



**FAUNA**  
*of*  
**AUSTRALIA**



**36. FAMILY HYDROPHIIDAE**

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## DEFINITION AND GENERAL DESCRIPTION

The family Hydrophiidae, or true sea snakes, includes the majority of marine serpents and is the most completely marine of all extant reptilian taxa. Reptiles of other marine groups either lay their eggs on land (marine turtles, laticaudid snakes) or have freshwater or terrestrial species in addition to marine ones (acrochordids, colubrids, crocodylians). The Hydrophiidae never come out on land voluntarily and all live in salty water except two lake-locked species that have a marine origin.

The family is characterised by several features that reflect their adaptation to a marine environment. These include valvular nostrils, a lingual fossa and a vertically compressed, paddle-shaped tail; all species are viviparous (Cogger 1992). There are two subfamilies in Australian waters, the Ephalophiinae which comprises five genera and 11 species and the Hydrophiinae containing seven genera and 20 species.

Books dealing with the general biology of sea snakes include Dunson (1975a) and Heatwole (1987) and there are a number of review papers (Pickwell 1972; Heatwole 1977a, 1977c, 1978a; Cogger & Heatwole 1978; Minton & Heatwole 1978; Limpus 1987). Cantor (1841) and Bergman (1949, 1962) described the anatomy and/or presented meristic data. Hibbard (1975) reviewed their sensory perception. Vigle & Heatwole (1978) and Culotta & Pickwell (1993) compiled bibliographies on the Hydrophiidae. The Australian species have been reviewed (Cogger 1992) and catalogued (Cogger, Cameron & Cogger 1983), and faunas of Australian regions treated (Shuntov 1971; Dunson 1975b; Heatwole 1975c, 1977d; Limpus 1975b; Minton & Heatwole 1975; Redfield, Holmes & Holmes 1978).

## HISTORY OF DISCOVERY

Sea snakes, along with marine turtles, were among the first Australian reptiles to be recorded by early European navigators and explorers. The abundance of sea snakes in our northern waters, especially the North-West Shelf, the Arafura Sea and the Gulf of Carpentaria, was noted as early as 1699 (Dampier 1703–1709).

The first of the species occurring in Australian waters to be described formally was the pelagic, yellow-bellied sea snake, *Pelamis platurus*, by Linnaeus in 1766, under the name *Anguis platara*. Not until 1804 was the first sea snake described based on an Australian specimen, the olive sea snake, *Aipysurus laevis* Lacépède, 1804. Only in 1869 was the first species, *Emydocephalus annulatus* Krefft, described by an Australian-based researcher.

Throughout the 19th century species of sea snakes were occasionally described and named, although because of the great individual and geographic variation in these snakes, combined with small museum samples, many species were soon synonymised. Many species, though occurring in Australia, were described from Asian populations. Not until late in the present century was it found that many of these widespread species consisted of two or more species with strong regional endemism.

The first major study of local and regional sea snake distribution patterns was made by Soviet fisheries research vessels in the late 1960s (Shuntov 1971). In surveys ranging from the Gulf of Carpentaria to the Arafura and Timor Seas, Shuntov recorded 18 species of sea snakes. He found major regional differences in the taxonomic composition of sea snake catches, and significant seasonal differences in sea snake abundance. However, his results have not been corroborated by subsequent studies. Heatwole (1975d) reviewed the sea snakes of the Gulf of Carpentaria and between April and December 1976 surveys of sea

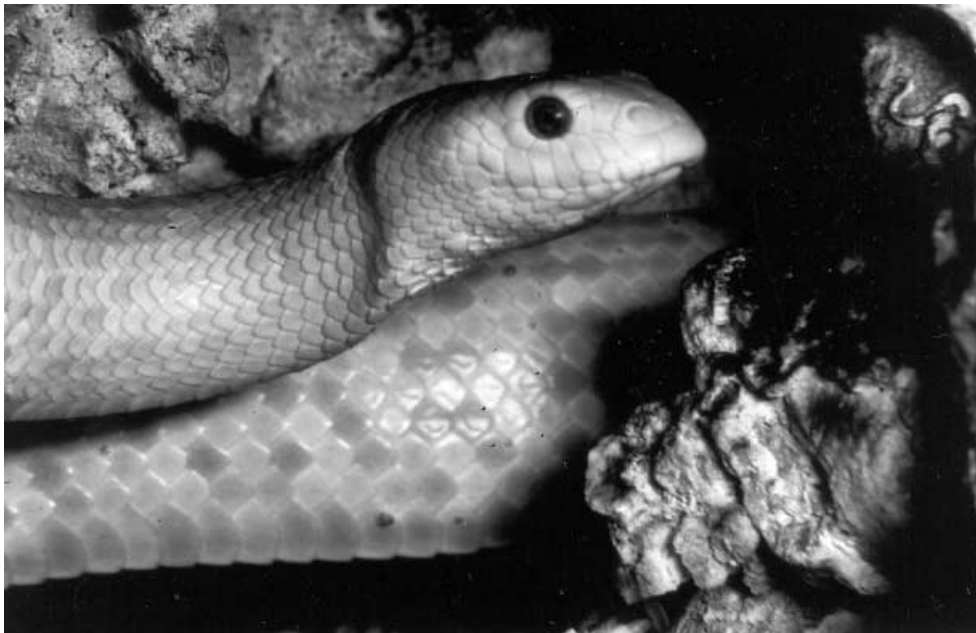
snakes in eastern waters of the Gulf of Carpentaria were undertaken by CSIRO scientists as adjuncts to surveys of potential commercial penaeid prawn fisheries in the region (Redfield *et al.* 1978). These surveys found significant overall increases in sampling abundance in October, but there were different seasonal patterns of relative abundance between the different species sampled. Redfield *et al.* (1978) were unable to reconcile the significant differences between their results and those of Shuntov (1971) and Heatwole (1975d).

## MORPHOLOGY & PHYSIOLOGY

### External Characteristics

Sea snakes vary greatly in size and body form. The smallest Australian species (for example, *Ephalophis greyi*, *Hydrelaps darwiniensis* and *Parahydrophis mertoni*) grow to only 0.5 m in total length, whereas the largest species (for example, *Astrotia stokesii*, *Aipysurus laevis*, *Hydrophis elegans*) may reach more than 2 m in length. Body form is highly variable. Generalist fish eaters are similar in form (apart from the flattened tail and some lateral compression) to terrestrial snakes, whilst species that feed on burrowing eels (Ophichthidae, Congridae and Moringuidae) have small to minute heads and forebodies, followed by large, deep hindbodies up to 10 times the diameter of the head and neck.

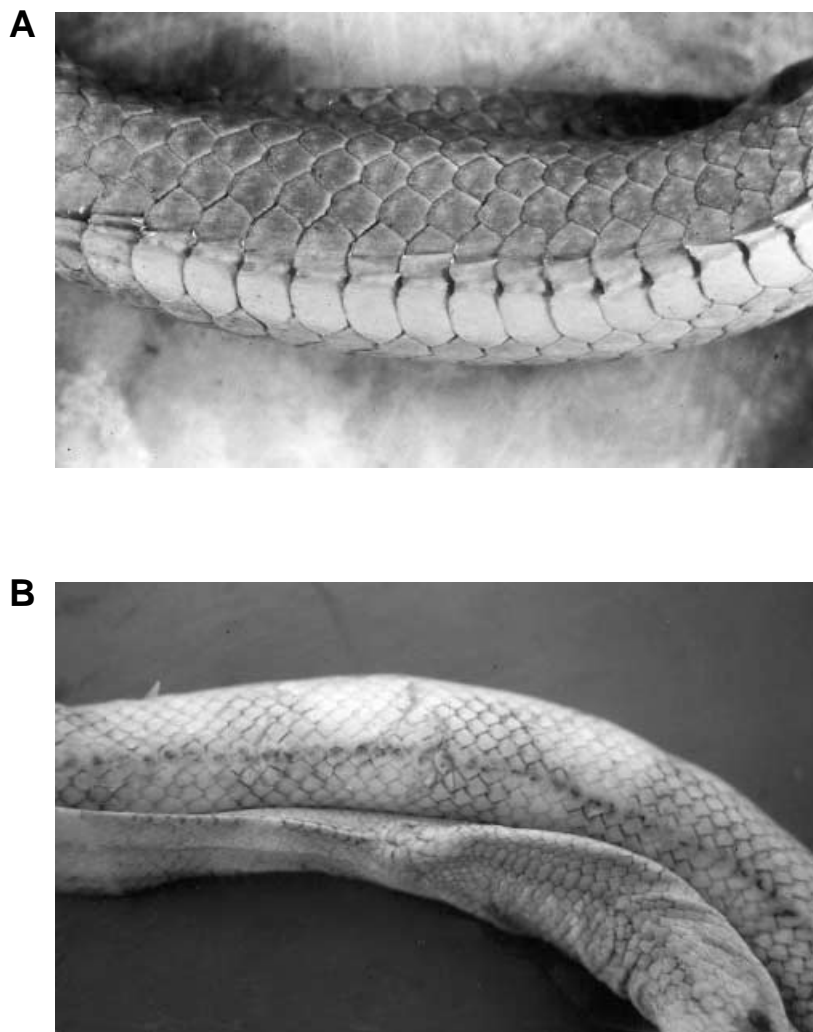
Externally sea snakes have a suite of common features associated with a fully aquatic marine existence. These include the presence of fleshy, valvular nostrils and a fleshy lingual fossa, which together effectively seal the respiratory passages and prevent the entry of water into the lung when the snakes are submerged. The flaps of these valves are activated by spongy, erectile tissue. In most species the nostrils are situated on the upper surface of the snout (Fig. 36.1) to allow the snake to breathe at the surface without exposing the rest of its body to aerial predators such as raptors.



**Figure 36.1** *Aipysurus laevis* hiding in a crevice. Note the dorsally placed valvular nostrils, flattened tail and new skin. [Photo by C. Pollitt]

The scales are generally very small, arranged in 15 to 69 rows around the mid-body. The broad belly scales (gastrosteges) which characterise most terrestrial snakes and which are a primary mechanism in locomotion on land, are generally absent in sea snakes (Fig. 36.2). However, in some groups of sea snakes, notably members of the subfamily Ephalophiinae, the belly scales are much wider and appear to be used in terrestrial-style locomotion over mangrove and reef flats. This group also has much larger body scales than most other sea snakes.

The scales of sea snakes vary not only in size, but also in shape and relief. Many have scales which are keeled (Fig. 36.2A), tubercular or both, giving a very rough feel when handled. In many species, especially those of *Disteira*, *Lapemis* and *Hydrophis*, the rougher scales are restricted to the lower flanks and belly and are often much more developed in males. This suggests that scale tuberculosity is a secondary sexual character facilitating the male's hold on the female before or during copulation.



**Figure 36.2** Ventral surface of two sea snakes showing different degrees of reduction of the gastrosteges. **A**, partly reduced gastrosteges of *Aipysurus laevis*, keeled centrally to enhance stability in the water; **B**, gastrosteges of *Hydrophis elegans*, reduced to the same size as the rest of the scales. [Photos by H. Heatwole]

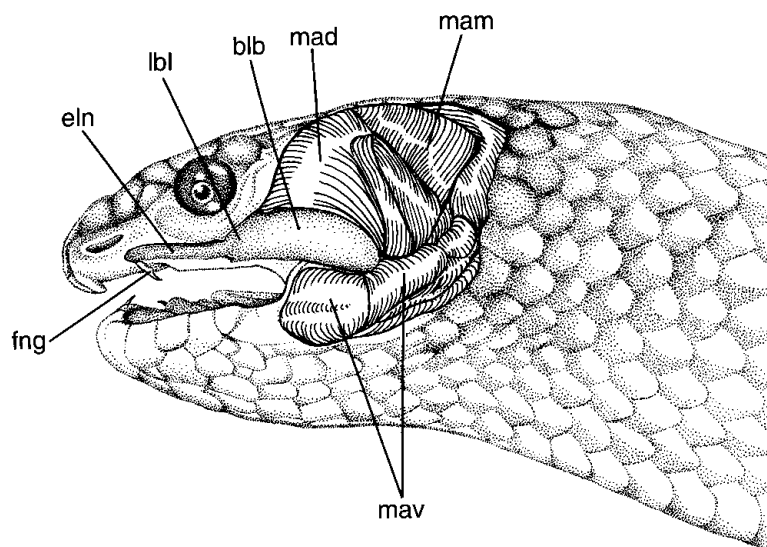
### Locomotion

Sea snakes propel themselves through the water by the laterally compressed paddle tail which produces an undulatory movement of the body. This movement directs a rearwards force against the liquid medium, in contrast to terrestrial snakes which propel themselves by using small irregularities in the substrata for purchase by their broad, backwardly directed ventral scales. Morphological adaptations reflect these different modes of locomotion. For example, the vertebral column of many sea snakes is weak and does not provide sufficient strength to cope well with terrestrial conditions. Hydrophiids do not take purchase on the substrate and accordingly their gastral plates are either somewhat narrowed or the same size and shape as other body scales (Fig. 36.2B). On the other hand, their propulsive surface has been increased by development of a broad paddle-shaped tail (Fig. 36.1; Pls 7.8-11) and in some species by a lateral flattening of the body until it is nearly ribbon-shaped (for example, *Astrotia stokesii*).

### Feeding and Digestive System

Most hydrophiids are venomous. Venom is produced by a pair of modified salivary glands, which lie on either side of the face along the posterior part of the upper jaw (Fig. 36.3), and is stored in a central lumen of the gland. The larger posterior portion tapers anteriorly into an elongate region towards the fang, into which the gland empties (Limpus 1978a). Unlike viperid snakes, in which these regions are morphologically and functionally distinct (see Chapter 24; Fig. 35.11), the glands of sea snakes are indistinct and the protein-secreting and mucus-secreting functions not clearly separated. The proportion of the gland devoted to mucus production is lower in sea snakes than in most terrestrial elapids (Gopalakrishnakone & Kochva 1990) and is probably related to a lesser need for lubrication of food when swallowing underwater.

The fangs of hydrophiids are located in the front of the mouth (Fig. 36.3). Usually there is only one on each side of the head although sometimes a second, replacement fang may be present. They are sharply pointed, slightly recurved



**Figure 36.3** Head of *Aipysurus laevis*, dissected to show the venom apparatus. Venom gland terminology follows that of Limpus (1978a). **blb**, bulbous region of venom gland; **eln**, elongate region of venom gland; **fng**, fang; **lbl**, lower bulbous region of venom gland; **mad**, dorsal part of *m. adductor mandibulae externus*; **mam**, *m. adductor mandibulae externus medialis*; **mav**, ventral part of *m. adductor mandibulae externus*. (After Zimmerman 1991) [T. Wright]

and have a central canal through which venom is extruded when the *m. adductor externus superficialis* applies pressure on the venom gland. In most sea snakes the fang is hypodermic-like, with a completely enclosed central canal exiting from a small orifice at the tip. *Astrotia stokesii* is an exception in that the venom canal opens through a groove in the fang throughout much of its length (Limpus 1978a).

Venom and the venom apparatus seem to have evolved in a feeding rather than a defensive context (Heatwole 1987). There are several lines of evidence for this. The few species (for example, *Emydocephalus annulatus* and *Aipysurus eydouxii*) that have secondarily adopted a diet of inactive food (such as fish eggs) and no longer need to subdue prey have nearly lost their venomous qualities and apparatus (Limpus 1978b; Minton 1983), though presumably they have as much need of defence as other hydrophiids. Also, some highly venomous species are reluctant to bite in defence; others do bite defensively but often fail to inject venom ('blank' bites).

Hydrophiid venoms are a mixture of a number of toxic proteins and polypeptides, spreading agents and lubricants. Venoms from several species have been fractionated and individual toxins purified and their chemical properties characterised (Tu & Toom 1971; Tu, Tzu & Beiber 1975), including amino acid sequences (Wang, Liu, Hung & Blackwell 1976; Maeda & Tamiya 1976, 1978; Fox, Elzinga & Tu 1977; Tamiya 1985). Common ingredients are short-chain toxins (60 to 62 amino acid residues) and long-chain toxins (66 to 74 amino acid residues) and phospholipases (Tamiya 1985). The exact composition of venom varies interspecifically although some toxins are common to several species.

Sea snake venoms may function as neurotoxins (Fraser 1904; Carey & Wright 1961; Barber, Puffer, Tamiya & Shynkar 1974; Tu *et al.* 1975; Fohlman & Eaker 1977; Tamiya, Maeda & Cogger 1983), as myotoxins and as nephrotoxins. Unlike some terrestrial snakes, they have very little haemotoxic activity (Minton & Minton 1969). The most important and swiftest mode of action is neurotoxic (Sutherland 1983). The venom of *Aipysurus laevis*, a generalist predator (see below), has differing effects on prey species. Eels are especially resistant whereas experimentally envenomated fish show changes in ventilatory rate (Zimmerman & Heatwole 1992), impairment of the ventilatory system with incomplete mouth closure and eventual cessation of opercular movements (Zimmerman, Gates & Heatwole 1990). Death is probably by asphyxiation. Part of the interspecific differences in prey resistance may reflect mode of respiration. At high venom doses, fish known to employ cutaneous respiration (for example, blennies), and hence be less severely influenced by loss of ventilatory capability, survived longer than fish such as pomacentrids which rely more heavily on gill respiration (Zimmerman, Heatwole & Davies 1992). The locomotory system was also affected. There was progressive loss of coordination of the fins and the fish developed an inability to maintain position and buoyancy; they leaned to one side and tended to sink (Zimmerman *et al.* 1990). The action of the venom not only subdues prey, but aids in its recovery should the snake lose it.

### **Respiration, Circulatory System and Diving**

Sea snakes can dive to depths as great as 100 metres (Heatwole 1978a) and regularly remain submerged for periods of half an hour to two hours (Heatwole 1978a; Graham, Gee, Motta & Rubinoff 1987b), and perhaps longer.

The metabolic rate of sea snakes is not greatly different from that of terrestrial snakes of equivalent body size (Table 37.1) (Heatwole 1978a) and lowered metabolism does not seem to be a major adaptation to diving. However, the

temperature of sea snakes is nearly identical to ambient sea temperature (Graham 1974b; Heatwole 1981b) and cooler water at depth could retard metabolic rate and lengthen submergence time.

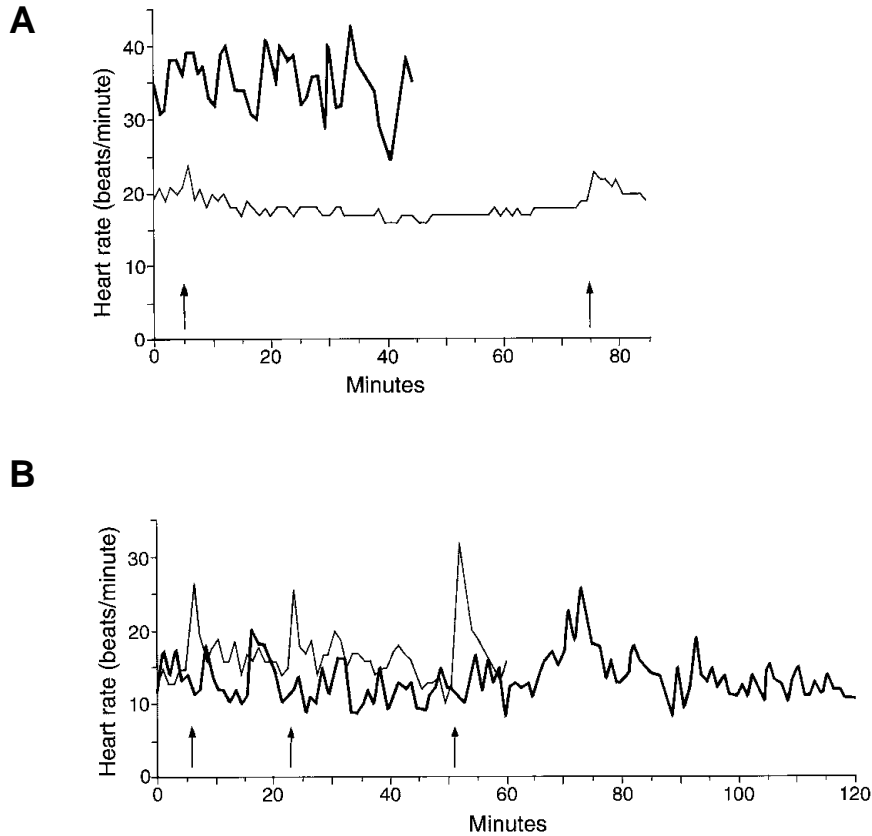
The blood of sea snakes has been compared with that of terrestrial snakes and other aquatic snakes. Differences in blood quality seem more related to activity and sluggishness than to diving capacity (Seymour 1976). Sea snakes have much lower blood volumes than the aquatic file snake, *Acrochordus granulatus* (Feder 1980), but blood volumes are not markedly different from terrestrial snakes; some species have a slightly higher blood volume than terrestrial snakes (Table 37.1; Pough & Lillywhite 1984; Heatwole & Dunson 1987). In general the similarities of haematology and metabolism of sea snakes and terrestrial snakes are more conspicuous than are the slight differences.

The lung of sea snakes, like that of terrestrial snakes, is a single tube that is longitudinally regionalised. The anterior end, known as the tracheal lung, is morphologically a modified trachea although functionally it acts as a lung, is highly vascularised and is involved in gaseous exchange (Heatwole & Seymour 1975b). The middle part of the lung, the bronchial lung, is the main avenue for gaseous exchange. It leads into a poorly vascularised section, the saccular lung, and serves mainly as an air storage compartment. In terrestrial snakes this part is thin and membranous, but in sea snakes it is muscular. Contraction of these muscles moves gas forward to the respiratory surfaces and mixes stored air with that of the anterior sections of the lung (Heatwole & Seymour 1975b).

Two evolutionary pathways are available to air-breathing diving vertebrates. Birds and mammals have the classic diving syndrome. This involves peripheral vasoconstriction of the blood (and hence oxygen) supply to the muscles and some internal organs, anaerobic metabolism of the blood-starved tissue with a resultant build-up of lactic acid, and diving bradycardia (lowered heart rate) with a reduced blood circuit, primarily to the heart, lungs and brain (see Elsner 1969). Diving bradycardia is independent of activity; strenuously active animals still have a lowered heart rate while submerged. By contrast, sea snakes have a higher heart rate while breathing (breathing tachycardia) than when not breathing, either submerged or at the surface (Fig. 36.4; Heatwole 1977e; Heatwole, Seymour & Webster 1979). The normal (resting) heart rate of sea snakes occurs when submerged; it is increased with activity in *Aipysurus laevis* (Fig. 36.4A), but changes little with activity in the laticaudid, *L. colubrina* (Fig. 36.4B) (Heatwole 1977b). Breathing tachycardia facilitates more effective transfer of oxygen to the blood during breathing.

Sea snakes usually surface for only a few seconds to take one or a few breaths (Heatwole 1978a); consequently they lack the time and ventilation that would be required to pay back an oxygen debt. Also, their blood has been shown to remain aerobic during voluntary diving (Seymour & Webster 1975). Sea snakes have solved the oxygen debt problem by using cutaneous respiration. Some species can absorb up to one-third of their oxygen requirements through the skin and lose up to 94% of their carbon dioxide production (Graham 1974a; Heatwole & Seymour 1975a). Elimination of carbon dioxide while underwater prevents it from building up enough to cause an acid imbalance in the blood. The capacity for cutaneous respiration is related to the degree of aquatic adaptation and to habitat. Hydrophiids generally respire more effectively through the skin than do other aquatic snakes, terrestrial snakes and most turtles (Table 37.1; Standaert & Johansen 1974; Heatwole & Seymour 1978; Seymour 1982).

Hydrostatic pressures in deep water can have a profound effect on air-breathing organisms. At depth, the lungs are hydrostatically compressed, and nitrogen is absorbed into the blood. During ascent, pressure decreases and dissolved nitrogen tends to come out as bubbles. These can cause serious discomfort,



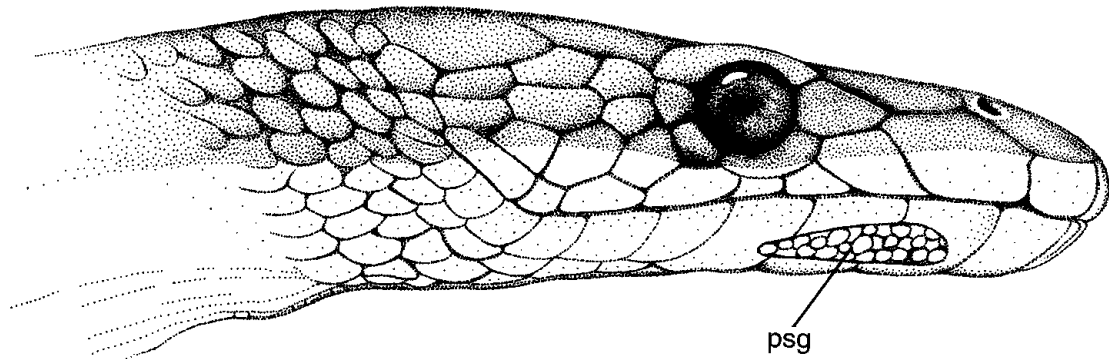
**Figure 36.4** Comparison of the heart rates of an inactive snake (thin line) and one during nearly continuous activity (thick line). Arrows indicate breaths of the inactive snake. **A**, the hydrophiid, *Aipysurus laevis*; **B**, the laticaudid, *Laticauda colubrina*. (After Heatwole 1977b) [W. Mumford]

disability and even death in humans, a disorder known as Caisson's disease or the 'bends'. Sea snakes do not suffer the bends either because they normally stay on the surface for only a short time and dive to depth again before the symptoms appear or, more likely, because lung nitrogen dissolved under pressure dissipates through the skin into the sea and blood concentrations do not build up (Graham 1974a).

Cardiac shunts may also serve to reduce the danger of the bends. As explained in Chapter 24, the functional separation of oxygenated and deoxygenated blood in squamate hearts allows the systemic return to the heart to be shunted to the systemic output (right-to-left-shunt) and bypass the lungs during diving. This would result in slower uptake of gas and thus a reduced threat of the bends. The shunt in this direction would also enhance cutaneous respiration at the expense of pulmonary respiration. By employing such shunts a sea snake can regulate the relative contribution of lungs and skin to respiration according to immediate circumstances, as well as the rate of nitrogen absorption into the blood and thereby avoid the bends. (Seymour 1974, 1982; Seymour, Spragg & Hartmen 1981). *Hydrophis coggeri* (cited as *H. belcheri*) has extensive shunts with 76% of its blood flow bypassing the pulmonary circuit, almost three times the value for a laticaudid (Seymour 1978).

Terrestrial, and especially arboreal, snakes tend to have the heart situated close to the anterior end, thereby shortening the length of the blood column to the head and permitting maintenance of blood pressure in the brain when the head is lifted vertically. Because of the equalising effect of external hydrostatic pressure, snakes in water are less subject to gravitational gradients than those in





**Figure 36.5** Head of *Pelamis platurus*, showing the posterior sublingual gland, or salt gland, in the lower jaw. It is located beneath the tongue sheath and empties into it. **psg**, posterior sublingual gland. (After Dunson 1979)  
[T. Wright]

air and require less control of axial blood pressures when in a vertical position. Accordingly, sea snakes have lower blood pressures and poorer regulation of blood pressure in compensation for postural changes than do terrestrial snakes and the heart is located closer to body midlength (Lillywhite 1976, 1987a, 1987c, 1988; Lillywhite & Pough 1983). When tilted in air their blood tends to pool in the posterior part of the body and they have problems in supplying blood to the brain.

The buoyancy requirements of sea snakes change with different activities. A snake ascending to breathe or maintaining position at the surface expends less energy if it is buoyant, whereas one foraging at the bottom exerts itself less if it is heavier than water. The lungs are the hydrostatic organs that assist in regulation of buoyancy (Graham, Gee & Robinson 1975; Graham *et al.* 1987b). At the surface, *Pelamis platurus* fills the lung sufficiently to float. Before diving it exhales some of the air but still maintains slightly positive buoyancy. Upon submergence buoyancy decreases through hydrostatic compression of the lung volume with depth and also metabolism of oxygen without equivalent replacement in the lung by carbon dioxide, which is dissipated to the sea via the skin as described above. Neutral or negative buoyancy is attained. These adjustments make for easier maintenance of position at depth and on the surface, although the snake still has to contend with a slight tendency to float during descent and to sink during ascent.

### Excretion and Osmoregulation

Body fluids of sea snakes are hypotonic to sea water and thus there is a tendency to lose water and to gain salts. Mechanisms to counteract these tendencies are required to maintain a proper balance of salts and water in the body. Sea snakes, like other snakes (and birds), conserve water by being uricotelic, that is, the waste products of nitrogen metabolism are excreted as uric acid or urate salts. However, the kidneys of sea snakes do not play a major role in ionic regulation; the urine is hypo-osmotic to the blood plasma and less salt is excreted than through extra-cloacal routes (Dunson 1968, 1979). In hydrophiids most salt excretion is via the posterior sublingual gland, located in the lower jaw just beneath the tongue sheath (Dunson 1979) (Fig. 36.5). It actively transports cations as a brine into the tongue sheath. When the snake protrudes its tongue the brine is pushed out of the mouth into the sea. The sublingual gland has probably evolved independently into a salt-excreting gland in the Hydrophiidae, Laticaudidae and Acrochordidae (Dunson & Dunson 1973).

The effectiveness of this gland varies among species. Maximum concentration of the brine correlates positively with relative size of the gland. *Hydrophis semperi*, one of the two species of sea snakes now lake-locked, has retained a functional salt gland. On the other hand, some completely marine species have tiny salt glands with extremely low rates of secretion (Dunson & Dunson 1974). Other factors must be involved in their salt balance.

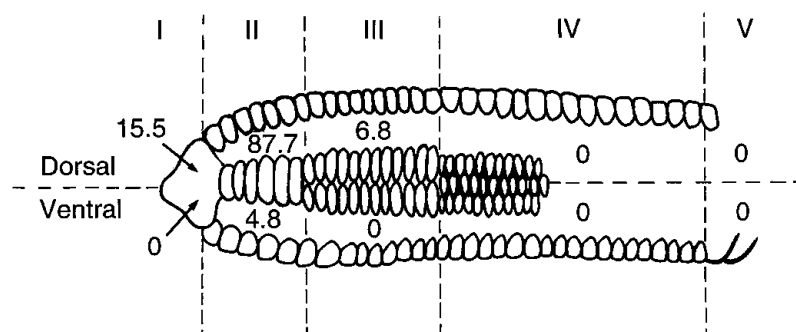
The skin of sea snakes is important in osmoregulation. The outer keratin layers act as a barrier against salts entering the body (Dunson & Robinson 1976). More salts move outward through the skin than inward (Dunson & Stokes 1983), thereby counteracting the tendency to accumulate salts from the environment. Water passes through the skin more easily than do salts, so that influx exceeds efflux and therefore assists the retention of water. The directionality of salt and water movement in sea snake skin is the reverse of that in freshwater snakes (Dunson 1978), which have opposite problems; they live in a dilute medium and need to get rid of water and gain salts from the environment.

### Sense Organs and Nervous System

Hibbard (1975) reviewed the sense organs and optic tectum of sea snakes. In general, the retinal structure of hydrophiids suggest effective diurnal vision. However, there are interspecific differences. Species of *Aipysurus* probably have better vision than other taxa as they have more distinct stratification of the inner plexiform layer of the retina and better development of the optic tectum. *Astrotia stokesii* has a pure cone retina and small cone receptors. *Hydrophis elegans* probably has the poorest vision of the species studied.

Sea snakes are unique among reptiles in possessing cutaneous photoreception (Zimmerman & Heatwole 1990). Light-sensitivity in the tail of *Aipysurus laevis* is most highly developed on the upper side and toward the tip (Fig. 36.6). Detection of light by the tail warns the hiding snake to withdraw the tail along with the rest of the body when hiding in crevices. Many sea snakes often hide in crevices among corals or other cover when not foraging for food or surfacing to breathe.

The olfactory epithelium of sea snakes is similar to that of other reptiles although some olfactory structures are reduced. The vomeronasal organ is well developed (Poran pers. comm.). Bowman's glands are present. The tongue is an important adjunct to olfaction through its use in transferring scented particles from the external medium to the sensory area of the vomeronasal organ. Taste buds may be present on the roof and floor of the mouth, but are absent from the tongue.



**Figure 36.6** Sensory map of the tail of *Aipysurus laevis*. The numbers indicate the percentage of light stimulations to which the snake responded by moving its tail out of the beam. (After Zimmerman & Heatwole 1990)

[T. Wright]

The inner ear of sea snakes has a well-developed sensory epithelium that senses both static and kinetic changes in equilibrium. However, the cochlear portions serving acoustic functions, especially the basilar papilla, are poorly developed in comparison to those of other reptiles. It is likely that sea snakes rely more heavily on vision and olfaction than on hearing.

### Exocrine Glands

Sea snakes possess the same cephalic glands found in terrestrial snakes, including Harderian, sublingual, anterior sublingual, venom, labial and nasal glands (Burns & Pickwell 1972). The sublingual gland is a salt gland excreting concentrated brine and functioning in osmoregulation (see Excretion and Osmoregulation). The venom gland is discussed in Feeding and Digestion.

*Pelamis platurus* is known to have scent glands in the base of the tail. These actively secrete, although they are small in comparison to those of terrestrial snakes (Weldon, Sampson, Wong & Lloyd 1991). Their function is unknown. Little is known of the endocrine glands of sea snakes.

### Reproduction and Development

All hydrophiids are live-bearers and, unlike the laticaudids, do not come out onto land to breed. Those that have been studied are truly viviparous in that after ovulation the developing eggs continue to receive nutrients from the mother via an allanto-placenta (Kasturirangan 1951).

Some sea snakes have strongly seasonal reproductive cycles, despite living in a relatively equable environment. The female gonadal cycle of *Aipysurus laevis* from the Great Barrier Reef is synchronous, with ovulation occurring in October and parturition in April, coinciding with the beginning and end of the monsoon season, respectively (Burns 1985). *Enhydrina schistosa* in Malaysia has a synchronous peak in gamete production by both sexes in September. Gestation extends over the warmer wet season from November to February–March (Voris & Jayne 1979). *Hydrophis brookii*, *Hydrophis melanosoma* and *Hydrophis torquatus* from the same locality and *Lapemis curtus* (= *Lapemis hardwickii*) from another Malaysian locality have similar reproductive cycles (Lemen & Voris 1981). Other species, however, have loosely seasonal or aseasonal reproduction. For example, the reproductive cycle of *Hydrophis caerulescens*, from the same locality as the *L. curtus* population mentioned above, was spread out over the year.

There may be regional differences in reproductive phenology. The conflicting reports of aseasonality and seasonality in *Pelamis* (see Kropach 1975) may arise from geographic differences in reproductive cycles. Lemen & Voris (1981) reported regional populations of several species being out of phase and Burns (1985) noted that in the Gulf of Carpentaria, gravid *A. laevis* are found in the cooler winter months as well as in summer and reproduction there must be less seasonal than on the Barrier Reef. Even in populations with synchronous reproduction not all mature individuals necessarily participate in each year's breeding activity. Only about half of the mature females of *A. laevis* breed in any one year. Burns (1985) suggested that it may take females two years to accumulate the energy required to produce young.

In general, sea snakes produce small numbers of young. The average clutch size ranges from three to nine for most species and larger females produce more young than smaller ones (Voris 1964; Voris & Jayne 1979; Lemen & Voris 1981). Considerable amounts of energy and materials are expended in reproduction. The young usually are large, with individual neonates in most species weighing 5 to 11% and entire clutches 28% to 38% of their mother's weight, an exceptionally large investment compared to that of terrestrial snakes

(Table 36.1). *Enhydrina schistosa* is an exception, with clutch sizes averaging 18.3 and some numbering over 30. Reproductive effort per clutch is about the same as in other sea snakes (39%), but like terrestrial snakes, this species tends to produce many small young (neonates average 2.1% of their mother's weight), rather than few large ones.

**Table 36.1** Reproductive characteristics of some sea snakes. Data from Lemen & Voris (1981).

Species	Mean clutch size	Mean reproductive effort (%)		Mean embryo weight (g)
		Per embryo	Per clutch	
<i>Aipysurus eydouxii</i>	4.4	6.6	28.9	10.8
<i>Enhydrina schistosa</i>	18.3	2.1	38.9	11.4
<i>Hydrophis brookii</i>	4.9	8.7	38.3	8.9
<i>Hydrophis caeruleus</i>	5.9	5.6	32.7	5.9
<i>Hydrophis fasciatus</i>	3.3	10.9	35.8	10.6
<i>Hydrophis melanosoma</i>	6.0	4.6	28.1	9.7
<i>Hydrophis torquatus</i>	5.5	6.3	34.9	6.2
<i>Lapemis curtus</i>	3.3	8.3	27.8	23.5
<i>Thalassophina viperina</i>	3.5	9.1	31.8	19.9

Some of the effort expended in reproduction is wasted through infertility. Lemen & Voris (1981) reported that 5 to 20% of the oviducal eggs in nine species of hydrophiid were infertile, and that 6 to 60% of gravid females contained at least one infertile egg.

## NATURAL HISTORY

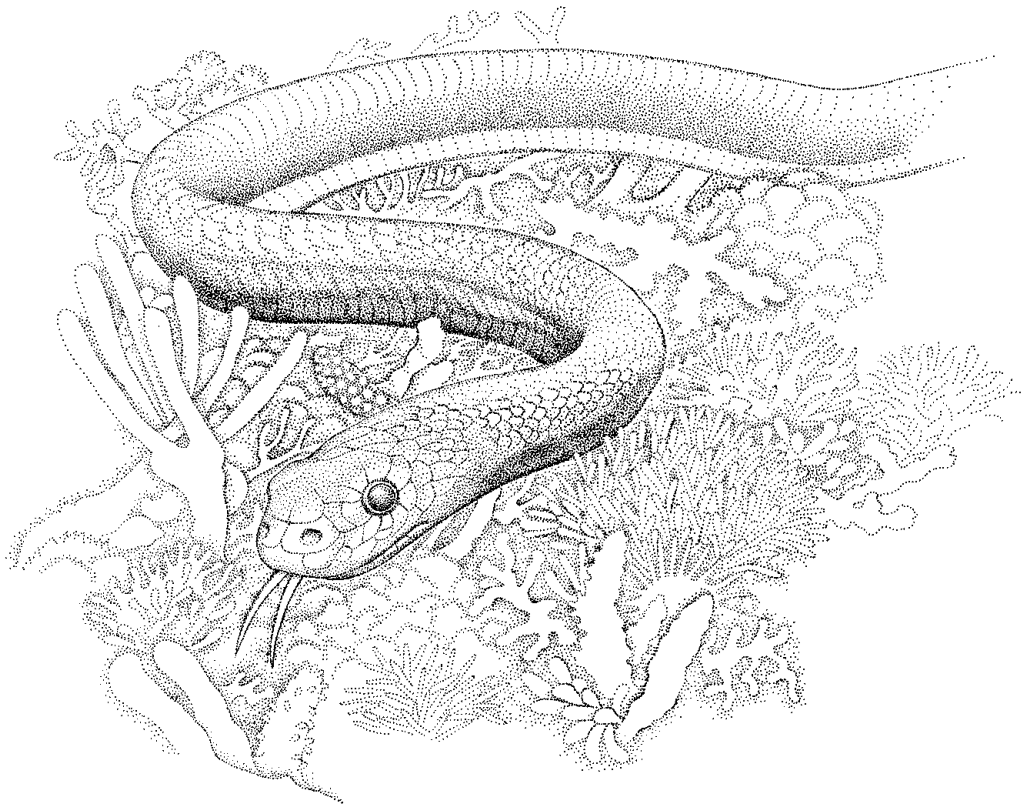
### Life History

Young snakes grow rapidly at first. Juvenile *Enhydrina schistosa* grow at an average rate of 0.5 g/day, without any seasonal decline (Voris & Jayne 1979; Voris 1985). They mature at about 18 months of age at which time growth rate declines. Females give birth for the first time at about 2 years of age. Only 10 to 20% of the newborn survive the first year and only about 6% of the females survive to reproduce. Only a tiny fraction of the population consists of animals four years of age or older (Voris & Jayne 1979).

Sea snakes often are locally abundant, yet few attempts have been made to measure population densities. The traditional mark/recapture method of estimating population size is difficult to use in a marine environment and has not always been successful. For example, Kropach (1975) marked 961 *Pelamis* but only four were recovered. Greater success was achieved for *Enhydrina schistosa* and an estimate of 900 to 1400 juveniles and about 1350 adults in an enclosed bay was obtained (Voris, Voris & Jeffries 1983; Voris 1985).

## Ecology

The food of most sea snakes consists of fish and occasionally some marine invertebrates. Some are highly specialised and take only fish of one or a few types, or of a particular body form (Voris 1972). For example, *Enhydrina schistosa* feeds mostly on tachysurid and plotosid catfish and pufferfish (Voris, Voris & Liat 1978), *Microcephalophis gracilis*, and *Hydrophis melanosoma* eat eels almost exclusively and *Ephalophis greyi* and *Astrotia stokesii* seem to specialise on fish with a goby-like shape (Voris & Voris 1983). In general, most species of sea snakes feed primarily on sedentary fishes that either dwell on the bottom or inhabit burrows or crevices; eels and goby-like fish are especially prevalent in sea snake diets. Some species, however, are generalised feeders and take a variety of fish from many different families, including free-swimming ones (Voris & Voris 1983; Rasmussen 1989). Fishes from 19 families have been identified in the stomach of the pelagic *Pelamis platurus* (Kropach 1975). *Aipysurus laevis* is another generalist feeder. The works of McCosker (1975), Limpus (1975b), Voris & Voris (1983) and Burns (1984) collectively indicate that this species feeds on fishes of at least 17 families and six different body-shape types as well as fish eggs, prawns, squids, molluscs and moulting crabs. The fishes included bottom-dwelling as well as free swimming species and both diurnally and nocturnally active forms. *Aipysurus laevis* forages in crevices at night and during the day (Fig. 36.7; Heatwole, Minton, Taylor & Taylor 1978). The state of digestion of prey suggested that free swimming, nocturnal species are taken from crevices during daytime inactive periods, and that diurnal forms are taken from nocturnal retreats (McCosker 1975).



**Figure 36.7** Diurnal foraging by *Aipysurus laevis* over a mixed coral bottom.  
(After photo by C. Pollitt) [T. Wright]

The habitat preferences of most sea snakes are largely unknown. Generally, individual species or species groups tend to have preferred habitats based on such factors as water depth, nature of bottom (coral, sand, mud), turbidity and season (Fig. 36.8). Many of these preferences simply reflect the occurrence of prey species. For example, many of the small-headed species of *Hydrophis* feed exclusively on garden eels which are restricted to sandy or some consolidated muddy substrates. The major habitats may be categorised as follows (the examples given are not exclusive to those habitats):

Coral reef habitats are selected by species which feed on crevice-dwelling fishes or fish eggs. Typically, such species browse the coral crevices looking for prey. Included in this group are *Emydocephalus annulatus* and most species of *Aipysurus*.

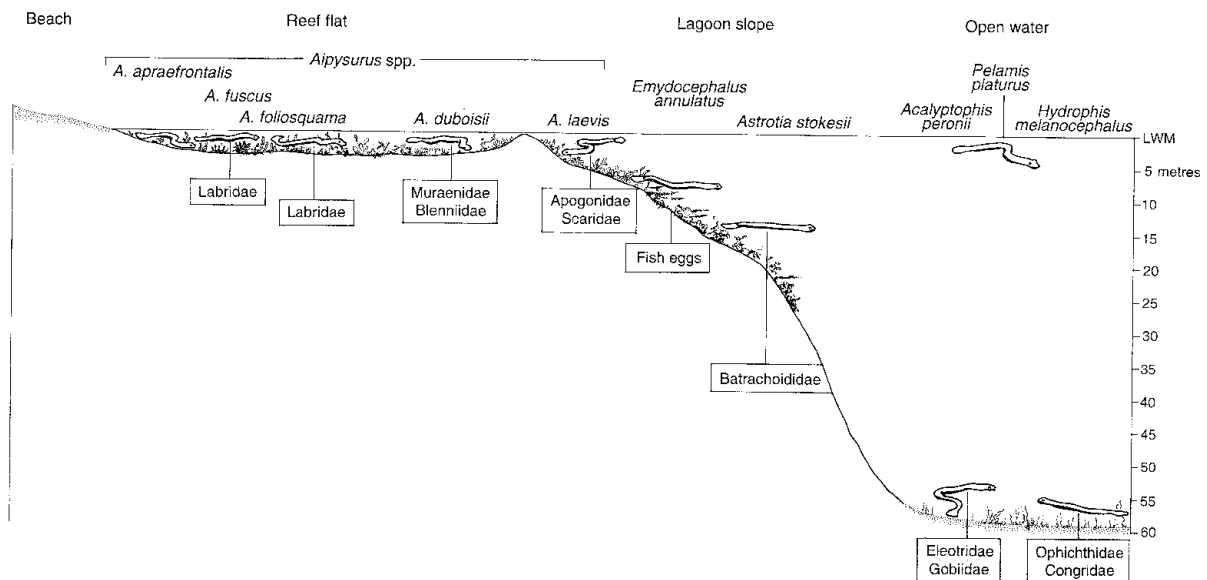
Coastal mangrove habitats are utilised by several smaller ephalophine species which feed on mudskippers and small crustaceans. This group includes *Hydrelaps darwiniensis*, *Ephalophis greyi* and *Parahydrophis mertoni*.

Turbid waters of estuaries and river mouths are the preferred habitat of *Enhydrina schistosa*, which may also travel long distances upstream into freshwater reaches of larger rivers.

Shallow inshore waters of moderate turbidity over mixed sandy/muddy substrata are the preferred habitat of many species, both ephalophiine and hydrophiine. It is typified by the productive shallow seas of the Gulf of Carpentaria. Species found commonly in this habitat complex are *Lapemis hardwickii*, *Hydrophis elegans*, *Hydrophis mcdowelli* and *Hydrophis ornatus*.

Deep (to 100 m), clear waters off coral reefs are preferred by many of the small-headed species such as *Hydrophis coggeri* and *Disteira kingii*, especially those which feed exclusively on burrowing eels.

Sea snakes often occur in mixed populations, sometimes in conjunction with other marine snakes such as laticaudids, homalopsines and acrochordids. Species richness varies widely and ranges from one to more than ten (Dunson 1975a; Dunson & Minton 1978). Ashmore Reef off northwestern Australia has ten resident species (plus a presumed stray), spatially separated into three zones:



**Figure 36.8** Diagram of the spatial and ecological separation of sea snakes on the leeward edge of Ashmore Reef, Australia. The preferred prey of several hydrophiid species is indicated; prey categories overlap considerably at the familial level, but not at the species level. (After McCosker 1975)

[W. Mumford]

corals in shallow water, muddy or sandy substrata in deep water, and open surface water (pelagic) (Fig. 36.8; Minton & Heatwole 1975; McCosker 1975). There is further ecological segregation by diet; no overlap occurs in the prey taken at the species level (McCosker 1975). Smaller assemblages of three to five species in the southern Coral Sea show similar habitat separation (Heatwole 1975c). Two species widely occupying the same habitat had different food habits, *Aipysurus laevis* eating mainly fish and *Emydocephalus annulatus* feeding exclusively on fish eggs. In studies of assemblages from several localities, Glodek & Voris (1982) and Voris & Voris (1983) also found separation by habitat, but where overlap occurred, syntopic species tended to differ in diet.

Redfield *et al.* (1978) recorded 17 species in the sea snake assemblage of the Gulf of Carpentaria; *Lapemis curtus* (= *Lapemis hardwickii*) accounted for 61% of the individuals. Previous reports by Shuntov (1971) and Heatwole (1975d) from the Gulf found other species dominating and it was suggested that those differences might reflect an effect of the prawn-fishing industry in the intervening time between studies. However, biased sampling may also have been involved, or regional differences over such a large area; it is likely that more than one assemblage was included in these investigations. The problem is currently under study.

Many species of sea snake have extensive distributions and individuals may wander widely. For example, *Pelamis platurus*, which occupies slicks on the surface of the ocean, may be carried by currents and storms. It is often found far out of its breeding range and is one of the most common species cast up alive on beaches. Some species, however, have very limited home ranges. Individually marked *Aipysurus laevis* confined their activities to a section of reef edge 150 m or less in length (Burns 1984). The home ranges of different individuals overlapped broadly and there was no evidence of territorial defence.

The tiger shark (*Galeocerda cuvieri*) and sea eagles (*Haliastur indus*; *Haliaeetus leucogaster*) commonly prey on sea snakes (Heatwole 1975a). Other species of sharks and birds as well as some predatory teleosts and mammals also may occasionally take them (MacLeish 1972; Heatwole, Heatwole & Johnson 1974; Heatwole 1975a; Heatwole & Finnie 1980). Attempted predation upon sea snakes may be frequent as suggested by a high incidence of missing tails or bite-like injuries (up to 24%) and of scars on the back presumably inflicted by bird talons (up to 7%) (Heatwole 1975a).

*Pelamis platurus* seems to suffer less from predators than do other sea snakes and its conspicuous black and yellow pattern has been interpreted as an advertisement of its venomous nature (Kropach 1975; Ineich 1988). Attacks on this species, but without evident ingestion, by gamefish (Paulson 1967) and seabirds (Wetmore 1965; Reynolds & Pickwell 1984) have been reported. Only two instances of predation (by a pufferfish and a seal) have been authenticated under natural conditions (Heatwole & Finnie 1980; Pickwell, Bezy & Fitch 1983). Rubinoff & Kropach (1970) showed that hungry predatory fish from areas in which *P. platurus* occurred avoided live or dead *Pelamis* and even pieces of skinned meat. By contrast, naive fishes allopatric with *P. platurus* sometimes ingested them and occasionally died from having been bitten. *Pelamis platurus* also is noxious in other ways and detection of these qualities may be chemoreceptive rather than visual. Weldon (1988) found that snappers (*Lutjanus* spp.) tended to reject pieces of *P. platurus* after snout contact with them, and when they were eaten often they were regurgitated. The skin had a stronger emetic effect than pieces of skinned meat, and snake skin extracts rendered pieces of fish meat less palatable.

Commensals of sea snakes include diatoms, foraminiferans, hydrozoans, serpulid polychaetes, bivalve molluscs, higher algae, bryozoans and barnacles (Zann, Cuffey & Kropach 1975); the last three are the most commonly encountered. Two species of barnacles, *Platylepas ophiophilus* and *Octolasmis grayii*, are exclusive to sea snakes. The former has morphological adaptations that allow it to penetrate the host's tissues and adhere more effectively (Zann 1975) whereas the latter merely adheres to the skin's surface (Jeffries & Voris 1979). Barnacles have been recorded from most species of sea snake for which adequate samples were available and infestations were often high, sometimes reaching 50 to 75%. Barnacles tend to clump together and are more prevalent toward the tail. Frequent skin-shedding by sea snakes periodically rids them of most commensals (Zann *et al.* 1975). Because of its pelagic habit, *Pelamis platurus* does not have access to solid substrata for anchoring the skin during ecdysis, and it coils and knots itself as a means of loosening and freeing the skin (Pickwell 1971).

Ectoparasitic ticks and mites, such as those reported from laticaudids (see Chapter 37), are not known from hydrophiids, probably because of their more completely marine life history. Nematodes and platyhelminths are recorded from the digestive tract (Kropach 1975). Digenean trematodes of the family Hemiuridae include *Plicatrium visayanensis* from the stomach and small intestine of *Hydrophis ornatus* (Bush & Holmes 1984), *Sterrhurus carpentariae* from the stomach of *Lapemis hardwickii* (Bush & Holmes 1979) and lung flukes of the genera *Hydrophitrema* and *Pulmovermis* from various species (Vercammen-Grandjean & Heyneman 1964; Ko, Lance & Duggan 1975).

### Feeding Behaviour

Like terrestrial snakes, sea snakes swallow large prey whole and can consume fish of a diameter at least up to twice that of their own necks (Voris & Moffett 1981). They capture prey in several ways. *Pelamis platurus* floats at the surface and small fish seeking shelter under it are struck and eaten. Vibrations produced by the motion of the fish induce the snake to slowly turn the head toward the source, sometimes with open mouth, followed by a rapid sideways lunge. Backward swimming occurs in response to presence of fish or to light tactile response and is often a component of the feeding sequence (Kropach 1975).

Some sea snakes rely on capturing confined prey. They examine crevices among coral or burrows in the sand (Heatwole *et al.* 1978), all the while flicking out the tongue (Fig. 36.7). When the tongue touches a fish and relays odours from it to the chemosensory Jacobson's organ in the roof of the mouth, the snake lunges and bites. The captured fish is held until its struggles abate under the effect of the injected venom. It is then released and the snake moves entirely around its circumference, flicking out its tongue against the edges. This appears to be a means of ascertaining whether the prey is of a size that can be swallowed.

Another means of prey capture is exemplified by the piscivorous *Enhydrina schistosa* which inhabits muddy water of low visibility. It cruises near the bottom and when it bumps into fish or comes close to them, it strikes laterally to effect the capture. It maintains its hold until the fish stops struggling, then works around to the head end and swallows it head first. During swallowing, the snake turns its head away from the direction of swimming and faces its tail (Voris *et al.* 1978).

It appears that vision is of little importance in any of these methods of prey capture. Indeed, sea snakes probably cannot identify a fish as a prey item by sight. If a captured fish is lost from the jaws of a crevice feeder, but lying nearby in full sight, the snake does not recognise it and initiates a random search pattern



while sticking out the tongue. If the fish is accidentally contacted by the tongue, it is immediately seized and feeding continues. Similarly, *Pelamis* cannot retrieve lost prey (Kropach 1975).

The three species of fish-egg-eating hydrophiids, *Emydocephalus annulatus*, *Emydocephalus ijimae* and *Aipysurus eydouxii* (Voris 1966; Gopalakrishnakone & Kochva 1990) have a unique feeding method. Contraction of the specialised *m. geniomucosalis*, which links the oral mucosa to the lower jaw, probably allows them to suck in fish eggs along with substantial quantities of sand (McCarthy 1987a, 1987b).

### Economic Significance

In 1982 the Commonwealth Government permitted the export of a limited number of skins of sea snakes taken as a by-catch of commercial prawn fishing in tropical Australia. Under the provisions of the Wildlife Protection (Regulation of Exports and Imports) Act 1982 (proclaimed in 1984), this export trade could only be continued as part of a management program under the Act; this trade continues until the present (1993). In an unpublished report to the Conservation Commission of the Northern Territory, Ward (1993) cited the sea snake by-catch of northern Australian prawn trawlers during 1989-90 as exceeding 200 000 specimens; the mean catch rate of sea snakes in his study was similar to the 0.26 snakes/hour recorded by Heatwole & Burns (1987).

As part of the sea snake management program, the Commonwealth Government has provided funds to various agencies to place sea snake 'observers' on commercial fishing vessels; this had led to the accumulation of a large, but mostly unpublished, body of data on sea snake distribution and local and regional taxonomic composition. However, despite these surveys, the knowledge of the broad distribution patterns of Australian hydrophiid sea snakes has changed little from that documented by various authors in Dunson (1975a).

In some parts of Asia, sea snakes are used as food by humans and domestic animals, and the skins are a source of leather; important fisheries occur in the Philippines and Japan. In Australia, sea snakes are not an item of human diet but there is a growing sea snake leather industry (both illegal and legal) (see Heatwole 1987). The sea snake (*pagi* or *ger*) is the subject of one of the many string games devised by the Torres Strait Islanders (Haddon 1912).

The main practical interest in sea snakes in Australia arises from their threat to human health and life. The potential danger of a snake depends on several factors. They include the likelihood of encounter, the potency and amount of venom delivered, the aggressiveness of the snake and the length of the fangs (a measure of how deeply the venom can be injected). Sutherland (1983) and Heatwole (1987) have reviewed these topics. Here, they are summarised briefly.

The venom of Australian sea snakes (except for those that eat fish eggs) is extremely toxic, by an order of magnitude greater than that of most dangerous viperids, but about the same or slightly lower than that of the most toxic terrestrial elapids. Its direct myotoxic effect is a clinical characteristic of serious hydrophiid envenomation of humans and laboratory animals (Fohlman & Eaker 1977), in which muscle fibres are attacked and break down. Muscle damage from myotoxins causes the release of myoglobin and creatine phosphate into the blood and eventually into the urine. Excess myoglobin could block kidney tubules and cause kidney damage (Zimmerman & Heatwole 1987). In addition to such a potential secondary effect, whole venom of *Aipysurus laevis* and six fractions derived from it all have a direct myotoxic effect (Zimmerman, Heatwole, Andreopoulos & Yong in press c).

Venom yields are lower than for many dangerous terrestrial snakes, and fangs are shorter (an exception is *Astrotia stokesii* which has long fangs and can deliver a massive dose of venom). Taking all these factors into consideration, most of the Australian sea snakes should be considered as potentially lethal.

The most aggressive and dangerous species of sea snakes inhabit muddy estuaries. In South-East Asia those species inflict many serious and sometimes fatal bites on people operating hand-seines, barefooted in shallow, turbid waters (Reid 1956, 1975; Murthy & Rao 1977). In Australia, most sea snake bites are sustained by crews of prawn trawlers. Serious envenomations seldom result because by the time the sea snake is brought to the surface it has exhausted its venom against fish or restraining ropes of the net and can give only a 'blank' bite. The species most often encountered directly by the general public are those that live in the clear water of coral reefs. Fortunately, those species usually become aggressive only if disturbed or mistreated and are seldom a danger to a sensible diver or swimmer. Unprovoked attacks are extremely rare but do occur occasionally (Heatwole 1975e, 1978b; Zimmerman 1988a, 1988b). Even when provoked into biting, often no venom is delivered (Heatwole 1990).

Given the potential danger of sea snakes and the more frequent contact between them and humans as a result of the developing leather industry and increasing tourism to waters inhabited by snakes, it is likely that sea snakes will become of greater medical importance in the future. There are antivenoms that protect against sea snake envenomation; that of the terrestrial Australian tiger snake (Elapidae) is one of the more effective ones readily available (Baxter & Gallichio 1976). One should be wary of folk remedies as many of the supposed 'cures' merely reflect recovery from blank bites, not from real envenomations (d'Aulaire & d'Aulaire 1980). For a more detailed treatment of the medical aspects of sea snake bite see Sutherland (1983).

## BIOGEOGRAPHY & PHYLOGENY

### Distribution

Approximately 50 species of hydrophiid sea snakes are known. With the exception of *Pelamis platurus*, which ranges across the Indian and Pacific Oceans from the east coast of Africa to the west coast of the Americas, the remaining species are found from the Persian Gulf to South-East Asia, New Guinea, Australia, and the islands of the south-western Pacific as far east as Fiji. They are abundant and species-rich throughout the shallow seas and inshore waters of tropical Australia. Of the 31 species recorded from Australian waters, 15 (48%) are endemic, 12 (39%) are shared with South-East Asia, while four (13%) are shared with the western Pacific.

Hydrophiid sea snakes have been recorded also from the colder waters of the southern oceans: from northern Tasmania, Victoria and South Australia (Cogger 1975). These latter records are presumed to be of individuals caught up in the strong summer Eastern Australian Current which sweeps down the eastern coast from the warm waters of the Great Barrier Reef. These individuals are unable to return to their feeding and breeding grounds, and ultimately find themselves in waters which are lethally cold. This summer influx of snakes is accompanied by a parallel influx of larval tropical fish species (Paxton pers. comm.).

Only one species, *Pelamis platurus*, appears to be a regular winter visitor to the seas off the south-east and south-west coasts of Australia. These intrusions were long regarded as waifs. For example, Dunson & Ehlert (1971) suggested that the lower lethal limit for this species lies between 14.5° and 17°C. However, Cogger (1975) showed that this species is not only a regular inhabitant of the cooler winter waters off New South Wales (mean winter surface temperature 16°C),

but that reproduction also occurs in these waters at this time. Because the mean size of *Pelamis platurus* in cooler eastern Australian waters is significantly larger than that recorded from eastern Pacific populations, the eastern Australian population may be genetically distinct.

Apart from the ubiquitous *Pelamis platurus*, two broad distribution patterns stand out. The first is a large suite of species which range from the east coast across the top of Australia (the Gulf of Carpentaria and the Arafura Sea) to the north-west shelf and the tropical coast of Western Australia. These include three species of *Aipysurus* (*laevis*, *eydouxii* and *duboisii*), *Acalyptophis peronii*, *Astrotia stokesii*, *Disteira major* and *D. kingii*, *Emydocephalus annulatus*, *Enhydrina schistosa*, three species of *Hydrophis* (*elegans*, *mcdowellii* and *ornatus*) and *Lapemis hardwickii*.

However, differences in dominant colour phases between eastern and western populations suggest that in some instances gene flow between populations of the same species on either side of Torres Strait may be low. Indeed, both *Emydocephalus annulatus* and *Hydrophis coggeri* appear to have a geographic discontinuity of approximately 1500 km between their populations on either side of Torres Strait.

There is a second, smaller group of species apparently confined to the waters west of Torres Strait: three species of *Aipysurus* (*apraefrontalis*, *foliosquama* and *fusca*), *Ephalophis greyi*, *Parahydrophis mertoni* and *Hydrelaps darwiniensis*.

For most other species recorded from Australian waters, records are few, or so isolated, that the extent of their ranges within Australian waters remains speculative.

### Affinities

The first rigorous phenetic classification of the Hydrophiidae was proposed by Smith (1926) based on morphological and cranial characters. Smith had included all marine snakes (including those in the genus *Laticauda*) within a single family, the Hydrophiidae. These were characterised by the presence of proteroglyphous ('fixed front fang') dentition, dorsal, valvular nostrils, posteriorly compressed bodies, short tongues in which typically only the cleft portion is protrusible, strongly developed caudal hypophyses and neural spines, and paddle-shaped tails. Within this family, Smith recognised two distinct subfamilies: the Laticaudinae with relatively broad belly scales, forward-projecting maxilla, broad parietal bones and a separate median prolongation of the rostral shield (*Laticauda* spp., *Aipysurus* spp. and *Emydocephalus* spp.) and the Hydrophiinae, to include all other marine snakes, with much reduced belly scales, a more posteriorly-located maxilla, narrow parietal bones and a fused median prolongation of the rostral shield.

In a major review of the world's sea snake fauna, using numerical taxonomy and cladistic principles, Voris (1977) concluded that there are three major monophyletic stocks of independent origin: Smith's Hydrophiinae and two separate groups within Smith's Laticaudinae: *Laticauda* spp. and *Emydocephalus* spp./*Aipysurus* spp.

Earlier, McDowell (1967, 1969a, 1969b, 1972a) had begun a series of detailed studies on the comparative anatomy, cranial osteology and external morphology of sea snakes. He concluded that three distinct monophyletic groups of hydrophiids can be recognised: the *Hydrelaps* group (*Hydrelaps*), the *Aipysurus* group (*Ephalophis*, *Aipysurus* and *Emydocephalus*) and the *Hydrophis* group (remaining hydrophiid genera). Seven genera (including five from Australia) can be recognised in the *Hydrophis* group: *Hydrophis*, *Acalyptophis*, *Kerilia*, *Thalassophis*, *Pelamis*, *Disteira* and *Lapemis*. Within the *Hydrophis* group three

subgroups (which McDowell accorded subgeneric status) can be recognised: *Hydrophis*, *Leioselasma* and *Aturia*. Some workers have treated these subgenera as full genera (for example, Kharin 1984).

Burger & Natsuno (1974) subsequently combined McDowell's *Ephalophis* and *Hydrelaps* subgroups into a new subfamily: the Ephalophiinae.

McDowell also examined the phylogenetic relationships between various groups of sea snakes, and between sea snakes and other proteroglyphous snakes. He concluded that laticaudid sea snakes represent a radiation separate from and independent of that of hydrophiid sea snakes, and that hydrophiid sea snakes are most closely allied to, and indeed are confamilial with, the Australasian radiation of terrestrial elapid snakes, all of which should be placed together in the family Hydrophiidae.

McDowell's conclusions were first interpolated into a new higher classification of snakes by Smith, Smith & Sawin (1977), who placed the laticaudids in a separate Tribe (Laticaudini) within the subfamily Elapinae of the family Elapidae. Other sea snakes were placed in four separate tribes (Ephalophini, Hydrelapini, Aipysurini and Hydrophiini) within the subfamily Hydrophiinae of the family Hydrophiidae. All Australasian terrestrial proteroglyphs were also included in this family.

Burger & Natsuno (1974) had argued earlier that the apparent independent origin of laticaudids from other marine snakes was best reflected in their assignment to separate families under the umbrella of a superfamily Elapoidea. This approach has generally been followed by subsequent authors who, while acknowledging the close phylogenetic relationships between all existing proteroglyphous snakes and the strong evidence for common ancestry, have tended to continue to recognise all three groups as distinct families: Elapidae, Hydrophiidae and Laticaudidae (for example, Cogger 1983) or as subfamilies (McCarthy 1986). The reason for this is not simply inherent conservatism; rather, the classification proposed by McDowell is based on weighting of certain characters (for example, heart position, arching of maxilla) for phylogenetic analysis. The relationships between these three groups remain speculative.