K appear to predominate in C. porosus from SAL 2–3, given the low Na and high K content of the urine. Evidence for renal or extra-renal Na excretion in C. acutus is equivocal at present and unlikely to be clarified without recourse to more detailed analyses of Na and water budgets.

5.2. Osmoregulation in fresh water, SAL 1

The only approximation to a Na and water budget for a crocodilian in fresh water is that of Taplin (1982) for C. porosus (Fig. 4). The Estuarine Crocodile is unable to maintain Na balance when unfed in fresh water, despite evidence of some capacity for active uptake of Na. The vast majority of the Na exchange is integumental. The small net Na loss across the integument, 0·38 μmol/100 g.h, is comparable to the urinary loss of 0·24 μmol/100 g.h. The overall Na loss would be readily compensated by feeding. For example, a 200 g hatchling would lose 14·4 μmol Na/100 g.day, which could be replaced in 0·6 g w. wt of food with a Na content of 50 μmol/g w. wt. This intake is only one-third of the amount required to satisfy energetic requirements at the resting metabolic rate predicted from equations of Bennett and Dawson (1976), given an energy content in food of 20 kcal/g w. wt. (Driver, 1981). Water fluxes in SAL 1 are very similar in magnitude to those in SAL 4 and, once again, integumental exchange dominates the budget. The small net influx across the integument is insufficient to compensate for urinary losses which are, presumably, obligatory. Water balance is achieved by drinking.

Interestingly, there is nothing in the data available to suggest that the euryhaline C. porosus is less well adapted to life in fresh water than other crocodilians. Urinary Na losses are similar in C. porosus, C. johnstoni and A. mississippiensis. None is known to have any remarkable capacity for active uptake of Na. The effective half-life for Na turnover is similar in the four species tested to date, but is perhaps more rapid in A. mississippiensis than in the crocodylines (Table 10). It is not clear whether differences in integumental water permeability or urination rate in Ca. crocodilus [Section 4.4.(a)] are unreliable estimates or reflect a greater degree of adaptation to a fresh-water existence.

The higher rates of Na turnover (Table 10) and poorer ability to absorb Na from dilute media suggest that the crocodilians are less well adapted than some fresh water

turtles for hyperosmotic osmoregulation. It is surprising, therefore, that published data on urinary Na losses in the turtles point in quite the opposite direction. Dunson (1979) estimated urinary and faecal Na loss in the soft shell turtle, *Trionyx*, at 1·2 μmol/ 100 g.h. Measurements of urine flow and Na concentration in the same species give a value of 3·6 μmol/100 g.h. (Dantzler & Schmidt-Nielsen, 1966; Bentley & Schmidt-Nielsen, 1970; Seidel, 1975). Both values are an order of magnitude higher than in crocodilians. *Trionyx* is also reported to void urine containing 20 mmol Na/l (Seidel, 1975), four times higher than is typical of crocodilians and other turtles (Bentley *et al.*, 1967; Trobec & Stanley, 1971). The turtle *Chrysemys picta* has a urination rate 2–3 times as high as crocodilians (Dantzler & Schmidt-Nielsen, 1966). The high urinary losses of these fresh-water specialist turtles are surprising and may, like those of *Ca. crocodilus*, be an abnormal response to cloacal cannulation. As with so many aspects of osmoregulation, the validity of these flow measurements is difficult to assess in the absence of detailed Na and water budgets. Integrated studies of the partitioning of salt and water fluxes are an urgent need for fresh-water reptiles if experimental artifact is to be distinguished from true physiological function.

5.3. *Feeding and osmoregulation*

While feeding is ultimately an important factor in maintenance of salt and water balance in any habitat, it appears to be a major proximate factor affecting osmoregulation and survival of at least one salt water crocodilian, *C. porosus*. Thus an understanding of the quantitative contribution of food intake to electrolyte and water balance budgets will be crucial to a proper understanding of this species' osmo-regulatory capabilities. The majority of laboratory studies of crocodilian osmo-regulation reported to date have concentrated on fasting animals. Part of the reason for the dearth of studies on feeding crocodilians has been the difficulty of maintaining them in salt water in the laboratory, especially as hatchlings. This difficulty does not necessarily reflect on their physiological capabilities as they are not the easiest animals to maintain in the laboratory at the best of times, even in fresh water. In our own work in Australia we have tended to shy away from the somewhat equivocal answers which can derive from work on laboratory-reared animals and have concentrated on the analysis of what might be termed 'natural experiments'. From this has derived a clear demonstration of the importance of feeding and facultative drinking for *C. porosus* across a range of sizes. A similar approach has been taken to the analysis of lingual gland function and salinity tolerance in *C. johnstoni* (Taplin, Grigg & Beard, 1985, unpubl. obs.). Extension of these field studies to quantitative measurements of sodium and water budgets in free-ranging *C. porosus* have proven both fruitful and frustrating. Valuable data on turnover rates are now available for actively feeding *C. porosus* in hyperosmotic salt water but integration of these data with complementary laboratory studies has proven difficult.

In a study of 62 *C. porosus* from SAL 2 and SAL 4 habitats, Grigg et al. (1986) measured Na and water fluxes over a 7–18-day period. The results are summarized in Fig. 6. Hatchlings and larger crocodiles in this study apparently responded differently to experimental disturbance; the hatchlings feeding and growing, the larger crocodiles losing weight in both salinity regimes and dehydrating in SAL 4. The weight loss and dehydration were attributed to partial or complete inhibition of feeding in the larger
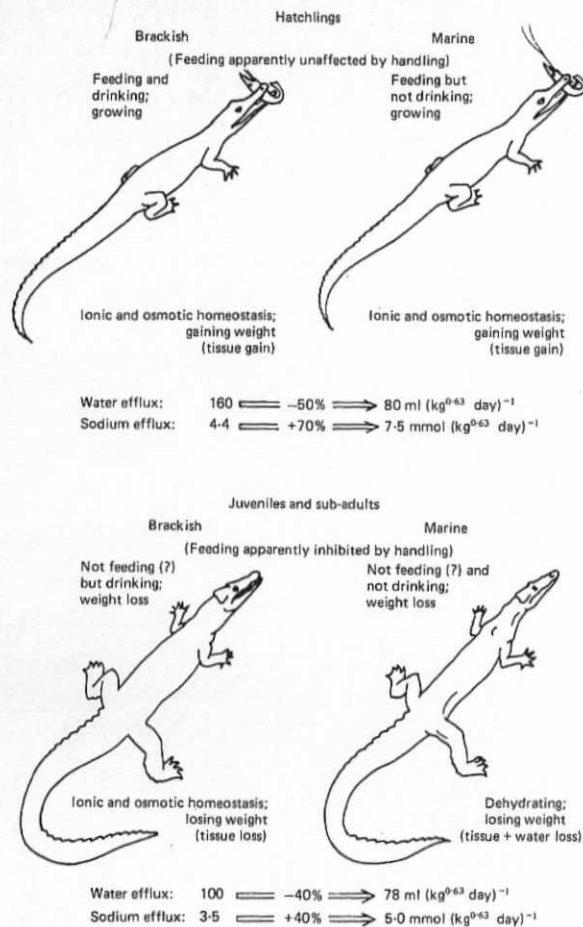
Fig. 6. Summary model of Grigg et al.'s (1986) interpretation of Na and water fluxes in free-living *C. porosus* in hyperosmotic ('marine') and hypo-osmotic ('brackish') sections of an estuary. Actively feeding juveniles and adults, as well as hatchlings, are able to maintain plasma homeostasis in hyperosmotic conditions as long as there is adequate food intake (Grigg *et al.*, 1980; Grigg, 1981; Taplin, 1984a). Hence, the weight loss of juveniles and subadults is thought to be an artifact, the result of feeding being partially or completely inhibited following capture, handling and release during the study. Reproduced with permission from Grigg et al. (1986).

animals. Nevertheless, feeding or not, *C. porosus* can effect a considerable reduction in water turnover in sea water (Fig. 6). Given the lack of evidence for changes in diffusional water permeability (Section 4.2) it seems that this reduction is related to lower drinking and urination rates in SAL 4. This is consistent with evidence of marked changes in drinking behaviour and mode of nitrogen excretion between hypo- and hyper-osmotic conditions (Sections 4.4 and 4.5). Though the field data are qualitatively consistent with the model of osmoregulation developed for *C. porosus*, quantitative consistency was not achieved. Na and water fluxes measured in the lab are 30–50 % lower than the field data for apparently fasting crocodiles would predict (Grigg *et al.*, 1986). There is room for caution in extrapolation from laboratory to field even when data from both sources are available.

In the laboratory, *C. acutus* and *A. mississippiensis* have been found reluctant to feed in simulated SAL 4 conditions (Dunson, 1982; Lauren, 1985). Alligators in fresh water or 5 ‰ salt fed readily but stopped feeding in the first week after transfer to hyperosmotic salt water (Lauren, 1985). *C. acutus* fed and gained weight most rapidly in 10 ‰, gained weight more slowly in 18 ‰, and lost weight in 26 and 35 ‰ salt water (Dunson, 1982). Occasional provision of hypo-osmotic drinking water in addition to food was sufficient to reverse the loss of weight in sea water (Mazotti and Dunson, 1984). The estuarine terrapin, *Malaclemys*, shows some parallels to *C. acutus* (Dunson, 1985). Hatchling *Malaclemys* show a growth optimum near 9 ‰ salt water and appear unable to thrive in sea water without access to hypo-osmotic salt water. No tests of growth rates as a function of salinity have been attempted for *C. porosus*. Studies of natural populations of *C. porosus* provide little evidence of any effect of salinity on growth rates of hatchlings (Webb *et al.*, 1978; Magnusson & Taylor, 1981; Messel & Vorlicek, 1984). However, none of these studies was designed specifically to test the effect of salinity *per se* and there are many confounding factors.

Further studies of salt and water budgets and growth rates of actively feeding crocodiles across the salinity spectrum are needed to clarify our understanding of crocodilian osmoregulation. Care needs to be taken that laboratory studies on animals from one geographical area are not extrapolated too readily to field studies on different populations. A greater integration of field and laboratory studies, perhaps making use of the semi-natural facilities available at crocodile farms, will be necessary if unequivocal answers are to be found. It remains to be demonstrated that the increased body weight of captive *C. acutus* in simulated SAL 3 conditions (Mazotti & Dunson, 1984) is not due in part or in whole to gross disturbance of volume regulation, as has been observed in *C. johnstoni* held unfed in SAL 2 conditions (Taplin, unpubl. obs.). While this seems most unlikely from the data available, it is a hypothesis which could be tested readily by simultaneous measurement of osmotic and ionic homeostasis with growth rates. Comparative studies of *C. acutus* and *A. mississippiensis* should focus on those osmoregulatory mechanisms which appear most likely to differ between the two species; renal function and extra-renal salt excretion. Superficial similarities of osmoregulatory capability may mask quite fundamental differences in strategy. A concentration of effort on osmoregulation and feeding could also clarify the inter-relationships between nitrogen metabolism and electrolyte and water budgets. Nitrogen may well be a far more important osmolyte than Na, K or Cl (Nagy & Shoemaker, 1977; Taplin, 1982). Much information is available on nitrogen excretion in *Alligator*

and its role in Na and water conservation (Coulson & Hernandez, 1964, 1970, 1983; Shoemaker & Nagy, 1977). However, the apparent differences in renal and extra-renal Na excretion between *Alligator* and some or all of the Crocodylinae call into question the applicability of the *Alligator* model to all crocodilians.

One further aspect of feeding and osmoregulation in crocodilians deserves some attention. It has been suggested that vulnerable small crocodiles might select food items of relatively low Na and high water content as a form of behavioural osmoregulation (Dunson, 1982; Taplin, 1982). Analysis of the salt and water content of food items has provided no support for the hypothesis (Taplin, 1985). Nonetheless, the nitrogen content of food may impose a considerably greater osmotic load on the excretory system than do electrolytes such as Na (Shoemaker & Nagy, 1977). In the absence of information on nitrogen, salt, and water balance in feeding animals it would be premature to conclude that the estuarine/marine crocodiles are not selecting prey which allows them to minimize net excretory water loss.

6. EVOLUTIONARY ASPECTS OF CROCODILIAN OSMOREGULATION

The modern crocodilians have traditionally been regarded as a fresh water stock, one or two species of which have made inroads into estuarine but not truly marine environments. Recently, however, Densmore & Dessauer (1982) and Taplin (1982) have proposed independently that some or all of the extant Crocodylinae might be derived from sea-going ancestors. Densmore and Dessauer based their hypothesis on the remarkably small biochemical differences they found among crocodyline blood proteins, which indicated a post-Pliocene radiation of the group and, hence, dispersal across substantial oceanic barriers (Densmore, 1983). Taplin, on the other hand, was attempting to explain the occurrence of salt glands in all of the Crocodylinae and their absence from alligatorids. The biochemical and physiological lines of evidence are remarkably concordant and have been combined to generate a scenario for eusuchian evolution which is markedly different from the traditional view (Taplin, 1984c; Taplin *et al.*, 1985). The living Crocodylinae are considered to be derived quite recently from some sea-going ancestor(s) with physiological characteristics comparable to those of *C. porosus*, which has the ability to disperse through and colonize island archipelagos. The Alligatoridae are regarded as an essentially fresh-water stock, lacking lingual salt glands, which have been largely restricted throughout their history to fresh-water environments and, hence, the major continental land masses. It might be noted that only a single major oceanic crossing via the Atlantic or Pacific oceans is required to explain the present circumtropical distribution of the Crocodylinae. The African, Indo-Asian and Australasian distributions are all explicable through relatively short coastal or marine movements.

It will be important to the further development and testing of these ideas that there be no confusion over the relevance of physiological studies to the proposed scheme. For example, contrary to Densmore's (1983) suggestion, the existence of salt glands in *C. porosus* is not particularly crucial in establishing that substantial marine excursions by crocodiles might have occurred. The zoogeographical hypothesis put forward requires only that some ancestral crocodile(s) have the capacity to cross oceanic barriers, to colonize estuarine and, subsequently, fresh water habitats, and to develop reproductive isolating mechanisms during geographic isolation from the parent stock. The

dispersive abilities of *C. porosus* are amply demonstrated by its occurrence throughout Indo- and Austral-Asia and this species is known to be capable of colonizing and reproducing in inland fresh-water habitats (Taplin, 1984*a*). The presence of salt glands serves only to explain some of the physiological basis for this dispersive and colonizing ability. More significant from the zoogeographical point of view are the observations that *C. porosus* is very flexible in the habitats it can live and breed in, that hatchling *C. porosus* are extremely euryhaline (Taplin, 1984a), that *C. porosus* is not obviously a less efficient osmoregulator in fresh water than other crocodilians (Taplin, 1982) (Section 5.2), and that salt glands have been found in all of the 'fresh-water' Crocodylinae examined to date and in none of the Alligatoridae (Taplin *et al.*, 1982) (Section 4.7). The first two findings suggest that at least one crocodilian has physiological capabilities which equip it to invade and successfully colonize both coastal and inland environments. The third finding provides a sound basis for questioning the immediate fresh water origins of many or all of the Crocodylinae.

A reinvasion of fresh water by estuarine/marine crocodilians is somewhat contrary to the argument of Dunson (1986) that reinvasion by more specialized or highly derived estuarine/marine species (of turtles) is unlikely because of their competitive disadvantage in fresh water. The nature of this 'competitive disadvantage' deriving from physiological specialization for an estuarine existence is not clear. Nor am I aware of any hard evidence demonstrating the role of competition in structuring guilds of any aquatic reptiles. In any case, invoking competition as a factor preventing estuarine-freshwater transitions is of limited heuristic value. Any observed occurrence of derived fresh water taxa among basically marine stocks can be explained away superficially as having originated at a time when competitors were not present. Given that fresh water derivatives are common among marine taxa as diverse as crustaceans, gastropods, elasmobranchs, teleosts, cetaceans and sirenians (Darlington, 1957; Potts & Parry, 1964; Domning, 1982; Gaskin, 1982), it would hardly be surprising to find examples among the aquatic reptiles.

7. CONCLUSIONS

The preceding analysis has revealed many aspects of crocodilian osmoregulation of which we are largely ignorant – hardly a surprising fact given the dearth of workers in the field. Recapping on some of the deficiencies outlined earlier, we need information about the following major areas.

- The occurrence of crocodilians in saline habitats, the salinity regimes they encounter and their patterns of plasma and urine composition as a function of salinity and body size.
- The physiology of aestivation in crocodilians, with particular reference to the function of lingual salt glands in regulation of salt and water balance.
- The osmoregulatory capabilities of neonatal crocodilians and the significance of low sodium levels in embryos and neonates.
- Drinking strategies of crocodilians in salt and fresh waters and their relationship to integumentary water and sodium permeabilities.
- Renal and cloacal function in fresh- and salt-water populations with particular regard to the relationship between sodium and water reabsorption and nitrogen excretion.

- Lingual gland function in fresh- and salt-water populations and acclimatory responses of the glands to changes in the salinity regime.
- Neuroendocrine control of salt gland excretion and its integration with regulation of renal function.

In all of the above there is abundant opportunity for comparative studies of the major crocodilian lineages, especially between the more common alligatorids and crocodylines. Such comparisons should be pursued with vigour while we still have opportunity to make them. The worldwide decline of crocodilians is proceeding apace and the opportunities to study important local populations are diminishing rapidly. Extensive rather than intensive studies will be essential in the short term if we are to develop a proper understanding of the range of physiological capabilities present among the crocodilians. Nowhere is this more true than for the salt water *Caiman* populations of southern and central America which can provide crucial insights into hypoosmotic regulation in the Alligatoridae and the hypothesis that stenohalinity in alligatorids has had significant zoogeographical consequences (Section 6).

Together with these extensive and often superficial investigations will need to go some intensive studies of osmoregulation in individual species. Once again, however, there will be profit in designing comparative studies in which standardized methodologies allow more direct comparisons of results than have been possible in the past. There is a need for determinations of complete sodium and water budgets for both fresh- and salt-water crocodilians. Attempts to construct quantitative budgets provide by far the best opportunities for discriminating experimental artifact from physiological function, yet there are few examples in the literature of aquatic reptiles. The extension of budgetary studies to analyses of nitrogen budgets in fasted and feeding crocodilians would allow better assessments of the role of food intake in osmoregulation. The ongoing development of the crocodile farming industry may well provide opportunities to address this problem. The existing farms are grappling with substantial husbandry problems in trying to minimize disease and maximize production. The feasibility of rearing various of the Crocodylinae in salt water has yet to be explored but offers good opportunities for integration of pure and applied science.

8. SUMMARY

1. The osmoregulatory strategies of crocodilians in both saline and fresh-water environments are discussed and dissected into their separate components.

2. Contrasts between members of the Alligatoridae and the Crocodylinae emerge repeatedly in aspects such as integumental permeabilities, functioning of the renal/cloacal system, and the presence of lingual salt-secreting glands.

3. These contrasts contribute to the view that the alligatorid and crocodyline stocks are more divergent than has been suspected previously. In particular, there is cogent evidence of a significant marine phase in the evolution of the Crocodylinae but not of the Alligatoridae.

4. The physiological evidence to support this view of a very basic dichotomy among the eusuchians is reviewed in detail and avenues which would contribute most to its critical evaluation are identified.

9. ACKNOWLEDGEMENTS

10. REFERENCES

ABERCROMBIE, C. L. (1978). Notes on West African crocodilians. *Journal of Herpetology* **12** (2), 260–262.

ALVAREZ DEL TORO, M. (1975). Morelet's crocodile. *Wildlife, World Conservation Yearbook, 1975*, pp. 88–91.

ANNANDALE, N. (1915). Fauna of the Chilka Lake. Reptiles and Batrachia. *Memoirs of the Indian Museum* **5**, 167–174.

BAYLY, I. A. E. (1967). The general biological classification of aquatic environments with special reference to those of Australia. In *Australian Inland Waters and their Fauna* (ed. A. H. Weatherley), ANU Press, Canberra.

BENNETT, A. F. & DAWSON, W. R. (1976). Metabolism. In *Biology of the Reptilia. Physiology A* (ed. C. Gans and W. R. Dawson), vol. 5, pp. 127–223. Academic Press, New York.

BENNETT, J. M., TAPLIN, L. E. & GRIGG, G. C. (1986). Sea water drinking as a homeostatic response to dehydration in hatchling loggerhead turtles, *Caretta caretta*. *Comparative Biochemistry and Physiology* **83** A (3), 507–513.

BENTLEY, P. J. (1962). Studies on the permeability of the large intestine and urinary bladder of the tortoise (*Testudo graeca*) with special reference to the effects of neurohypophysial and adrenocortical hormones. *General and Comparative Endocrinology* **2**, 323–328.

BENTLEY, P. J. (1971). *Endocrines and Osmoregulation*. Springer-Verlag, Berlin.

BENTLEY, P. J. (1976). Osmoregulation. In *Biology of the Reptilia, Physiology A* (ed. C. Gans and W. R. Dawson), vol. 5, pp. 365–411. Academic Press, London.

BENTLEY, P. J. (1982). *Comparative Vertebrate Endocrinology*, 2nd ed. Cambridge University Press, Cambridge.

BENTLEY, P. J., BRETZ, W. L. & SCHMIDT-NIELSEN, K. (1967). Osmoregulation in the diamondback terrapin, *Malaclemys terrapin centrata*. *Journal of Experimental Biology* **46**, 161–167.

BENTLEY, P. J. & SCHMIDT-NIELSEN, K. (1965). Permeability to water and sodium of the crocodilian, *Caiman sclerops*. *Journal of Cellular and Comparative Physiology* **66**, 303–309.

BENTLEY, P. J. & SCHMIDT-NIELSEN, K. (1966). Cutaneous water loss in reptiles. *Science* **151**, 1547–1549.

BENTLEY, P. J. & SCHMIDT-NIELSEN, K. (1970). Comparison of water exchange in two aquatic turtles, *Trionyx spiniferus* and *Pseudemys scripta*. *Comparative Biochemistry and Physiology* **32**, 363–365.

BIRKHEAD, W. S. & BENNETT, C. R. (1981). Observations of a small population of estuarine inhabiting alligators near Southport, North Carolina, USA. *Brimleyana 1981*, pp. 111–118.

BOGERT, C. M. & COWLES, R. B. (1947). Moisture loss in relation to habitat selection in some Floridian reptiles. *American Museum Novitates* no. 1358, 1–34.

BRADSHAW, S. D. (1972). The endocrine control of water and electrolyte metabolism in desert reptiles. *General and Comparative Endocrinology*, supplement 3, 360–373.

BRAZAITIS, P. (1973). The identification of living crocodilians. *Zoologica* **58** (4), 59–101.

BROWN, C. R. & LOVERIDGE, J. P. (1981). Effect of temperature on oxygen consumption and evaporative water loss in *Crocodylus niloticus*. *Comparative Biochemistry and Physiology* **69** A, 51–58.

BURGESS, W. W., ALVAREZ, A. M. & MARSHALL, E. K. (1933). The site of the antidiuretic action of pituitary extract. *Journal of Pharmacology and Experimental Therapeutics* **49**, 237–249.

CAMERON, W. M. & PRITCHARD, D. W. (1963). Estuaries. In *The Sea* (ed. M. N. Hill), vol. 8, pp. 306–324. John Wiley, New York.

CLOUDSLEY-THOMPSON, J. L. (1968). Water relations of crocodiles. *Nature* **220** (5168), 708.

CLOUDSLEY-THOMPSON, J. L. (1969). Water relations of the young Nile Crocodile. *British Journal of Herpetology* **4** (5), 107–112.

COTT, H. B. (1961). Scientific results of an enquiry into the ecology and economic status of the Nile Crocodile, (*Crocodylus niloticus*) in Uganda and northern Rhodesia. Transactions of the Zoological Society of London **29**, 211–356.

COULSON, R. A. & HERNANDEZ, T. (1959). Source and function of urinary ammonia in the alligator. *American Journal of Physiology* **197**, 873–879.

COULSON, R. A. & HERNANDEZ, T. (1964). *Biochemistry of the Alligator: A Study of Metabolism in Slow Motion*. Louisiana State University Press, Baton Rouge.

COULSON, R. A. & HERNANDEZ, T. (1970). Nitrogen metabolism and excretion in the living reptile. In *Comparative Biochemistry of Nitrogen Metabolism* (ed. J. W. Campbell), pp. 639–710. Academic Press, New York.

COULSON, R. A. & HERNANDEZ, T. (1983). *Alligator Metabolism: Studies on Chemical Reactions in vivo*. Pergamon Press, London.

COWAN, F. B. M. (1985). Short term acclimation of *Malaclemys terrapin* to saltwater. *Comparative Biochemistry and Physiology* **68** A, 55–59.

COX, J. (1984). Crocodile nesting ecology in Papua New Guinea. Field Doc. no. 5, Livestock Division, Department of Primary Industry, PNG.

DANTZLER, W. H. (1976). Renal function (with special emphasis on nitrogen excretion). In *Biology of the Reptilia, Physiology A* (ed. C. Gans and W. R. Dawson), vol. 5, pp. 447–503. Academic Press, London.

DANTZLER, W. H. (1980). Renal mechanisms for osmoregulation in reptiles and birds. In *Animals and Environmental Fitness*, vol. 1, pp. 91–110. Pergamon Press, New York.

DANTZLER, W. H. & HOLMES, W. N. (1974). Water and mineral metabolism in Reptilia. In *Chemical Zoology. Vol. IX. Amphibia and Reptilia* (ed. M. Florkin and B. Scheer), pp. 277–336. Academic Press, New York.

DANTZLER, W. H. & SCHMIDT-NIELSEN, B. (1966). Excretion in fresh-water turtle (*Pseudemys scripta*) and desert tortoise (*Gopherus agassizii*). *American Journal of Physiology* **210**, 198–210.

DARLINGTON, P. J. (1957). *Zoogeography: the Geographical Distribution of Animals*. Museum of Comparative Zoology, Harvard.

DENSMORE, L. D. (1983). Biochemical and immunological systematics of the Order Crocodilia. In *Evolutionary Biology* (ed. M. K. Hecht, B. Wallace and G. T. Prance), vol. 16, pp. 397–465. Plenum, New York.

DENSMORE, L. D. & DESSAUER, H. (1982). Low protein divergence of species within the circumtropical genus *Crocodylus*. Result of a post-Pliocene trans-oceanic dispersal and radiation? *Federation Proceedings* **41** (4), abstr. 4293.

DERINAYAGALA, P. E. P. (1930). *A Coloured Atlas of Some Vertebrates from Ceylon*. Vol. 2. Tetrapod Reptiles. Ceylon Government Press.

DIEFENBACH, C. O. DAC. (1973). Integumentary permeability to water in *Caiman crocodilus* and *Crocodylus niloticus* (Crocodilia: Reptilia). *Physiological Zoology* **46**, 72–78.

DILL, D. B. & EDWARDS, H. T. (1931). Physicochemical properties of crocodile blood (*Crocodylus acutus*, Cuvier). Journal of Biological Chemistry **90**, 515–530.

DOMNING, D. P. (1982). Evolution of manatees: a speculative history. *Journal of Palaeontology* **56**, (3), 599–619.

DOWNES, M. C. (1971). Regional situation report – Papua New Guinea. *Proceedings 1st Working Meeting IUCN Crocodile Specialists Group*, IUCN, Gland, Switzerland.

DRIVER, E. A. (1981). Calorific values of pond invertebrates eaten by ducks. *Freshwater Biology* **11** (6), 579–581.

DUNSON, W. A. (1967). Sodium fluxes in freshwater turtles. *Journal of Experimental Biology* **165**, 171–182.

DUNSON, W. A. (1970). Some aspects of electrolyte and water balance in three estuarine reptiles, the Diamondback Terrapin, American and 'Saltwater' crocodiles. *Comparative Biochemistry and Physiology* **32**, 161–174.

DUNSON, W. A. (1976). Salt glands in reptiles. In *Biology of the Reptilia. Physiology A* (ed. C. Gans and W. R. Dawson), vol. 5, pp. 413–445. Academic Press, London.

DUNSON, W. A. (1978). Role of the skin in sodium and water exchange of aquatic snakes placed in seawater. *American Journal of Physiology* **235** (3), R151–R159.

DUNSON, W. A. (1979). Control mechanisms in reptiles. In *Mechanisms of Osmoregulation* (ed. R. Gilles), pp. 273–322. John Wiley, New York.

DUNSON, W. A. (1980). The relation of sodium and water balance to survival in seawater of estuarine and freshwater races of the snakes, *Nerodia fasciata*, *N. sipedon* and *N. valida*. Copeia 1980 (2), 268–280.

DUNSON, W. A. (1981). Behavioural osmoregulation in the Key Mud Turtle, *Kinosternon b. baurii*. *Journal of Herpetology* **15** (2), 163–173.

DUNSON, W. A. (1982). Salinity relations of crocodiles in Florida Bay. *Copeia* 1982 (2), 374–385.

DUNSON, W. A. (1985). Effect of water salinity and food salt content on growth and sodium efflux of hatchling diamondback terrapins. *Physiological Zoology* **58** (6), 736–747.

DUNSON, W. A. (1986). Estuarine populations of the Snapping Turtle (*Chelydra*) as a model for the evolution of marine adaptations in reptiles. *Copeia* 1986 (3), 741–756.

DUNSON, W. A. & HEATWOLE, H. (1986). The effect of relative shell size in turtles on water and electrolyte composition. *American Journal of Physiology* 250 (Regulatory Integrative Comparative Physiology), R1133–R1137.

DUNSON, W. A. & MOLL, E. O. (1980). Osmoregulation in sea water of hatchling emydid turtles, *Callagur borneoensis*, from a Malaysian sea beach. *Journal of Herpetology* 14 (1), 31–36.

DUNSON, W. A. & STOKES, G. D. (1983). Asymmetrical diffusion of sodium and water through the skin of sea snakes. *Physiological Zoology* 56 (1), 106–111.

DUNSON, W. A. & WEYMOUTH, R. D. (1965). Active uptake of sodium by the softshell turtle *Trionyx spinifer*. *Science* 149, 67–69.

ELLIS, T. M. (1981). Tolerance of seawater by the American Crocodile, *Crocodylus acutus*. *Journal of Herpetology* 15 (2), 187–192.

ELLIS, T. M. & EVANS, D. H. (1984). Sodium balance in the American Alligator. *Journal of Experimental Zoology* 231, 325–329.

EVANS, D. H. (1973). The sodium balance of the euryhaline marine loggerhead turtle, *Caretta caretta*. *Journal of Comparative Physiology* 83, 179–195.

EVANS, D. H. (1979). Fish In *Comparative Physiology of Osmoregulation in Animals* (ed. G. M. O. Maloiy), pp. 305–390. Academic Press, London.

EVANS, D. H. & ELLIS, T. M. (1977). Sodium balance in the hatchling American Crocodile, *Crocodylus acutus*. *Comparative Biochemistry and Physiology* 58 A, 159–162.

FERDINAND, L. (1884). *Zur Anatomie der Zunge*. Reidel, München.

FITZSIMONS, J. T. & KAUFMAN, S. (1977). Cellular and extracellular dehydration and angiotensin as stimuli to drinking in the common iguana, *Iguana iguana*. *Journal of Physiology (London)* 265, 443–463.

GABY, R., McMAHON, M. P., MAZOTTI, F. J., GILLIES, W. N. & WILCOX, J. R. (1985). Ecology of a population of *Crocodylus acutus* at a power plant site in Florida. *Journal of Herpetology* 19 (2), 189–198.

GASKIN, D. E. (1982). *The Ecology of Whales and Dolphins*. Heinemann, London.

GILLES-BAILLIEN, M. (1970). Urea and osmoregulation in the diamondback terrapin, *Malaclemys centrata centrata* (Latreille). *Journal of Experimental Biology* 52, 691–697.

GIST, D. H. & DE ROOS, R. (1966). Corticoids of the alligator adrenal gland and the effects of ACTH and progesterone on their production *in vitro*. *General and Comparative Endocrinology* 7, 304–313.

GREGORY, P. T. (1982). Reptilian hibernation. In *Biology of the Reptilia*, Vol. 13. *Physiology B* (ed. C. Gans and F. H. Pough), pp. 53–154. Academic Press, London.

GRIFFITH, R. W., UMMINGER, B. L., GRANT, B. F., PANG, P. K. T. & PICKFORD, G. E. (1974). Serum composition of the coelacanth, *Latimeria chalumnae* Smith. *Journal of Experimental Biology* 187, 87–102.

GRIGG, G. C. (1981). Plasma homeostasis and cloacal urine composition in *Crocodylus porosus* caught along a salinity gradient. *Journal of Comparative Physiology* 144, 261–270.

GRIGG, G. C., TAPLIN, L. E., HARLOW, P. & WRIGHT, J. (1980). Survival and growth of hatchling *Crocodylus porosus* in saltwater without access to fresh water. *Oecologia (Berlin)* 47, 264–266.

GRIGG, G. C., TAPLIN, L. E., GREEN, B. & HARLOW, P. (1986). Sodium and water fluxes in *Crocodylus porosus* free-living in marine and brackish conditions. *Physiological Zoology* 59 (2), 240–253.

GROOMBRIDGE, P. (1982). *IUCN Amphibia–Reptilia Red Data Book*, part 1. IUCN, Gland, Switzerland.

GUGGISBERG, C. A. W. (1972). *Crocodiles : their Natural History, Folklore and Conservation*. Wren, Victoria.

HEDGPETH, J. W. (1957). *Treatise on Marine Ecology and Palaeoecology*, vol. 1. Geological Society of America, New York.

HUANG CHU-CHIEN, (1978). A general account of our country's amphibian and reptilian resources. *Natural Resources* 2, 92–100.

HUANG CHU-CHIEN, (1982). The ecology of the Chinese Alligator and changes in its geographical distribution. *Proceedings 5th Working Meeting IUCN Crocodile Specialists Group*. Gland, Switzerland.

JOANEN, T. & McNEASE, L. (1972). Population distribution of alligators with special reference to the Louisiana coastal marsh zones. American Alligator Council Symposium, Lake Charles, Louisiana. 12 pp. Mimeograph.

KHALIL, F. & HAGGAG, G. (1960). Xanthine oxidase and arginase in the liver and kidney of reptiles. *Zeitschrift für Vergleichende Physiologie* 43, 269–277.

KING, F. W., CAMPBELL, H. W. & MOLER, P. E. (1982). Review of the status of the American Crocodile. *Proceedings 5th Working Meeting IUCN Crocodile Specialists Group*. Gland, Switzerland.

KIRSCHNER, L. B. (1970). The study of NaCl transport in aquatic animals. *American Zoologist* 10, 365–376.

KOOISTRA, T. A. & EVANS, D. H. (1976). Sodium balance in the green turtle, *Chelonia mydas* in seawater and in fresh water. *Journal of Comparative Physiology* 107, 229–240.

KUSHLAN, J. A. (1982). The status of crocodilians in South Florida., *Proceedings 5th Working Meeting IUCN Crocodile Specialists Group*, Gland, Switzerland.

KUSHLAN, J. A. & MAZOTTI, F. J. (1988). Population biology and status of the American Crocodile in South Florida. *Proceedings 7th Working Meeting IUCN Crocodile Specialists Group*, Gland, Switzerland. (In the Press.)

LANCE, V. & LAUREN, D. J. (1984). Circadian variation in plasma corticosterone in the American Alligator, *Alligator mississipiensis*, and the effects of ACTH injection. *General and Comparative Endocrinology* 54, 1–7.

LANG, H. (1919). Notes in K. P. Schmidt, Contributions to the herpetology of the Belgian Congo based on the collections of the American Congo Expedition (1909–15). *Bulletin of the American Museum of Natural History* 39 (20), 425–435.

LAUREN, D. J. (1985). The effect of chronic saline exposure on the electrolyte balance, nitrogen metabolism, and corticosterone titer in the American Alligator, *Alligator mississipiensis*. *Comparative Biochemistry and Physiology* 81 A (2), 217–223.

LeBRIE, S. J. (1972). Endocrines and water and electrolyte balance in reptiles. *Federation Proceedings* 31 (6), 1599–1608.

LeBRIE, S. J. & ELIZONDO, R. S. (1969). Saline loading and aldosterone in water snakes, *Natrix cyclopion*. *American Journal of Physiology* 217, 426–430.

LeFEVRE, M. D. (1973). Effects of aldosterone on the isolated, substrate-depleted turtle bladder. *American Journal of Physiology* 225, 1252–1256.

MAGNUSSON, W. E. & TAYLOR, J. A. (1981). Growth of juvenile *Crocodylus porosus* as effected by season of hatching. *Journal of Herpetology* 15 (2), 242–245.

MAZOTTI, F. J. (1983). Ecology of *Crocodylus acutus* in Florida. Unpublished Ph.D. Thesis, University of Pennsylvania.

MAZOTTI, F. J. & DUNSON, W. A. (1984). Adaptations of *Crocodylus acutus* and *Alligator* for life in saline water. *Comparative Biochemistry and Physiology* 79 A, 641–646.

MAZOTTI, F. J., BOHNSACK, B., McMAHON, P. & WILSON, J. R. (1986). Field and laboratory observations on the effects of high temperature and salinity on hatchling *Crocodylus acutus*. *Herpetologica* 42 (2), 191–196.

McCANN, C. (1940). A reptile and amphibian miscellany. *Journal of the Bombay Natural History Society* 41 (4), 742–764.

McNEASE, L. & JOANEN, T. (1978). Distribution and relative abundance of the alligator in Louisiana coastal marshes. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 32, 182–186.

MEDEM, F. (1976). Project 748. Orinoco Crocodile – status survey. *World Wildlife Yearbook, 1975–76*, pp. 191–193.

MEDEM, F. (1981a). *Los Crocodylia de Sur America*, vol. 1. Ministeria de Educacion Nacional, Bogota.

MEDEM, F. (1981b). *Los Crocodylia de Sur America*, vol. 2. Ministeria de Educacion Nacional, Bogota.

MESSEL, H. et al. (1979–85). *Surveys of the Tidal River Systems in the Northern Territory of Australia and their Crocodile Populations*. A series of 19 Monographs. Pergamon Press, Sydney.

MESSEL, H. & VORLICEK, G. C. (1984). A review of the growth of *C. porosus* in northern Australia. *Proceedings 6th Working Meeting IUCN Crocodile Specialists Group*, Gland, Switzerland.

MINNICH, J. E. (1979). Reptiles. *Comparative Physiology of Osmoregulation in Animals* (ed. G. M. O. Maloiy), pp. 391–641. Adademic Press, London.

MINNICH, J. E. (1982). The use of water. In *Biology of the Reptilia, Physiology C* (ed. C. Gans and F. H. Pough), vol. 12, pp. 325–395. Academic Press, London.

NEILL, W. T. (1971). *The Last of the Ruling Reptiles : Alligators, Crocodiles and their Kin*. Columbia University Press, N.Y.

OWEN, R. (1866). *On the Anatomy of Vertebrates*. Vol. 1. *Fishes and Reptiles*. Longman, Green, London.

PANG, P. K. T., GRIFFITH, R. W. & ATZ, J. W. (1977). Osmoregulation in elasmobranchs. *American Zoologist* 17, 365–377.

PLOTKIN, M. J., MEDEM, F., MITTERMEIER, R. A. & CONSTABLE, I. D. (1983). Distribution and conservation of the Black Caiman (*Melanosuchus niger*). In *Advances in Herpetology and Evolutionary Biology* (ed. A. G. J. Rhodin and K. Miyata), pp. 695–705. Museum of Comparative Zoology, Cambridge, Massachusetts.

POOLEY, A. C. (1962). The Nile Crocodile *Crocodylus niloticus*. Notes on the incubation period and growth rate of juveniles. *Lammergeyer* 2 (1), 1–55.

POOLEY, A. C. (1971). Notes on the ecology of the Lake St Lucia crocodile population. *Proceedings 2nd Working Meeting IUCN Crocodile Specialists Group*. Gland, Switzerland.

POOLEY, A. C. (1980). The status of crocodiles in Africa – 1980. *Proceedings 5th Working Meeting IUCN Crocodile Specialists Group*, Gland, Switzerland.

POTTS, W. T. W. & PARRY, G. (1964). *Osmotic and Ionic Regulation in Animals.* Pergamon Press, London.

PRITCHARD, D. W. (1952). Estuarine hydrography. *Advances in Geophysics* 1, 243–280.

REESE, A. M. (1915). *The Alligator and its Allies.* Putnam, New York.

REESE, A. M. (1925). The cephalic glands of *Alligator mississipiensis*, Florida alligator, and *Agkistrodon*, Copperhead and Mocassin. *Biologia Generalis* 1, 482–500.

ROBERTSON, J. D. (1963). Osmoregulation and ionic composition of cells and tissues. In *Biology of Myxine* (ed. A. Brodal and R. Fange), pp. 503–515. Universitetsforlaget, Oslo.

ROSE, C. (1893). Über die Nasendruse und die Gaumendrusen von *Crocodylus porosus*. *Anatomischer Anzeiger* 8, 745–751.

ROSENBLATT, M. B. (1936). A chemical study of the blood of *Alligator mississipiensis*. *Journal of Biological Chemistry* 116, 81–86.

ROSS, C. A. (1984). Crocodiles in the Republic of the Phillipines. *Proceedings 6th Working Meeting IUCN Crocodile Specialists Group*, Gland, Swizerland.

SAWYER, W. H. & SAWYER, M. K. (1952). Adaptive responses to neurohypophysial fractions in vertebrates. *Physiological Zoology* 25, 84–98.

SCHMIDT-NIELSEN, K. (1969). The neglected interface: the biology of water as a liquid–gas system. *Quarterly Reviews of Biophysics* 2 (3), 283–304.

SCHMIDT-NIELSEN, B. & DAVIES, L. E. (1968). Fluid transport and tubular intercellular spaces in reptilian kidneys. *Science* 159, 1105–1108.

SCHMIDT-NIELSEN, K. & FANGE, R. (1958). Salt glands in marine reptiles. *Nature* (London) 182, 783–785.

SCHMIDT-NIELSEN, B. & SKADHAUGE, E. (1967). Function of the excretory system of the crocodile (*Crocodylus acutus*). *American Journal of Physiology* 212 (5), 973–980.

SEIDEL, M. E. (1975). Osmoregulation in the turtle *Trionyx spiniferus* from brackish and fresh water. *Copeia* 1975 (1), 124–128.

SHOEMAKER, V. H. & NAGY, K. A. (1977). Osmoregulation in amphibians and reptiles. *Annual Reviews of Physiology* 39, 449–471.

SINGH, L. A. K. & BUSTARD, H. R. (1982). Geographical distribution of the gharial, *Gavialis gangeticus* (Gmelin) in Orissa, India. *British Journal of Herpetology* 6, 259–260.

SKADHAUGE, E. (1977). Excretion in lower vertebrates: function of gut, cloaca and bladder in modifying the composition of urine. *Federation Proceedings* 36 (11), 2487–2492.

SKADHAUGE, E. (1978). Osmoregulation and hormones in reptiles. In *Environmental Endocrinology* (ed. I. Assenmacher and D. S. Farner), pp. 217–221. Springer-Verlag, Berlin.

STOKES, J. D. & DUNSON, W. A. (1982). Permeability and channel structure of reptilian skin. American Journal of Physiology 242, F681–F689.

TAGUCHI, H. (1920). Beitrage zur Kenntnis über die fienere Struktur der Eingeweideorgane der Krokodile. *Mitteilungen aus der Medizinischen Fakultat der K. Japanischen Universitat zu Tokio* 25, 119–188.

TAPLIN, L. E. (1982). Osmoregulation in the Estuarine Crocodile, *Crocodylus porosus*. Unpublished Ph.D. thesis, University of Sydney.

TAPLIN, L. E. (1984a). Homeostasis of plasma electrolytes, sodium and water pools in the Estuarine Crocodile, *Crocodylus porosus*, from fresh, saline and hypersaline waters. *Oecologia* 63, 63–70.

TAPLIN, L. E. (1984b). Drinking of fresh water but not seawater by the Estuarine Crocodile, *Crocodylus porosus*. *Comparative Biochemistry and Physiology* 77 A, 763–767.

TAPLIN, L. E. (1984c). Evolution and zoogeography of crocodilians: a new look at an ancient order. In *Zoogeography and Evolution in Australia – Animals in Space and Time* (ed. M. Archer and G. Clayton), pp. 361–370. Hesperian Press, Perth.

TAPLIN, L. E. (1985). Sodium and water budgets of the fasted estuarine crocodile, *Crocodylus porosus*, in sea water. *Journal of Comparative Physiology* 155 B, 501–513.

TAPLIN, L. E. & GRIGG, G. C. (1981). Salt glands in the tongue of the Estuarine Crocodile. *Science* 212, 1045–7.

TAPLIN, L. E., GRIGG, G. C. & BEARD, L. (1985). Salt gland function in fresh water crocodiles: evidence for a marine phase in eusuchian evolution? In *Biology of Australasian Frogs and Reptiles* (ed. G. C. Grigg, R. Shine and H. Ehmann), pp. 403–410. Surrey Beatty and Sons, Sydney.

TAPLIN, L. E., GRIGG, G. C., HARLOW, P., ELLIS, T. M. & DUNSON, W. A. (1982). Lingual salt glands in *Crocodylus acutus* and *C. johnstoni*, and their absence from *Alligator mississipiensis* and *Caiman crocodilus*. *Journal of Comparative Physiology* 149, 43–47.

TAPLIN, L. E. & LOVERIDGE, J. P. (1988). Nile Crocodiles, *Crocodylus niloticus* and Estuarine Crocodiles, *Crocodylus porosus*, show similar osmoregulatory responses on exposure to seawater. Comparative Biochemistry and Physiology. 89A: 443–448.

THORSON, T. B. (1968). Body fluid partitioning in Reptilia. *Copeia* 1968 (3), 592–601.

TROBEC, T. N. & STANLEY, J. G. (1971). Uptake of ions and water by the painted turtle, *Chrysemys picta. Copeia* 1971 (3), 537–542.

VARONA, L. S. (1966). Nota sobre los Crocodilidos de Cuba y descripcion de una nueva especie del Pleistoceno. *Poeyana* 16 A, 1–34.

VARONA, L. S. (1976). *Caiman crocodilus* en Cuba. *Miscellanea Zoologica* 5, 2.

VILLIERS, A. (1958). Tortues et Crocodiles de l'Afrique Noire Française. *Inst. Française d'Afrique Noire, Initiations Africaines* 15, 1–354.

VOIGHT, W. G. & JOHNSON, C. R. (1976). Aestivation and thermoregulation in the Texas tortoise, *Gopherus berlandieri. Comparative Biochemistry and Physiology* 53 A, 41–44.

WEBB, G. J. W., MESSEL, H., CRAWFORD, J. & YERBURY, M. J. (1978). Growth rates of *Crocodylus porosus* (Reptilia: Crocodylia) from Arnhem Land, northern Australia. *Australian Wildlife Research* 5, 385–399.

WHITAKER, R. (1980). Assistance to the crocodile skin industry, Papua New Guinea. Interim report on the status and biology of crocodiles in Papua New Guinea. Field Document no. 1, Wildlife Division, Department of Lands and Environment, PNG.

WHITAKER, R. & BASU, D. (1983). The gharial (*Gavialis gangeticus*): a review. *Journal of the Bombay Natural History Society* 79 (3), 531–548.

WHITAKER, R. & WHITAKER, Z. (1978). Preliminary crocodile survey – Sri Lanka. *Journal of the Bombay Natural History Society* 76 (1), 66–85.