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Lungfish as environmental indicators

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Abstract

Lungfish fossil material is widespread, and the records are almost continuous in some continents, from the time that lungfish first appeared. Lungfish live for a long time, and the dentition is never replaced during the life of the fish. Tooth plates, the parts most often preserved in lungfish, can provide information about how the fish lived, what it could have eaten, and how good the environment was. For many reasons, lungfish are good indicators of environmental health. However, analysis of the diseases present in fossil populations over time shows that the story is not positive for the future survival of the Australian lungfish. Mesozoic lungfish tooth plates show only a few examples of caries, and the range of diseases present in the dentitions of Cenozoic and living populations includes erosion, caries, abscesses, hyperplasia, parasitic invasion and osteopenia. Some lungfish tooth plates from Cenozoic environments show attrition, as do specimens from living lungfish, suggesting that the fish did not have enough food. Comparison of Mesozoic material with specimens from younger deposits suggests that the condition of lungfish populations and their environments has deteriorated over time.

Introduction

Analysis of ancient environments explains far more than the conditions under which animals lived in the past. It has implications for living animals, and for the potential survival of groups that are at risk, such as the living Australian lungfish, *Neoceratodus forsteri*. This species is now confined to a few rivers in southeast Queensland, and most of the environments have been converted into reservoirs for water storage and flood mitigation. These reservoirs do not provide a good environment for lungfish (KEMP 2011).

Lungfish tooth plates from Australian Cenozoic deposits have been used to define ancient environments in Australia (KEMP 2005). This continent is geologically old, and has an excellent record of dipnoan fossils, beginning in the Devonian and continuing until the present day, with the exception of the Jurassic when conditions may not have been suitable for the preservation of lungfish material, or deposits that contain lungfish remain unrecognised. In deposits where they are found, there may be large numbers of lungfish, and preservation, at least of the dentition, is reasonable. Notable among the Mesozoic deposits are the lungfish of the Cretaceous localities at Dinosaur Cove in Victoria (Eumerella Group, Early Cretaceous), in Queensland at Longreach and Winton (Upper Cretaceous Winton Formation), and the opal deposits in Lightning Ridge (Griman Creek Formation, Early Cretaceous), Coober Pedy and Andamooka in South Australia (Bulldog Shale, Early Cretaceous). Comparative material is found in central Australia, in the Namba, Etadunna, Wipijiri, and Katapiri Formations, all mid-Tertiary localities, and in younger deposits at Bullock Creek (Camfield Beds) and Riversleigh (Carl Creek Limestones) in northern Australia (KEMP 2005). Material from the living lungfish is also available, from the Brisbane River and Enoggera Reservoir. The map provides locations of fossil sites and of the populations of living lungfish that have been used for comparison (Fig. 1).

Lungfish evolve slowly, and many characters of the dentition and jaw bones are similar or even almost identical in genera of different ages, particularly among members of the families Ceratodontidae and Neoceratodontidae from the southern hemisphere. Lungfish in the past, in the Mesozoic and in the Cenozoic, faced similar problems of disease and environmental damage compared with the living lungfish, although the situations are not always exactly parallel. However, information from the many fossil relatives of *Neoceratodus* in Australia can be gathered and applied to the situation faced by lungfish now, as humans continue to invade and spoil their environments.

This contribution describes diet related wear and pathologies in Mesozoic lungfish tooth plates. Equivalent conditions in material from Cenozoic localities have already been described (KEMP 2003, 2005). The information obtained from this work suggests that threats to living lungfish are considerable, and have increased over time.

Materials and methods

Institutional abbreviations: AMNH, American Museum of Natural History, New York; **AM**, Australian Museum, Sydney, New South Wales, Australia; **LRF**, Lightning Ridge Opal and Fossil Centre, Lightning Ridge, New South Wales, Australia; **MV**, Museum of Victoria, Melbourne, Victoria, Australia; **QM**, Queensland Museum, Brisbane, Queensland, Australia.

Lists of material with geological information

The extinct condition of a taxon is indicated with the symbol "†".

†*Ceratodus diutinus*: **AM F 75220** (Surat Basin, Lightning Ridge area, Grawan Field, New South Wales, Griman Creek Formation, Early Cretaceous). **AM F 75641** (Surat Basin, Grawan, New South Wales, Wallangulla Sandstone Member, Griman Creek Formation, Early Cretaceous). **QM F 18830** (Canary Station, near Boulia, West Queensland, Great Artesian Basin, Rolling Downs Group, Toolebuc Formation, Early Cretaceous). **QM F 14417** (Surat Basin, Lightning Ridge Opal Fields, Grawan Field, New South Wales, Wallangulla Sandstone Member, Griman Creek Formation, Early Cretaceous).

†*Metaceratodus wollastoni*: **AM F 64917** (Longreach, Queensland, Winton Formation, "Mid" Cretaceous). **AM F 75221** (Lightning Ridge, New South Wales, Griman Creek Formation, Early Cretaceous). **MV P 166372** (Lake Eyre, South Australia, Winton Formation, "Mid" Cretaceous). **MV P 12555** (Lightning Ridge, New South Wales, Griman Creek Formation, Early Cretaceous). **MV P 175701** and **MV P 175702** (both Solitary Hill, South Australia, Winton Formation, "Mid" Cretaceous). **MV P 160345**, **MV P 160346** and **MV P 160348**, (all Simpson Desert, South Australia, Winton Formation, "Mid" Cretaceous). **MV P 186415** (Slippery Rock Pillar, Otway Group, Dinosaur Cove, Victoria, Early Cretaceous). **QM F 12074** and **QM F 12666** (both Lightning Ridge, New South Wales, Griman Creek Formation, Early Cretaceous). **LRF 588** (Lightning Ridge, New South Wales, Griman Creek Formation, Early Cretaceous). **LRF 726** (Lightning Ridge, New South Wales, Griman Creek Formation, Wallangulla Sandstone Member, Early Cretaceous). **LRF 321** (Lightning Ridge, New South Wales, Griman Creek Formation, Wallangulla Sandstone Member, Early Cretaceous). **LRF 1214** (Lightning Ridge, New South Wales, Griman Creek Formation, Wallangulla Sandstone Member, Early Cretaceous). **QM F 3949** (4 Miles South of Clarafield Station, Winton Formation, "Mid" Cretaceous).

†*Neoceratodus nargun*: **MV P 157247** (Shore Platform, Point Lewis, Cape Otway, Victoria, Otway Group, Early Cretaceous). **MV P 182182** (Cape Otway, Victoria, Otway Group, Early Cretaceous). **MV P 186036** (Eagle's Nest Rock, Victoria, Early Cretaceous). **MV P 186401** (Punchbowl, Victoria, Early Cretaceous).

†*Archaeoceratodus avus*: **MV P 186138** (San Remo Back Beach, Strzelecki Group, Early Cretaceous, Victoria). **MV P 10057** (Cape Patterson, Victoria, Strzelecki Group, Early Cretaceous).

Normal lungfish tooth plate structure

Four species of lungfish from Mesozoic deposits in Australia, †*Ceratodus diutinus* (KEMP 1993), †*Metaceratodus wollastoni* (CHAPMAN 1914, KEMP 1997a), †*Neoceratodus nargun* (KEMP 1983, 1997b) and †*Archaeoceratodus avus* (WOODWARD 1906a, KEMP 1997b), all members of the families Ceratodontidae and Neoceratodontidae, have been used in this analysis. Tooth plates of these species have four to seven ridges in each jaw, and the ridges are separated by clefts of varying depth, usually becoming shallower from front to back of the tooth plate. On the occlusal surface between the ridges are furrows that show wear, and along the ridges are crests that may be sharp or rounded. On the labial margins of the ridges are cusps, produced as the tooth plate grows from the enamel bone junction, and eventually worn away at the occlusal surface. Around the unworn surface of the enamel, which is covered by gingiva in life, are lines extending from the new cusps. These are particularly noticeable on the labial face of the tooth plate. Like the cusps, they wear away from the occlusal surface.

In all of these species, the lower tooth plates are separated by a wide gutter and are slightly angled to each other, because of the long symphyseal process on the prearticular bone and the way these bones fit together. The gutter accommodates the long tongue during suctorial feeding activities. The upper tooth

Fig. 1.
Map of Australia, showing fossil lungfish localities (●) and the two localities from which specimens of the living lungfish *Neoceratodus forsteri* were collected (★).

plates are almost contiguous in the midline, and lie flat. Matching lungfish tooth plates, from the same fish, can be picked out from a mixed pile of tooth plates because they fit together so closely, with the first ridge of the lower tooth plate fitting within the furrow behind the first ridge of the upper tooth plate. The posterior heel of the lower tooth plate overhangs the posterior part of the upper tooth plate.

Wear characters on lungfish tooth plates

Tooth plates of derived lungfish have a combination of characters, some intrinsic and therefore useful for diagnostic purposes, and some a result of growth and wear (BEMIS 1987; KEMP 1977a,b). The latter group cannot be used for taxonomic purposes, but are useful for an analysis of dental function. This has implications for the understanding of the way the fish lived.

Lungfish of the families Neoceratodontidae and Ceratodontidae can use the jaws in one of two ways. They can move the jaws up and down, producing a crushing action, or they can operate the articulation in a sub-terminal rotation grinding movement. These have different effects on the dentition. Grinding causes rounded furrows to appear on the occlusal surface of the tooth plates, shallow if the food is soft and deep if the food is rough (KEMP 2005: fig. 1A). Depth of the furrows is also affected by the age of the fish. The longer the fish lives the more often it will have chewed or ground its food, and the tooth plates are permanent (KEMP 2001, 2003). Crushing causes facets to form on the occlusal surface between the ridges of the tooth plates (KEMP 2005: fig. 1B). Again, the depth of the furrows depends on how rough the food is, as well as the age of the fish.

Depth of the faceted or rounded furrows is increased if the fish is eating a high proportion of siliceous plant material, or hard shelled invertebrates. If food items are soft and easy to masticate, such as worms and soft shelled invertebrates, the depth of the furrows will be reduced. Heavy wear with deep furrows suggests a harsh diet, and smooth wear with shallow furrows indicates a soft diet (KEMP 2005).

Another form of dental wear, called attrition, occurs when teeth are ground together without food being present (KEMP 2005: fig. 5A,B). This form of wear produces a flat occlusal surface, with striations running along the tooth plate, and sometimes notches at the ends of the ridges A high proportion of tooth plates in a population that show attrition indicates that fish had nothing to eat, or that food is not plentiful. It can also suggest that fish did not feed for reasons related to stress, such as disease, crowding, or competition for suitable resources (KEMP 2005).

Assessing the age of a lungfish

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. Estimates vary widely, from a conservative 30 to 70 years to over a hundred. Captive lungfish, protected and well fed, have been known to survive for many years.

Lungfish may grow rapidly or slowly, depending on environmental conditions. In a rich environment like the Brisbane River, growth is rapid, and size alone is not a reliable guide to the chronological age of the fish (KEMP 1987). Scales of lungfish of known age kept in captivity have more growth lines than they should if the lines are deposited annually, and too few to define growth over a shorter interval (KEMP 2005). The lines vary considerably in thickness, and do not reflect regular increments in the size of the fish.

Tooth plates show growth lines in dentine and enamel, but wear continually from the occlusal surface, so the earlier lines are lost. Skull bones can be thin enough to reveal lines of bone deposition, varying, as do the lines in the scales, in thickness and intensity, but all of the bones have dense areas where the bone was first laid down and no lines are visible in these places (KEMP 1999). Lungfish are known to live for a long time (KEMP 2005, JAMES et al. 2010), although methods for the assessment of the age of a lungfish are either not useful or not completely verified, such as analysis of scales using carbon dating (JAMES et al. 2010). A single adult fish was apparently about 70 years old when tested with this method. Otoliths that show incremental lines are occasionally present in *N. forsteri* (GAULDIE et al. 1986) although the otoliths of this species usually consist of fragments of calcium carbonate without any lines (RETZIUS 1881).

It is possible to make an approximate guess of the ages of specimens in fossil lungfish populations by considering the size of tooth plates, in conjunction with the incidence of certain structural characteristics, such as the development of spur and step wear on the posterior margin of the tooth plates. Normal occlusion between lungfish tooth plates means that a very precise fit develops between the tooth plates. As the fish ages, a spur develops on the lower plate, with a corresponding step on the upper plate (KEMP 2005: fig. 5B). 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, since more reliable methods are not yet available (KEMP 2005).

All of the Mesozoic tooth plates considered in this paper belong to adult fish.

Pseudopathology

Lungfish tooth plates are affected by taphonomic events after the fish dies and the skeletal elements are disarticulated, and these can simulate the effects of disease. This is why they are called pseudopathologies (WELLS 1966). These changes must not be confused with naturally occurring disease conditions or events that happened during the life of the animal, and are usually obvious. Effects of abrasion by water or constant movement against sand or rocks leaves a smooth polished surface in parts of the tooth plate that would not normally experience such effects, as in many of the tooth plates from Lightning Ridge (Fig. 2A). Invasion of the dental or bone structure by plant rootlets or by burrowing organisms can leave irregular tracks in the hard tissues on parts of the tooth plate that would not experience much wear, because they are partially covered by epithelium in life (Fig. 2B). This is present in the large lower tooth plate of †*Metaceratodus wollastoni* from Longreach, in the Winton Formation of central western Queensland.

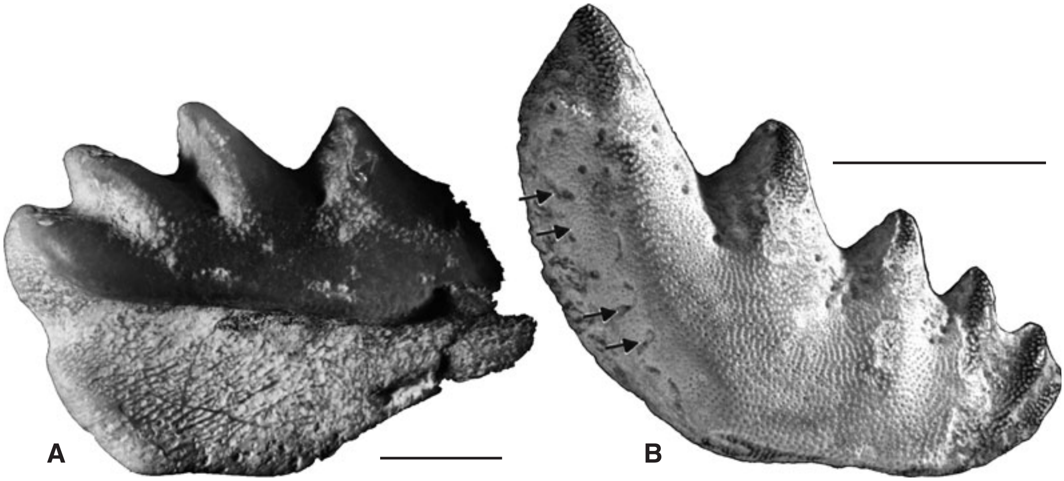


Fig. 2.
Pseudopathology. **A,** Unnatural polish in a specimen of †*Metaceratodus wollastoni* from the Lightning Ridge Opal and Fossil Centre (LRF 588). Scale bar = 1 cm. **B,** Channels bored by small worms on the medial surface of ridge 1 of a lower tooth plate of †*Metaceratodus wollastoni* (MV P 166372, Lake Eyre, South Australia, Winton Formation, "Mid" Cretaceous). Scale bar = 2 cm. Despite the pseudopathology, a carious lesion (arrow) is present in A, and the tooth plate illustrated in B shows soft grinding wear.

Lungfish populations in the Mesozoic

The condition of tooth plates from the Mesozoic deposits contrasts sharply with that of tooth plates from several Cenozoic localities in Australia, where diseased material is common and wear usually extreme (KEMP 2003, 2005). These fossil species had a dentition, and jaw architecture, similar to those of the living *Neoceratodus 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. All of the fossil localities had different characteristics, and each one sheds light on the plight of living lungfish. No fossil locality in Australia is exactly like the Brisbane River or Enoggera Reservoir in recent times, but certain comparisons can be made.

Mesozoic deposits in Australia often include significant numbers of fossil lungfish tooth plates, but preservation, on the surface or as opalised casts, is not conducive to an analysis of wear. The large numbers of small tooth plates, referred to †*Ptychoceratodus phillipsi*, from the early Triassic Arcadia Formation of central Queensland (KEMP 1996) are severely worn by water and other environmental influences, and unfortunately reveal little of conditions in the environment in which they lived, apart from the possible presence of a fast flowing river. Material from the Blina Shale of Western Australia, also Triassic, is poorly preserved in coarse grained sandstone, and not useful for analysis of dental wear and pathologies (COSGRIFF 1967). There are other Triassic deposits in Australia that have lungfish, but most have one specimen or only a few of each species (WOODWARD 1906a, WADE 1935, WALDMAN 1973, DZEIWA 1980, RITCHIE 1981, KEMP 1994). Following current dating of Mesozoic deposits in Australia, Jurassic material is entirely absent (WOODWARD 1906b).

Abrasion of the tooth plates, that is using the tooth plates while food is present, has specific effects on the permanent dentition of a lungfish. Sub-terminal rotational grinding movements of the tooth plates while feeding results in the formation of shallow furrows on the occlusal surface between the ridges, and rounded ridge crests. Furrows are not usually incised as far as the mediolingual margin. Depth of the furrows will depend in part on the age of the fish, and on the nature of the food, with harsher items resulting in greater wear. If the jaws are used to crush food, ridge crests will be sharp, not rounded, furrows will show a facet, and will be incised to the mediolingual margin of the tooth plate. If no food is present while the fish moves the jaws, the tooth plate will have a flat polished surface without furrows or ridge crests. This is characteristic of attrition. Most of the Mesozoic tooth plates examined, that are appropriately preserved for analysis, show shallow furrows that are not incised as far as the mediolingual margin. This suggests a diet

Fig. 3.
A large tooth plate of †*Metaceratodus wollastoni* from the "Mid" Cretaceous Winton Formation in Queensland (QM F 12074). Wear is smooth and there are no pathologies on this specimen. Scale bar = 3 cm.

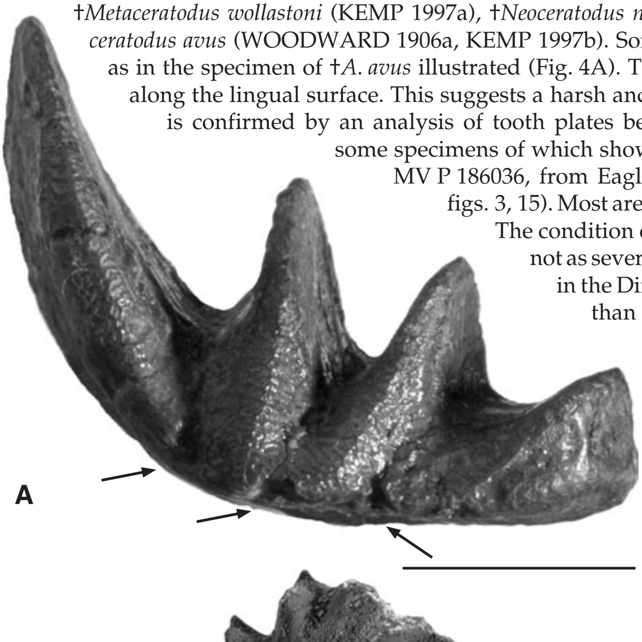
of soft food that was easy to chew. One, the specimen of †*A. avus* illustrated in Fig. 4A, shows deep rounded furrows reaching the mediolingual face, suggestive of a harsher diet. None show attrition.

Cretaceous deposits in Queensland are more useful, and contain reasonable numbers of tooth plates with attached bones (KEMP 1997a,b). When the tooth plates are preserved in rock and not abraded by lying exposed on the surface for many years, it is possible to make a reasonable assessment of their condition.

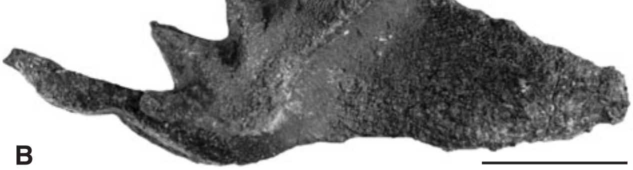
Lungfish tooth plates from some of the localities within the Winton Formation are unaltered and not damaged during preservation (Fig. 3). Few of these tooth plates show any evidence of disease, and wear is smooth. This suggests that they ate soft food, and that the environment in which they lived was clean. The tooth plates from this deposit are often large, suggesting a long life untroubled by problems of overcrowding or of getting enough to eat.

Fossils of an earlier age, from Dinosaur Cove in Victoria, include several species of lungfish, †*Metaceratodus wollastoni* (KEMP 1997a), †*Neoceratodus nargun* (KEMP 1983, 1997b) and †*Archaeoceratodus avus* (WOODWARD 1906a, KEMP 1997b). Some show signs of heavy wear during life, as in the specimen of †*A. avus* illustrated (Fig. 4A). This tooth plate has several carious lesions along the lingual surface. This suggests a harsh and dirty environment and rough food. This is confirmed by an analysis of tooth plates belonging to a second species, †*N. nargun*, some specimens of which show heavy wear and carious lesions, such as MV P 186036, from Eagle's Nest Rock, in Victoria (KEMP 1997b: figs. 3, 15). Most are smoothly worn and not diseased (Fig. 4B). The condition of †*M. wollastoni* tooth plates is similar but not as severe as in the other two species. Environments in the Dinosaur Cove deposits were less favourable than the habitats offered by the Winton Formation in Queensland. However, none of the tooth plates shows any of the disease conditions so common in lungfish from Tertiary environments.

Lungfish tooth plates are common in opal bearing deposits of eastern and southern Australia, and at least two species are represented, †*Metaceratodus*



A



B

◁ **Fig 4.**
Two tooth plates from the Early Cretaceous of Victoria. **A,** †*Archaeoceratodus avus* (MV P 186138) showing heavy wear and some caries on the mediolingual face. **B,** †*Neoceratodus nargun* (MV P 186401) showing smooth wear. Scale bars A = 34 cm and B = 2 cm.

Fig 5.
Two tooth plates from the Early Cretaceous Griman Creek Formation, Lightning Ridge area, Grawan Field, New South Wales. **A,** †*Ceratodus diutinus*, with smooth wear and no pathologies (AM F 75220), and (**B**) †*Metaceratodus wollastoni* with a carious lesion on the mediolingual face (LRF 1214). Scale bar = 2 cm.

wollastoni and †*Ceratodus diutinus* (KEMP 1993). The living Australian lungfish may also be present in these places (KEMP & MOLNAR 1981). Unfortunately for an analysis of palaeopathology, these fossils are pseudomorphs, preserved as natural casts. In addition, they show a degree of post mortem polish that suggests they were abraded in water before preservation, although the palaeoenvironment is generally described as having stagnant or slow moving water, which is likely to include large numbers of pathogenic bacteria. Despite this, they appear to be healthy (Fig. 5A) with only a few instances of caries (Fig. 5B).

Discussion

Adult lungfish are able to adjust to life in many diverse environments, as in the various Cenozoic localities, and in the rivers and wetlands of southeast Queensland now. Some of these may not be completely suitable for lungfish and environments may lack suitable food, or spawning sites and places for young fish may be absent. Steep banks and fluctuating water levels in spring mean that submerged aquatic plants do not grow where they are needed, and food items are less plentiful (KEMP 1995, 2011). Two factors cause the water levels in Australian lakes, rivers and reservoirs to fluctuate, one applying equally well to fossil localities and to present day environments, and the other a result of human interference with natural sites. Rainfall is not constant, and Australia is affected by periodic severe droughts and huge floods (Australian Bureau of Meteorology Records). Fossil localities were also affected by such fluctuations, at least in parts of central Australia (CALLAN & TEDFORD 1972). At the present time, rivers, lakes and particularly reservoirs are affected by water use for agriculture, industry and domestic purposes, especially in spring when crops require irrigation and fish are trying to spawn. Other factors affecting lungfish populations include overcrowding and competition for available food, or poor water quality (KEMP 2005).

Oral secretions help to preserve mammalian teeth because they contain large concentrations of phosphates, and water does not continually wash the secretion away. This does not operate in the lungfish oral cavity, which is confluent with the water of the reservoir or river because water enters the mouth continuously to allow for a respiratory current over the gills. This means that 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, and if the surrounding water is acidic, the tooth plates may be damaged (KEMP 2005). The water of the Brisbane River is neutral (pH 7.4 to 7.8), and damage on the tooth plates is limited to small carious lesions, usually on the mediolingual surface (KEMP 2005: fig. 5B). In Enoggera Reservoir, the water is acidic (pH 5 to 6). Tooth plates from Enoggera Reservoir show considerable damage, and the erosion and caries exposes the pulp cavity in most of the fish from this reservoir (KEMP 2005: fig. 5A).

A species of nematode worm may invade the bones and teeth of the lungfish, forcing the bone and dentine grow around them in little burrows with an opening to the soft tissue around the bone or tooth plate. This particular parasite causes deformation of the tooth and affects the ability of the fish to feed. It is rare, but when it occurs it is harmful (KEMP 2005: figs. 9, 10). The presence of the worms, and the distortion of the hard tissues, results in severe malocclusion. It is found in living *Neoceratodus forsteri* from the Brisbane River, and in a related species from mid-Tertiary deposits in central Australia (KEMP 2005). None of the Mesozoic tooth plates examined for this project show the condition.

Occasionally, in old lungfish with broken tooth plates, overgrowth, or hyperplasia, of dental tissue, resulting in malocclusion and feeding difficulties, becomes a serious problem. The condition is found in a number of lungfish populations, even in a specimen of *Ceratodus latissimus*, a Triassic lungfish from Aust Cliff, near Bristol in England (KEMP 2001: fig. 11A). It is a consequence of the permanent nature of the tooth plates, and of their continuous growth. As lungfish age, the tooth plates can become diseased, and parts of one tooth plate may break away (KEMP 2001: figs. 12, 13). This means that the opposing tooth plate cannot wear effectively, and continues to grow until it damages the soft tissues of the opposing jaw. Although the growth of the dental tissue is benign, consequences for the fish are serious. Damaged soft tissues may become infected, and the jaws do not close properly, nor can the fish chew its food effectively (KEMP 2001, 2003). Osteopenia, another consequence of the long life of lungfish, can be severe in old specimens, such as most of the material collected from Enoggera Reservoir and a few specimens from the Brisbane River (KEMP 2003: fig. 8C,D) Bone becomes thin and fragile, although the tooth plates are not affected. The condition occurs in Cenozoic fossils as well, particularly in specimens from the Namba and Katapiri Formations.

Dental decay, or caries, is a common pathology among Tertiary populations of lungfish, and is even found in Devonian lungfish of the Gogo Formation in Western Australia (KEMP 2003: fig. 2). This condition may develop as a result of mechanical injury from harsh items in the diet, trapping of damaging items between the teeth and the gums, or exposure to stagnant water containing infective organisms. In a few specimens, caries may become severe enough to expose the pulp cavity and cause an abscess in the pulp cavity below the tooth plate, or actually in the dental tissue itself. Because the denteons that run through the hard tissue contain blood vessels, pathogenic bacteria can enter the tooth plate and cause infections (KEMP 1991, 2003). 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. The tooth plates of lungfish are surrounded by oral epithelium which invests the growing regions of the tooth plate close to the dental/bone junction. Injury to this area by broken tooth plates is not only possible, it is common. However Mesozoic tooth plates are free of any evidence of breakage of the dental tissue, and of infection of the soft tissues.

Dental caries is quite common in Devonian lungfish, such as †*Chirodipterus australis* and †*Pillararhynchus longi* from the Gogo Formation of Western Australia (KEMP 2003: fig 2). Although they are free of severe wear, and most pathological conditions, many of the tooth plates from this deposit show dental caries in the posterior and medial surface of the tooth plate that would have been covered by the oral epithelium in life. These fish probably had an easy life, and the caries merely reflects their age.

There are large numbers of tooth plates of the Triassic †*Ceratodus latissimus*, particularly from Aust Cliff in southern England, but these were healthy, with no dental caries (AGASSIZ 1833–43: 131). Only one specimen has overgrowth of one ridge (KEMP 2001: fig.11A). The teeth from this deposit are heavily worn, but the occlusal surfaces are smooth, so food was not abrasive, and the fish must have lived in a good environment.

Information from Mesozoic populations in Australia is unfortunately confined to the Cretaceous deposits of eastern Australia, because of unsuitable preservation or lack of material. Nevertheless, the general health of lungfish populations in the Cretaceous was similar to that of earlier geological epochs, with little disease and wear indicative of reasonable environments and adequate food, with a few exceptions such as †*Archaeoceratodus avus* from Dinosaur Cove.

Cenozoic lungfish present a different picture (KEMP 2005). Some, such as the lungfish of the Wipajiri Formation, resemble the present day population of the Brisbane River. These places all had large numbers of adults and juveniles, and wear on the tooth plates was smooth. They were however much healthier and the tooth plates show little damage and disease. Others, like material from the Namba and Katapiri Formations, conform in many characteristics to the recently extinct population in Enoggera Reservoir. Large fish only are found here, bones show severe osteoporosis, and the tooth plates have many age or environmentally related conditions, such as heavy crushing wear, and attrition. Like the new weirs and reservoirs built over the Burnett and Brisbane Rivers, these deposits are based on localities that had fluctuating water levels (CALLAN & TEDFORD 1976), and no suitable habitat for embryos and young fish could have become permanently established (KEMP 1995, 2011).

Other populations, such as the fish of the Etadunna Formation, may have been sustained by active recruitment, but the dentition shows evidence of harsh food. The lungfish of the Carl Creek Limestones at Riversleigh in North Queensland, or the Camfield Beds in the Northern Territory, are quite different from all the other fossil populations. They lived in a poor and overcrowded environment with little food. Fish in these places are unusually small, although they were actively spawning and young fish were recruited into the adult population (KEMP 2005).

The initial study of wear and disease in the lungfish dentition from the Brisbane River and from Enoggera Reservoir was conducted on fish collected around 1980. At that time, the condition of the dentition of the lungfish from lakes and rivers in Queensland was poor, worse than in any fossil deposit. The only saving grace was that the Brisbane River had some juvenile lungfish, and disease conditions, while commoner than they were among the fossils, were not likely to overwhelm the fish (KEMP 2005). 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 only fish found with nematode infection inside the tooth plates and bones comes from this locality. This situation has changed recently, and spawning events in many parts of the Brisbane River system have ceased (KEMP 2011).

Brisbane River fish had smoothly worn tooth plates with few pathologies, suggesting that most of the food consumed was soft and easy to chew. Acid related damage of the tooth plates was unusual, and the only instance of attrition, resulting from grinding of the teeth without food present, came from the single fish affected by parasitic infection of the teeth and bones. This would have resulted in malocclusion (KEMP 2003). Most of the dental pathologies that were found were related to trauma, causing breakage of the tooth tissue (KEMP 2001). Lungfish are unable to repair breaks in their dentition (KEMP 2001).

Material collected from Enoggera Reservoir, in 1981, some years after the removal of the water hyacinth caused loss of recruitment in the reservoir, consists of large tooth plates only. This confirms that successful spawning and recruitment had ceased in Enoggera Reservoir. All of the specimens show heavy occlusal wear, and crushing movements of the jaws indicating that the diet available in this habitat was limited. The number of tooth plates with signs of attrition is higher among Enoggera fish than it is among Brisbane River fish. As in the solitary Brisbane River fish with attrition, affected tooth plates have other disease problems as well, such as dental decay and overgrowth of one tooth plate following breakage of the matching tooth plate. Removal of dental material from the tooth plates as a result of the acid environment is exceptionally high. 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. Osteoporosis, as a result of age or of a poor diet, is found in most of the material from this reservoir collected at that time. The isolated environment of Enoggera Reservoir may have allowed the fish to survive to a great age, but there was little food and acid, stagnant water (KEMP 2005). The question of the health of Enoggera Reservoir fish is now academic, as the population is extinct.

Despite the fact that lungfish are tough and adaptable, environments impose significant constraints on them, especially when they have been altered by human interference. Water quality in the Mesozoic must have been reasonable, and significantly poorer in the Cenozoic, partly because of increasing aridity in Australian environments. The situation in lungfish habitats is now much worse (KEMP 2011), with the creation of new water impoundments that have changed lungfish environments completely. The future of the last surviving lungfish in Australia is now in doubt.

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