The sea snakes of New Caledonia (Elapidae, Hydrophiinae)

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Résumé

Seuls des serpents marins de la famille des Elapidae sont présents en Nouvelle-Calédonie. Ils appartiennent tous à la sous-famille des Hydrophiinae qui regroupe également les Elapidae terrestres australiens et mélanésiens (serpent tigre, taipan, ...). La vie marine est apparue de façon indépendante à au moins deux reprises dans cette lignée. Les Elapidae marins de Nouvelle-Calédonie comprennent trois espèces du groupe des serpents marins amphibies (ovipares ; les tricots-rayés du genre Laticauda) et 12 espèces du groupe des serpents marins vrais (ovovivipares), soit au total 15 espèces. Les affinités du peuplement sont partagées entre d'une part la région australienne et d'autre part l'Asie. Deux espèces ne sont connues que par un unique spécimen de Nouvelle-Calédonie (Lapemis curtus et Hydrophis spiralis) et la présence de populations reproductrices devra y être confirmée. La présence de populations reproductrices de Laticauda frontalis n'est pas non plus attestée. Il pourrait s'agir, dans ces trois cas, d'individus erratiques transportés accidentellement par les courants marins lors d'anomalies climatiques comme les cyclones, colonisation non suivie par l'installation d'une population reproductrice. Hydrophis laboutei, décrit récemment à partir de deux exemplaires, n'a pas été retrouvé depuis et sa répartition devra être précisée. Le genre Laticauda et Emydocephalus annulatus font l'objet de recherches importantes (écologie) en Nouvelle-Calédonie. Les techniques les plus modernes à présent disponibles en écologie devraient pouvoir être appliquées aux serpents marins vrais autres que E. annulatus (les espèces du genre Hydrophis par exemple) car leur biologie et leur écologie strictement marines demeurent pratiquement inconnues.

Abstract

Only sea snakes of the family Elapidae are present in New Caledonia. They all belong to the subfamily Hydrophiinae comprising also Australian and Melanesian terrestrial elapids (tiger snake, taipan, ...). Marine life has appeared independently at least two times in that lineage. Marine elapids of New Caledonia comprised three species of amphibious sea snakes (oviparous sea kraits; the locally called 'tricots-rayés' of the genus Laticauda) and 12 species of the true sea snakes group (ovoviviparous), in total 15 marine snake species. Affinities of the sea snakes of New Caledonia are shared between on one hand the Australian area and on the other hand Asia. Two species are known by only one specimen from New Caledonia with unknown collect localities (Lapemis curtus and Hydrophis spiralis) and the occurrence of reproductive populations has to be confirmed. The occurrence of reproductive populations for Laticauda frontalis has also to be assessed. These three cases could correspond to erratic specimens accidentally transported by ocean currents during climatic anomalies like hurricanes, a colonisation not followed by the installation of a reproductive population. Hydrophis laboutei, recently described from only two specimens, has never been found again since its original description and its distribution has to be determined. The genus Laticauda and Emydocephalus annulatus are subjects of important researches (ecology) in New Caledonia. The most modern techniques nowadays available in ecology should also be applied to true sea snakes others than E. annulatus (e.g. species of the genus Hydrophis) since their strictly marine biology and ecology are nearly completely unknown.

Introduction

Neglected for a long time by herpetologists, sea snakes of New Caledonia are nowadays subject to particular attentions, notably the study of ecology of the most abundant and easy to study species (sea kraits and another species that feeds only on fish eggs, *Emydocephalus annulatus*). Their systematic

and their distribution have been revised in a recent synthetic book (Ineich & Laboute, 2002) also giving the first data on their ecology. This book reports first occurrence of several species previously unknown for the area, but most are still known by less than five specimens in New Caledonia, often by one or two specimens only. These marine reptiles all belongs to the family Elapidae also comprising species like Afro-Asiatic cobras, African mambas and American coral snakes. The diversity of that group is highest in Australia where one can find, among others, tiger snake or the famous taipan. Sea snakes are present in Persian Gulf, on the whole tropical Indian Ocean and tropical and subtropical Pacific Ocean, but their diversity is maximal in the Indo-Australian area. They are absent from the Red Sea, Atlantic Ocean and Mediterranean Sea. The diversity of sea snakes decreased rapidly when going away from the Indo-Pacific area in both directions and one rapidly only just find one remaining species, in the East as in the West, the Yellow-bellied Sea Snake, *Pelamis platura*. The sea snakes of interest to us there all belongs to the same lineage than Australian and Melanesian terrestrial elapids with which they share a common ancestor (subfamily Hydrophiinae). Among these sea snakes two clades can be distinguished. The first comprised amphibious forms of the genus Laticauda Laurenti, 1768, apparently all oviparous [sea kraits or 'amphibious sea snakes', represented by three species in New Caledonia] and the second comprised the 'true sea snakes' [represented by 12 species in New Caledonia]. These later never come to land and their reproduction is ovoviviparous: they give birth to live offspring. Both groups possess different phylogenetic origins and their marine life is related to at least two different independent evolutionary events. Amphibious sea snakes comprised 8 species in the World, all placed in the genus *Laticauda*, whereas true sea snakes comprised 57 species (Ineich, 2004; Heatwole et al., 2005; Kharin, 2005b), thus totalising 65 marine elapid species. Despite their diversity in New Caledonia (15 species), their relative abundance and their frequent occurrence on Noumea main beaches (Baie des Citrons, Anse Vata), theses snakes are responsible of few envenomations (see e.g. Anonymous, 2005). A determination key of New Caledonian sea snakes is found in Ineich & Laboute (2002).

Origin of our knowledge

The lack of venomous terrestrial snakes has been reported for New Caledonia since a long time (Trouessart, 1898). First acquired knowledge on New Caledonian sea snakes is based on some old specimens deposited in national museums (MNHN of Paris and NHM of London mostly) and were included in the Monograph of Malcolm A. Smith (1926). Very few of the 15 species presently known are reported in that book from New Caledonia. The first study totally devoted to New Caledonian sea snakes dated from 1958 (Gail & Rageau, 1958), but is not well documented and has several determination mistakes. Some studies followed, but only concerned ectodermic parasites of amphibious sea snakes (Rageau, 1960, 1967; Rageau & Vervent, 1959). The first serious ecological study on sea snakes of New Caledonia concerned amphibious sea snakes (Saint Girons, 1964a); this excellent work was later translated from French in 1990 by American herpetologists and published a second time (Saint Girons, 1964b). Our knowledge about distribution of those snakes in New Caledonia were later improved by some American and Australian field trips, notably to Chesterfield Islands (Minton & Dunson, 1985). Some other punctual works also permitted a better knowledge on their biology (see e.g. Rancurel & Intes, 1982; Bauer & DeVaney, 1987; Zimmerman et al., 1994); a first synthesis based on recently collected material was done by Ineich and Rasmussen in 1997, followed by the Monograph of New Caledonian herpetofauna published on 2000 by Bauer and Sadlier which put together knowledge on that group at that time. It is mostly through collections and numerous underwater observations made by the IRD of Noumea (Philippe Bourret, Pierre Laboute and Jean-Louis Menou) that our knowledge has progressed (Ineich & Rasmussen, 1997). Later a new species for Science has been described from New Caledonian waters and two others reported for the first time from there (Rasmussen & Ineich, 2000). Those collections allowed publication of a recent synthesis book, largely illustrated by excellent submarine photographs (Ineich & Laboute, 2002; see also Bauer, 2002). Ecological studies undertaken by Richard Shine (University of Sydney, Australia) and by Xavier Bonnet and François Brischoux (CNRS of Chizé, France) still continue (see e.g. Bonnet et al., 2005; Shine et al., 2003a, 2003b, 2004, 2005; Shine, 2005). The Thesis of François Brischoux dealing with the ecology of amphibious sea snake populations of New Caledonia will be soon submitted and certainly will provide new and interesting information about these reptiles.

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[a more complete bibliography of sea snakes can be found in Ineich (2004)]

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List of taxa

Laticauda frontalis (De Vis, 1905) - Vanuatu sea krait (Plature du Vanuatu)

Kharin (1984b) revised the genus Laticauda and split it in two genera, Laticauda sensu stricto and the new genus Pseudolaticauda Kharin, 1984. Pseudolaticauda comprised two species, P. semifasciata (Reinwardt, 1837) and P. schistorhynchus (Günther, 1874), but its validity was generally not accepted. Later the study of geographical variation of the populations of Laticauda colubrina (Schneider, 1799) allowed to show that this binomen comprised a complex of four species about which the revalidated Laticauda frontalis mostly limited to Vanuatu and whose occurrence in New Caledonia has to be confirmed, a first new species, Laticauda saint-gironsi Cogger and Heatwole, in press, restricted to New Caledonia and Loyalty Islands, a second new species, Laticauda guineai Heatwole, Busack and Cogger, 2005, only present south of Papua New Guinea and L. colubrina (Schneider, 1799) sensu stricto with a large distribution in south-east Asia, Indo-Malay archipelago, Indonesia and Melanesia (Heatwole et al., 2005).

L. frontalis is known from New Caledonia by a unique specimen without precise location from Paris Museum collections (MNHN 3966) and three specimens from Loyalty Islands deposited at Sydney University (MM 633) and Paris Museum (MNHN 1886.0385 and 0388). The occurrence of reproductive populations in New Caledonia has not yet been assessed. Biology and ecology of that species are well known in Vanuatu (Reed et al., 2002; Shine et al., 2002a, 2002b). Concerning New Caledonia, nothing is known about biology and distribution of the species.

Laticauda saintgironsi Cogger and Heatwole, in press – Saint Girons' sea krait (Plature de Saint Girons) This species is reported and diagnosed by Heatwole et al. (2005), but its original description has not yet been published (Cogger & Heatwole, 2006). Nearly all reports of L. colubrina or L. cf. colubrina for New Caledonia refers to that new species (see e.g. Ineich & Rasmussen, 1997; Bauer & Sadlier, 2000; Ineich & Laboute, 2002). It is one of both most common snakes of New Caledonia. Its mean size varies around 90 cm, but larger specimens are reported. This amphibious snake is feeding in the sea, mainly among small species of moray eels or other anguilliform fish, and returned to land to digest them, shelter, shed skin and reproduce; nearly 30 species of unknown moray eels for New Caledonia have been found in stomachs of that snake and of L. laticaudata (Ineich et al., 2006). Biology of Saint Girons' sea krait is relatively well known, at least during its terrestrial part of life (Ineich & Laboute, 2002) and the Thesis of François Brischoux will certainly give rise to interesting additional data. Recent field works realised on Fiji (Shetty & Sivasundar, 1998; Shetty & Shine, 2002a, 2002b) showed that L. colubrina presents an important phylopatry, and clearly showed that individuals from one island generally return to the same island; such a situation also seems to occur in New Caledonia for L. saintgironsi.

Laticauda laticaudata (Linnaeus, 1758) – Brown-lipped sea krait (Plature à bandes)

This amphibious species shows a large distribution encompassing Indian subcontinent, Indo-Malay archipelago, South China Sea, Philippines, Indonesia and the Australian area as far in the east as Niue Island. Its mean size is situated around one meter, with a known maximum of 1.36 m. It's a common species in the New Caledonian great lagoon. This snake is much more nocturnal than *L. saintgironsi* and less terrestrial in its habits (Bonnet *et al.*, 2005). It frequents the lagoon to feed, and comes back to land to digest preys and reproduce. Its alimentation is relatively distinct from that of the previous species and notably differences exist between sexes in both species (Ineich *et al.*, submitted).

Acalyptophis peroni (A.M.C. Duméril, 1853) - Horned sea snake (Acalypte de Péron)

This species is the only member of its genus. Its size varies from 80 to 110 cm, with a known maximum reaching nearly 130 cm. This snake is present from Gulf of Thailand to Vietnam and as far as the Australian area in the east. It is an ubiquitous animal, sometimes nocturnal, which occupies loose sandy-silty bottoms, seagrass beds and solid substrates, from coastal bays to inlets, on the whole New Caledonian great lagoon. The species is characteristic by the presence of folded and/or spiny scales on the top of its supraocular plates. It seems to mainly feed on gobies but juvenile also eat commensal shrimps of the genus *Alpheus*. Its biology is not well known (Ineich & Laboute, 2002).

Aipysurus duboisi (Bavay, 1869) – Dubois' sea snake (Aipysure de Dubois) Kharin (1981) revised the genus Aipysurus Lacepède, 1804 and recognised two subgenera: Aipysurus and Smithohydrophis Kharin, 1981. He placed that species in the subgenera Aipysurus. This author also provides an identification key for the species of the genus. Kharin (1984b) diagnosed the new subfamily Aipysurinae and include only two genera in it: Aipysurus (7 recognized species) and Emydocephalus Krefft, 1869 (2 species), both primitive true sea snake species still showing clearly enlarged ventral plates. A. duboisi has been described from a specimen nowadays lost and collected on Loyalty Islands (Lifou). This snake is present from Western Australia to New Caledonia in the east and to New Guinea north. Its mean size varies between 70 and 80 cm, with a known maximum of 148 cm. It mostly occupies sandy-silty sedimentary zones covered by seaweed or invertebrates that could serve him as shelter (gorgonian and antipatharian corals, sponges). It occurs from shallow waters until depths of up to 50 meters and even more (one collected at 80 meters; see Ineich & Laboute, 2002). This snake is less active, and shows a body often covered by phoretic seaweed. It feeds on various benthic fish that he stalks among the seabed.

Aipysurus laevis (Lacepède, 1804) - Olive sea snake (Aipysure lisse)

Kharin (1981) revised that genus and placed the species in the subgenus *Aipysurus*. This snake is common in the waters of the Australian Great Barrier Reef and its biology is well known. Olive sea snake is present from Western Australia to Loyalty Islands in the east and to New Guinea in the north. It's a common species in the great lagoon of New Caledonia. Its mean size varies from 110 to 150 cm, but its maximal known size reaches about 200 cm. Females are larger than males. This snake, particularly active at night, occurs mostly in coral reefs located between 3 and 50 m depth, but does not really appreciate external slope. It is not shy about swimming right up to divers, attracted by their bright face mask but is generally not aggressive. It's a generalist feeder, preying upon several reef fish. It gives birth to 1 to 5 large sized offspring.

Emydocephalus annulatus (Krefft, 1869) - Turtle-headed sea snake (Emydocéphale annelé)

This species feeds only on fish eggs (McCarthy, 1987) that it really browse on coral blocks (Shine et al., 2004) with the help of an adapted mouth musculature. In New Caledonia, it appreciated eggs of damselfish, blennies and gobies. Eggs' searching is made by smelling rather than vision. Shine (2005) has shown that in that species vision is very important to recognize a sexual partner and that pheromones are only active during physical contacts. Vision is however efficient only at short distances, below one meter, and the snake often can mix a black snake like object with a congener. Mean size of that snake varies from 70 to 90 cm. Male can be distinguished from the female by the presence of a larger rostral spine. That spine allows him to stimulate the female during copulation and has no role in feeding as previously though (Guinea, 1996). This snake occurs from northern Australia to the Timor Sea at west, and as far as Loyalty Islands in the east. It is common and abundant in the New Caledonian great lagoon and easy to observe in the sea on the beaches around Noumea. It is a typical clear water and coral reef species, often seen in groups of specimens separated by several meters among each other. A recent work has shown that probably exist a strong social cohesion between specimens of that species belonging to a same group (Shine et al., 2005). Marking, capture-recapture method allows to show that specimens of a same group are synchronously recaptured during time. This behaviour seems to be placed in parallel with the phylopatry observed by Laticauda colubrina on Fiji and could have been selected by evolution for the greater ability of a group of individuals to succeed in a colonisation rather than a unique snake on disseminated oceanic islands like those of the southern Pacific.

Hydrophis coggeri (Kharin, 1984) - Cogger's sea snake (Hydrophide de Cogger)

This species was originally described by Kharin (1984a) in the genus *Leioselasma* Lacepède, 1804, a genus with uncertain validity but still in use (Kharin, 2005a, 2005c). Kharin (2005b) later placed the species in the subgenus *Leioselasma* inside the genus *Hydrophis* Latreille in Sonnini and Latreille, 1802. The genus *Hydrophis* comprised a large number of species (nearly 40) about which six are present in New Caledonian waters. This species is present from Timor Sea and north coasts of Sulawesi (Indonesia) as far as northern Australian coasts, southern New Guinea, New Caledonia, Vanuatu and Fiji. It was recently reported from Loyalty Islands (Ineich & Borsa, 2003). Its mean size is nearly 100 cm and known maximal size is about 137 cm. Females are larger and heavier than males. It is a ubiquitous species, mainly nocturnal, occurring around seabeds with loose organic material and sediment within the 1-40 m depth range. It is also found along the coast, near mangroves, in low water and on white coral seabeds behind the barrier reef. This snake mainly feeds on Ophichthidae and Congridae fish. Viviparous like all true sea snakes, it gives birth to 1 to 8 offspring.

Hydrophis laboutei Rasmussen and Ineich, 2000 - Laboute's sea snake (Hydrophide de Laboute)

This species was only recently described based on two unique specimens. It was no more reported since that time. Kharin (2005b) placed it in the subgenus *Chitulia* Gray, 1849, inside the genus *Hydrophis*. Its mean total length is around one meter. Its actual distribution is limited to Chesterfield Islands (2,20° 21,98' S; 161° 4,87' E). This animal seems to occupy depth sea since one of both types was collected at 62 m depth. Its biology, alimentation and reproduction are unknown.

Hydrophis macdowelli Kharin, 1983 - McDowell's sea snake (Hydrophide de McDowell)

This species was only described in 1983 (Kharin, 1983). Kharin revised that group of sea snakes and later (Kharin, 2004, 2005b) placed that species in the subgenus *Hydrophis* inside the genus *Hydrophis*. It is a small animal which only rarely reach over 50 to 60 cm total length; the known maximum is 90 cm. Its distribution seems to be limited from northern Australia to southern New Guinea and to New Caledonia in the east. It's a highly wary snake occurring around grey bottoms in the middle of the lagoon at depths ranging from 10 to 40 m. McDowell's sea snake actively forage for prey in burrows that fish dig in the sediment.

Hydrophis major (Shaw, 1802) - Olive-headed sea snake (Hydrophide cerclé)

Kharin (2005b) placed that species in the genus *Disteira* Lacepède, 1804 inside the new tribe of Disteirini, but that position is not accepted by all. It's a large snake with a known maximum total length of 156 cm; mean size varies around 120 cm. This snake is present from western Australian coasts to New Caledonia and is still imperfectly known. It seems to search for muddy waters with numerous seaweeds and feed on small fish captured near coral reef cavities. It gives birth to a mean of 9 offspring and this number varies from 6 to 12.

Hydrophis ornatus ornatus (Gray, 1842) - Ornate sea snake (Hydrophide orné)

Kharin (2005b) placed that species in the subgenus Chitulia inside the genus Hydrophis. Australian populations are classically attributed to H. ornatus ocellatus (Gray, 1849) whereas those of New Caledonia and Asia are attributed to H. ornatus ornatus. The validity of those forms and their status have to be assessed, but they clearly should correspond to two distinct species. Occurrence of black ocellus-shaped markings on the sides is never observed in New Caledonian and Asiatic populations, whereas it is constant in Australia. Biology and ecology of that species in Thailand are reviewed by Rasmussen (1989). It's a small species with a mean size varying from 85 to 100 cm in Australia whereas it is only around 70 cm in New Caledonia (Ineich & Laboute, 2002). Known maximum size in New Caledonia is 78.7 cm total length for an adult female. The species is distributed from Indian Ocean, Persian Gulf, Indo-Malay archipelago, South China Sea, Philippines, Indonesia, to northern Australia, New Guinea to New Caledonia. It's a common species in Australia and it was reported as far south as Tasmania. It seems to occupy a great number of habitats, even going up some estuaries in Australia, but precise knowledge is still lacking. Its alimentation seems to be specialised against consumption of gobies directly taken from their burrows on grey substrates.

Hydrophis spiralis (Shaw, 1802) - Yellow sea snake (Hydrophide spirale)

This species is sometimes included in the genus Leioselasma but this position is not regularly followed (see David & Ineich, 1999); Kharin (2005b) placed it in the subgenus Leioselasma inside the genus Hydrophis. It was reported from New Caledonia by a unique specimen with unknown collect location. It's a large animal (1582 cm total length in New Caledonia) and a specimen from Malaysia (Penang) of 1745 cm total length is the record size for an elapid sea snake. This species occurs from Indian Ocean to the Indo-Malay archipelago, South China Sea and as far as Indonesia and? New Caledonia. This snake seems to prefer depth waters and surfaces only to warm up. It is an active swimmer that feeds on anguilliform fish.

Lapemis curtus (Shaw, 1802) - Short sea snake (Lapémide court)

Lapemis hardwickii Gray, 1835 is generally considered as a synonym of that species but that position is not unanimously shared; this later binomen is sometimes still used to designate Australian area populations. This snake is heavily built and its mean size is around one meter with a known maximum of 128 cm. It occurs from Persian Gulf to Australian waters and New Caledonia from where it is presently known by a unique specimen with unknown collect location. It frequents unclear waters around sandy and muddy seabeds, but also clear waters around coral reefs and even some estuaries in Australia but prefers soft bottoms. It's generally a diurnal animal with a skin often covered with different parasites and phoretic organisms. It feeds on a wide variety of fish and probably small crustaceans.

Pelamis platura (Linnaeus, 1766) – Yellow-bellied sea snake (Pélamide bicolore)

Biology, ecology and distribution of that species have been reviewed by Ineich (1988). This species is certainly the best known sea snake but finally is not really representative of the group. It's the only species in its genus. Its mean size is around 60 to 90 cm with a maximum known of 113 cm. The species occupies a wide distribution area encompassing nearly all tropical and subtropical marine areas of Indian Ocean and Pacific Ocean from Madagascar to Central America coasts. This snake is present in open sea and is the only pelagic sea snake. It commonly lives at surface and preys on fish in slicks which are channels of vegetation and floating debris created by ocean currents. The Yellow-bellied sea snake is present between 35 to 50 m depth. It's an ecological generalist feeding on numerous fish. It gives birth to 2 to 8 offspring of about 25 cm total length. Its high densities, e.g. around Central America coasts, certainly makes it being one of the most abundant snake in the World. Global earth warming could facilitate its range extension in the coming years.

Originality of New Caledonian sea snakes and biogeographical affinities

Sea snakes of New Caledonia clearly shows double affinities: on one side they comprise typical Australian species related to coral reefs (e.g. Acalyptophis peroni, Aipysurus duboisi and A. laevis, Emydocephalus annulatus, Hydrophis coggeri and H. macdowelli) and on the other side taxa with rather Asiatic affinities as Laticauda sp., Hydrophis spiralis and H. o. ornatus, absent or very rare in the waters located between New Guinea and Australia. The occurrence of resident populations for several species has to be confirmed (Laticauda frontalis, Lapemis curtus, Hydrophis spiralis). Specimens of those three species from New Caledonia also could correspond to erratic individuals arrived through accidental natural transport and not resident in the area. The distribution of Hydrophis laboutei has to be clarified by complementary collects or observations.



Acalyptophis peroni



Acalyptophis peroni



Aipysurus duboisi



Aipysurus duboisi



Aipysurus laevis



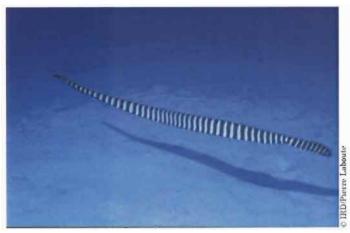
Emydocephalus annulatus



Emydocephalus annulatus



Hydrophis coggeri



Hydrophis laboutei



Hydrophis macdowelli



Hydrophis major



Hydrophis ornatus



Hydrophis ornatus



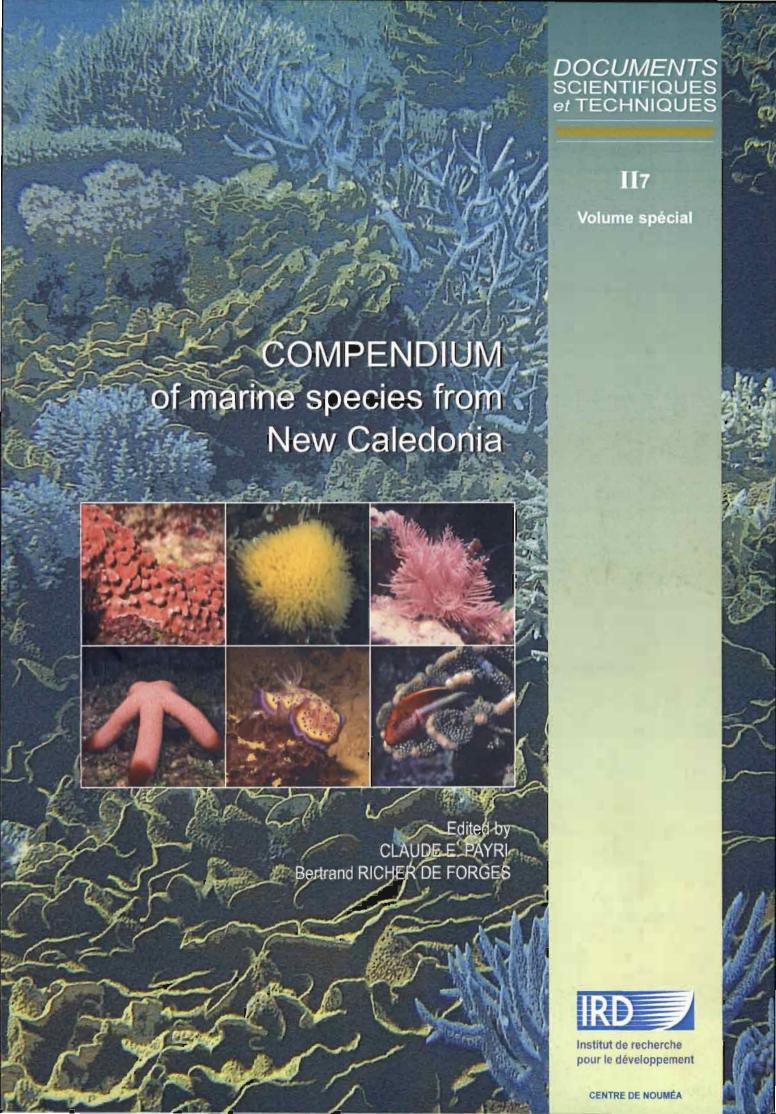
Laticauda colubrina



Laticauda laticauda



Pelamis platura







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