

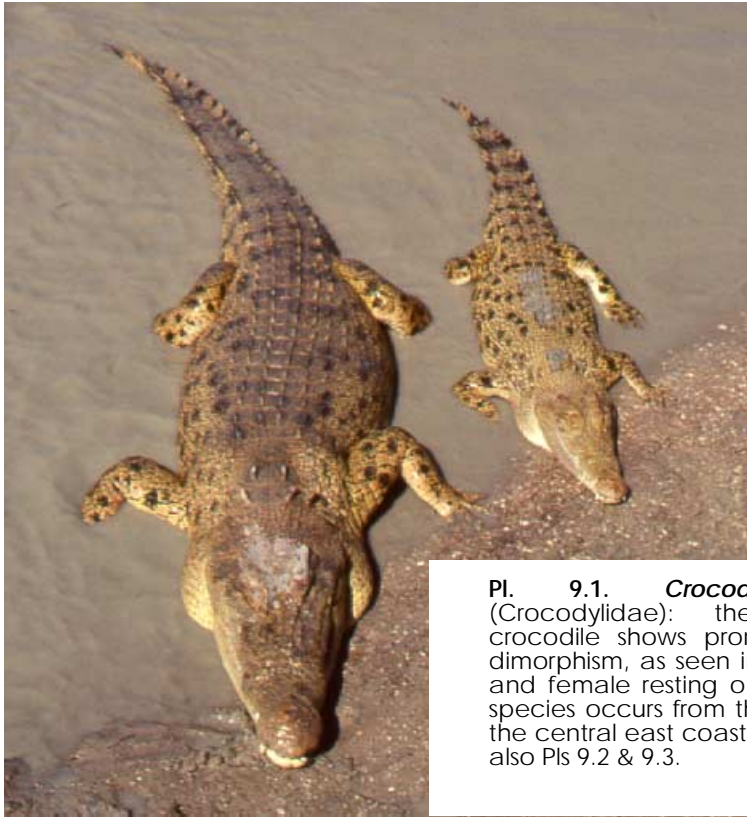


FAUNA *of* AUSTRALIA



40. MORPHOLOGY & PHYSIOLOGY OF THE CROCODYLIA

Gordon Grigg & Carl Gans



Pl. 9.1. *Crocodylus porosus* (Crocodylidae): the salt water crocodile shows pronounced sexual dimorphism, as seen in this male (left) and female resting on the shore; this species occurs from the Kimberleys to the central east coast of Australia; see also Pls 9.2 & 9.3. [G. Grigg]



Pl. 9.2. *Crocodylus porosus* (Crocodylidae): when feeding in the water, this species lifts the tail to counter balance the head; see also Pls 9.1 & 9.3. [G. Grigg]



Pl. 9.3. *Crocodylus porosus* (Crocodylidae): the snout is broad and rounded, the teeth (well-worn in this old animal) are set in an irregular row, and a palatal flap closes the entrance to the throat; see also Pls 9.1 & 9.2. [G. Grigg]



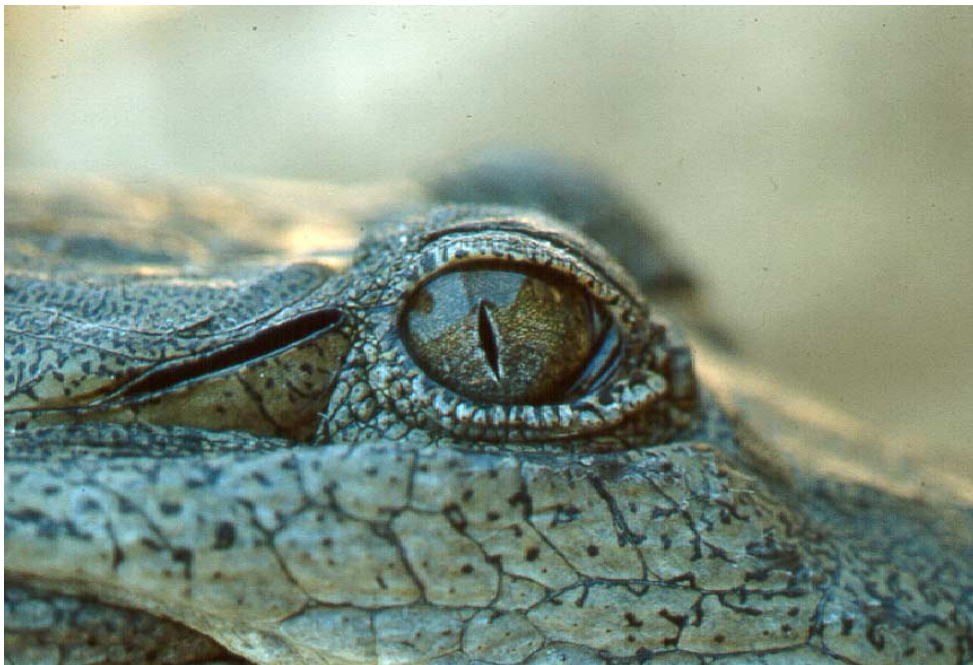
Pl. 9.4. *Crocodylus johnstoni* (Crocodylidae): the freshwater crocodile is found in rivers and billabongs from the Kimberleys to eastern Cape York; see also Pls 9.5–9.7. [G.J.W. Webb]



Pl. 9.5. *Crocodylus johnstoni* (Crocodylidae): the freshwater crocodile increases its apparent size by inflating its body when in a threat display; see also Pls 9.4, 9.6 & 9.7. [G.J.W. Webb]



Pl. 9.6. *Crocodylus johnstoni* (Crocodylidae): the freshwater crocodile has a long, slender snout, with a regular row of nearly equal sized teeth; the eyes and slit-like ears, set high on the head, can be closed during diving; see also Pls 9.4, 9.5 & 9.7. [G.J.W. Webb]



Pl. 9.7. *Crocodylus johnstoni* (Crocodylidae): the eyes and the slit-like ears are set high on the head, and can be closed during diving; see also Pls 9.4–9.6. [G. Grigg]

EXTERNAL CHARACTERISTICS

The 22 species of extant crocodilians (Order Crocodylia) are remarkably similar. Various morphological details have been used to subdivide them into three families, the Alligatoridae (the caimans, *Caiman*, *Palaeosuchus*, *Melanosuchus*, and alligators *Alligator*), the Crocodylidae ('true' crocodiles, *Crocodylus* and dwarf crocodile *Osteolaemus*) and the Gavialidae (the Gharial *Gavialis* and False Gharial *Tomistoma*) whose affinities are uncertain within and without the group. Australia has two species of crocodiles, the saltwater or estuarine crocodile, *Crocodylus porosus* and the freshwater crocodile, *C. johnstoni*. Readable and well-illustrated reviews of the biology of world crocodilians may be found in Webb & Manolis (1989) and Ross (1989).

The remarkably homogeneous extant species are the remnants of a large radiation which peaked in the Mesozoic. Their hard parts are impressively similar to those of fossil forms of the Triassic (see Steel 1973). The three extant lineages were distinct by the Upper Cretaceous. With the birds, they are the only surviving archosaurs, the group which included the dinosaurs. Relationships between the modern crocodilians have been examined extensively (Cohen & Gans 1970; Densmore & Owen 1989; Densmore & White 1991).

These large amphibious and carnivorous reptiles inhabit tropical and subtropical lakes, rivers and coasts. They lay their eggs in nests constructed on land. Their morphology and physiology have been shaped by similar lifestyles, allowing many generalisations about the group of crocodilians as a whole. Research work, concentrating on the few more easily available species, has emphasized homogeneity within the group rather than differences among its members.

Body Form and Size

Crocodilians are sturdy lizard-shaped reptiles, with a well-armoured head and trunk and with horny skin and scales, reinforced with bony plates (Pl. 9). In modern Crocodylia, at least, the head is generally flattened and the snout elongated. The nasal capsules lie near the tip of the snout, and nostrils which can close in the external nares tend to be raised above the tip of the snout; thus submerged crocodilians are inconspicuous when drifting toward terrestrial prey. Members of the Alligatoridae tend to have broad snouts (Fig. 40.1A, B), whereas those of the Crocodylidae range from broad to long and slender (Fig. 40.1C, D). In gavialids the snout is extremely slender (Fig. 40.1E, F).

Crocodilians have laterally compressed tails, webbed hind feet, and the nostrils, eyes and ears are placed high along the head and snout, all consonant with aquatic habits (Pl. 9.3, 9.7). Skull and jaws are solid and together with the strong peg-like teeth can maintain an effective hold on prey. The palatal flap, a rigid plate of tissue at the rear of the oral cavity, closes the posterior buccal space (oesophagus and glottis) against the entry of water. A well-developed hard palate permits ventilation from nostril to glottis, bypassing the mouth (Fig. 40.2). The nostrils can be closed tightly during submergence.

Adult crocodilians are large and species show an enormous size range. The smallest are species of *Palaeosuchus* and *Osteolaemus* which grow to an adult size of 1 to 1.5 m. Males of *Crocodylus porosus* more than 7 m in length and weighing perhaps 2000 kg, are the largest of the extant reptiles. Crocodilians show a pronounced sexual dimorphism. Males grow larger and often more rapidly than females, even though they attain sexual maturity at an equivalent age (Pl. 9.1). Apart from size, there is no external indication of sex. The alimentary, urinary and reproductive systems open to the exterior via the midventral longitudinal slit of the cloaca.

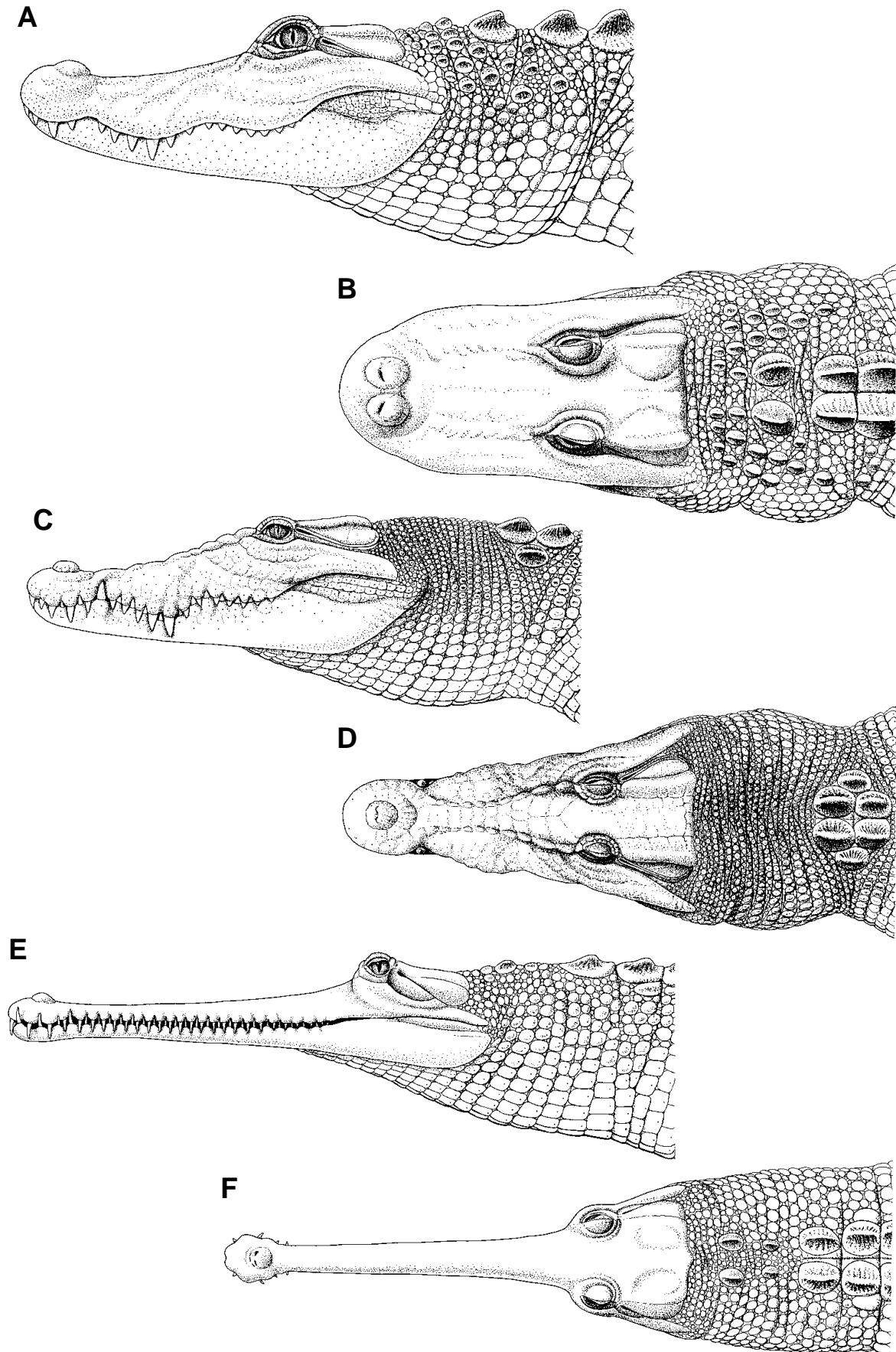


Figure 40.1 Head shapes and dentition in Crocodylia. **A, C, E**, lateral views; **B, D, F**, dorsal views; **A, B**, Alligatoridae; **C, D**, Crocodylidae; **E, F**, Gavialidae. [D. Kirshner]

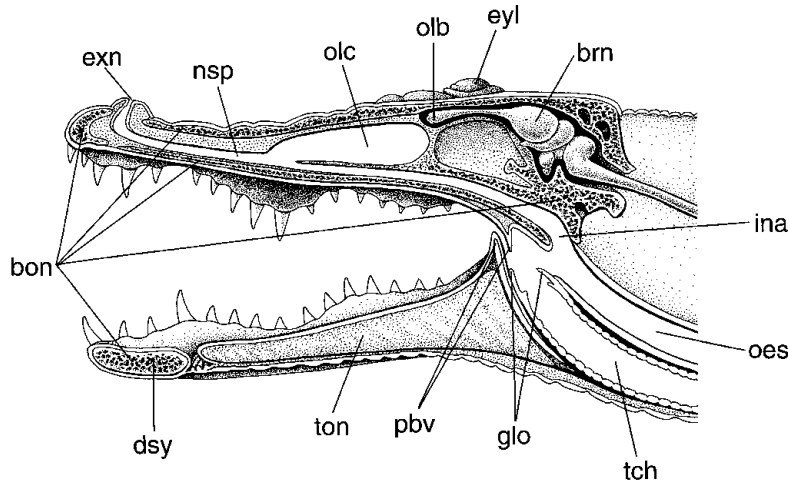


Figure 40.2 Sagittal section of the head of *Crocodylus porosus*. **bon**, bones of the skull; **brn**, brain; **dsy**, dentary symphysis; **exn**, external nares; **eyl**, eyelid; **glo**, glottis; **ina**, internal nares; **nsp**, nasal passages; **oes**, oesophagus; **olb**, olfactory bulb; **oic**, olfactory chamber (location of conchae); **pbv**, palato-buccal valve; **tch**, trachea; **ton**, tongue. [D. Kirshner]

Skin and Scalation

The skin is covered with keratinised scales, or scutes, many of which are reinforced with bony plates, or osteoderms. Interspecific differences in scales can be used for identification (Brazaitis 1987). Osteoderms are most prevalent in the dorsal and nuchal scutes which commonly bear conspicuous ridges, and in the belly scales of some species. The nuchal, dorsal and some of the rectangular and keeled scutes are covered by hard, wear-resistant beta-keratin. Since they are vascularised, scutes may act as heat absorbers or radiators (see Thermoregulation). The fields of scutes are embedded in the intermediate skin under a covering of alpha-keratin which provides an important barrier to water and electrolyte exchange. This facilitates the homeostasis of body fluids in a wide range of salinities (see Salt and Water Regulation). Flexible skin covers the neck and the flanks, whereas the abdomen and sides of the tail are sheathed in large, flat, squarish scutes arranged neatly in rows.

Crocodilian scales bear a pore that is generally thought to be sensory, analogous to the lateral line of fishes. Higher densities of small scales around the head, particularly on the upper and lower jaws (Pl. 9.3, 9.6), concentrate this supposed mechanosensory apparatus. Alternatively, the pores could be a source of a detergent-like or oily substance (perhaps a modification of betakeratin) since mud seems to flush off them easily in the wild.

Often the prominent paired gular and paracloacal integumentary glands are everted at capture. The gular glands lie in ventral folds of skin at the angles of the jaw and the paracloacal glands are embedded in the lateral walls of the cloaca. Their holocrine secretions are primarily lipid. The histology of the gular glands has been described in *Alligator mississippiensis* and *C. porosus* (Weldon & Sampson 1988; Wright & Moffat 1985). Secretions analysed from both pairs of glands in most crocodilian species contain sterols, free fatty acids, triglycerides, steryl esters and aliphatic alcohols and, commonly, hydrocarbons (Weldon, Scott & Tanner 1990; Weldon & Tanner 1991). The proportions differ between sexes, and among glands and individuals for the gular and paracloacal glands, suggesting different functions. Secretions, presumably from the paracloacal glands, could be detected in the air after a headslap in

A. mississippiensis; an oily sheen, then appeared on the water surface (Vliet 1989). LeBuff (1957) suggested that alligators spray secretions from the gular glands while bellowing, but the volume of material would seem to be insufficient for that. Wright & Moffat (1985) speculated on a glandular role in predator deterrence. Immature alligators respond to exudates of both glands by increased rates of gular pumping (Johansen & Wellington 1982; see Sense Organs), suggesting that a pheromonal role in intraspecific communication is quite likely. Pooley (pers. comm.) noted that female *C. niloticus* rub their chin glands over males before nesting, and during courtship each investigates the other's head and tail base and rubs its gular area over the other's head (Kofron 1991). Clearly pheromonal chemistry deserves more study.

MUSCULAR SYSTEM

The crocodilian muscle masses seem to reflect the general tetrapod pattern (Frey 1988a, 1988b). Until recently, they have been described mainly on the basis of juveniles, in spite of the fact that their proportions change allometrically. Also, the few studies of functional analysis reflect particular species. The obvious differences in muscular types or relative masses among species have yet to be documented.

The crocodilian muscles reflect the general short fibre phenomenon (Gans & Gaunt 1992). Jaw closing muscles appear to be much more massive than the openers and the jaws of even of medium-sized specimens can be held shut comparatively easily, especially when coupled with the leverage attainable by grasping the snout. Much of aquatic propulsion depends on the axial musculature. However, terrestrial locomotion is effected by the muscles of limbs and the associated girdles. Some ventilation is powered by the intercostals, but much of inhalation reflects the contraction of the *m. diaphragmaticus*, a striated muscle that connects the liver to the pelvic girdle (Gans & Clark 1976).

SKELETAL SYSTEM

The crocodilian skeleton is typical of that of tetrapods in general and of archosaurs in particular, with the skull and pelvis particularly specialised (Romer 1956). Also of interest are the structure of the head vertebrae (atlas and axis), the osteoderms, and the gastralia, or stomach ribs, which protect the ventral surface. Steel (1973), Iordansky (1973) and Langston (1973) provide useful reviews of the structure of both modern and extinct crocodilian skulls.

As archosaurs, crocodilians are diapsid, although the post-temporal fenestrae are reduced. Palatal and external mandibular fenestrae (Fig. 40.3) and ossified laterosphenoids are present. The wall of the braincase is ossified, but supratemporals and postfrontals are absent. The pterygoid and quadrate adhere tightly to the lateral wall of the braincase and the otic notch closes posteriorly. All species lack a parietal (pineal) foramen. The premaxillae are expanded postero-dorsally, isolating the external nares from the maxillae. Internal nares are prolonged posteriorly by a secondary palate formed of the palatal processes of the premaxillae, maxillae, palatines and pterygoids and the secondary choanae open within the pterygoids (Fig. 40.3).

The premaxilla, maxilla and dentary bear peg-like conical thecodont teeth (Iordansky 1973). The largest teeth of the upper jaw are premaxillary 4 in the Alligatoridae, premaxillary 5 in the Crocodylidae, and maxillary 9 and 11 and dentary 1, 4, 11 and 12 throughout this group. The vertically undulating jawline coincides with the distribution of the largest teeth, thus accentuating the pseudoheterodonty, particularly in the shorter-snouted species. In the long-snouted, fish-eating crocodilians, the teeth are more uniform in size, approaching a homodont condition, and the jawline is straight rather than

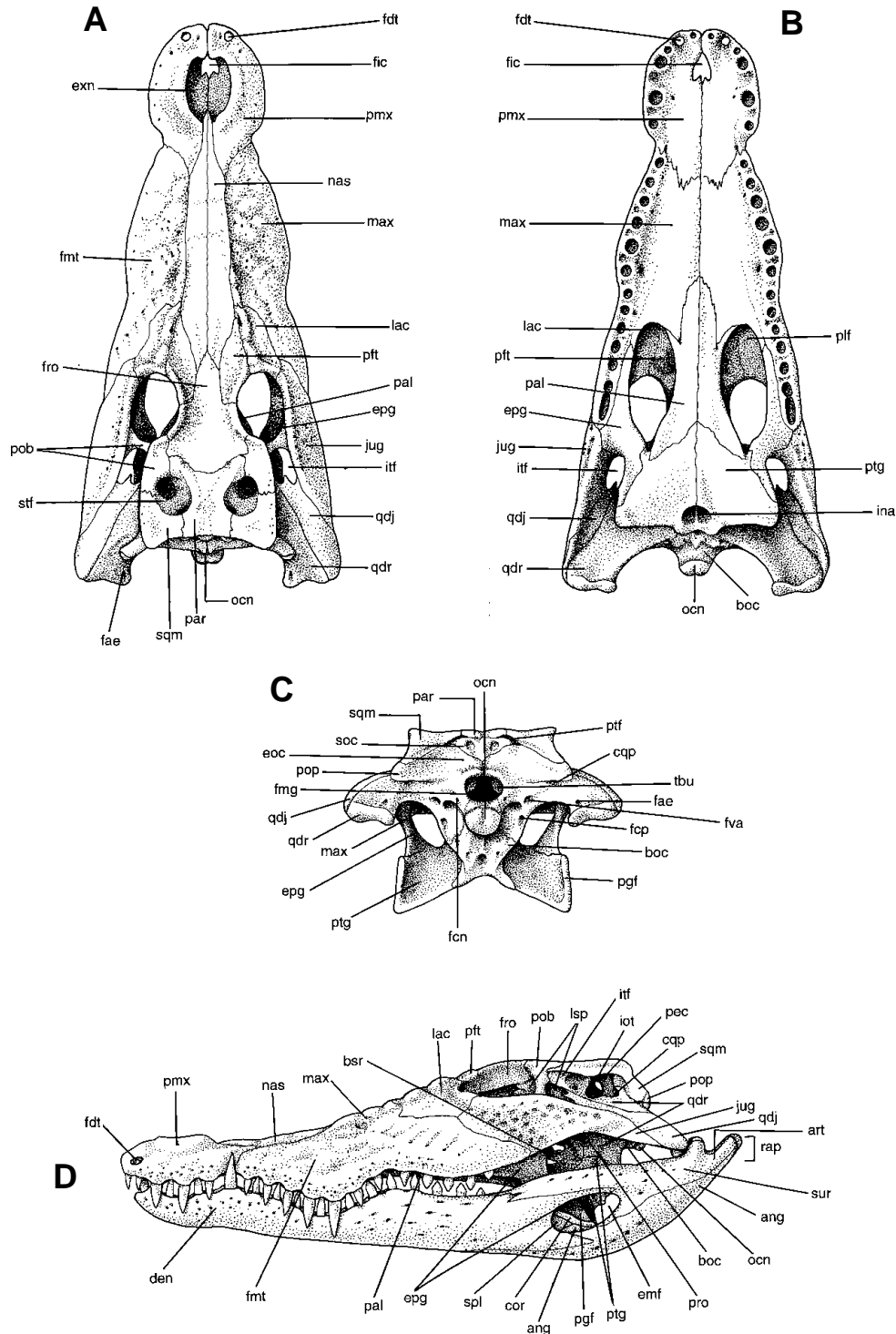


Figure 40.3 Skull of *Crocodylus porosus*. **A**, dorsal view; **B**, ventral view; **C**, posterior view; **D**, lateral view. **ang**, angular; **art**, articular; **boc**, basioccipital; **bsr**, basisphenoid rostrum; **cor**, coronoid; **cqp**, cranio-quadrato passage; **den**, dentary; **emf**, external mandibular fenestra; **eoc**, exoccipital; **epg**, ectopterygoid; **exn**, external nares; **fae**, foramen aëreum; **fcn**, foramen of cranial nerve XII; **fcp**, foramen caroticum posterius; **fdt**, foramen for first dentary tooth; **fic**, foramen incisivum; **fmg**, foramen magnum; **fmo**, swelling over alveolus of fifth maxillary tooth; **fro**, frontal; **fva**, foramen vagi; **ina**, secondary choanae (internal nares); **iot**, incisura otica; **itf**, inferior temporal fossa; **jug**, jugal; **lac**, lacrimal; **lsp**, laterosphenoid; **max**, maxilla; **nas**, nasal; **ocn**, occipital condyle; **pal**, palatine; **par**, parietal; **pec**, transverse canal between middle ear cavities; **pft**, prefrontal; **pgf**, lateral pterygoid flange; **plf**, palatal fenestra; **pmx**, premaxilla; **pob**, postorbital; **pop**, paraoccipital process; **pro**, prootic; **ptf**, posttemporal fenestra; **ptg**, pterygoid; **qdj**, quadratojugal; **qdr**, quadrate; **rap**, retroarticular process; **soc**, supraoccipital; **spl**, splenial; **sqm**, squamosal; **stf**, superior temporal fossa; **stp**, supraoccipital; **sur**, surangular; **tbu**, tympanic bulla.

undulating. In the Alligatoridae, the 4th dentary tooth fits into a pit in the upper jaw at the junction of premaxilla and maxilla, and the mandibular tooth rows lie inside the upper tooth rows at occlusion. In the Crocodylidae and Gavialidae, upper and lower teeth alternate at occlusion, and the 4th dentary tooth fits into a lateral notch at or near the junction of the pre-maxilla with the maxilla. Thus the teeth of crocodiles are far more conspicuous than those of alligators when the mouth is closed. Teeth generally are replaced continuously with new ones growing from below in the same socket, but this process slows down and stops in older individuals; some of the largest individuals are likely to be edentulous.

Cranial sculpturing becomes more complex with age as a result of secondary dermal ossifications on the dorsal surface. Some (*Osteolaemus* species and *Palaeosuchus palpebrosus*) have palpebral osteoderms in the upper eyelids. The middle ear region is modified extensively, and the quadrate is inclined so that the hinge of the jaw is displaced far posteriorly. Cranial growth is allometric and the naris-eye dimension increases several times faster than that between eye and condyle. As the olfactory bulbs lie close to the nares, the proportions of the brain reflect those of the skull.

Many cranial bones are pneumatized, and have gas-filled cavities connected to the Eustachian tubes of the middle ear and the nasal passages. These may equalise pressure in the inner ear (Colbert 1946), or isolate the inner ear from underwater sounds when listening above water (Iordansky 1973). However, pneumatization also reduces the cranial mass (and inertia), while maintaining its strength, which is an important consideration in both buoyancy and feeding.

The nine cervical vertebrae are keeled ventrally. The last two to five of the 15 to 16 dorsal vertebrae lack free ribs. The caudal vertebrae bear relatively long neural and haemal spines, as well as chevron bones on the anterior two-thirds. The cervical ribs are solid and the dorsal ones articulate ventrally with two partly calcified elements, the ventral-most of which reaches the sternal system. The most superficial gastralia are located between the sternal region and the pelvic girdle. The shoulder girdle is simple and plate-like, and the three components of the pelvic girdle radiate from the articular fossa.

LOCOMOTION AND BUOYANCY

Crocodylians are amphibious, but travel most easily in water which they traverse with sinuous movements of the strong, laterally compressed tail, holding the limbs at the sides. On land they have several gaits (Brinkman 1980; Kálin & Knüsel 1944; Parish 1987): walking, high walking with the body held clear of the ground, running and, in some species, a galloping gait in which limbs of the two sides move in unison, driven by dorsoventral flexion of the vertebral column (Fig. 40.4). They also undulate down steep slopes. Galloping is a conspicuous escape movement in *C. johnstoni* (Webb & Gans 1982). Although they can travel at great speed, such bursts are shortlived as they are sustained by anaerobic metabolism. Crocodiles can travel substantial distances both overland (Pooley & Gans 1976; Webb pers. comm.) and by sea (Walsh & Whitehead 1993).

They are excellent swimmers, under water or at the surface. When chasing or fleeing from other individuals, as is common in the breeding season, they may plane along the water surface, driven by the thrashing tail (Pl. 9.2). The anterior half of the chest and abdomen serve as a hydroplane, and creating significant bow wave and wake in the process. The tail can be used to accelerate the body completely out of the water or to launch a rapid lunge at prey. However, most movements made by crocodylians are silent and surreptitious, often with only the

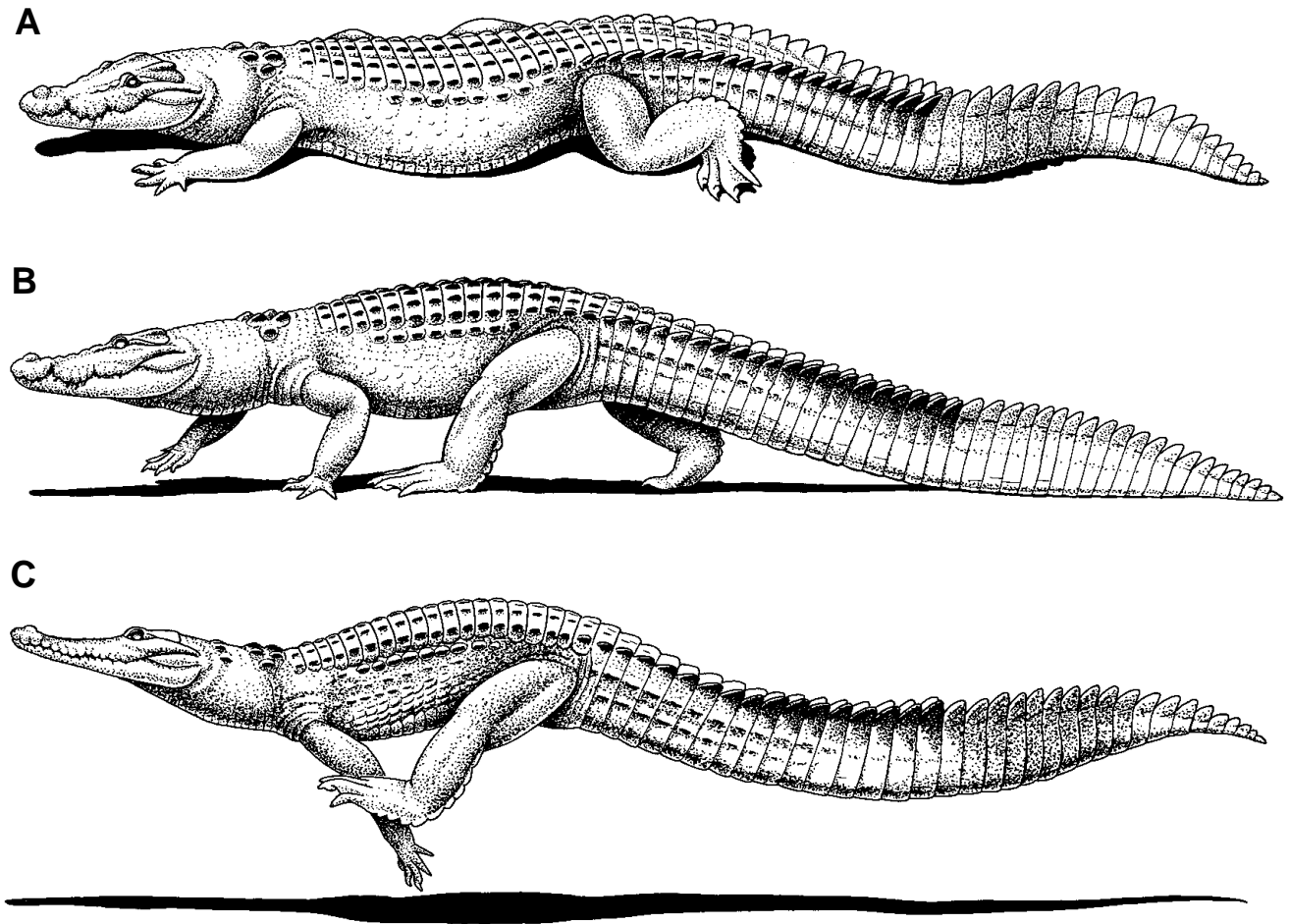


Figure 40.4 Gaits of crocodiles on land. **A**, *Crocodylus porosus* walking; **B**, *C. porosus* high walking; **C**, *C. johnstoni* galloping. [D. Kirshner]

nostrils, eyes and the top of the skull platform emergent. They brace themselves against the bottom with the hind legs and tail to anchor themselves in a current and use tidal currents to provide low energy transport up and down estuaries.

Crocodylians manage their buoyancy very skilfully. They are denser than water (Kirshner 1985), and achieve neutral buoyancy by appropriate inflation of the lungs. Shallowly breathing crocodilians are able to float at the water surface for long periods, the water line constant within a couple of millimetres just below the eye (Fig. 41.3). They are able to lie immobile on the bottom between breaths for many minutes, or hours in larger individuals (see Respiration). It is unlikely that pulmonary volume can be modified by muscular contraction during a dive, but negative buoyancy increases with depth as the lungs are compressed and as oxygen is removed and replaced with a smaller volume of carbon dioxide.

Most larger crocodilians accumulate gastroliths (stomach stones), including individuals which live in areas where stones are uncommon, implying that some effort may be made to collect them. Larger crocodiles have a larger burden of stones (Cott 1961). Buoyancy hypotheses have been considered in some detail by Kirshner (1985) in relation to experiments performed on juvenile *C. porosus*. The gastroliths do not increase specific gravity, because the crocodiles compensate for added load by inhaling more deeply. Consideration of ontogenetic changes in body proportions tends to support the views of Cott (1961) and Brander (1925), who argue that the stones may function as a counterpoise for the weight of the head, which increases proportionally with increasing age.

Some authors have suggested that the gastroliths have digestive significance (see Chapter 41), analogous to the role of gravel in the avian gizzard in the trituration of foods. This hypothesis is, however, unconvincing and the counterpoise one remains most likely (Kirshner 1985).

FEEDING AND DIGESTION

Crocodylians are carnivorous, sit-and-wait predators, which rely on swift attack from the water to seize large terrestrial prey and immobilise it before it is swallowed. Smaller prey is commonly taken by a sideways strike of the head, which reduces the change of cranial momentum. It may then be broken up by being lifted from the water and ‘whiplashed’, in a similar manner to that used by monitor lizards. Large prey may be stored until it starts to disintegrate. In cooperative feeding, several individuals grasp a single prey item and dismember it by twisting in opposite directions.

The hard palate and the palatal flap at the back of the buccal cavity allow food to be held in the mouth for long periods without interrupting the respiratory flow, while prey is dismembered or drowned. Food is commonly picked up near the anterior tips of the jaws. It is repositioned and shifted toward the oesophagus, by inertial feeding (Gans 1969), in which the jaws quickly release and shift the food to a new position before it can fall far. This is obviously more effective in air than in water and, in addition to breathing, may explain why ingestion usually occurs with the head above the water. The head is then lifted clear of the water and the tail is lifted as a counterbalance if the prey object is large. To pick up food on land, a crocodilian turns the head and much of the body to the side, as the neck is comparatively inflexible (Fig. 41.2).

The crocodilian gut is comparatively short and simple and the viscera are typically reptilian (Chiasson 1962). General reviews of digestion and the digestive system in reptiles are given by Dandridge (1974), Parsons & Cameron (1977), and Guard (1980). Chunks of food are swallowed whole and pass to the stomach via a long oesophagus. The stomach lies posterior to the heart, which is positioned about midway between the front and rear limbs. The cardiac sphincter occurs at the junction of the oesophagus with the cardiac sac at the left anterior corner of the stomach. The cardiac sac is divided into left and right halves by a thick collar of muscle and spongy tissue, which may operate as a gizzard. The pyloric region is much smaller, and opens to the duodenum via a pyloric sphincter (Chiasson 1962). It is likely that the cardiac (or fundic) stomach has a glandular epithelium which secretes HCl and pepsinogen, whereas the pyloric portion secretes mucus. As crocodilians do not secrete chitinases (Jeuniaux 1963), chitinous and keratinous remains, snail opercula and fur accumulate in crocodilian gut contents. Such indigestible remnants are likely to be cast out via the mouth, as in many avian species. Though data from the wild are lacking, ejection of hair and fur balls by captive occurs routinely.

Crocodylians digest flesh and bones fully, including that from fresh carcasses, and cache only very large prey for its initial dismemberment. Concerning control mechanisms, gastrin/ cholecystekinin-like hormones are secreted by the pyloric mucosa, and emphasise the similarity of Crocodylia to other vertebrates. Further studies are needed of the nature of digestive enzymes and the control of digestion.

THERMAL RELATIONS

Crocodylians are ectotherms. Their body temperature reflects their behaviour in relation to the thermal heterogeneity of the habitat (see Chapter 41), modified to some extent by physiological mechanisms. Reptilian thermoregulation has been reviewed comprehensively by Huey (1982), Bartholomew (1982) and Avery

(1982). The thermal relations of crocodilians are affected markedly by their large size and by the long time they spend in water. Except for large individuals (Grigg 1977), body temperatures will therefore be at or near ambient water temperature much of the time, commonly 25° to 28°C for *C. porosus* in northern Australian estuaries (Messel *et al.* 1979–85). During the day, crocodilians often leave the water to bask (Pl. 9.4). Rates of temperature increase are governed by thermal time constants, which are strongly mass-related (Grigg, Drane & Courtice 1979), and thus heating is quite slow in large individuals. Radiotelemetered and directly observed values from animals on a thermal gradient or in a naturalistic captive environment show that temperature in active individuals ranges from about 25° to 35°C, and mainly between 30° and 33°C. These values are comparatively low for reptiles. Indeed, upper lethal temperatures seem to be in the vicinity of 35°C (Grigg pers. obs.). As crocodilians live in many places where ambient air temperatures are higher than this, they need to avoid high temperatures frequently by seeking shade or by returning to the water. *Crocodylus porosus* sometimes coat themselves with a thick layer of mud, which presumably assists in reducing insolation.

Thermoregulatory behaviour seems to be more pronounced in alligators and caimans, which inhabit thermally variable environments, than in crocodiles (Lang 1987). Basking, shade-seeking, and shifts into and out of water are the most important thermoregulatory behaviours; size is implicated also, particularly whenever thermoregulation is augmented by physiological mechanisms. Large individuals have some measure of thermal stability because of their high thermal inertia during heating and cooling (Grigg 1977; Grigg, Taplin, Harlow & Wright 1980); no studies in the wild have been reported. Also, large reptiles in general may heat rapidly but cool more slowly (thermal hysteresis; Fraser & Grigg 1984) as the result of lower thermal conductance during heating. Thermal hysteresis has been documented in the Alligatoridae (Smith 1975a, 1976c, 1976d, Smith, Standora & Robertson 1984) and Crocodylidae (Grigg & Alchin 1976; Grigg *et al.* 1980; Loveridge 1984). The change in thermal conductance is affected by control over dermal blood flow (Grigg & Alchin 1976), particularly flow to the scutes of the limbs (Turner & Tracy 1983) which are particularly well supplied with blood vessels. The importance of thermal hysteresis in the wild animals remains to be determined.

Crocodilians sometime select specific body temperatures with a degree of precision. Thus larger hatchlings of both Alligatoridae and Crocodylidae in a thermal gradient select higher temperatures (+1.5° to 4.0°C) after feeding and lower ones during fasting (reviewed by Lang 1987). Increased temperatures may reduce digestion time. Selection of lower temperatures may conserve energy in larger individuals because of the effect of temperature on metabolic rate. Grigg (1978) and Smith (1975b) have reported quite high Q_{10} values in crocodilians (2.7 to 3.1), suggesting markedly enhanced energy conservation at low body temperatures. Another example of selection of high temperatures is described Lang (1987) as ‘behavioural fever’, in which juvenile American alligators increased their temperatures by 2° to 5°C following infection with the pathogenic bacterium, *Aeromonas hydrophila*. The thermophily has been interpreted as a mechanism for resisting the infection, in a manner analogous to the endothermic fever developed in infected birds and mammals.

There are some exceptions to the preceding generalisations about crocodilian thermoregulation. Some caimans, such as both species of *Palaeosuchus*, live in jungle streams where the closed canopy suggests they have minimal, if any, basking behaviour. They may construct their nests near termite mounds, the warmth of which may facilitate incubation of the eggs (Magnusson, Lima & Sampaio (1985); see also Reproduction). Similarly, in winter the body temperature of American alligators may drop to 5°C in very cold water. Some have been observed under an ice-layer, but they maintain an open breathing hole

(Brisbin, Standora & Vargo 1982). *Crocodylus johnstoni* in northern Australia and *C. niloticus* in southern Africa also become dormant in the cooler, dry season (Walsh 1989; Pooley 1982), and retreat into caverns excavated or enlarged in river banks.

RESPIRATION AND CIRCULATORY SYSTEM

Lungs and Ventilation

The paired lungs are well developed and well perfused, and lie in the thorax, served by a trachea which originates anteriorly in a glottis which can be closed. The latter lies on the floor of the posterior pharyngeal cavity and is supported by the cartilaginous hyoid plate. Interestingly, in large *C. porosus* and perhaps in other species, the trachea forms a large loop in the upper thorax, reminiscent of a water-trap, but its function is unknown. The anatomy and functioning of the respiratory system have been described by Gans & Clark (1976). During ventilation the glottis is lifted into close proximity to the internal nares, and the gases then pass above the secondary palate to and from the exterior via the external nares (Fig. 40.2). The palatal flap at the rear of the buccal cavity prevents the entry of water into the posterior pharynx, even when the open mouth holds prey. During swallowing, the glottis is closed and depressed, and the palatal flap opened.

In crocodilians, the liver is connected to the body wall by an annulate connective tissue sheet which divides the pleural and visceral cavities (Fig. 40.5). Inspiration is effected by contraction of portions of the intercostal muscles which distend the rib cage, and of the *m. diaphragmaticus* which retracts the liver caudally. Expiration is by contraction of the superficial intercostal muscles, and of the transverse abdominal muscles which move the liver forward, thereby decreasing the pleural volume.

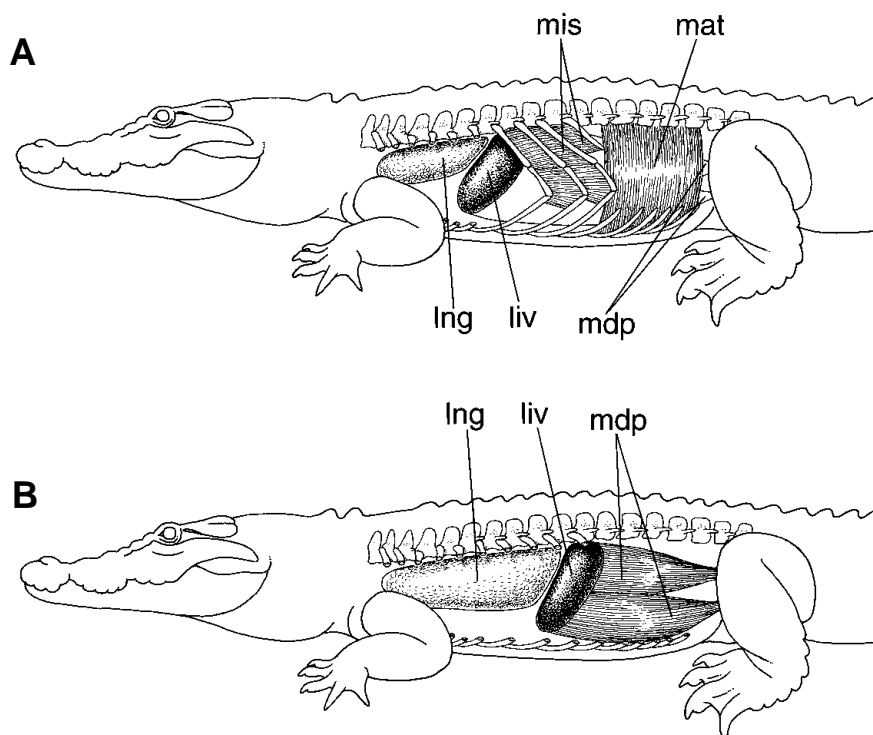


Figure 40.5 Respiration in *Crocodylus porosus*. **A**, expiration; **B**, inspiration. **lng**, lungs; **liv**, liver; **mat**, *m. abdominalis transversus*; **mdp**, *m. diaphragmaticus*; **mis**, *m. intercostalis superficialis*. [D. Kirshner]

Apart from their importance as an oxygen store and a carbon dioxide sink, crocodilian lungs are important in controlling buoyancy. Indeed, the volume of the lungs in a swimming or diving individual is determined by buoyancy requirements, not oxygen store demands (Kirshner 1985). Wright & Kirshner (1987) report that whereas the relationship of oxygen requirements with body mass has an exponent of approximately 0.75, buoyancy requirements scale with body mass at 0.91, almost in direct proportion. This implies an increased maximum duration of aerobic dives in larger individuals. Thus, at 25°C a resting 1000 kg animal would be able to undertake aerobic submergences of approximately 110 minutes, compared to 20 minutes for a 1 kg animal.

Heart and Circulation

Functionally the crocodilian heart appears to be the most sophisticated of all vertebrate hearts. Unlike other reptiles, crocodilians have a complete four-chambered heart with two atria and two ventricles. Structure and pressure balance are similar to those of birds and mammals, with a high pressure (60 to 100 mm Hg) systemic circuit and a low pressure (15 to 20 mm Hg) pulmonary circuit. However, as detailed below, the system also incorporates a number of unusual features which endow strong pulmonary bypass capabilities.

The major anatomical and functional specialisations (Fig. 40.6) have been the focus of much interest and speculation for more than 150 years (Panizza 1833b). Firstly, the left systemic arch persists as a small vessel which leaves from the right ventricle, alongside the pulmonary arch! It runs dorso-laterally above the lungs to join the dorsal aorta (right systemic arch) via a small connecting vessel. However, anatomy suggests that most of its flow would be directed towards the coeliac artery rather than the dorsal aorta (Fig. 40.6). Secondly, left and right systemic arches communicate where they cross, via a small foramen of Panizza in their common wall. Functional aspects of this unusual anatomy have been studied by many workers in many species (White 1970; Webb 1979a; Greenfield & Morrow 1961; Sabatier 1873; Pettersen, Axelsson & Nilsson 1992; Grigg & Johansen 1987; Axelsson, Fritsche, Holmgren, Grove & Nilsson 1991).

The persistence of the left systemic arch and its connection from the right ventricle to the coeliac artery and the dorsal aorta affords a pulmonary bypass shunt (Grigg 1989, 1992). Normally, blood enters the left aorta from the right aorta via the foramen of Panizza, and the valves at the base of the left aorta remain closed to the right ventricle because its pressure remains lower than that in the left aorta. Hence, the left aorta normally carries well-oxygenated blood which reflects its origin from the right aorta. However, towards the end of aerobic breath-hold dives, and probably in anaerobic dives as well, the blood pressure rises in the right ventricle under the influence of pulmonary circuit vasoconstriction. At this stage, some low oxygen blood, otherwise destined for the lungs, is directed into the left aorta and then towards the gut; it does not mix with any of the oxygenated blood until downstream of the dorsal confluence, and thus preserves a well-oxygenated supply for the head and brain. The circumstances under which this extraordinary pulmonary bypass is used under natural conditions still require study, perhaps by radiotelemetry of the flow from the major vessels.

Grigg (1989, 1992) has speculated that the shunt pathway may even allow a complete shutdown of the pulmonary circuit, perhaps during anaerobic respiration, and the whole body is then supported by perfusion driven by the single right ventricle. Indeed, Pettersen *et al.* (1992) experimentally blocked both pulmonary arteries and achieved this result, with reversed flow through the foramen of Panizza, although whether this occurs under natural circumstances is unknown.

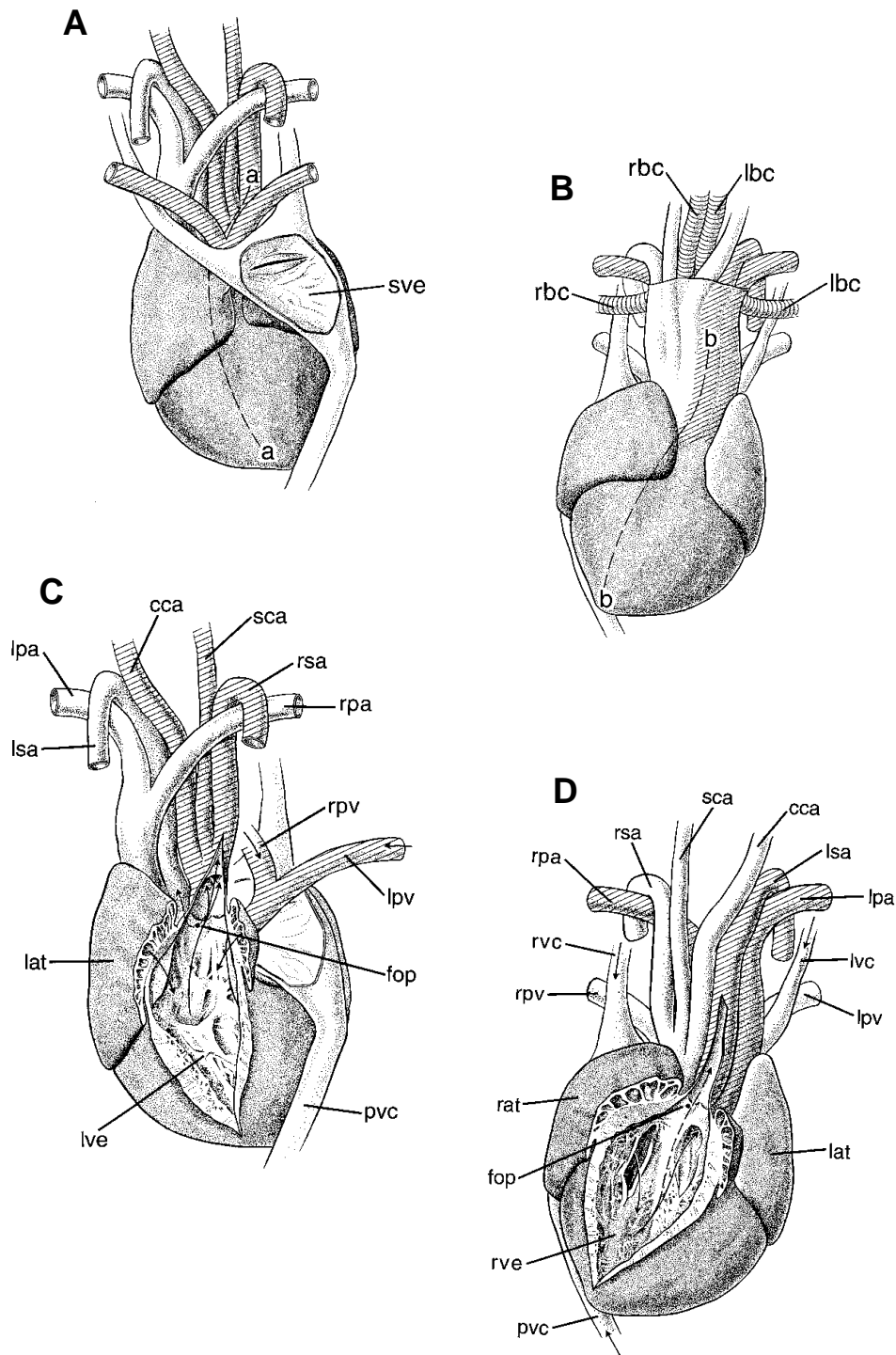


Figure 40.6 Morphology of the heart of *Crocodylus porosus*, shown in dorsal view (A, C), and ventral view (B, D). In C and D, the heart is opened along lines a-a and b-b shown in A and C respectively. C, arrows indicate blood flow during normal breathing, from left atrium to left ventricle to right systemic arch, and through the foramen to the left systemic arch; D, solid arrows indicate blood flow during normal breathing, from right atrium via the right ventricle to the pulmonary arch. The dashed arrow shows the direction of flow via the pulmonary bypass shunt. **cca**, common carotid artery; **fop**, foramen of Panizza; **lat**, left atrium; **lbc**, left bronchus; **lpa**, left pulmonary vein; **lpv**, left pulmonary vein; **lsa**, left systemic arch; **lvc**, left anterior vena cava; **lve**, left ventricle; **pvc**, post vena cava; **rat**, right atrium; **rbc**, right bronchus; **rpa**, right pulmonary vein; **rpv**, right pulmonary vein; **rsa**, right systemic arch; **rvc**, right anterior vena cava; **rve**, right ventricle; **sca**, subclavian artery; **sve**, sinus venosus. (After Grigg 1989) [J. Jeffery]

Aside from the heart and associated blood vessels, the blood system is essentially similar to that in other reptiles. A renal portal system is present.

The extensive lymphatic system is the most complex and modified among the reptiles (Ottaviani & Tazzi 1977). It differs from those of other reptiles in the absence of the great sinuses and has finer and more plexiform trunks which are generally similar to those of mammals. As the flow of lymph is driven largely by hydrostatic pressure, the similarity may reflect its association with a blood vascular system which operates at higher pressures than those of most reptiles.

Gas Transport

Oxygen is transported by haemoglobin contained in oval nucleated erythrocytes. The mean haematocrit of a sample of 96 wild individuals of *C. porosus* was 24.8% (range 19.1 to 31.3%; Gruca & Grigg 1980), but this declined in captivity, presumably as a correlate of reduced activity. Grigg & Cairncross (1980) described oxygen equilibrium curves for *C. porosus* over a range of temperatures and carbon dioxide tensions (Fig. 40.7A, B). They reported a general descriptive equation:

$$\log_{10} P_{50} = 0.4163 + 0.0200 T^{\circ}\text{C} + 0.3763 \log_{10} P_{\text{CO}_2}$$

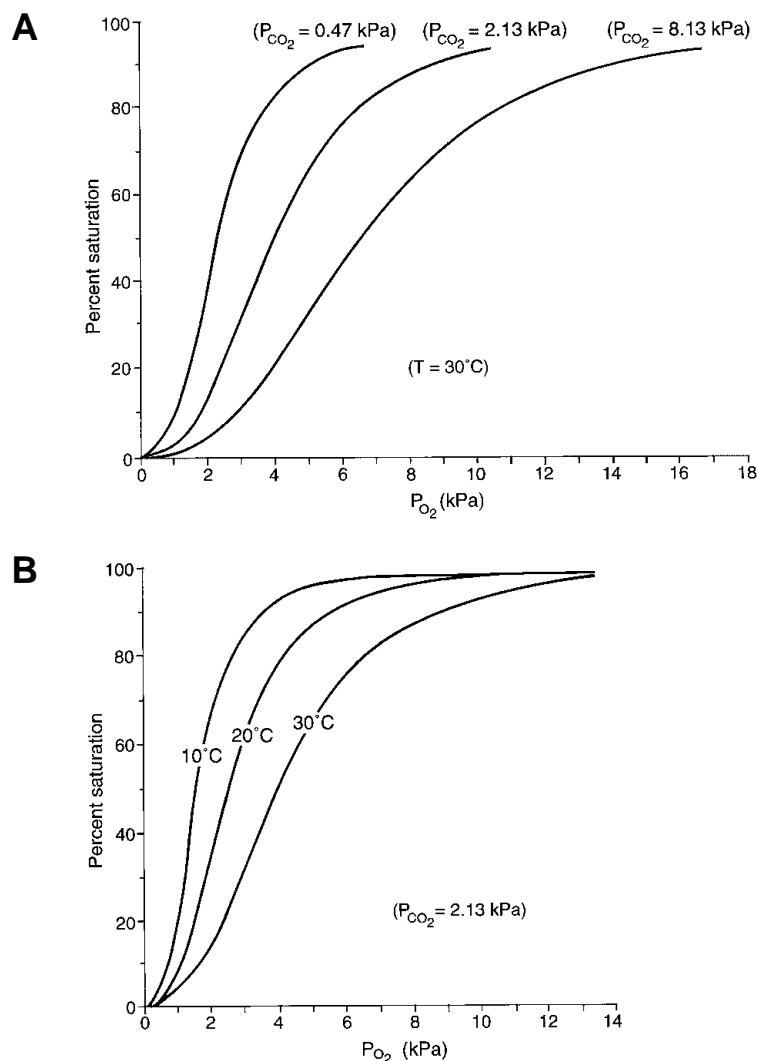


Figure 40.7 Respiratory relationships in *Crocodylus porosus*. **A**, the effect of increased P_{CO_2} on blood oxygen levels; **B**, the effect of temperature on blood oxygen levels. (After Grigg & Cairncross) [W. Mumford]

Of particular interest, however, is the strong sensitivity of oxygen affinity to carbon dioxide (Bauer & Jelkman 1977) and a comparatively low 'fixed acid' Bohr effect. Grigg & Gruca (1979) have interpreted this as an adaptation to diving which relies on anaerobic rather than aerobic metabolism. Rapid blow-off of carbon dioxide at the end of a dive results in a rapid left-shift of the curve and facilitates reloading of the blood with oxygen. Metabolism of accumulated lactic acid, on the other hand, takes much longer and any effect on the oxygen equilibrium curve would be slow. This interpretation was supported by Seymour, Bennett & Bradford (1985). Studying solutions of crocodilian haemoglobin, Bauer & Jelkman (1977) also reported low sensitivity to changes in pH, and, most significantly, the lack of 2,3-DPG or other red cell organic phosphates (RCOP). In most vertebrates RCOPs act as ligands, which bind to haemoglobin within the red cells and reduce the very high affinity of unliganded pigment into the physiological range. Grigg & Gruca (1979) confirmed this lack in *C. porosus* and *C. johnstoni*. Noting that dialysis of human haemoglobin to remove bound RCOP also enhances the sensitivity of oxygen affinity of the haemoglobin to carbon dioxide and reduces the 'fixed-acid' Bohr effect (Duhm 1976). Grigg & Gruca proposed that the loss of RCOP, which seems to be a general occurrence in crocodilians post-hatching, may provide the mechanism for the adaptive, low 'fixed acid' Bohr effect described above. Interestingly, *C. porosus* has two RCOPs during embryonic life, and two distinct haemoglobins (Grigg, Wells & Beard 1993). In early embryos, haemoglobin is present and sensitive to ATP which is present in high levels. Later, embryonic haemoglobin is replaced by the adult type, ATP is replaced by 2,3-DPG, but in small quantities (Fig. 40.8A, B) and, intriguingly, oxygen affinity of the adult haemoglobin type is unaffected by either ATP or 2,3-DPG. It is, of course, strongly affected by carbon dioxide.

As might be expected from a high dependence on anaerobically-supported activity, crocodilian blood has a high capacity for carrying and buffering carbon dioxide (Grigg & Cairncross 1980; Seymour *et al.* 1985).

Gas Exchange and Metabolism during Diving

Cutaneous gas exchange is negligible in *C. porosus* (Wright 1986) and should be in other species also, as *C. porosus* is among the species with least dermal ossification. Biphasic ventilation of the lungs is periodic, interrupted by apneas during which pulmonary pressures (of submerged animals) are slightly above ambient. At least in captivity, crocodilians frequently rest for hours submerged in shallow water and periodically lift the snout to the surface to ventilate the lungs. During such behaviour, juvenile *C. porosus* may be supported entirely aerobically in 10 to 12 minute voluntary dives (Wright 1985). Lung P_{O_2} falls from approximately 120 to 140 mm Hg, while P_{CO_2} rises from approximately 20 to 40 mm Hg. Meanwhile, arterial oxygen saturation falls from 95% to approximately 30%, but blood lactate remains throughout at resting levels of about 1 mMol l⁻¹. At any disturbance, however, bradycardia is initiated and blood lactates rise three or four fold very rapidly, indicating the implementation of anaerobic metabolism. If dives are prolonged by force, blood lactates rise to 20 mMol l⁻¹ after 40 to 50 minutes. In larger individuals, the time period of these events is much slower, as discussed above.

The acidbase status of *C. porosus* has been examined at rest and after exhaustive exercise (Seymour *et al.* 1985). Whereas normal plasma pH is approximately 7.43, it falls to 7.0 after 5 minutes of exercise; lactate rises to 20 to 30 mMol l⁻¹. Struggles associated with capture cause pH values to drop as low as 6.4, but recovery occurs by respiratory compensation as carbon dioxide is excreted,

followed by metabolic reduction of lactate. Full recovery may take 1 to 2 days. The frequent death of large crocodilians after a prolonged struggle at the time of capture most likely reflects a pronounced lactic acidosis.

SALT, WATER BALANCE AND EXCRETION

Ionic balance has been reviewed recently by Taplin (1988) and Mazzotti & Dunson (1989). Species of the Alligatoridae and Crocodylidae are good ionic and osmotic regulators. They maintain plasma osmotic pressures of approximately 300 mOsm l^{-1} and the ionic composition is similar between species. The skin provides a significant barrier to the movement of both water and ions. With a smaller surface area/mass ratio, larger individuals can tolerate exposure to osmotic stress for longer than smaller ones when osmotic values depart from normal. Maintenance of internal homeostasis is frequently managed against a threat of flood or drought in fresh and salt water respectively.

Whereas most crocodilians are found in fresh water, some Crocodylidae (notably *C. porosus* and *C. acutus*) occur routinely in hyperosmotic estuarine habitats while many others are exposed at least to brackish environments (Taplin 1988). Hatchlings of *C. porosus* are able to survive and grow without access to fresh water (Grigg *et al.* 1980; Taplin 1984). Hatchlings of *C. acutus* also enter hyperosmotic water from nest sites around the Florida Keys, but they are

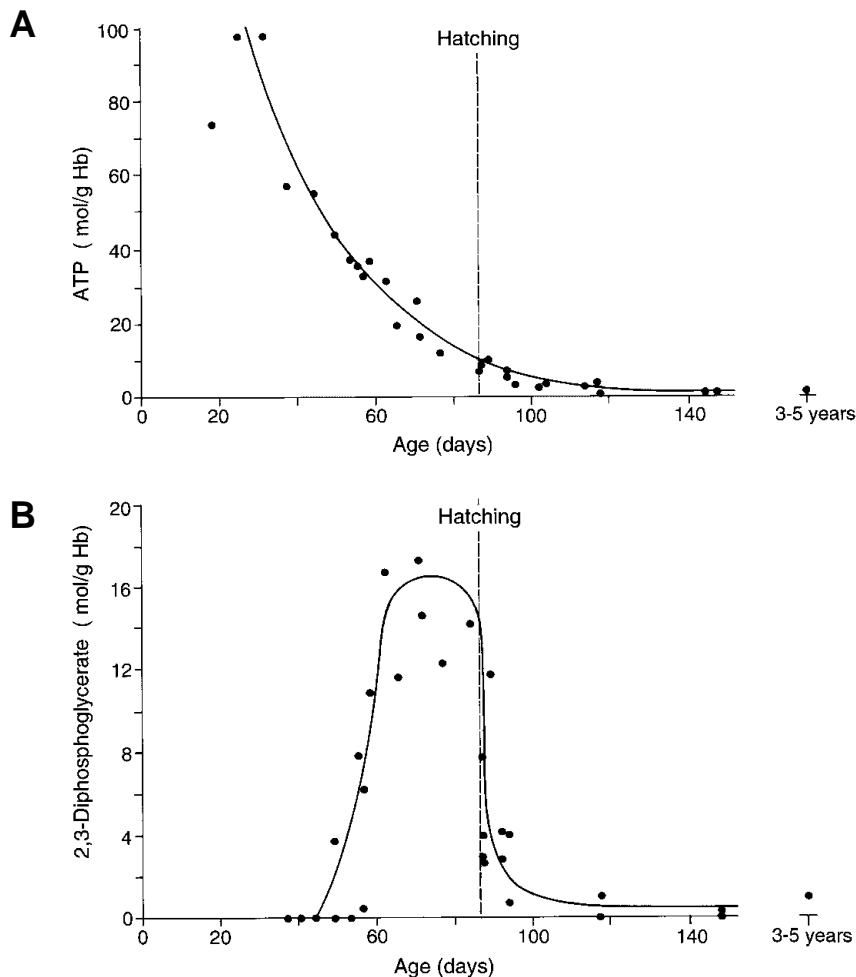


Figure 40.8 Ontogenetic changes in red cell organic phosphates before and after hatching in *Crocodylus porosus*. **A**, ATP levels; **B**, 2,3-DPG levels.

[W. Mumford]

thought to make use of floating lenses of fresh water from rainstorms (Mazzotti & Dunson 1984, 1989; Mazzotti, Bohnsack, McMahon & Wilson 1986). It is unknown whether they could survive without drinking fresh water.

No studies suggest that any of the Alligatoridae can live indefinitely in hyperosmotic conditions. However, the American alligator *A. mississippiensis* sometimes ventures temporarily into salt water, and *Caiman latirostris* occurs in estuaries in southern Brazil.

The mechanisms which support crocodilian ionic and osmotic homeostasis are essentially the same as those in other reptiles (Minnich 1979, 1982; Dunson 1976; Dantzler 1976). Mesonephric kidneys are the organs of ionic and osmotic regulation and of nitrogen excretion, supported by the cloaca, and lingual salt glands in the Crocodylidae but not Alligatoridae. All crocodilians lack a bladder. In fresh water, the cloacal urine is copious, clear and dilute, and excess nitrogen is lost as ammonium ions, excreted as ammonium bicarbonate (Coulson & Hernandez 1959, 1983).

Under hyperosmotic conditions, the urine of *C. porosus* is opaque white/cream and often reduced in volume. Nitrogen is excreted as insoluble uric acid, which achieves a water saving, as in birds (Grigg 1981; Grigg, Taplin, Green & Harlow 1986). The liquid fraction is low in sodium and never hyperosmotic to the plasma, but in salt water the cloacal urine contains small quantities of urea, plus significant excess potassium and divalent cations (Grigg 1981).

More information is needed about the composition of the ureteral urine in both the Alligatoridae and Crocodylidae. At least in crocodiles, the urine is presumably subject to water reabsorption by sodium pumping, probably after temporary reflux to the distal colon, in the manner of birds (Skadhauge 1977). This would account for the low levels of sodium in the cloacal urine of individuals of *C. porosus* in salt water, referred to above. The excess sodium is excreted via salt glands.

Lingual salt glands appear to be present in all crocodylids. Some 23 to 93 discrete lobulated glands open by conspicuous pores onto the surface of the tongue (Fig. 40.9A; Taplin & Grigg 1981; Taplin, Grigg, Harlow, Ellis, & Dunson 1982; Taplin, Grigg & Beard 1985; Taplin 1988). The ultrastructure of these glands (Fig. 40.9B, C) is very similar to the (non-homologous) glands of marine turtles. Salt glands have not, however, been found in any member of the Alligatoridae (Taplin 1988; Grigg & Beard unpub. obs.) and a study of captive *A. mississippiensis* suggests that it cannot maintain homeostasis in hyperosmotic water (Lauren 1985). The situation in both *Gavialis* and *Tomistoma* is unclear. The buccal morphology of *Tomistoma* suggests the presence of similar lingual glands, whereas *Gavialis* has glands that are distributed differently. Data on secretory capabilities are lacking. Taplin *et al.* (1985) have postulated a marine phase in the evolution of the Crocodylidae, but not for the Alligatoridae, an idea developed subsequently in a historical zoogeographic context (Taplin & Grigg 1989).

Typical concentrations of salt gland secretions, using the methacholine stimulation method, approach or exceed that of sea water ($\text{SW} = 1000 \text{ mOsm l}^{-1}$, compared with plasma at approximately 300 mOsm l^{-1}), with sodium and chloride the dominant ions (see review by Taplin 1988). Rates of flow differ among species. Rates of sodium secretion range from less than $10 \text{ (C. johnstoni)}$ to more than $40 \text{ uMol } 100\text{g}^{-0.7}\text{hr}^{-1}$ (*C. porosus* and *C. acutus*). Questions have been raised about the relevance of measuring secretory performance of glands stimulated artificially by methacholine chloride (Mazzotti & Dunson 1984; Mazzotti *et al.* 1986) and, by implication, about the functional significance of the glands. However, isotopic measurements of sodium effluxes in *C. porosus* living in natural hyperosmotic habitats show that the field efflux is less than the maximum measured in the laboratory (Grigg *et al.* 1986), and apparently the salt

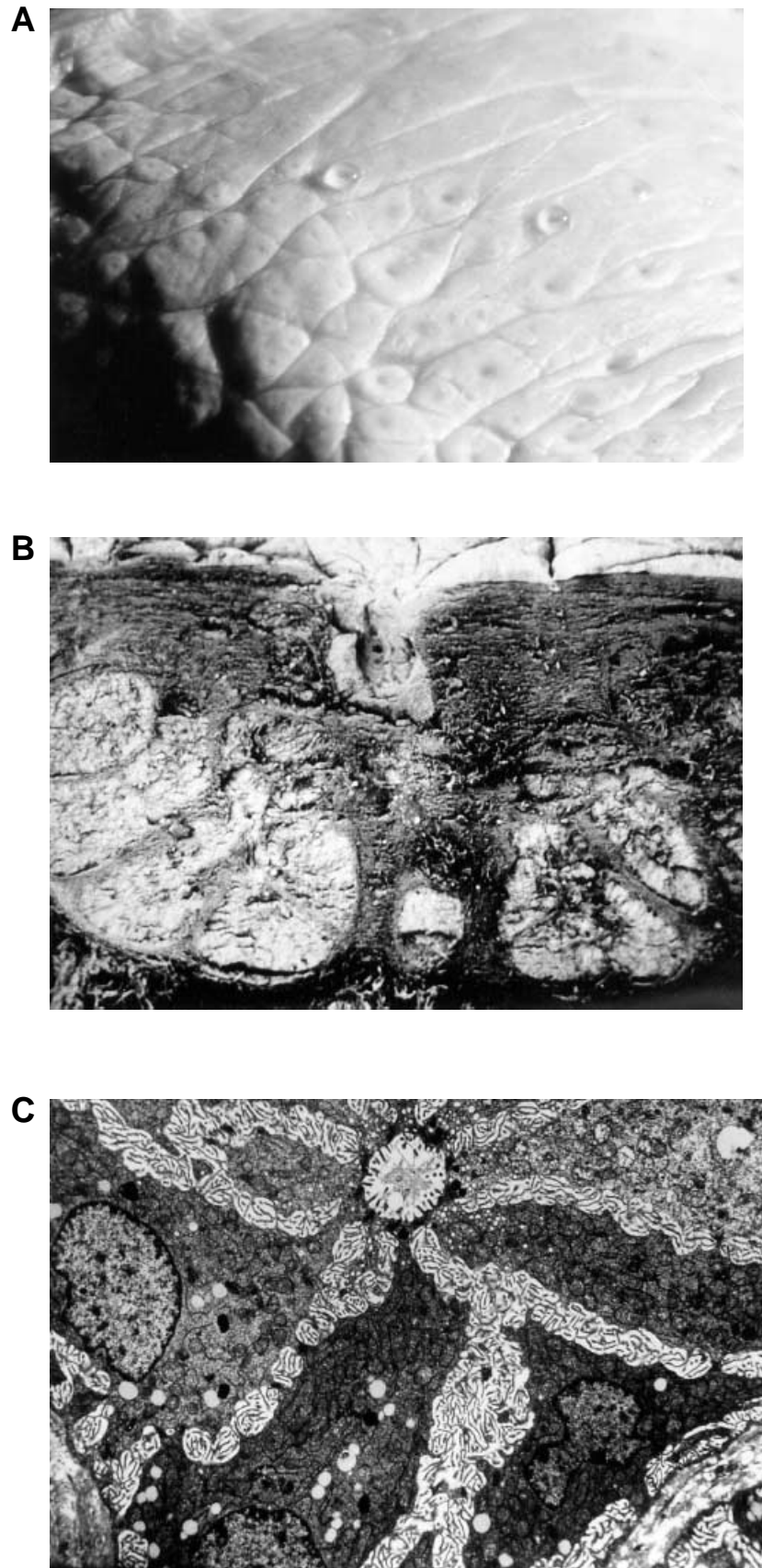


Figure 40.9 Salt glands of *Crocodylus porosus*. **A**, secreted droplets welling from pores on the surface of the tongue; **B**, scanning electron micrograph of a thick section of the tongue showing lobules comprising a single salt gland; ducts from the gland unite to form a pore on the surface of the tongue; **C**, transmission electron micrograph of a lobulated gland in transverse section.
[Photos by L.E. Taplin]

glands are sufficiently competent to maintain homeostasis under these conditions. Hatchling *C. porosus*, indeed, are known to survive and grow in hypersaline creeks at salt concentrations nearly twice that of sea water, where fresh water is unavailable during the dry season (Taplin 1984). In comparison to a control group kept in fresh water, captive hatchling *C. porosus* maintained for months in 570 mOsm salt water showed increased vascularisation of the lingual glands (Franklin & Grigg in press).

There is evidence of some physiological adaptation in *Crocodylus johnstoni*, which does occur in brackish waters, though uncommonly (Messel *et al.* 1979–1985). Individuals captured in the Limmen Bight River, Northern Territory, in hyperosmotic salinities sometimes in excess of 600 mOsm l⁻¹, exhibited plasma homeostasis, with values comparable to individuals from a nearby fresh water population (Taplin, Grigg & Beard 1993). Salt gland performance is lower than that of *C. porosus*, in both concentration and rate. Whether or not *C. johnstoni* can tolerate hyperosmotic conditions indefinitely, and to what maximum concentration, remains unknown.

SENSE ORGANS AND NERVOUS SYSTEM

Before dismissing the mental capabilities of crocodilians, it is as well to remember the complexity of their predatory and reproductive behaviour (see Reproduction) and their homing capacities (Walsh & Whitehead 1993). Reptilian brains are about one tenth the mass of avian or mammalian brains at comparable body size and crocodilians appear to be no exception (Jerison 1969).

Crocodilians are well provided with sense organs, having good vision, hearing, olfaction and senses of touch. The eyes are well situated for vision in air by an almost submerged individual. While submerged, a translucent ‘third eyelid’, the nictitating membrane, moves across horizontally to protect the eye. When underwater vision is probably restricted to sensing light and dark. Touch receptors and ears are probably the main operational sense organs underwater.

The structure of the crocodilian eye was reviewed by Underwood (1970). The eye may be closed by depression of the upper eyelid, which is protected by a bony scute. Binocular vision is implied, as the cornea subtends an angle of 128°, with 25° of overlap in the forward fields in *C. porosus* Pettigrew & Grigg 1990). Of importance in night vision is the tapetum lucidum, a layer of retinal cells containing guanine crystals, which reflects incoming light, and serves as an image intensifying system. The reflective tapetum allows crocodilians to be located easily at night, the eyes reflecting the beam of a spotlight or flashlight. The iris is a vertical slit by day, and opens to a wide circle at night.

The ear was discussed by Baird (1970). Crocodilians vocalise when in distress and during aggressive behaviour, and are said to have excellent auditory capabilities. The tympanic membranes are concealed and protected by flat rectangular flaps that may be raised and lowered by muscles (Pl. 9.7). Presumably they are closed during diving, though reception of underwater sounds is an important aspect of social communication (see Reproduction). The middle ear, surrounded by bone, is more complex than in other reptiles and shows similarities to the ears of birds.

Olfaction originates from receptors within the nasal cavities (Parsons 1970). The nasal cavities are the most complex among the reptiles and are essentially similar within the Crocodylia. The nasopharyngeal ducts are elaborated dorsally in a series of sinuses, sacs and blind ducts. Adult crocodilians lack Jacobson's organs. The olfactory bulbs of the forebrain are well-developed, consistent with the importance of olfaction.

Experiments on *A. mississippiensis* (Weldon *et al.* 1990) have shown that alligators use chemical cues to locate food both on land and under water. Gular pumping increases in the presence of meat odours and probably serves to improve the efficiency with which air is sampled by olfaction. Taste is probably involved as well in the contact identification of food, as taste buds occur on the tongue (Bath 1906) and posterior palate (Ferguson 1981).

REPRODUCTION

A detailed natural history of reproduction is outside the scope of this chapter. It has been reviewed recently in excellent, well-illustrated books about crocodilians in general (Ross 1989) and *C. porosus* and *C. johnstoni* in particular (Webb & Manolis 1989). Another valuable reference is Webb, Manolis & Whitehead (1987), and much of the detail referred to below has come from these sources, plus personal experience.

Briefly, crocodilians have a complex social hierarchy which is established by aggression and by elaborate social signalling (Vliet 1989). Large males are dominant and territorial and are thought to fertilise most of the females in a particular area. Most observations have been made on small numbers of captive species, and their relevance to wild populations can only be inferred. Studies on *A. mississippiensis*, *C. niloticus* and *C. porosus*, coupled with elements of similar behaviour recorded in other species, suggest that all crocodilians are probably broadly similar in their reproductive biology.

Mating behaviour of *C. porosus* observed in captivity in north Queensland provides an example which seems to be typical of crocodilians in general. Mating occurs in the water. Females usually approach the male and an elaborate, sometimes prolonged courtship ensues. The individuals swim together, often in circles, make body contact frequently and rub their head over the other body (see comments on gular and paracloacal glands). The female may flee a short distance, and draw the male into a chase before circling is resumed. Typically females show headlifting, submissive postures. Copulation occurs when the male curls his tail under the female, lying to the side. In shallow water, both individuals may be seen lying on their sides.

All Alligatoridae, half of the Crocodylidae and *Tomistoma* nest in mounds. The remaining species use holes. *Crocodylus acutus* nests sometimes in a hole and sometimes in a mound. Mound nesters lay their eggs in a nest constructed from grass or other vegetation, litter, and sand or soil in various proportions, depending upon what is available at the site. The mound is constructed using material dug up with the hind legs, or from vegetation torn off with the teeth (Fig. 41.4).

Crocodylus johnstoni lays an average of 13 eggs (range four to 21; weight 65 to 75 g) in August, during the north Australian dry season. Eggs are laid about six weeks after mating into a hole which is dug with the hind feet into the sandy substrates of a river bank. Though incubation time is temperature dependent, under average field conditions *C. johnstoni* hatch after about eleven weeks. *Crocodylus porosus* is a mound nester and, unlike *C. johnstoni*, breeds in the wet season. After courtship at the end of the dry season, nests are built at the onset of 'the wet'. If the wet season begins early, the nesting season may be quite prolonged and tapers off towards March and April. *Crocodylus porosus* lays 50 to 60 eggs, which are heavier than those of *C. johnstoni*, weighing about 100 g (range 70 to 140). The number and size of the eggs reflects the age and size of the mother. At normal field temperatures, incubation takes about 80 to 90 days. Clutch characteristics of specific populations of *C. porosus* and *C. johnstoni* are discussed in Chapter 41.

Parental care and the temperature dependence of the sex of the young are two features of crocodilian reproduction of particular interest. Persistent and often ancient anecdotal reports about maternal care were confirmed by observations on captive *C. niloticus* (Pooley & Gans 1976) and have since been extended to other species, including *C. johnstoni* and *C. porosus*. Females commonly guard their nests, though the effectiveness of this behaviour as a predator deterrent is doubtful. At the end of incubation, hatchlings emerging from the eggs in the nest cavity emit characteristic, staccato, rasping vocalisations. These sounds encourage the female to excavate the nest and to collect emergent hatchlings in the jaws and carry them to the water. Several trips may be required to transport a whole clutch. Eggs not yet hatched may be taken in the mouth and manipulated to release the young. Pods of hatchlings seem to be defended by the mother (and the father) for some time after these have entered the water, but more data are needed about this behaviour and its effectiveness.

As is typical for many turtles and some lizards, the sex of crocodilian hatchlings is determined by the incubation temperature, rather than genetically. Reviews of aspects of temperature sex determination (TSD) may be found in Webb *et al.* (1987), Webb & Cooper-Preston (1992) and Deeming & Ferguson (1992). Crocodiles and alligators are slightly different. At constant incubation temperatures, *A. mississippiensis* and *Caiman crocodilus* eggs produce males above 32°C and females below 31°C, with mixed sex ratios in between. Crocodiles eggs also produce females when incubated below 31°C, and a mixture of sexes is produced between 31° and 32°C. Embryos incubated between 32° and 33°C hatch as males, and females dominate in the mixture of sexes above 33°C. Experiments with constant incubation temperatures are misleading as sex is likely to be determined during brief intervals.

The influence that a very small difference in temperature may provoke is of great interest, as is the phenomenon itself in evolutionary and ecological terms. Nest site selection, which determines incubation temperature, therefore has a marked influence not only on the duration to hatching and the survivorship of the eggs, but on their sex as well. Most natural nests produce a mixture of males and females, but some produce only a single sex. The temperature regime of both holes and mounds is buffered compared to diurnal fluctuations; metabolism of the eggs themselves contributes to elevated temperatures, and decomposition of vegetation may be an important heat source of heat in mound nests. Whatever the mechanisms, measurements in the nest cavities generally show temperatures above but close to 30°C, with little diurnal variation. Periods of heavy rainfall may provide an exception, as shown by Magnusson (1979) in a nest of *C. porosus*. Eight days were required to regain the warmth lost after several days of cyclonic rain, during which the nest cavity temperature declined from 32°C to 25°C.

Much more needs to be learned of the morphology and physiology which supports crocodilian reproduction. Illustrations of the male and female reproductive (and urinary) systems are available in Chiasson (1962). The single, rigid penis is pulled out and forward by muscles. A middorsal, open groove receives sperm through juxtaposition with the vasa deferentia, which open dorso-laterally through the cloacal wall. The testes are paired and adjacent to the kidneys. They undergo a conspicuous annual cycle in size and activity (see below). The clitoris of females is much smaller than the penis, but lies in the same position.

The oviducts open anteriorly to receive ova from the paired ovaries, adjacent to the kidneys. Longitudinal differentiation and specialisation of the oviducts has been described in detail (Palmer & Guillette 1992), and appears to be more similar to birds than to other reptiles, again emphasising the archosaurian connection. Unlike other reptiles, the eggshell membranes and the calcareous shell are formed in different regions of the oviduct, as they are in birds. Thus,

the whole clutch is treated sequentially, egg by egg, in different parts of the oviduct. Fertilisation presumably occurs in the anterior end of the oviduct. Albumen proteins are secreted in the oviducal tube, shell membranes are secreted in the anterior uterus, and the calcareous shell is deposited by the posterior uterus. Each of the two oviducts opens into the cloaca via a vagina with a narrow lumen which spirals through the muscular cloacal walls (Palmer & Guillette 1992). How these walls relate functionally to the role of a vagina as a receptacle for a penis, is unclear and the appropriateness of the term is uncertain.

The coordination of the anatomical, physiological and behavioural events involved in reproduction and subsequent care of the developing embryo is achieved by endocrine regulation, under the influence of environmental factors. Thus, photoperiod, temperature, rainfall, nutritional status and social factors all influence the level of circulating reproductive hormones. This has received closest attention in *A. mississippiensis* (Lance 1987; Lance 1989) and *C. niloticus* (Kofron 1990). The reproductive cycle of *A. mississippiensis* commences in March (early spring) as air and water temperatures increase. In males, testis mass, plasma testosterone ($>50 \text{ ng ml}^{-1}$) and spermatogenesis peak around April. Mature spermatozoa appear from midMay when mating occurs. Testosterone and testis size decline rapidly after spermiation and the testes are fully regressed in July and August. There is a small peak in testosterone in September, with no visible changes in testicular histology. In females, plasma oestradiol peaks in mid April ($>600 \text{ pg ml}^{-1}$), and ovarian follicles increase from 5 to 45 mm in diameter in May, at ovulation. Testosterone is high also in preovulatory females (approximately 1.5 ng ml^{-1}), but its function is unknown. Plasma progesterone shows a peri-ovulatory surge to 16 ng ml^{-1} , with a rapid decline during the two to three weeks between ovulation and oviposition. During incubation, while the female remains at the nest, ovarian steroids are undetectable. These patterns are broadly similar to those in other tetrapods, but Lance (1989) has drawn attention to the need for more work on the pituitary gonadotropins and other aspects of the endocrine regulation of reproduction in crocodilians. The large size and difficulty of handling sexually mature individuals, and their limited availability, assure that both heroic and herculean efforts will be needed to answer many of the questions which remain on the physiology of crocodilian reproduction.