



FAUNA *of* AUSTRALIA



37. FAMILY LATICAUDIDAE

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DEFINITION AND GENERAL DESCRIPTION

The nasal scales of laticaudids are separated by one or two internasal scales. This feature, in conjunction with wide gastrosteges running the full width of the venter, like those of land snakes, separates this group from the Hydrophiidae. Oviparity is the sole proven means of reproduction. Sea kraits are amphibious and move freely on land.

The snakes of the family Laticaudidae constitute a discrete taxonomic group which represents either an independent lineage originating from terrestrial elapids, or an early separation from the hydrophiid sea snake lineage (Voris 1977).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The laterally positioned nostrils, broad ventral scales and a cylindrical body form are laticaudid characters that are considered primitive for sea snakes. The body scales are smooth, imbricate and arranged in 19 to 25 rows at mid length. The tail is laterally compressed, an advanced feature shared with hydrophiids. Usually laticaudids have conspicuous light and dark bands, and superficially resemble kraits, a feature giving rise to their common name, sea kraits. Banding is probably an advertisement of their noxious qualities, and some eels that can hardly be distinguished from *Laticauda colubrina* unless they are in hand are believed to be Batesian mimics (Pernetta 1977).

Locomotion

Aided by their wide ventral scales, sea kraits move on land in a manner similar to terrestrial snakes. They are competent climbers amongst rocks and vegetation (Mao & Chen 1980). In water, rhythmic lateral undulations of the body and flattened tail propel the animal forward. Laticaudids are usually sedentary on land, though rain stimulates them to be active (Guinea 1987).

Feeding and Digestive System

Sea kraits have potent venom and hollow fangs positioned at the front of the mouth. Prey is located underwater by foraging in crevices while protruding the tongue. Detected prey is envenomated and then swallowed, usually head first. Digestion may take several weeks (Saint Girons 1964).

Despite their effective venom apparatus, sea kraits are docile and reluctant to bite defensively, even when roughly handled, although bites to humans have been recorded (Punay 1975). Lethal doses (LD₅₀) for laboratory mice are: *Laticauda colubrina* 0.42 mg kg⁻¹; *L. laticaudata* 0.18 to 0.30 mg kg⁻¹; *L. semifasciata* 0.28 to 0.50 mg kg⁻¹ (Tamiya 1975). The toxicology, immunology, biochemistry and physical properties of sea krait venom are relatively well known through the publications of Tamiya & Arai (1966), Uwatoko, Nomura, Kojima & Obo (1966a), Uwatoko, Nomura, Kojima & Obo (1966b), Tu & Salafranca (1974), Low (1979), Kim & Tamiya (1982), Guinea, Tamiya & Cogger (1983), Tamiya, Sato, Kim, Teruuchi, Takasaki *et al* (1983), Singh & Guinea (1984), Takasaki, Kuramochi, Shimazu & Tamiya (1988), Obara, Fuse, Tsuchiya, Nonomura, Ménez & Tamiya (1989), Rowan, Harvey, Takasaki & Tamiya (1989) and Fuse, Tsuchiya, Nonmura, Ménez & Tamiya (1990).

Respiration, Circulatory System and Diving

Sea kraits are seen most often on land or foraging in shallow water near the islands they use for refuge (Gail & Rageau 1958), and consequently have a reputation as less capable divers than many hydrophiids. However, *L. colubrina* was observed at a depth of 45 m and when disturbed the snake swam into deeper water, estimated to be greater than 60 m (Mebs, pers. comm.). Usually, the species dives voluntarily for 15–25 minutes and has been recorded submerged for longer than 50 minutes (Heatwole 1975b; 1981a). Its maximum capacity for breathhold is unknown. When actively foraging in shallow water (less than 13 m deep), *L. colubrina* may surface every few minutes (Cogger, Heatwole, Ishikawa, McCoy, Tamiya & Teruuchi 1987).

The single tubular lung of sea kraits comprises three distinct sections (Heatwole & Seymour 1975b). The anterior tracheal section is a modified trachea and retains remnants of the tracheal cartilages. This part and the lung proper, or bronchial section, are heavily vascularised and collectively form the vascular lung which functions as the major gas exchange organ. The third and most posterior section is the saccular lung, which is not vascularised, plays no part in gas exchange and has only a minimal role in buoyancy (Heatwole 1981a). In water, the breathing cycle of *L. colubrina* consists of a number of quick breaths at the surface followed by a long period of apnea while submerged, much like the rhythm exhibited by hydrophiids. However, unlike hydrophiids, sea kraits can shift from this 'aquatic rhythm' to a 'land rhythm' of more regularly spaced breaths, similar to that of terrestrial snakes (Heatwole 1981a).

In many hydrophiids the capacity for prolonged submergence is enhanced significantly by cutaneous respiration. Sea kraits have less than half the capacity of hydrophiids to take up oxygen through the skin (Table 37.1; Heatwole & Seymour 1978). Sea kraits do not exhibit true diving bradycardia (Heatwole 1977b), nor is their blood especially adapted for oxygen storage (Seymour 1976; Heatwole & Seymour 1976). Indeed, they resemble terrestrial snakes more than hydrophiids in the temperature sensitivity of the oxygen carrying capacity of their blood (Table 37.1; Pough & Lillywhite 1984).

Blood flow to the lung, and hence pulmonary uptake of oxygen and nitrogen by the blood, can be regulated through intrapulmonary and intraventricular shunting of the systemic cardiac output. Compression causes non-uniform lung collapse, an increase in partial pressure of oxygen in the lung and arteries, and enhances shunting. Protection from the bends is afforded by maintenance of arterial nitrogen levels below those of the lung through increased shunting and by loss of nitrogen through the skin (Seymour 1978, 1989). *Laticauda colubrina* has a lower capacity for shunting and for cutaneous gaseous exchange than an hydrophiid and consequently is less well adapted to deep diving (Table 37.1). In deep water it could actually lose oxygen to the sea (Seymour 1987).

Osmoregulation

Excess salt is removed from the body of sea kraits by a sublingual salt-excreting gland that discharges into the tongue sheath. The skin is resistant to inward passage of salt (Dunson 1984). Laticaudids drink freshwater when it is available, which assists osmoregulation (Guinea 1987, 1991).

Table 37.1 Comparison of physiology, lung morphology and diving ability of the Acrochordidae, Laticaudidae, Hydrophiidae, Colubridae (Homalopsinae), Elapidae and Boidae. Apart from extrarenal excretion, sea snakes appear to have few specialised physiological adaptations to their marine environment. (Data sources: metabolic rate, cutaneous respiration, relative heart weight and relative lung volume, Vinegar, Hutchinson & Dowling 1970; Heatwole & Seymour 1975; Heatwole & Seymour 1978: blood volume (% mass), Lillywhite, Smits & Feder 1988: blood volume (haematocrit %), Seymour 1976; Pough 1979; Heatwole & Dunson 1987): extrarenal excretion, Minnich 1979: cutaneous diffusion, Dunson 1984)

	Acrochordidae	Laticaudidae	Hydrophiidae	Colubridae Homalopsinae	Elapidae	Boidae
Metabolic rate	Low	High	High	High	High	Low
VO ₂ (ml 100 g ⁻¹ h ⁻¹)	0.2–0.4	–	0–1.1	–	–	0.5–4.0
Cutaneous respiration	High	Low	High	Low	Low	Low
(ml O ₂ 100 g ⁻¹ h ⁻¹)	0.07–0.2	0.74–0.89	1.5–1.94	0.4–2.25	–	0.06
% of O ₂ requirements	7–13%	–	12–33%	–	–	3%
Blood volume	High	Low	Low	Low	Low	Low
% mass	12.5–13.3	5.9–6.5	5.5–9.9	3.9–13.3	–	–
Haematocrit %	41–57	24–34	26–35	32.2	28	25–29
Relative heart weight %	0.26	0.52	0.11–0.79	–	0.43	–
Lung morphology	Lobular	Vascular & sacular	Vascular & sacular	Sacular	Sacular	Sacular & paired in primitive forms
Relative Volume (ml g ⁻¹ body weight)	0.22–0.39	0.32	0.1–0.89	–	–	–
Diving ability	Shallow	60 m	100 m	Shallow	Shallow	Shallow
Extrarenal excretion	Sublingual gland	Sublingual gland	Sublingual gland	Premaxillary gland	None	None
Rate (mEq 100 g ⁻¹ h ⁻¹) Na, K, Cl	–, –, .39	33.9, 2.7, 36.7	218, 9.2, 169	–	–	–
Cutaneous diffusion	High	Low	High	Low	Low	Low

Reproduction

All species of laticaudids that have been studied are oviparous (Saint Girons 1964; Pernetta 1977; Guinea 1981; Bacolod 1983; Toriba & Nakamoto 1987). Reports of viviparity in *Laticauda colubrina* (in Singapore, Smith 1930) and in *L. crockeri* have not been substantiated (Cogger *et al.* 1987). Clutch sizes vary with species: two to 10 eggs in *L. colubrina* (Pernetta 1977; Guinea 1981); one to five eggs in *L. laticaudata*; three to 10 eggs in *L. semifasciata* (Bacolod 1983). In this last species, clutch size increases with size of the female and the relative clutch mass (RCM) is 21.1% of the mother's weight. Hatchling males are significantly larger (43.1 g) than females (40.0 g) and the sex ratio among hatchlings is skewed in favour of males (61%) (Toriba & Nakamoto 1987).

NATURAL HISTORY

Life History

Reproductive seasonality is geographically variable. In the Philippines, *L. colubrina* breeds aseasonally (Gorman, Licht & McCollum 1981; Bacolod 1983). The same species has a twice-yearly breeding cycle in Sabah (Steubing 1988) and a single breeding season in Fiji, in the warm summer months (Guinea 1981, 1987). The eggs are deposited in rock crevices and caves (Herre & Rabor 1949; Bacolod 1983). Incubation periods vary from about 123 days for *L. colubrina* (Guinea 1987) to 140 days for *L. semifasciata* (Nakamoto & Toriba 1986).

Ecology

Laticauda colubrina forages on coral reefs (Fig. 37.1) and rests and seeks shelter on adjacent land, often on very small islands or cays. Movement to and from the sea coincides with nocturnal high tides (Heatwole 1987). All species of sea kraits are piscivorous. *Laticauda colubrina* and *L. laticaudata* feed almost exclusively on moray and conger eels (Muraenidae and Muraenesocidae) (Pernetta 1977; Voris & Voris 1983; Moriguchi 1988); known departures from this diet are so rare that when they occur they occasion comment. *Laticauda semifasciata* eats various bony fish species (Voris 1972). A gudgeon, *Eleotris*, forms the sole diet of *L. crockeri* in Lake Te-Nggano, Rennell Island, Solomon Islands (Cogger *et al.* 1987).

Predators on sea snakes include sea eagles and some predatory fishes, especially tiger sharks (Heatwole 1975a), and these may prey on sea kraits as well. Guinea (1987) reported crabs preying on sea kraits.

Laticauda colubrina is host to the ectoparasitic ticks, *Amblyomma nitidum* and *Aponomma* sp. (Zann, Cuffey & Kropach 1975) and parasitic mites have been found in the respiratory tract of *L. laticaudata* (Gail & Rageau 1958). Parasites recorded for *Laticauda semifasciata* include flagellate protozoans, digenetic trematodes, nematodes, trombiculid mites and unidentified larval helminths (Telford 1967). Barnacles frequently encrust the skin of sea kraits (Gail & Rageau 1958).



Figure 37.1 *Laticauda colubrina* foraging on a coral reef at a depth of 10 m at Pig Island, near Madang, Papua New Guinea. [Photo by D. Mebs]

Behaviour

The body temperature of *L. colubrina* approximates that of their immediate environment, although the full range of fluctuation in environmental temperature is not experienced because snakes select cool microhabitats. In New Caledonia, body temperatures of snakes on land range from 27° to 28°C in the cooler part of the year and 28° to 30.5°C in snakes in shade or near shelter in warmer seasons; the mean is 27.8°C (Saint Girons 1964). Those in the Philippines are similar (mean 28.4°C; range 26.7° to 30.1°C; Heatwole 1981b). Temperatures of more exposed snakes in hotter periods reach temperatures of 30° to 33° C (mean 31.2° C). At night body temperatures dropped to 12° to 18° C, depending on the season. Snakes foraging in the water had temperatures of 17° to 19°C and 20° to 21°C, depending on the season.

Terrestrial aggregations of sea kraits are common in localities throughout their distribution. Estimates of the numbers of *Laticauda colubrina* using specific islands range from 600 and 721 on small islands in Sabah (Steubing 1988; Lading, Steubing & Voris 1991) to 1400 on Sausau Island, Fiji (Guinea 1987) and 1700 on Signal Island, New Caledonia (Saint Girons 1964).

Economic Significance

Laticaudids are used for stock and human food in parts of Asia and they are important in the leather industry. In the Philippines in the early 1970s, 4000 to 5000 kg of dried sea snake meat per month was ground for pig and poultry food, and 180 000 to 200 000 skins per year were exported to Japan (Punay 1975). *Laticauda semifasciata* and *L. laticaudata* were two of the principal species involved. In addition, local trade in *Laticauda* leather reached 5000 pieces per month. A sea snake industry operates in the Ryukyu Islands. No data are available on the annual catch, but receipt of about 1000 individuals of *L. semifasciata* on a single day was observed once (Heatwole 1987). In Australia, laticaudids are too rare for commercial exploitation. Potential danger to sea kraits comes from overexploitation by the leather industry, introduced predators (Guinea 1981), destruction of reefs by humans (Steubing 1988) and wanton slaughter (Saint Girons 1964).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Sea kraits are restricted to tropical waters of the western Pacific and eastern Indian Oceans (Fig. 37.2; Heatwole 1978a). The broadest distribution is shared by *Laticauda colubrina* and *L. laticaudata* which are broadly sympatric from India to southern Japan and to the eastern coast of Australia. *Laticauda semifasciata* ranges from southern Japan to Indonesia, with one subspecies, *L. s. schistorhynchus* restricted to Niue (Cook Islands), Tonga and Samoa. *L. crockeri* is known only from Lake Te-Nggano, Rennell Island, Solomon Islands (Cogger *et al.* 1987). Only *L. colubrina* and *L. laticaudata* have been recorded from Australian territorial waters, and then only as isolated individuals, not as breeding populations (Cogger, Cameron & Cogger 1983). Though this may reflect the low collecting effort in parts of northern Australia (Cogger 1975b), present information suggests that sea kraits occur in Australia only as waifs brought by oceanic currents from Melanesia. Their absence from the Australian coastline west of Torres Strait has been attributed to a cold water barrier in the Timor Sea during lowered sea levels in the Pleistocene (Cogger 1975b), or alternatively, to competitive exclusion by the hydrophiid *Aipysurus* (McCarthy 1986).

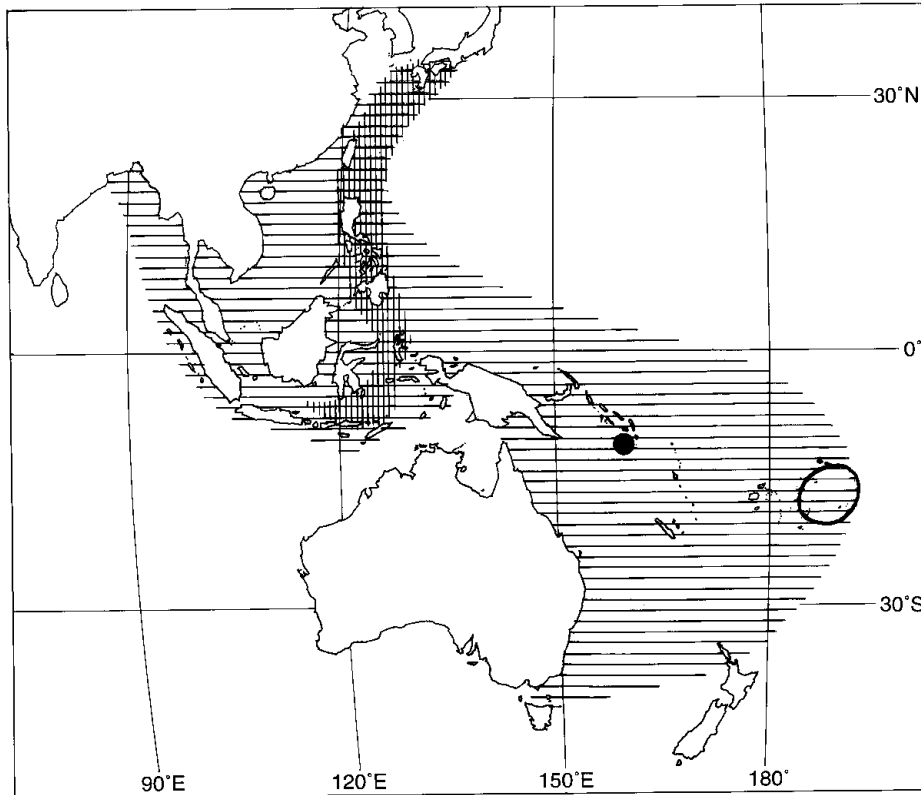


Figure 37.2 Distribution of sea kraits. Horizontal shading, *Laticauda colubrina*, *L. laticaudata*; vertical shading, *L. semifasciata*; open circle, *L. schistorhynchus*; closed circle, *L. crockeri*. (After McCarthy 1986)
[W. Mumford]

Affinities with other Groups

Burger & Natsuno (1974) accorded sea kraits full familial rank as the Laticaudidae, an arrangement supported by amino acid sequences of neurotoxins (Tamiya 1985). We follow Cogger *et al.* (1983) in accepting that assignment, pending further studies. For a more detailed discussion of the relationships of sea snakes and sea kraits, see Chapter 36.

Historically, sea kraits have been grouped most often in the subfamily Laticaudinae, as part of either the family Hydrophiidae (Smith 1926) or Elapidae (Dowling 1967; McDowell 1972a). Smith's concept of the subfamily was broader than currently accepted, and included, in addition to sea kraits, the hydrophiines *Aipysurus* and *Emydocephalus*. Some herpetologists assigned sea kraits to rankings lower than subfamilial level. Smith, Smith & Sawin (1977) considered them only as a tribe within the Elapidae. Because of the similarities in haemoglobin fingerprinting and serology linking sea kraits and other sea snakes, Mao & Chen (1980) included *Laticauda* within the Hydrophiidae and dispensed with the subfamilial designation, Laticaudinae.

Affinities within the Taxon

Kharin (1984) proposed splitting the sea kraits into two genera, *Laticauda* and *Pseudolaticauda*. This division is not supported by morphological (McCarthy 1986; Cogger *et al.* 1987) or toxicological (Slowinski 1989) studies and accordingly we retain all of the sea kraits in the single genus, *Laticauda*.

The species form three distinct complexes based on head colouration, presence or absence of an azygous prefrontal shield, division or not of the rostral shield, and numbers of scale rows around the body (Cogger *et al.* 1987). The *Laticauda colubrina* complex contains *L. colubrina* and *L. frontalis*, the *Laticauda laticaudata* complex comprises *L. laticaudata* (two subspecies of doubtful validity; McCarthy 1986) and *L. crockeri* (Cogger *et al.* 1987), and the *Laticauda semifasciata* complex includes two subspecies of the nominate species (Guinea *et al.* 1983).