The Natural History of the Australian Lungfish

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Abstract

Aspects of the biology, phylogeny, distribution, appearance and adaptations to the environment of the Australian lungfish, Neoceratodus forsteri, are described. Lungfish are long lived benthic omnivores, well adapted to an unaltered natural environment, which includes a stable water level, flowing and still areas, and stands of submerged water plants (macrophytes) or roots along the bank to shelter the vulnerable eggs, embryos and hatchlings. Since the original scientific description in 1870, the phylogenetic position of the Australian lungfish has been controversial and is undecided to this day, because of conflicting evidence derived from different sources. First described from material obtained in the Burnett River, lungfish were soon discovered in the Mary River, and a population in the Brisbane River, considered to be the result of translocation, is also likely to be a natural population, and to have been in that river at the time of the original discovery of lungfish. The onset of oviposition by wild lungfish is associated with a rising photoperiod, and not affected by the synodial cycle, by rainfall, or by water quality parameters such as oxygen content, pH, conductivity and temperature. Submerged plants or rootlets along the bank are essential the attachment of eggs, and the protection of eggs and hatchlings, but do not affect the initiation of spawning. Spawning is cyclical, with good years followed by poor years, and lungfish return to the same sites to spawn every year. The distribution of the Australian lungfish has contracted significantly over time, and analysis of characteristics of related fossil populations shows that some fossil populations suffered from the same problems that are now being imposed on the living Australian lungfish, such as loss of hatchling habitat and poor quality of their environment. Unless these conditions are reversed, or a reasonable recovery plan is implemented soon, wild populations of the lungfish will be lost.

Introduction

Living lungfish, including the Australian lungfish, belong to a group of fish that first appeared in the fossil record of the early Devonian, about 420 million years ago. They are not among the earliest of the fish that appeared in the fossil record, which had mostly become established in the Ordovician and Silurian. However, they play a small but significant part in the radiation of fish groups during the Devonian, and the fossil record of lungfish is continuous to the present day. The divergence of the two major divisions of living lungfish, represented by the Monopneumona, with one living genus and species, the Australian lungfish, Neoceratodus forsteri, and the Dipneumona, with Lepidosiren paradoxa in South America and several species of Protopterus in Africa, can be followed from their common origin among fossils of the Mesozoic. The Australian lungfish is the only surviving species of an extensive Australian fossil fauna.

Lungfish belong in the class Osteichthyes, meaning fish that have bone in the skeleton. They are usually classified, within this large group, with the living coelacanth and related fossil species, as sarcopterygians, or lobe finned fishes, because the paired fins have a muscular base. Apart from obvious links with other sarcopterygian fish, fossil and living, relationships of the living lungfish with other vertebrates, such as amphibians, are controversial. Analyses based on morphology or on palaeontology can be interpreted to support different phylogenies (Schultze, 1994; Holmes 1985; Rosen et al. 1981). Some structural characters, such as the cartilaginous skull of the living Australian lungfish, suggest links with the elasmobranchs and evidence derived from development, such as the formation of the scales, indicate close relationships with actinopteryigians. Other characters, like the unusual forms of dentine and enamel in the tooth plates (Kemp and Barry 2006, Barry and Kemp 2007), or the mode of growth of the dentition (Kemp 2003), suggest few close relationships with other fish groups or with tetrapods. Even the analysis and comparison of DNA gives no consistent results, with some studies supporting a close sister group relationship between lungfish and tetrapods (Zardoya and Meyer, 1996, 1998), others suggesting that coelacanths are closer to the tetrapods than are lungfish (Laurin and Ricqles 2000), and others assigning this position to actinopteryigians or to lungfish with an equal possibility of correctness (Kikugawa et al. 2004).

All of the three living genera of lungfish have been used as counters in the systematic and phylogenetic arguments current since the fish were first described (Conant 1987), Neoceratodus least of all because it was discovered later than the other two genera (Krefft, 1870; Gunther 1871). Although evidence on the origin of lungfish in relation to other groups of fishes, and their possible sister group status with the tetrapods, is not completely reliable, an evolutionary progression within the lungfish can be traced without difficulty in the fossil record. The divergence of the two major divisions of living lungfish, the Dipneumona, with Lepidosiren from South America, and four species of Protopterus from Africa, and the Monopneumona, with one species of Neoceratodus from Australia, can be followed from their common origin in the Mesozoic. Further, the evolutionary progression within the lungfish should not be regarded as degeneration or regression to a basal state. It is a process of refinement, resulting in species that are well adapted to their natural environments.

Discovery and early history of lungfish research

The discovery of three different types of living lungfish by naturalists, and their naming and description in scientific terms, caused considerable excitement among scientists in the nineteenth century, and the fish were quickly adopted as “missing links” (Conant 1987). Obviously, these discoveries were not news to indigenous African and South American peoples, or to Australian Aborigines and European settlers, who had all been exploiting lungfish populations as a food source for many years. They were, however, new to science, and added new ideas to scientific knowledge at the time of their discovery.

In 1859, Gerhardt Krefft, a young German naturalist, settled in Australia, and was engaged as assistant to the Curator of the Australian Museum in Sydney. In 1861, he was promoted to Curator, a position he held until 1874. During his time at the Australian Museum, Krefft became friendly with Mr William Forster, Agent General for

New South Wales, and later Minister for Lands in the New South Wales Government. For many years, Forster, who owned land in the Wide Bay District of Queensland, tantalised Krefft with his stories of an unusual fish to be found there, known as a "fresh water salmon" to the local settlers. Krefft wanted proof that such a fish existed, and eventually Forster was able to provide some specimens, collected by his nephew, William McCord, who lived on the family property in Queensland close to the Burnett River. The fish, gutted and preserved in salt, were sent to Sydney.

Krefft announced the discovery of Ceratodus forsteri, an "amphibious creature inhabiting northern streams and lagoons" in the Sydney Morning Herald, on Tuesday, January 18th, 1870. The name Ceratodus was chosen because Krefft recognised the similarity of the teeth of the new specimen to fossil material described as such by Agassiz in 1838, and in honour of Mr Forster. Krefft pointed out that Ceratodus was not, as Agassiz had thought, a shark, and Agassiz subsequently wrote to Krefft to congratulate him on his discovery and agree that his "sharks" were "sharks no longer". The name Ceratodus, still used in Queensland as a common name for the Australian lungfish, was later changed to Neoceratodus. This name is now used to distinguish the living Australian lungfish from related fossil forms.

Many details of the structure of the new fish were not available to Krefft because of poor preservation of his material. He notes that "the specimen before me is somewhat mutilated and without intestines." He describes the similarities of the new animal to Lepidosiren, and mentions the broad flat head, small eyes and four limbs in the shape of "flappers". The fish has ten rows of cycloid scales on each side, the third row from above being marked by the lateral line. In front of each pectoral fin are a large gill opening with well developed gills, and a large pair of "nostrils" just below the upper lip, communicating by a short tube with the "roof of the mouth". He points out that the skeleton is made partly of bone and partly of cartilage. The vertebrae are entirely cartilaginous, but the palate, jaws, upper part of the skull and the hyoid consist of bone.

Krefft provided more details of his discovery in the proceedings of the Royal Society of London, later in 1870, in a paper entitled "Description of a giant amphibian allied to the genus Lepidosiren, from the Wide Bay District, Queensland" (Krefft, 1870). Krefft was correct in assigning the new fish to the genus Ceratodus, based on the similarities of the teeth to those of the fossils described by Agassiz. He was correct in stating that the new species was related to Lepidosiren paradoxa, although the similarities are not particularly obvious. Lepidosiren paradoxa is a slender fish, dark grey or almost black in colour with white or yellow spots. The scales are reduced, covered by thick skin, and the long, paired fins are filamentous in form. The Australian lungfish has a large heavy body, dark brown dorsally and pink ventrally, with a flattened head, paddle shaped fins and large obvious scales covered by soft glandular epidermis. He was wide of the mark in calling N. forsteri an amphibian, despite its general resemblance to a giant salamander like Cryptobranchus. One way in which the Australian lungfish does resemble an amphibian is in its eggs and embryos, but these were not discovered for another 14 years (Caldwell, 1884), and were not available to Krefft when he made his determination.

Thus the first scientific paper on the Australian lungfish caused a renewal of the controversy on the correct phylogenetic position of the lungfishes, a debate that is unresolved to this day. For several reasons, this was largely independent of the discussions concerning the status of the South American and African lungfishes. The Australian lungfish has many more basal characters than its relatives, and has always been classified in a separate group, the Monopneumona, referring to the single, dorsal lung. Protopterus and Lepidosiren belong in the Dipneumona, because of their double lungs. In many aspects of its morphology, physiology and behaviour, the Australian species differs from the other living lungfishes. A more comprehensive description of the Australian lungfish (Gunther, 1871), using fresh material from the Mary River, placed the new species firmly in the class Pisces, and indicated in no uncertain terms that lungfish were not, and could not be, amphibians.

Caldwell, who was the first to find lungfish eggs in the Burnett River, published a brief description of the egg and its development in 1885. Semon, who also worked on fish from the Burnett River, collected and described a comprehensive series of eggs, embryos and young hatchlings (Semon, 1899), and took material back to Germany for further analysis, providing the basis for morphological descriptions of development of N. forsteri that have rarely been surpassed by subsequent researchers. He was also the first to find the elusive wild hatchlings, less than an inch long, among water plants near the banks of the Burnett River (Semon, 1893). Around this time, naturalists on the Burnett River began to take an interest in lungfish, among them Illidge who was the first to raise young fish (Illidge, 1893) and O'Connor, who carried out the work of translocation lungfish to rivers and lakes in south east Queensland (O'Connor, 1895, 1902).

The distribution of the Australian lungfish

Although one of many species of lungfish that were widespread over eastern Australia in Cainozoic times, the distribution of the Australian lungfish is now restricted to rivers and lakes of south east Queensland, east of the Great Dividing Range. Originally described from specimens collected in the Auburn River, a tributary of the Burnett River, in southeast Queensland (Krefft 1870), it was soon discovered in the neighbouring Mary River (Gunther, 1871). The species has been described as occurring naturally only in the Burnett and Mary Rivers (Welsby 1905, Brooks et al. 2002), but there is one suggestion that it was also present in the Fitzroy River, north of the Mary and Burnett Rivers, in historical times (de Castelnau 1876a). There is evidence that the Brisbane River population is natural, as are the lungfish of the Mary and Burnett Rivers (Kemp 1987).

At the time of discovery of the lungfish, the Burnett and Mary River systems consisted of numerous tributaries that united to form meandering rivers, with many long deep pools and short stretches of rapid flow. Although these rivers, in the past, were likely to be converted into a chain of water holes in dry periods, the water holes were deep and extensive, and retained populations of plants and animals, including lungfish, throughout the drought (Spenser, 1892). South of the Mary River, and separated from it by the mountains of the D'Aiguillar ranges, is the Brisbane River system. Prior to 1895, when O'Connor began moving lungfish around the state, there are no written records of lungfish in this system, and many local people are unaware even today that it contains lungfish. The Brisbane River is similar to the Mary River in fauna and flora, and in water composition, but is much deeper and flows faster in the unaltered reaches. The Fitzroy system differs from the three southern Rivers in flora, fauna and water composition.

Late in the nineteenth century, in a series of actions best described as ecological vandalism, a large number of adult lungfish were collected from a small region of the Mary River at Miva, and transported to new homes in other river systems in southeast Queensland (O'Connor, 1895). This action was taken because of fears that the lungfish would become extinct, and the significance of catching so many lungfish in one small place for the chances of extinction of the species was lost on the perpetrators. At the time, the distribution of lungfish, apart from the Mary and Burnett Rivers, was not known.

O'Connor, who carried out the work of catching and transporting the lungfish, notes that the fish were fairly abundant at Miva. Of one hundred and nine adult lungfish caught, eleven escaped when the pond in which they were kept flooded during the night, and 29 died. The survivors were distributed to other sites over a six month period from May to December 1895. O'Connor (1897) states that the fish were 33-45 inches in length, and 9-14 pounds in weight, and thought that at least two thirds of them were female.

O'Connor states that eight lungfish were placed in the North Pine River, "a mile above tidal influence" in May 1895. A population is still present in this system. Later in May of this year, eighteen fish were placed in Enoggera Reservoir in the hills to the west of Brisbane, where they became established. In July 21 fish were taken to the Condamine near Warwick, and sixteen fish went to the Coomera River. Lungfish were caught in the Condamine, in 1923, and were apparently breeding, as one of the specimens found was smaller than the fish originally released nearly thirty years before. Lungfish have been caught in tributaries of the Condamine River in recent years (Kemp 1995). O'Connor (1902) notes that lungfish have been seen in the Coomera River, and some may have been caught there. Five were released in a lagoon near the Albert River in November 1895. There have been no published reports since of the results of this translocation. In December 1895, eight lungfish were placed in a dam near Cressbrook, close to the upper reaches of the Brisbane River, on the property of the McConnell family. This dam is a small farm dam, and the name does not refer to the Cressbrook Dam, which was not built until 1982.

In a subsequent letter (O'Connor 1902), quoted in full by Welsby (1905), O'Connor admits that some of the lungfish involved in the first introductions to new river systems died in transit. North Pine River received only three living lungfish, and the dam near Cressbrook, close to the Brisbane River, only five. Four were placed in the lagoon near the Albert River. Numbers as low as this could mean that the translocations were not in fact successful, or, if large numbers of lungfish were found subsequently in the river system or lake, simply added to an existing population. For the last translocation, to the Coomera River, fish were transported in boxes covered in damp water plants, a method subsequently used to send the fish by sea to London a few years later. None of these died.

O'Connor mentions that lungfish were involved in a fish kill in the upper reaches of the Brisbane River (O'Connor 1902, cited by Welsby, 1905)

> "News came from Cressbrook that a few ceratodi had been seen among a number of dead fish near or on the banks of the Upper Brisbane. An extraordinary mortality prevailed among the fishes in the Upper Brisbane at this time, about two years ago. It was believed that all the fishes in the river died from some unexplained cause."

The five fish, which were not actually placed in the Brisbane River, have been presumed to be the progenitors not only of the fish that formed part of the fish kill a few years later, but also of the entire present population of lungfish in the Brisbane River. However, the dam in question communicates with the Brisbane River only during times of flood. Although flooding does affect rivers in Queensland regularly, the major flood in the Brisbane River valley occurred in 1893, two years before O'Connor carried out his work. Although there were several floods in the Brisbane River system between 1895 and 1902, rainfall in the Cressbrook area was not extreme, and may not have caused flooding in a farm dam.

Even if all five of the introduced lungfish from Miva were healthy when they were placed in the farm dam, and survived there, and if a flood did cause the dam to communicate with the river, they may not have entered the river system. For the lungfish in question to have survived and entered the Brisbane River, produced enough descendants to be involved in a fish kill a few years later, and still leave progeny over for extending further into the river, the five specimens would have had to have included mature adults of both sexes, to have escaped quickly from the dam, settled in the river, spawned and produced progeny which would have had to become adult in their turn, all in the space of six or seven years.

This is an unlikely combination of events for several reasons. Although growth rate of juveniles in the Brisbane River can be rapid, the propensity of lungfish for recruiting young to the adult population is not high in the Burnett River (Bancroft 1912, 1918), or in the Brisbane River (Kemp 1987). Lungfish are cryptic in colouring and not easy to catch with net, hook or line, and they could easily have been present in the Brisbane River prior to the introduction of five fish into the original dam near Cressbrook. There could also have been one or more unrecorded introductions at some point. It is also worth noting that both adults and young from the Brisbane River differ in many points of morphology, such as the colours of juveniles, details of development, the size and timing of appearance of the paired fins, and possible differences in spawning behaviour, from Mary River fish that were used as stock for Cressbrook. Both differ from fish found in the Burnett River. The molecular signature of the lungfish from the Brisbane River also differs from those found in the Burnett or the Mary Rivers (Brooks et al. 2002; Lissone, 2002). The population of lungfish in the Brisbane River is most probably a natural population.

North of the Burnett River is the Fitzroy River and its extensive system of tributaries, including the Dawson River where the primitive osteoglossid, Scleropages leichardtiii, is found. This species has several points of similarity with N. forsteri. Both have large scales with a reticulate pattern, both have pinkish flesh and both have been named Barramundi or Dawson River Salmon (Whitley 1929). There the obvious similarity ends.

There is no actual record of a lungfish from the Fitzroy River system, but there is one intriguing possibility. Scientific interest in lungfish from Australia in the 1870's was already intense when another species, Neoceratodus blanchardi, was described, on this occasion by a French diplomat called de Castelnau, in a detailed paper that is full of inconsistencies (de Castelnau, 1876a). He describes the specimen as silver in colour and 60 cm long. Locality details recorded in the Museum of Natural History in Paris, where the specimen is kept, list the origin as the Fitzroy River. However, the fish preserved in the Paris Museum is an ordinary adult N. forsteri, brown and pink in colour and nearly a metre long, as de Castelnau later admitted (de Castelnau 1876b). Lesions on the ventral surface and scales suggest that it was transported a considerable distance before it was preserved. It may have been collected from the Rockhampton Market, as de Castelnau states, but it is more likely that it originated in the Burnett River, and not in the Fitzroy River near Rockhampton.

Stories that lungfish have been found in the Norman or the Gregory Rivers, in North Queensland, have been current for many years. De Castelnau mentions the possibility of a lungfish from the Norman River. Aboriginals have described and provided drawings of a fish from North Australia that bears some resemblance to N. forsteri. A letter in the archives of the Queensland Museum requests information on the identity of a fish resembling the lungfish seen in the Gregory River. No actual specimen to support these stories has yet been found. The stories may refer to the fork-tailed catfish, which is brown and has a head similar in shape to that of a lungfish.

As part of the effort to preserve the lungfish from extinction, Bancroft tried to establish a lungfish hatchery In Brown Lake on Stradbroke Island off the coast of Queensland (Bancroft, 1933). His efforts were bedevilled by a lack of financial support, and the hatchery did not succeed. Nor was he successful in establishing a separate population of lungfish in Blue Lake on Stradbroke Island. The waters of the Blue Lake are soft, and can become highly acid under certain circumstances. Although lungfish are tolerant of a wide range of water conditions, this may have been too much for them. In addition, Bancroft transplanted lungfish to Lake Manchester, one of the storage reservoirs built across small creeks in the hills to the west of Brisbane. Although it is not a perfect environment for lungfish, and has few suitable sites for eggs and hatchlings, they have survived in this reservoir. The current status of the population in the reservoir is not known.

Appearance

For the purposes of this description of the biology of N. forsteri, the following criteria, used during the analysis of spawning carried out in the Brisbane River from 1977-2006, are employed to place the morphological changes in lungfish into categories useful for the analysis of data such as the time taken to hatch in the wild, and the numbers of new eggs laid in spawning sites. Stage 1-10 are described as cleavage stages, 11-16 are blastulae, 17-25 are early neurulae, 26-35 are head development, 36-40 are prehatching, 41-51 hatchling, and 52 - 62 are juveniles. Fish older than stage 62, with rosettes of sensory openings on the snout instead of single pits are subadult, until they reach a length of 80 cm, when they are labelled adult. The change to multiple openings occurs when the fish are over 200 cm in total body length. Developmental stages are described in Kemp (1982, 1999).

Adult lungfish are large fish, with a round, stocky body, a pointed tail, flat head and paddle shaped fins. Adult N. forsteri attain a size of up to 1.5 metres in length in the Burnett River (Brooks et al. 2002). They are smaller in the Brisbane River, usually only just over a metre long. The body and the posterior and lateral surfaces of the head are covered in large overlapping scales covered by a slimy epidermis. The colour varies, depending on the environment and origin of the fish, usually dark brown or olive brown dorsally, and ventrally, reddish orange. The eyes are small, often bluish in colour. The anterior surface of the head is free of scales, and rich in sense organs. Neuromasts of the lateral line system open in clusters around the eyes, on the snout, and on the mandible, and continue down the trunk as a single line of openings, flanked above and below by lines of electroreceptive pits. Two distinct rows of sensory pits cross the dorsal and lateral surfaces of the head. There are also many single electroreceptive pits on the snout.

The mouth of lungfish is small and the anterior and posterior openings of the olfactory organs lie inside the mouth, the anterior opening partially rostral to the lower lip, and the posterior opening labial to the second ridge of the pteryogopalatine tooth plates. These are frequently described as nares, choanae or nostrils, but they are not used for the passage of air (Atz 1954; Greenwood and Oliva, 1959) and are not nostrils or nares in the sense of the mammalian structure. On either side of the head, and covering the base of the large pectoral fins, is the bell shaped fleshy operculum, which protects the gills. Movements of the operculum draw water over the gills. Pelvic fins lie slightly anterior to the cloaca. Pectoral and pelvic fins are pointed, as is the diphycercal tail, and have scales along the muscular axis, similar in arrangement to scales on the tail. The scales decrease in size as they approach the thin membranous margins of both fins and tail, which are free of scales.

Adults of the Australian lungfish have two pigments in the skin, melanin enclosed in melanophores under the epidermis, and a red pigment, possibly ferritin, also enclosed in cells below the epidermis. Lungfish tissues contain masses of this orange pigment, dissolved in oil. This accounts for the pink colour of the flesh and earned the lungfish the name of “Burnett River salmon”. Large droplets of oil, stained by ferritin, are found in the thick dermal tissues below the skin, and other tissues, such as the retina, include minute globules of oil. This pigment is responsible for the bright colours on the bellies of lungfish that are ready to spawn. Reduction of the ferritin in the chromatophores of the skin in adults that are not spawning leaves the underside pale pink. Melanophores confer on the lungfish the uniform dark brown colour, sometimes tinged with olive, of the head and dorsal trunk. This uniformity is relieved by patches of intense dark pigment on the tail, sufficiently individual to be used to identify the different fish (Kemp 1987). Albino lungfish are known, particularly in specimens that originate in the Mary River. These are actually yellow in colour. One of the juveniles caught in Enoggera Reservoir in 1926 is albino. Early researchers have referred to a thin line of yellow tissue around the margins of the tail, prominent in the breeding season when the fish have “coloured up”. This is actually a characteristic of growth, and may be found in lungfish of any age. New epithelium around the growing tail has no melanophores, and is yellow in colour.

Differences in the appearance of lungfish as they grow have been described many times, usually for the definition of stages of development for embryological research (Semon, 1899; Whiting et al. 1992; Kemp, 1982, 1999). The stage of development, at which young fish may hatch in the wild varies from 41 to 45 (Kemp, 1982, 1994), and small fish use the egg case as a shelter for some weeks after hatching (Bancroft 1913). Some authors have used the length of young fish to describe the developmental stage (Bertmar 1966; Fox 1964), although this measurement alone is not a reliable guide, and fish of similar ages may vary considerably in length (Bancroft 1933). Additional problems arise when young fish are growing, between stages 52 and 60. Little change is visible externally, although significant development continues internally (Kemp 1999).

Subadult lungfish resemble the adult, although the colour of the belly is less intense. Colour is more variable, and depends on where the fish were caught. Subadult fish from the Brisbane River are uniformly dark, and fish from the Mary River often retain the mottled colourings of juveniles. Juvenile lungfish are similar in body form to the adults, except that the head is shorter and rounder and colour is more variable. The juvenile lungfish is mottled with darker and lighter patches, and the belly is quite pale. Eggs and embryos are green or brown in colour, thanks to included bile salts (Conant 1977), and the upper surface of the egg has granules of melanin pigment. Colours of small fish are cryptic, and although they use the discarded egg membranes as a shelter for a short time (Bancroft 1912, Kemp 1987), they soon move deeper into the weed mass. Prior to hatching, melanin pigment is formed, at stage 37, first in the eye, and then on the back and sides. Chromatophores containing ferritin appear later. By the time small lungfish are ready to hatch, the skin over the back and the head is speckled with diffuse melanocytes and scattered red chromatophores. The belly, like the egg, is green or brown, because lungfish hatch while the cells of the gut are still loaded with yolk globules, and these show through the unpigmented ventral skin. As the hatchling grows, yolk is used up and pigment cells spread over the belly, giving the young fish a more even colour. The pigment cells are capable of contracting in response to light for several weeks after hatching, until the pigment becomes too dense to show any effect of contraction.

Eggs are enclosed in a jelly membrane that rapidly collects detritus and algae. This confers some protection on the egg, which is often attached to the outer surface of leaves and roots, and not covered within the plant mass. Embryos and recently hatched lungfish are frequently described as similar to amphibian tadpoles, but this superficial resemblance, shared by other early fish such as Polypterus (Bartsch 1998), disappears as the hatchling grows.

Locomotion

Lungfish make use of a number of different muscular movements. The tail and the paddle shaped pectoral and pelvic fins are used for slow swimming actions, such as while the fish is moving through weed banks searching for food (Dean 1906). The pectoral and pelvic fins are also used underwater in alternating movements, as in many other aquatic animals, such as sharks, rays, Polypterus or salamanders. The fins may be used to brace the body against the substrate while the fish is ingesting food. Burrows in a substrate or under the riverbank are created by pushing with the snout and flushing the detritus away with streams of water from the mouth (Bartsch pers. com.). The tail and body musculature are used for rapid escape responses, usually mediated by the Mauthner neuron system. When these fast conducting nerves are stimulated, the fish will twist into a C-shape, and move away rapidly in an unpredictable direction.

Feeding movements do not usually involve active prehension in adult lungfish (Bemis 1984, 1986), although this is the method of choice in young lungfish attacking live food in an aquarium (Kemp 1987), and may be employed by adults on occasions. Feeding in adult N. forsteri involves strong suction, using the powerful hyoid apparatus, supported by strong occipital ribs in the throat, the mandibular muscles and the tip of the tongue, which fits neatly into a deep groove between the two prearticular tooth plates in the lower jaw (Bemis 1986; Kemp 1994). This mode of feeding may have been common among Devonian species such as Sorbitorhynchus (Wang et al. 1993), in which the hyoid is similarly constructed, and was probably the case among Mesozoic and Cenozoic dipnoans with similar jaw architecture to that of N. forsteri. Feeding movements in Protopterus are also suctorial, although these lungfish (Bemis 1986) do not have a gap between the mandibular jaw bones and could not use the tongue in the same way.

All of these movements develop along with the formation of fins and growth of the body musculature. Embryos at around stage 33 are able to move the head from side to side prior to hatching. Tail flexion follows as neural connections are completed (Whiting et al., 1992). Newly hatched fish cannot adopt an upright posture and are only capable of rapid escape responses, using the side to side flick of the tail, flopping onto lateral recumbency when they come to rest (Bancroft, 1912). They spend much of the time entangled among water plants and algae or lying on their sides, completely inactive (Bancroft, 1912). It takes weeks for the upright dorsoventral posture to develop, and this only happens after the ventral pre-anal fin fold regresses (Kemp, 1982, 1996). Hiding among water plants gives them support and shelter.

Respiration

The Australian lungfish is a facultative air breather, and respiration involves the gills most of the time (Kemp, 1987). Respiratory movements are carried out by rhythmic contractions of the bell shaped operculum, which moves water over the surface of the gill lamellae. Air may also be drawn into the mouth and passed into the lungs via the epiglottis when the fish rises to the water surface, and after the air has first been expelled from the lungs. Fish may then move forwards and dive into the water, or slide silently backwards into the water (Dean, 1906, 1912). Air is not passed through the olfactory passages between the openings in the mouth, as these are purely olfactory (Atz, 1954), and contain delicate stereocilia that could be damaged by the passage of air. Inhaling air through the mouth and into the lungs is carried out most frequently when fish are stressed, living in polluted water, or perhaps need additional oxygen, such as during the breeding season (Kemp, 1987). The noise made when lungfish expel air is responsible for the famed “mating call” of Kesteven (1945). It is certainly much in evidence during the spawning season, but it is arguable whether it is actually a mating call.

The diet of lungfish

Adult lungfish make use of a variety of aquatic plants and small water animals for food, although they are not really omnivorous, in that they reject some species of introduced water snail and certain plants, plentiful in the environment, are never found in the intestines. In rivers where food is abundant, the main diet of adult lungfish consists of filamentous algae, the leaves of aquatic macrophytes such as Vallisneria and Hydrilla, and native water snails, such as Plotiopsis balonnensis, small clams like Corbiculina, prawns, tadpoles, and small fish. They are not averse to ingesting their own young, if these are to be found among the water plants when the adults perform their suctorial feeding activities. In lake environments, the diet may be more restricted, and includes the leaves of plants, such as Hydrilla, as well as snails and prawns. An early paper records that they ingest the flowers of gum trees that have fallen into the water (Macleay 1883). It has even been suggested that plant material is taken in for the sake of digesting the minute algae and microscopic animals living on the leaves of water plants. Occasionally, adult lungfish are caught with their intestines filled with grass that grew on the bank of the river. This does not mean that the lungfish were able to crawl out of the river and graze on the bank. It happens when the river floods, and the fish can move over the bank to eat grass that they could not reach under normal circumstances.

Early work on newly hatched lungfish suggested that they fed on microscopic material such as algae, although it was later admitted that "conferva is insufficient as food" (Bancroft 1913) and the small fish died when around three quarters of an inch in length. In fact, young lungfish have a supply of yolk when they hatch, and this allows them to grow without actually feeding for several weeks. They die when the yolk supply runs out if they have not been provided with suitable food before this happens.

Young lungfish do not feed by filtering small organisms from the environment, despite the large number of active cilia on the head and within the oral cavity. In stages earlier than 44, before the oral cavity and the foregut have joined, small organisms are swept into the oral cavity and out again (Kemp 1996). After the mouth becomes patent, the organisms pass through the oral cavity and out under the operculum. Cilia in the oral cavity are reduced by this stage, but still present on the gill filaments. There is no structure capable of collecting the microscopic food particles and moving them into the intestines, and no trace of microscopic food items can be found in faecal pellets (Kemp 1996). Young offered microscopic food alone do not thrive.

Hatchling lungfish grow best if the first food that they are offered consists of small living invertebrates, such as daphnia or tubifex, and if they are given such items before they yolk supply runs out (Kemp 1981, 1982). Meckel’s cartilage in the lower jaw, and the corresponding articulation on the cartilaginous quadrate, start to form soon after the oral cavity joins the foregut. The young fish is able to move the jaws by stage 46, before the teeth erupt and before the yolk globules have disappeared from the intestinal epithelium. By stage 48, the fish have begun to eat small invertebrates, and by stage 51 they are voracious carnivores. They may also ingest filamentous algae, if provided with clumps of this material for shelter, but it is not digested. Young juvenile lungfish rely on animal food such as worms, prawns and snails, and the diet changes as they grow older to include plants.

Habitats and microhabitats

Although able to survive in stagnant water, lungfish are creatures of flowing rivers or deep pools in a river system, with dense stands of submerged aquatic plants around the borders. They can make, or find, submerged caves below the bank of the water hole or river. They may hide under submerged logs or, less often, among leaf litter and detritus on the substrate. Adult lungfish may be found in open water, or resting among submerged plants, often quite close to the surface of the water. Moving into shallow water on a submerged riverbank may be an extension of this behaviour. They are not capable of leaving the water and moving freely on a dry riverbank. Nor are they breathing air while resting close to the surface. Older lungfish can cope with many different environments, but the presence of submerged aquatic plants around the water's edge, or of dense masses of tree roots hanging in the water, is essential for the vulnerable eggs and early juvenile stages of the lungfish (Semon 1893, Kemp, 1995, 1996, Bancroft 1924).

Juveniles and young lungfish have not been found as often as the number of adult fish in a river or lake suggests they should be. Early researchers were sure that juveniles spend the first few years of their lives "buried in the mud", in the detritus of the river bed, and that this accounts for the apparent scarcity of young lungfish (Illidge, 1893; Bancroft, 1912). Semon, who studied the lungfish of the Burnett River, found hatchlings, not in mud but among water plants near the bank (Semon, 1893), an observation that has been confirmed since (Kemp, 1987; Brooks and Kind, 2002). At any rate, it is apparent from the records in the literature and from the register of the Queensland Museum that juvenile lungfish are not actually scarce. Research in the Mary, Burnett and Brisbane Rivers (Kemp, 1987; Brooks and Kind, 2002), and in Enoggera Reservoir (Longman, 1926), has shown that juvenile and subadult lungfish are in fact found in much the same places as adults, in deep flowing water amongst dense aquatic weeds, that are growing in a substrate not of mud but of sand, fine gravel or pebbles (Kemp, 1987) or floating on the surface of the water (Longman, 1926).

The hatchling environment is among submerged water plants (macrophytes) or tree roots close to the bank (Semon, 1893, Kemp, 1987), where older lungfish cannot live because they are too large. Unlike the African and South American lungfish, the Australian lungfish does not build a nest or protect its young. Instead, small lungfish hatch into the mass of plants or roots to which the eggs become attached. They are immature when they leave the egg capsule, and do not move around much for several weeks (Bancroft, 1912, 1913). They remain close to the egg capsule, and slip back inside it when danger threatens (Bancroft, 1913). In the sites where lungfish eggs are lodged, algae and protozoa grow on the leaves and roots, and small animals live among the algae. This microhabitat provides food and shelter for the young fish, and without this protection, newly hatched lungfish would not survive the first few weeks of life, when the young fish has no other protection (Kemp, 1995, 1996).

In a natural lungfish environment, such as the Brisbane River, the temperature varies between 13º C and 25º C. Surface water in full sun may be warmer by day, particularly in summer, but lungfish live in deeper water, among water plants, or in shady places. Eggs and embryos are less tolerant of temperature differences than adults and no lungfish are comfortable in low temperatures. The pH varies from around 6 in Enoggera Reservoir to 7.2-7.8 in the Brisbane River, and conductivity in most lungfish habitats in south east Queensland is high. Water is often shaded, with many aquatic plants, and the oxygen content tolerable. The water in many natural lungfish environments is stained brown with tannin and often turbid, so lungfish live mostly in subdued light. They are most often active during the night, from dusk to dawn. During the spawning season, they are also active during the day (Kemp, 1984).

Eggs of lungfish are large, and the jelly membranes pose some restrictions on oxygen uptake. Theoretical calculations indicate that they can obtain enough oxygen by diffusion through the membranes and the egg substance if they are in well oxygenated water. Unfortunately, unattached eggs may be swept into less well oxygenated water, and if they are trapped there, they are unlikely to survive.

The question of aestivation

The Australian lungfish lacks the capability to form structured burrows in dried mud that are lined by mucus, as the African lungfish may do, and, in the natural environment, they do not need to do so. As an early researcher, Spencer, said in 1892,

"It is always to be found in the deep pools, and not in the shallow waters, and it is important to notice that these pools are many of them of considerable extent, some more than a mile long. In the hottest summer, they contain a good supply of water and thus, though a ceratodus may, of course, find its way into a shallow pool which gets dried up, normally no such thing happens and the animal passes its whole life in water".

Spencer adds

" A further fable, pervading all the literature about Ceratodus ever since its discovery, is the statement of its embedding itself in the mud during periods of drought".

Semon, who collected eggs and studied lungfish development in the late nineteenth century, spent months observing the lungfish of the Burnett River, and agrees with Spencer

"As soon as I came to the Burnett, I tried to get acquainted with every detail concerning the fishes' summer sleep, the supposed formation of a cocoon and burial in the mud, for it to adopt a mode analogous to that of its African ally. But the result of my enquiries proved quite negative, and on the ground of my own observations, I must absolutely deny the existence of a summer sleep and the existence of a cocoon.

"I very much doubt if Ceratodus makes for itself a cocoon, as Protopterus does. It may possibly, but very rarely, bury itself in mud, but the fishermen with whom I spoke and who were perfectly well acquainted with the animal, knew nothing of its ever doing this".

Despite these denials, the story of Australian lungfish enclosed in mud or covered only in water plants has persisted, and there is a foundation in fact. The Australian lungfish has a limited ability to aestivate in a lagoon without water when covered by mud and partially dried water plants (Bancroft, 1918; Kemp, 1987). Lungfish can survive out of water, provided that the skin is kept moist in some way and they are not exposed to the sun.

Oviposition and development of lungfish in the wild

Oviposition in the Australian lungfish has been surveyed over the past 35 years, in Enoggera Reservoir and the Brisbane River. Analysis of the data obtained during this survey has provided information on the numbers of eggs laid in different sites and on the factors that govern oviposition in wild lungfish in these systems. Behaviour of lungfish during oviposition and the development of eggs and embryos in the river have also been observed.

Fertilisation in lungfish is external, and there is little obvious sign of sexual dimorphism in the adults. Females are said to have a vent that protrudes more than that of the males (Bancroft 1924), during the breeding season, and males are said to have more brilliant colours. In fact both sexes have vents of similar size, and both are highly coloured during the spawning season.

In the Brisbane River and in Enoggera Reservoir, lungfish return to the same spawning site every year. The lungfish lay eggs within masses of submerged water plants or roots, or close to areas that contain these, and spawning sites are specific and limited in extent. Apparently suitable weeds will be ignored in long stretches of a river or reservoir, and other sites overloaded with eggs.

Wild lungfish in natural situations display complex courtship behaviour, and there are no published reports of the process in its entirety. During the initial stages of courtship, fish follow each other through a bank of submerged aquatic plants such as Hydrilla verticillata (Grigg, 1965) or turn in tight circles in pairs at the surface of open water (Kemp, 1984). These behaviours continue for a while and may or may not lead to the actual release of gametes. Nor are they always conducted within, or close to, a mass of submerged weed. The behaviours are also performed in open water, especially in the Brisbane River where large stands of water plants are not always available, and where flow rates can be rapid. When the courtship rituals are followed by oviposition, the fish lie on their sides, intertwined. The female releases eggs, usually singly or occasionally in small clusters, close to masses of submerged weeds, and the male sprays milt over them (Kemp 1984).

Fish in the Brisbane River may spawn among water plants, and eggs can be found at the base of Vallisneria leaves, or deep within a mass of Callistemon rootlets, well attached in both places, suggesting that the adults have placed them there. However, fish may also spawn in open water, and eggs may be carried down in the current. Some are swept into masses of water plants such as Hydrilla, or filamentous algae such as Cladophora or Lyngbya, or Callistemon rootlets. Deposition of eggs on particular plants in the Brisbane River is therefore often accidental. In Enoggera Reservoir, fish that were spawning appeared to be pushing the eggs into the submerged roots of the water hyacinth (Kemp, 1984).

The outer jelly layer on a lungfish egg is only sticky for a short time after oviposition, so adults must have been close to an item if the eggs are actually attached. If they are simply washed into the mass of water plants by the current, after the outer layer of jelly has lost its adhesive properties, they lie in the root mass or among the algae or leaves of the plants without attachment. Survival of these eggs, and of the eggs that do not encounter a plant, is a matter of chance. Eggs that have not adhered to the plant may be shaken loose or swept away, and eggs that do not adhere may come to rest in deep water without adequate oxygen, refuges for young fish, and access to the small animals that the hatchling lungfish uses for food. Even when they are carried into well oxygenated, shallow water, refuges and food may be absent, if there are no water plants. The proportion of eggs that are closely attached to plants varies in different years, and the faster the current, the fewer the number of eggs that encounter a water plant.

For many years, lungfish in Enogerra Reservoir made use of submerged root masses of the introduced floating weed, water hyacinth, Eichornia crassipes, for spawning. The reservoir was built in 1867, one year after the water hyacinth spread throughout Queensland, and lungfish were placed in the reservoir in 1895 (O'Connor, 1896). The fish in this locality have always used water hyacinth for spawning, in specific localities where some flowing water was available. Juveniles have been found when water hyacinth was forked up onto the bank (Longman, 1928) and hatchlings have been caught among the roots, close to their egg cases (Kemp, 1987). Although the water is clean and of good quality, if slightly acidic, there are few native species of water plant suitable for the attachment of lungfish eggs in this reservoir. Although Enoggera reservoir is no longer used as a water supply, the level is not constant because of periodic drought and flooding. This means that native water plants such as Hydrilla verticillata do not become established around the margins of the lake, and, if no floating weeds are available, eggs will not be attached to a suitable substrate and will fall to the bottom of the reservoir and die. Water hyacinth was essential for spawning of Enoggera reservoir lungfish. Water hyacinth was cleared from the reservoir in 1974, and no lungfish eggs have been collected from Enoggera reservoir since this time.

Brisbane River lungfish have a wide choice of submerged water plants for spawning sites. Eggs may be found on a range of submerged water plants, such as Hydrilla verticillata, Vallisneria spiralis, Nitella, Chara, Cladophora, Rhizoclonium, Lyngbya, water hyacinth, and the submerged roots of Callistemon viminalis. Adult lungfish may ignore plants that occur naturally in their ancestral homes in favour of the water hyacinth, and will do so even when the natural water plants are readily available. All of these plants share the characteristic that they are found close to the banks of the river, in water that is shallow, at most a metre deep. Even if the water levels are low when the fish spawn, suitable materials to receive the eggs are usually present. Lungfish are not always particular where they spawn, so eggs may be found on sticks or discarded litter, such as floating beer cans, or on the empty shells of a large freshwater clam often found in the Brisbane River. They will also lay eggs on submerged mops made of acrylic fibre if these are present among the water plants in their usual spawning sites.

The list of plants that are not used for spawning is equally long, and it is often difficult to fathom the reasons why, since lungfish, particularly in the river, may never come into actual contact with the plants while they are spawning. Eggs are not found in, or attached to, species of Potamogeton, which forms dense stands in Enoggera Reservoir and in the Brisbane River. Potamogeton leaves are rough and the foliage is loose. Brachiaria mutica, a coarse grass that is found in Enoggera Reservoir and in the river, may produce stands of submerged plant matter, but these consist mostly of stems with sparse rootlets, and there are no thick bundles of root hairs. Adults may leave tracks through the submerged stems, presumably formed while they are moving around looking for food, but eggs are not found on this plant. The dense masses of rootlets and root hairs produced by the river bottle brush, Callistemon viminalis that grows along the river banks, are a popular place for eggs, but the roots of the willow tree, Salix babylonica, which has a similar habit, do not shelter eggs or young lungfish.

Time to hatching

Lungfish in the Brisbane River take between three and five weeks to emerge from the egg membranes. Cleavage and formation of a gastrula take 2 and 3 days respectively in the laboratory, and 4 or 5 days in the river. Embryos develop to stage 24 in 2-4 days at constant temperatures in the laboratory, but this process takes 4-6 days in the field. Similarly, development of the head, 6 days at constant temperature, takes 7-10 days in the wild, and stages capable of hatching, around stage 40, a further 4-8 days in the lab, and 9-17 days in the river. Eggs hatch in three to four weeks in the laboratory, at constant temperatures, and there is little difference in the times taken at 18 C and 22 C. In the field, where the temperature is variable, eggs hatch after a longer period, four or five weeks. There is little difference in times taken by eggs in the river to pass through the various stages, despite a range of temperatures from an average of 17 C in September to 22 C in November.

Triggers for oviposition

Lungfish lay eggs annually, between August and December, although spawning is more prolific in some years than in others, and the exact timing varies from one locality to another. Possible triggers include rainfall, temperature, a flush of fresh water into the river or lake, availability of water plants in the spawning site, photoperiod, the synodial cycle, and changes in pH or oxygen tension in the water.

Lungfish spawning in Enoggera Reservoir was monitored in three sites from 1969 to 1973. In the following year, the water plant used by lungfish for spawning in this locality, the water hyacinth, was destroyed (Kemp 1984). Lungfish spawned over a period of four weeks in Enoggera Reservoir, usually in late August or early September. Since 1974, searches of other species of plant in the reservoir have produced no eggs, although lungfish carried out their usual courtship behaviour. It is possible that lungfish have continued to spawn, but in the absence of suitable plants in the spawning sites, the eggs had no attachment sites and fell into deep water where they could not be found.

A detailed analysis of spawning in two localities of the Brisbane River from 1984 until 2006 indicate that lungfish spawn annually in specific sites, over a period of two to four months, from August or September until December. Eggs are found in water ten to fifty centimetres in depth. Some sites in the river are in full sun, and others in shade. Year after year, they spawn in the same places, on the same patches of submerged plant or in the same masses of algae or tree roots. This may reflect ownership of territories by specific males, a trait developed to a high degree by the African and South American lungfish (Kerr, 1950, Johnels and Svensson, 1954). During most of the years of the study, oviposition was apparently absent only if there were no suitable submerged aquatic plants to which the eggs could become attached, a situation that can happen if severe winter floods denude the river of plants. In recent years, this has changed.

The onset of oviposition appears to be related to increasing photoperiod in spring (Kemp, 1984). Spawning occurs at a time of rising photoperiod, whether it involves the initiation of spawning in any one year or the subsequent laying of new clutches of eggs after the start of oviposition. Spawning reaches a peak within a month of the initiation of oviposition, and then declines over the next few weeks. Fish in the Burnett River, the most northerly natural environment of the lungfish (Brooks el al., 2002), spawn slightly earlier than fish in the Brisbane River or in Enoggera Reservoir (Kemp, 1984).

The onset of spring rain, resulting in a flush of fresh water, is frequently claimed to be the trigger for spawning in lungfish. In fact, rain or a flush of fresh water, in the Brisbane River or in Enoggera Reservoir, rarely precedes spawning. The onset of oviposition occurs in most seasons before significant rains fall, and often before any spring rain falls. Levels of water in the Brisbane River, while not constant, are not highly variable. Water levels in Enoggera Reservoir can only be changed by rainfall, as the reservoir is not used to supply water. Rainfall over a year may have an indirect effect, because flooding can remove weed and food supplies, and drought can leave water plants on the shore dry, also reducing the availability of spawning sites. Equally, oxygen content, or pH, which vary little in the Brisbane River in spring and early summer, have no apparent effect on spawning in wild lungfish. Temperature does not control oviposition. Lungfish will spawn in the cool waters of August, and continue to lay eggs in warm water in October and November.

Poor conditions in the river, such as low oxygen levels, high conductivity, a drop in pH and increased levels of cyanobacteria in the water may affect spawning and the survival of eggs and young fish. Blooms of cyanobacteria in the Brisbane River have become common in recent years, partly as a result of severe drought in the region, and partly because water is being retained in upstream reservoirs and environmental flows are not reaching lower stretches of the Brisbane River. These have been sufficient to turn the water green.

The synodial cycle does not appear to initiate oviposition by wild lungfish in the Brisbane River, nor does it affect the production of new batches of eggs. Lungfish may spawn initially at any time of the lunar cycle, and new eggs continue to be laid throughout the spawning season, again without reference to the synodial cycle. This is the case whether eggs were laid first at new moon or full moon, or when spawning was initiated close to the first or last quarter. The original suggestion that lungfish spawning behaviour could be controlled by the synodial cycle was based on a misprint in a medical journal (Ross, 1966). Wild lungfish are not "lunar".

Availability of water plants is unlikely to exert any control over spawning, as eggs will be laid, but not be caught, if weed cover is low. While the presence of suitable submerged water plants or tree roots is important, availability of weed does not control the onset or the continuation of spawning. From 1991, most eggs were not placed on or in weed beds in the Brisbane River, but shed into the water column. Fish continue to spawn even when submerged plants are not available. The fish in Enoggera Reservoir continued to carry out their distinctive courtship behaviour for years after the water hyacinth was cleared, and may have produced eggs as usual. In the absence of water hyacinth, no eggs were found adhering to any other type of weed. However, survival of eggs, and recruitment of young, to the adult population, is controlled by the presence of suitable water plants or rootlets.

The short season always observed in the lungfish of Enoggera Reservoir despite the persistence of good conditions until 1973 suggests that only a few breeding pairs were active in this area. A longer season in the river may reflect the larger population and the larger number of breeding pairs in the river compared with the lake.

Cycles of spawning

Even under apparently good conditions, with weed available to catch the eggs, lungfish breeding seems to follow a cyclical pattern, with some years of good spawning seasons followed by several seasons of poor spawning. The occurrence of goods seasons of spawning is rarely abrupt. There is usually a slow loss followed by a slow return to good spawning years. Recruitment to the population tends to follow cycles too. Prolific seasons of 1978-79 were followed by good recruitment of juveniles in 1980-81.

Two areas of the river, both below Wivenhoe Dam, and separated by a long reach of deep, slow flowing water, 10 k in extent, were surveyed from 1984 to 2006. In the upstream area, lungfish laid eggs on both sides of the river from 1984 to 1998, and the site covered an area of 10 m of river bank on one side, and 30 metres of the other side. The long stretch on the opposite bank was overshadowed by Callistemon trees with roots extending into deep water. Fish spawned over the whole extent of this bank until 1996, when usage contracted to 10 and then to 5 metres.

Spawning in the upstream site attained a high point in 1984, followed by slow and continual reduction in egg numbers to 1988. In the spring following heavy winter rains in 1989, which caused floods severe enough to clear weed from the Brisbane River, no eggs were collected in the usual sites because the weed was either not there or because it was covered in silt. Numbers of eggs collected rose slowly from 1990 to peak in 1993-4, and dropped slowly again to 1998. Then spawning ceased on one side, when water plants like Lyngbya disappeared, and Callistemon roots were overgrown with masses of Brachiaria mutica. Lungfish did not spawn in 1999. After a slow recovery in 2000 and 2001, spawning in the upstream area stopped in 2002, without ever attaining the previous use of the area.

The downstream site consisted of patches of Vallisneria in shallow water, and Callistemon roots submerged in pools of deeper water. A deep channel with fast flowing water separated these sites from the opposite bank where Vallisneria grew in shallow, almost stagnant pools. Fish moved from one small area to another from year to year, sometimes using Callistemon roots in deep water, and sometimes pushing the eggs into the base of Vallisneria plants in shallow water. Spawning has never been prolific in the downstream site, which is often disturbed by human activity. Fish in this area may not spawn for several years.

Some of the variation in use of spawning areas may be explained by the number of pairs involved in spawning, a variable that is difficult to assess, as is the possibility that a male may be territorial, with females visiting to lay eggs. Lungfish in the Brisbane River are rarely seen. Involvement of more than one female is evident in some collections, because of variation in the size of the egg capsule and of the egg. Occasionally, eggs that are significantly smaller or significantly larger than the usual 3mm egg and 1 cm capsule are found, such as a 2.8mm egg and 8mm capsule, or a 3.5 mm egg and 1.3 cm capsule.

The prolonged drought of recent years in south east Queensland has reduced the water levels in spawning grounds so much that lungfish have few of their usual spawning sites left. The river runs only in deep channels where water plants are unsuitable or absent. These poor conditions may be the reason for the current reduction in egg numbers in both areas of the Brisbane River that were studied, and for the cessation of spawning in the upstream site over the last three years. This does not explain the cycles of spawning in previous years, nor does it explain why spawning did not occur in 1989 and 1999, before the current drought began. Lack of eggs in 1989 is related to the occurrence of a flood in winter, which removed all of the water plants from the spawning sites, and damaged the Callistemon roots. This did not occur in 1999, when conditions were reasonable.

Recruitment of young fish to the adult population

Low recruitment rates are a normal strategy for a species such as lungfish that can live for up to seventy years (Kemp, 1995). Recruitment of juveniles to the adult population is not well understood, although available evidence indicates that it is normally low. Relatively few hatchling lungfish have been collected from the wild since lungfish were first discovered over a hundred years ago. All were found among submerged plants or roots close to shore (Semon, 1893, Kemp, 1987).

A number of juveniles, ranging in length from 11-15 cm, were caught among water hyacinth dragged up onto the bywash in Enoggera Reservoir in 1928. These were found in March, and could have been young of the previous year. Small subadult fish, up to 28 cm long, also from water hyacinth forked up onto the bank of Enoggera Reservoir, were caught between September 1928 and July 1932 (Kemp 1987). These could have been about one year old, but assessing the age of wild caught lungfish is difficult (Kemp 2005; Brooks et al. 2002). Subadult lungfish from the Brisbane River, collected in 1961 and 1982, ranged from 25 cm to 41 cm, and weighed from 250 gm to 500 gm. Other, isolated, records of small lungfish from historical sources, mostly from the Burnett River, varied in length from 35 to 50 cm (Kemp 1987). These may not be indicative of successful recruitment in that they could be quite old and have fed poorly, or young of a year or two ago that have fed quite well. These results have largely been confirmed by an extensive search for young lungfish in the Burnett River, carried out after much of the river was altered by the building of weirs and reservoirs (Brooks et al 2002). Few hatchlings were found, and not many juvenile or subadult fish.

Bancroft, who worked extensively in the Burnett River system, searched for juveniles among submerged aquatic macrophytes many times after prolific spawning seasons, with little success. Bancroft concluded that recruitment of juveniles to the adult population occurs only once or twice in a century, and without effective conservation strategies, that the species would become extinct, This assessment proved to be unnecessarily pessimistic, while rivers remained unchanged by human intervention. In the last sixty years, the three major river habitats of lungfish have been converted into dams and reservoirs with fluctuating water levels. No water plants can become established along the banks of the weir, and there are no refuges or homes for the hatchling fish. This has changed the balance of the system and increased the risk to lungfish populations by reducing successful recruitment of young to the adult population. Rivers in south Queensland have already been extensively altered, and future plans include more reservoirs.

Predation and pathology

Although the African lungfish is still caught for food, the Australian lungfish is safe from such predation, except perhaps from fishermen who are unaware of the laws regarding lungfish, or who do not recognise the fish that they have caught. In the past, the lungfish lived with predators such as crocodiles, but these are no longer found in the rivers of south east Queensland. However, although the adults are relatively immune from predation, eggs, embryos, and young are not. Other fish, dragonfly larvae and other insects use them as food (Bancroft, 1912), and at least one common predator is capable of snipping the egg out of the egg case.

The incidence of trauma and disease in wild lungfish is low. Adult lungfish have effective defences against infection, and effective mechanisms of healing injury under most circumstances. However, lungfish live for a long time, and can be affected by the common diseases of senescence, such as osteoporosis and dental decay, particularly common in lungfish that live in lakes with acid water, such as Enoggera Reservoir (Kemp, 2005).

Neoplasia is rare in lungfish, and has been recorded only in Protopterus held in captivity (Hubbard and Fletcher 1985; Masahito, Ishikawa, and Takayama, 1984). Hyperplasia or hypertrophy of the tooth plates is known in N. forsteri, and a Devonian fossil, Sorbitorhynchus deleaskitus, has a lesion that would have been occupied in life by a large epidermoid cyst in the mandible (Kemp 1994).

Lungfish confined in a container with a rough substrate will suffer abrasion and subsequent thickening of the skin and scales on the ventral surface of the body and of the paired fins. The lesions will heal if the fish are transferred to more suitable conditions. This injury is always the result of a poor situation in captivity, sustained over a long period of time. One of the first lungfish caught, the specimen preserved in the National Museum of Natural History in Paris, has been damaged in this way. Apparently the fish came from the Rockhampton Market, a long distance from the Burnett River (de Castelnau 1876a). Lesions on its belly and fins suggest that it spent a considerable time in poor conditions before it was finally killed. It is probable that it was caught in the Burnett or Mary River and transported to Rockhampton.

Young lungfish may suffer from a number of problems, particularly in captivity. Live food may not be free of disease producing organisms. Oligochaete worms such as tubifex may harbour bacteria, and protozoa such as Microsporidia or Myxosporidia. Myxosporidial infection causes apparently healthy fish to swim in circles. Fish infected by Microsporidia fail to thrive, and are thin and pale, with clusters of clear, refractile organisms on the skin. Fish with these conditions should be euthanased.

Fish may develop bloat, or gas bubbles in the anterior intestine. This condition is never normal (Bancroft 1918). Affected fish float upside down at the surface of the water. Some species of crustacea, dried food, or food laden with bacteria, are most likely to produce bloat. It is possible to reduce the air bubble by gentle pressure on the abdomen in juveniles but hatchling fish are too small and delicate to be treated in this way, and are unlikely to recover spontaneously.

Small lungfish live amongst water plants or submerged tree roots, where algae and settling organisms are also present. This environment is perfect for gathering silt and dirt. All of this will settle on the egg cases, providing useful camouflage, and will also cover the hatchling while it rests in the habitat, and enter the egg case after holes appear in the membrane, but before the little fish hatches. In this dirty environment, small lungfish are able to keep the skin clean because many of the cells of the skin have cilia, which remove any material that settles on the fish, or enters the egg case (Kemp, 1996). As the fish grows, and becomes more active, ciliated cells disappear, and mucous secreting cells proliferate in the epidermis.

Wild lungfish harbour several metazoan parasites, some specific to lungfish, and others capable of infecting other animals as well. A monogenean tapeworm lays eggs on the teeth. It is virtually unknown in the Brisbane River, but particularly common in fish from Enoggera Reservoir (Whittington and Pichelin, 1991). Adult stages are not known. Nematode parasites frequently infect the gut, probably with little effect on the fish. Occasionally a nematode may infect the bones and teeth of the lungfish, and lesions in the tooth plate that are reminiscent of this parasite are known from fossil material as well (Kemp, 2005).

It is perhaps surprising, in view of the insistence on close relationships between N. forsteri and amphibians, that lungfish have not so far shown infection with chytrid fungus. Chytridiomycosis, a skin disease that has decimated some frog populations in Australia and around the world (www.deh.gov.au), has not been described in lungfish. Threats to the lungfish come from other sources.

Palaeoecology

Australia has an extensive fossil record of lungfish related to N. forsteri, extending back into the Eocene and lasting until the Pleistocene. The latter deposits include N. forsteri, but this species is not known with certainty from earlier epochs. The fossil species had tooth plates, and jaw architecture, similar to those of the living N. forsteri, and the ways in which the dentition was used are equivalent. Pathologies and wear conditions on the tooth plates of both fossil and living lungfish are comparable. Information derived from this analysis of fossil and living lungfish can be used to assess the population structure and environmental conditions in the past, and predict what may happen to living lungfish in the future (Kemp, 2005).

Many aspects of research into lungfish populations have been hampered by the lack of a precise method of assessing the age of a wild lungfish (Brooks et al., 2002). Growth in lungfish can be rapid or slow, depending on the conditions of the environment (Kemp, 1987), and it follows that size alone is not a reliable indicator of age. Scales of lungfish of known age kept in captivity have more growth lines than they should if the lines are deposited annually, but too few to reflect monthly or seasonal growth spurts (Kemp, 2005). Tooth plates show incremental lines in dentine and enamel, but wear continually from the occlusal surface. Skull bones can be thin enough to reveal incremental lines of bone deposition, but all of the bones have thicker areas where the bone was first laid down and no lines are visible in these areas (Kemp, 1999). It is however possible to estimate age in lungfish populations by considering the size of tooth plates, in conjunction with the incidence of certain structural characteristics, such as the development of osteoporosis and spur and step wear (Kemp, 2005). This method of estimating age in the living and fossil populations of fish is not exact, but can be used to gain some idea of population structure, in the absence of more reliable methods (Kemp, 2005).

The oral cavity of a lungfish is confluent with the surroundings because water enters the mouth continuously to allow for respiration. Therefore, the pH of the environment and the pH of the oral cavity are similar. Although mucous glands are present in the oral epithelium, this secretion is unlikely to have any protective effect on the dentition. Acidity of the surrounding water may be a factor in producing severe erosion, as is the length of exposure to acid conditions during the life of the fish (Kemp, 2005). Brisbane River fish live in a neutral environment and show little severe erosion of the tooth plates. Fish in Enoggera Reservoir live in acid water, and most have considerable erosion in the dentition, exposing the pulp cavity in many specimens.

Dental decay is a common pathology among lungfish tooth plates, and found in fossil and living specimens (Kemp, 2005). This condition may develop as a result of mechanical damage from harsh items in the diet, or exposure to stagnant water containing infective organisms. A high incidence of dental decay, and other pathologies such as abscesses or parasitic invasion of dental tissue in material from a locality indicates a poor environment.

Harsh food produces heavily abraded tooth plates, as well as a greater proportion of fish using crushing jaw movements. Soft food, and a grinding action in the jaws results in smoother wear of the occlusal surface. Attrition of dental material happens when teeth are ground together without food being present. A high proportion of tooth plates in a population that have attrition indicates that food is not plentiful, or that fish did not feed for reasons related to stress, such as disease, crowding, or competition for suitable refuges.

Until 1999, unaltered regions of the Brisbane River contained actively spawning populations of lungfish with significant recruitment, living in an environment with neutral water and plentiful food. However, despite this, the fish from this locality had a high incidence of caries in the dentition, and the only fish found with nematode infection inside the tooth plates and jaw bones came from this locality. Around half of the fish sampled showed signs of heavy wear. Few individuals used crushing movements of the tooth plates, suggesting that most of the food consumed was soft and easy to chew. Spur and step formation, a condition that develops over a long time, was also present in half of the tooth plates examined, confirming that a significant proportion of the population was in fact older than size alone might indicate. Erosion of the tooth plates was unusual, and the only instance of attrition, resulting from grinding of the teeth without food present, came from the fish affected by parasitic infection of the teeth and jaw bones. Dental decay was however common, and present in nearly a third of the fish examined, including a small specimen. Most of the pathologies found related to malocclusion and trauma, and it was possible that some harsh items are present in the diet (Kemp 2005).

Material collected from Enoggera Reservoir some years after removal of the water hyacinth consists of large tooth plates only, and indicates that successful spawning and recruitment has ceased in Enoggera Reservoir. All of the specimens show heavy occlusal wear, and many have spur and step wear as well. The high proportion using crushing movements of the jaws may be a response to a harsh diet. The number of tooth plates with signs of attrition is higher among Enoggera fish than it is among Brisbane River fish. As in the Brisbane River fish with attrition, concurrent pathology is present in Enoggera fish with this condition. Erosion of dental material from the tooth plates is exceptionally high, in keeping with the acidity of the environment. Carious lesions are present in all but one of the fish from this locality, and the levels of trauma, hyperplasia and abscess in the tooth plates is the highest recorded for any lungfish population, fossil or living. Osteopenia, as a result of age or of a poor diet, is found in most of the material from this reservoir. The environment of Enoggera Reservoir may permit the fish to survive to a great age, but it has little food and acid, stagnant water. Pathologies suggestive of a harsh diet are common. More important for the survival of the species, the lake provides no refuges for young lungfish, and there has been no recruitment to the lungfish population in this reservoir for many years (Kemp 2005). Lungfish in Enoggera Reservoir have now become extinct (J. Hall, pers. comm.)

No fossil locality is exactly like the Brisbane River or Enoggera Reservoir, but certain comparisons can be made. Some, such as the lungfish of the Wipajiri Formation, resemble the present day population of the Brisbane River, with large numbers of adults and juveniles, smooth wear on the tooth plates, and few dental pathologies. Others, like material from the Namba and Katapiri Formations, conform in many characteristics to the population in Enoggera Reservoir, Large fish only are present, and the tooth plates have many age related conditions, such as heavy wear, crushing jaw movements and attrition. Like the new weirs and reservoirs built over the Burnett River, these Formations are based on localities had fluctuating water levels, and there would have been no habitat for embryos and young fish. Others, such as the fish of the Etadunna Formation, may have had active recruitment, but the dentition shows evidence of harsh food. Others, like the lungfish of the Carl Creek Limestones at Riversleigh in North Queensland, or the Camfield Beds in the Northern Territory, suggest that the environment was depauperate and precluded growth to a large size Kemp, 2005). This has implications for living populations. Despite the fact that lungfish are tough and adaptable, environments impose significant constraints on them, especially when they have been altered by human interference.

Among the present day lungfish, wear characters, population structure, size, and age characters are similar to those of the fossil deposits, but incidence of the more serious conditions like pathology and caries and erosion is invariably greater in the living fish, and indicates that at the time of collection of the tooth plates from these areas, the populations were already under stress. The situation in lungfish habitats is now more difficult, with the creation of new weirs and reservoirs that alter environmental conditions fundamentally. The implications of these changes for the last survivor of an extensive fossil lungfish fauna are serious.

The future for the Australian lungfish

There is little doubt that weirs and reservoirs in the natural lungfish habitat do lungfish few favours. Water quality is poor, and promotes the growth of cyanobacteria. Food plants and animals do not become established, or are not able to live, in such conditions, and the water levels fluctuate depending on the demands placed on the reservoir, and spawning grounds previously used by the lungfish are deeply submerged. This means that no protected habitats exist for eggs and hatchling lungfish. Worse, occasional floods in water impoundments carry lungfish over concrete spillways, causing death and injury and isolating them in an unsuitable environment.

Conditions in Enoggera Reservoir, while the lungfish were actively breeding, were not the same as in new dams and weirs. By the time lungfish were introduced to Enoggera, the lake had been established for 20 years, and included water hyacinth. The reservoir is deep, with a constant inflow of fresh water. This is not always the case with new reservoirs.

Man made changes to lungfish habitats have caused acceleration to the contraction of lungfish habitat apparent in the past. Reasons for this are not always obvious, although it is not difficult to understand why it has happened in the last 50 years since dams and weirs have been built over natural rivers. Fossil lungfish populations died out because the environment became arid, but most were in trouble before such natural climatic events took place. The major lesson to be learned from the contraction in the range of lungfish in the past is that lungfish are completely dependent on the maintenance or persistence of an environment that they like. However, despite over a hundred years of research into the biology of lungfish, we do not yet know what exactly lungfish look for in an environment. This makes design of a recovery plan subsequent to extensive damage of an environment for lungfish almost impossible, particularly after the event.

Lungfish return to the same place every year to spawn. This is totally predictable. The extent of use of the site may vary, depending on the point in the cycle and the number of adult females visiting the site in any one year. However, the reason behind the choice of different sites is not clear.

We do not know what makes a site suitable in the opinion of the lungfish. It could be the position with respect to sun and shade, or the way in which water flows past the weed bank. It could be the quality and quantity of the water plants, and the small organisms attached to them, or the lack of adherent algal masses. Possibly the fish are territorial and the spawning site is part of the home range of the territory owner. Lungfish will utilise an artificial site if it is placed within a normal spawning site. If it is not within a normal site eggs will not appear on it. Lungfish will use one clump of weed and ignore another, for no reason apparent to human insight. Hyacinth grew all around the margin of Enoggera Reservoir, but the lungfish used only 3 sites. It follows that artificial spawning sites within a weir or reservoir will not be used by the lungfish unless they are in or near a site used previously, or within the territory of a male lungfish, and unless they conform to factors and criteria that only the fish understand and will accept. This is the one vital question for recovery plans in a man made lake, and it cannot be addressed by analyses of how often lungfish use a fish ladder, or how far they migrate in a river system. We do not know enough about how a lungfish relates to its environment to answer this question. Creation of a lake or a pond with stable water, plants and animals, however suitable to human eyes, and the introduction of lungfish to this environment, may not work if it does not conform to lungfish standards that we do not understand.

Unfortunately for lungfish and other endangered plants and animals, successive Queensland Governments are determined to convert natural river systems into foetid swamps in the name of conservation of water, and the supply of water to industry, agriculture and an ever increasing number of houses in Queensland. Recovery plans in the dams across the Burnett River, implemented after the dam is built, and artificial breeding systems, most of which are directed at the raising of lungfish for sale to the aquarium trade, are unlikely to save the species from extinction. Although lungfish have often spawned in a captive situation they do not do this reliably, not every year. If the government is concerned with the welfare of lungfish, they should preserve as National Parks, in each of the Brisbane, Mary and Burnett Rivers, a stretch of river, where lungfish are known to be abundant and which is free of the effects of foul water emanating from the reservoirs, unchanged for the future. If this is done, lungfish, and the animals and plants associated with them, may survive.

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Bibliography

Anonymous (W.H.J.) 1923. The palatability of Ceratodus. Brisbane Courier, Feb. 17.

Agassiz, L. 1833. Recherches sur les Poissons Fossiles. Vol. II, III. Neuchatel: Imprimerie de Petit-pierre. (Ceratodus: 46, 129-136).

Atz, J. W. 1952. Narial breathing in fishes and the evolution of internal nares. Quart. Rev. Biol. 27:366-377.

Bancroft, T. L. 1912. On a weak point in the life-history of Neoceratodus forsteri, Krefft. Proc. Roy. Soc. Queensland 23: 251-256.

Bancroft, T. L. 1913. On an easy and certain method of hatching Ceratodus ova. Proc. Roy. Soc. Queensland 25: 1-3.

Bancroft, T. L. 1918. Some further notes on the life-history of Ceratodus forsteri. Proc. Roy. Soc. Queensland 30: 91-94.

Bancroft, T. L. 1924. A suggestion for a biological laboratory on Stradbroke Island for the protection of Ceratodus. Proc. Roy. Soc. Queensland 36: 19-20.

Bancroft, T. L. 1928. On the life-history of Ceratodus. Proc. Linnean Soc. NSW. 53: 315-317.

Bancroft, T. L. 1933. Some further observations on the rearing of Ceratodus. Proc. Linn. Soc. NSW. 58: 467-469.

Barry J. C. and Kemp, A 2007. Protoprismatic enamel in the Australian lungfish, Neoceratodus forsteri (Osteichthyes: Dipnoi).Tissue and Cell, 39: 387-398.

Bartsch, P., Gemballa, S., and Piotrowski, T. 1997. The Embryonic and Larval Development of Polypterus senegalus Cuvier, 1829: its Staging with Reference to External and Skeletal Features, Behaviour and Locomotory Habits. Acta Zoologica (Stockholm) Vol. 78, No. 4, pp. 309-328.

Bemis, W. E. 1984. Morphology and growth of lepidosirenid lungfish tooth plates (Pisces:Dipnoi). J. Morphol. 179:73-93.

Brooks, S. G., and Kind, P. K. 2002. Ecology and demography of the Queensland lungfish (Neoceratodus forsteri) in the Burnett River, Queensland. (With reference to the impacts of Walla Weir and future water infrastructure development). Department of Primary Industries Final Report. The State of Queensland, DPI, Brisbane. 158 pp.

Caldwell, W. H. 1884. The eggs and larva of Ceratodus. J. Proc. Roy. Soc. N.S.W. 18:138.

Caldwell, W .H. 1885. On the development of the Monotremes and Ceratodus. J. Proc. Roy. Soc. N.S.W. 18: 117-122.

de Castelnau, F. 1876a. Memoire sur les poissons appeles Barramundi par les aborigines du nordest de L'Australie. J. de Zool. 5:129-136.

de Castelnau, F. 1876b. Remarques au sujet du genre Neoceratodus. J. de Zool. 5:342-343.

Conant, E. B. 1977. Green colour of bones and eggs in the African lungfish, Protopterus annectens, due to bile pigments. Amer. Zool. 17:911.

Conant, E. B. 1986. An historical overview of the literature of Dipnoi: Introduction to the bibliography of lungfishes J. Morphol. Suppl 1 5-13.

Dean, B. 1906. Notes on the living specimens of the Australian lungfish, Ceratodus forsteri, in the Zoological Society's collection. Proc. Zool. Soc. London 1906:168-178.

Dean, B. 1912. Additional notes on the living specimens of the Australian lungfish (Ceratodus forsteri) in the collection of the Zoological Society of London. Proc. Zool. Soc. London 1912:607-612.

Greenwood, P. H. 1986. Journal of Morphology supplement 1:163-179.

Greenwood, P. H. and Oliva, O 1959. Does a lungfish breathe through its nose? Discovery (New Haven) 20:18-19.

Grigg, G. C. 1965. Spawning behaviour in the Queensland lungfish, Neoceratodus forsteri. Aust. Natur. Hist. 15:75.

Gunther, A. 1871. Description of Ceratodus, a genus of ganoid fishes, recently discovered in rivers of Queensland, Australia. Trans. Roy. Soc. London 161:511-571.

Holmes, E. B. 1985. Are lungfishes the sister group of tetrapods? Biol. J. Linn. Soc. 25:379-397.

Hubbard, G.B. and Fletcher, K. C. 1985. A seminoma and a leiomyosarcoma in an albino African lungfish (Protopterus dolloi). J. Wildl. Dis. 21:72-74.

Illidge, T. 1893. On Ceratodus forsteri. Proc. Roy. Soc. Queensland 10:40-44.

Jarvik, E. 1980. Basic Structure and Evolution of Vertebrates. Vol. I 1980, Vol. 2 1981. New York: Academic Press.

Johnels, A. G. and Svensson, G. S. O. 1954. On the biology of Protopterus annectens. Ark Zool. 7:131-164.

Kemp, A. 1981. Rearing of embryos and larvae of the Australian lungfish, *Neoceratodus forsteri* (Krefft) under laboratory conditions. Copeia, 1981:776-784.

Kemp, A. 1982. The embryological development of the Queensland lungfish, Neoceratodus forsteri (Krefft). Memoirs of the Queensland Museum, 20:553-597.

Kemp, A. 1984. Spawning of the Australian lungfish, Neoceratodus forsteri (Krefft) in the Brisbane River and in Enoggera Reservoir, Queensland. Memoirs of the Queensland Museum, 21:391-399.

Kemp, A. 1987. The Biology of the Australian lungfish, Neoceratodus forsteri. Journal of Morphology, supplement 1:181-198.

Kemp, A. 1994. Pathology in developing eggs and embryos of Neoceratodus forsteri. (Osteichthyes: Dipnoi). Copeia, 1994:435-443.

Kemp, A. 1995. Threatened fishes of the world: Neoceratodus forsteri (Krefft 1870) (Neoceratodontidae). Environmental Biology of Fishes, 43:310.

Kemp, A. 1996. The role of epidermal cilia in development of the Australian lungfish, Neoceratodus forsteri (Osteichthyes: Dipnoi). Journal of Morphology, 228:203-221.

Kemp, A. 1999. Ontogeny of the skull of the Australian lungfish, Neoceratodus forsteri (Osteichthyes: Dipnoi).Journal of Zoology, 248: 97-137.

Kemp, A. 2002. Growth and hard tissue remodeling in the dentition of the Australian lungfish, Neoceratodus forsteri (Osteichthyes: Dipnoi). Journal of Zoology, 257:219-235.

Kemp, A. 2005. New insights into ancient environments using dental characters in Australian Cainozoic lungfish. Alcheringa, 29:123-149.

Kemp, A and Barry J. C. 2006. Prismatic dentine in the Australian lungfish, Neoceratodus forsteri (Osteichthyes: Dipnoi).Tissue and Cell. 38:127-140.

Kerr, J. G. 1950. A Naturalist in the Gran Chacao. Cambridge: Cambridge Univ. Press. (Lepidosiren Expedition:169-229).

Krefft, G. 1870. Description of a gigantic amphibian allied to the genus Lepidosiren, from the Wide-Bay District, Queensland. Proc. Zool. Soc. London 1870:221-224.

Kesteven, H. L. 1945. The origin of the Tetrapods. Proc. Roy. Soc. Victoria. Vol. LVII, Parts I and II, pp.93-138.

Kikugawa, K., Kazutaka K., Shigehiro K, Hiroshi S., Osamu I., Naoyuki I., and Takashi M. 2004. Basal jawed vertebrate phylogeny inferred from multiple nuclear DNA-coded genes. BMC Biology 2/3, pp.1-11.

Laurin, M., Girondot, M. and de Ricqles, A. 2000. Early tetrapod evolution. TREE Vol. 15, No.3, pp.118-123.

Lissone, I. 2003. Conservation genetics and the Australian lungfish Neoceratodus forsteri (Krefft 1870); a spatio-temporal study of population structure. Master of Science. thesis, Faculty of Science, The University of the Sunshine Coast, Sippy Downs, Queensland.

Longman, H. A. 1928. Discovery of juvenile lung-fishes, with notes on Epiceratodus. Mem. Queensl. Mus. 9:160-173. N:1 3 9 10 15 18 19 21.

Macleay, W. S. 1883. On some newly observed habits of Ceratodus forsteri. Zoologist 1883:506-507.

Masahito, P., Ishikawa, T. and Takayama, S. 1984. Spontaneous spermatocytic seminoma in African lungfish, Protopterus aethiopicus Heckel. J. Fish Dis. 7:169-172.

O'Connor, D. 1897. Report on preservation of Ceratodus. Proc. Zool. Soc. Queensland 12:101-102.

Rosen, D. E., Forey, P. L., Gardiner, B. G., and Patterson, C 1981. Lungfishes, tetrapods, paleontology, and plesiomorphy. Bull. Amer. Mus. Natur. Hist. 167:159-276.

Ross, L. S. 1966. Lunar lungfish. N. Engl. J. Med. 274:1388.

Schultze H-P. 1994. Comparison of hypotheses on the relationships of Sarcopterygians. Syst. Biol. 43 (2), pp.155-173.

Semon, R. 1893. Die aussere Entwickelung des Ceratodus forsteri. Denkschriften med-naturwissenschaftung gesellschaft Jena 4:29-50.

Semon, R. 1899. In the Australian bush. London: Macmillan, 552 pp.

Spencer, W. B. 1892. Note on the habits of Ceratodus forsteri. Proc. Roy. Soc. Victoria 4:81-84.

Spencer, W. B. 1892. A trip to Queensland in search of Ceratodus. Victorian Natur. 9:16-32. N:10 14 18 19.

Wang, S., V. Drapala, R.E. Barwick and K.S.W. Campbell 1993. The Dipnoan species, Sorbitorhynchus deleaskitus, from the Lower Devonian of Guangxi, China. Phil Trans. R. Soc. London B 340, pp.1-24.

Welsby, T. 1905. Schnappering and Fishing in the Brisbane River and Moreton Bay waters, a Wandering Discourse on Fishing Generally. Brisbane: Outridge Printing Co.

Whitley, G. P. 1929. The discovery of the Queensland lungfish. Aust. Mus. Mag. 3:363-364.

Whiting, H. P., and Bone Q. 1980. Ciliary cells in the epidermis of the larval Australian dipnoan, Neoceratodus forsteri. Zool. J. Linn. Soc. 68:125-137.

Whiting, H. P., Bannister, L. H. Barwick, R.E. and Bone Q. 1992. Early locomotor behaviour and structure of the nervous system in embryos and larvae of the Australian lungfish, Neoceratodus forsteri. Journal of Zoology, London 226:175-198.

Whittington, I. D. and Pichelin S. 1991. Attachment of eggs by *Concinnocotyla australensis* (Monogenea: Polystomatidae) to the tooth plates of the Australian lungfish, Neoceratodus forsteri (Dipnoi). International Journal for Parasitology 21: 341-346

Zardoya, R., and Alex M. 1996. The complete Nucleotide sequence of the mitochondrial genome of the Lungfish (Protopterus dolloi) supports its phylogenetic position as a close relative of land vertebrates. Genetics 142, pp.1249-1263.

Zardoya, R., and Axel M. 1996. Evolutionary relationships of the coelacanth, lungfishes, and tetrapods based on the 28S ribosomal RNA gene. Proc. Natl. Acad. Sci. USA 93 (9), pp.5449-5454.

Zylberberg, L. 1988. Ultrastructural data on the scales of the dipnoan Protopterus annectens (Sarcopterygii, Osteichthyes). Journal of Zoology, London, 216, 55-71.