The Biology and Systematics of Frogs

Contributions submitted to The University of Adelaide

by

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FOR THE DEGREE OF

DOCTOR OF SCIENCE

DECLARATION

I declare that none of the publications submitted here has been submitted for a degree at this or any other university.

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30th June 2002

I give consent to this copy of my thesis, when deposited in the University Library, being made available for loan and photocopying.

Michael J.Tyler

SUMMARY

The published work submitted for the degree falls into the following categories:

Biology
Systematics of New Guinea taxa
Systematics of Australian taxa
Studies of fossil taxa

To put the work in perspective the extent of previous knowledge of the frogs of New Guinea and Australia is summarised, revealing the inadequate state of the information available when I commenced my studies.

The biological information can be mainly described as being reproductive biology. By far the most significant, and one that attracted considerable attention from the world's media, was the discovery of gastric brooding in the Queensland frog *Rheobatrachus silus*. Because there was only limited knowledge of amphibian digestion it was necessary to undertake fundamental research to establish the nature of gastric secretion and peptide production, and to determine gastric emptying times and intestinal transit. It was finally demonstrated that the inhibitor of gastric secretion was prostaglandin E_2 secreted by the oviducts investing the eggs prior to their expulsion and fertilisation.

Field studies on the biology of other species established for the first time details of development, advertisement calls, etc. Much of the biological data was documented in the course of the first wet season investigations of the fauna of the Kimberley Division of northwest Western Australia, and the northern portion of the Northern Territory. These led to the considerable extension of the known fauna. Twenty-five species were added to the list of those known to inhabit the Kimberley, of which 17 were new to science. Similarly in the Northern Territory the known fauna was tripled from 14 species to 44 of which 14 were new to science.

In the case of New Guinea slightly more than one-third of the presently known species had been described when I commenced fieldwork there in 1960. I concentrated upon the numerous species then referred to the genus *Hyla* (now *Litoria*), transferring two species to the genera *Oreophryne* and *Nyctimystes* respectively. The former was from New Britain and represented the first record of the family Microhylidae from that island. The final result was the production in 1968 of a 200-page monograph.

In 1974 I reported the first frog fossil from Australia and in 1976 erected the new genus *Australobatrachus* for it and named the species *A. ilius*. This work was based on a comparative study of ilia. I have since identified numerous extant species from Pleistocene and Holocene cave deposits, and have named numerous new species from the Oligo-Miocene deposits at Riversleigh Station in northwest Queensland. The predominant species at Riversleigh is *Lechriodus intergerivus* which is notable historically and geographically, because the site bridges to some extent the disjunct distribution of the modern species between New Guinea and southeast Queensland.

Ninety papers and chapters are submitted. Of this total 81 are papers published in 46 journals of which 32 are overseas publications.

THE BIOLOGY AND SYSTEMATICS OF FROGS

Historical Background

A study of the biology and systematics of any group of organisms is likely to include a wide variety of approaches and experimental techniques. Almost every year the range of techniques available to the investigator increases, and multi-disciplinary studies become more popular. It follows that the understanding of the biology and systematics of frogs, on an historical scale, needs to take into account the technological limitations imposed upon contributors at any point in time. Available today is modern binocular dissecting microscope fitted with sub-stage and fibre optic lighting. H.W. Parker in the preparation of a monumental 1936 monograph.used the monocular microscope with a limited depth of focus and 60 watt globe.

Concepts of species have been modified whilst the technological changes have taken place. The big change has been recognition that pre-mating isolating mechanisms exist, and that one of them (advertisement calls) is as intrinsic a characteristic as the morphology of a species.

In the account that follows I describe former and current studies of the biology and systematics of frogs. I have been particularly concerned with the fauna of Australia and New Guinea, but have also studied and published papers on species from other continents and islands such as Africa, the Seychelles and Jamaica. However the historical overview will be confined to Australia and New Guinea.

The principal purpose of the account is to provide an understanding of the state of knowledge when I commenced my studies, so permitting the extent of my work, and the nature of its significance. to be evaluated.

In the case of the island of New Guinea, comprising the eastern half of Papua New Guinea, and the western half of Indonesian West Irian or Irian Jaya, the first species to be described was *Rana papua* by Lesson in 1830. The accumulation of further specimens leading to their eventual description was principally through the efforts of adventurers, or collectors funded by or based at European museums. Thus Luigi D'Albertis collected animals and anthropological specimens along the Fly River and on the Vogelkop Peninsula in 1872. His collections were deposited in the Museo Civico di Storia Naturale at Genoa where they were described by W. Peters and G. Doria in 1878. The entomologist Evelyn Cheesman of the British Museum of Natural History collected frogs in the course of her expeditions to remote areas. These are but two examples and they have in common the opportunistic nature of the accumulation of frog specimens: they were not the principal objective of the collectors.

Description of New Guinea taxa in the nineteenth century was dominated by the work of the Curator of Reptiles and Amphibians at the British Museum: George Albert Boulenger. He assembled a catalogue of the Museum's collections and personally described numerous species and genera from the island that are still considered valid.

For almost fifty years there were no further syntheses of the New Guinea frogs. Then, in 1923, P.N.Van Kampen produced a volume on the Amphibia of the "Indo-Australian Archipelago." In it he provided checklists of the islands and that for New Guinea included 85 species. Of the various families represented in that work, Parker's 1936 monograph on the Microhylidae of the world updated those species, and in 1940 he presented a treatment of the 'Australasian' (Australia plus New Guinea) species of the Myobatrachidae (as Leptodactylidae). The American entomologist P.J. Darlington took advantage of a Second World War posting to New Guinea. He collected insects, reptiles and frogs and forwarded the frogs to Arthur Loveridge at the Museum of Comparative Zoology at Harvard University. The new material prompted Loveridge to produce in 1948 an annotated catalogue of the Harvard and United States National Museum collections of New Guinea frogs.

Finally R.G. Zweifel of the American Museum of Natural History in 1958 produced a review of the hylid genus *Nyctimystes* which, at that time, was only known from New Guinea.

The above monographic works were the only ones available when I commenced my study of New Guinea frogs in 1960. Only a fraction of the frog fauna had been discovered, and the speciose genus *Litoria* (then referred to as a synonym of *Hyla*) was conspicuous in its lack of a taxonomic revision. With the sole exception of R.G. Zweifel no one was studying the frogs of New Guinea and the overall picture was chaotic.

The situation in Australia was somewhat better in that the known fauna was more efficiently documented. Early descriptions followed the pattern in New Guinea whereby specimens collected by expeditions of discovery were taken to Europe, and there described by herpetologists in museums. The principal contributors to this process were G.A. Boulenger in London and A.M.C. Dumeril and G. Bibron in Paris. Boulenger described genera and species from Australia, and in his catalogue of 1878 includes numerous new species.

The pattern of development of knowledge of the frogs, and other elements of the fauna, followed the colonial pattern whereby early settlers sent specimens overseas to taxonomists who described the new species. Thus the second person appointed as Director of the Botanic Gardens in Adelaide, sent collections to W.C.H. Peters in Berlin, leading to the publication of descriptions there in 1863. The few contributors based in Australia tended to be generalists and it was not until the early part of the twentieth century that a herpetologist with considerable expertise could be identified. That person was Dene B. Fry who as a young trainee produced some papers with illustrations of exceptional quality. He enlisted in the First World War and was killed in action in 1914. His tragic death arrested the description of the Australian frog fauna for several decades.

Few papers of any magnitude were published until A. Loveridge of Harvard University produced in 1935 a catalogue of Australian frogs in the collections there, followed in 1940 by H.W. Parker's review of the Myobatrachidae. Biological information was almost non-existent until A.R. Main of The University of Western Australia, together with his post-graduate students addressed the fauna of southern Western Australia and, later, the southeast of the continent. Main concentrated upon the nature of pre-mating isolating mechanisms in accordance with the biological concepts of species expounded by Ernst Mayr. Contemporaneously with Main's activities was the visit from 1952-1953 of J.A. Moore whose major revisionary work was finally published in 1961. Although focussed upon the fauna of eastern New South Wales, Moore investigated biogeographic trends throughout the continent, summarised the literature and nomenclature, and recognised 91 species.

One of those whose assistance Moore acknowledged was S.J. Copland who in 1957 revised the tree frogs then referred to the genus *Hyla* (now *Litoria* and *Nyctimystes*). Copland recognised 44 species and sub-species. It was in this concept of sub-species that Copland and Moore differed: Copland attributing weight to morphological differences that Moore was unable to recognise as being of any consequence. In retrospect it should be noted that Copland's distinctions were more often correct than inaccurate: of 19 sub-species recognised by him 13 have been shown to be good species, whilst Moore admitted to being a "lumper".

Personal Involvement

(a) New Guinea

In 1960 I spent six months in New Guinea, firstly working as Manager of a Bird of Paradise farm and coffee plantation, and subsequently studying frogs on a fulltime basis. My studies centred on the Waghi Valley at 2000 metres, from which I ventured into the adjacent moss forest and later crossed the Waghi-Sepik Divide, continuing to the headwaters of the Sepik River. I transported my collection to London and was awarded a grant to study it at the British Museum (Natural History). In 1967 I visited the island of New Britain and spent six weeks collecting. In both cases I was the first person to visit the islands specifically to collect frogs.

(b) Australia

I settled in Australia in 1961 and worked as a technician at the University of Adelaide. In 1962 I was appointed Honorary Associate in Herpetology at the South Australian Museum. At that time the museum collection of amphibians comprised about one dozen jars of poorly preserved specimens. I set about collecting local species and exchanging some of them with museums interstate and overseas, to improve the representation of Australian and foreign species. Particular attention was focussed upon representatives of families found in South Australia.

Being fully employed and able to undertake research only in my spare time, the nature of my activities had to be limited to those that could be pursued on a part-time basis. Behavioural studies were largely impossible and I found a need for taxonomic studies of Australia and New Guinea. In Australia there was a particular need for studies on the diversity of the fauna of the north which was largely unknown.

In 1974 I was awarded an M.Sc. degree. My thesis was concerned with the superficial mandibular musculature and vocal sac structure of diverse frogs representing nine families. I was subsequently appointed Lecturer in the Department of Zoology, and in the following year commenced fieldwork in the north of the Northern Territory and in the Kimberley Division of northwestern Western Australia. These studies have continued to the present day.

In the following paragraphs I provide details of my contributions to the Biology and Systematics of frogs, with particular emphasis upon those concerning the fauna of Australia and New Guinea.

CONTRIBUTIONS TO BIOLOGY

Numbers in parenthesis correspond with those on submitted papers

Monographs are enclosed in the accompanying box

As indicated earlier, my initial studies in herpetology were undertaken on a part-time basis, so that behavioural topics entailing regular or otherwise committed observations were simply not possible. It is for that reason that only two papers on biological topics were produced prior to my appointment to my first academic position in 1974. Of those two, one is particularly noteworthy **(2)**.

Whilst undertaking fieldwork in the New Guinea highlands in 1960 I found frogs that were extremely lethargic and exhibited large, subcutaneous bulging. Dissection revealed the presence of leeches. In some other frogs leeches were found within the peritoneal cavity.

Very few taxonomists studied leeches but I collaborated with K. H. Mann of Reading University who identified the specimens as a *Philaemon* species. Subsequently L. R. Richardson revised the taxonomy of land leeches and named it *Tylerbdella* in my honour. At a later stage I found that the leeches enter and leave the host via lesions in the wall of the cloaca, but the importance of the find is that it may possibly provide an insight into the evolution of endoparasitism.

In 1974 I received a phone call from G.J. Ingram of Brisbane. He told me that a captive specimen of *Rheobatrachus silus* had 'given birth' to a juvenile frog – the juvenile had been seen for the first time one morning swimming with the adult. My interpretation of this phenomenon was that it paralleled the situation in the Chilean frog *Rhinoderma darwini*, in which the male carries its young in the vocal sac beneath the tongue. However when I eventually had the opportunity to dissect the throat of the adult I found that it lacked a vocal sac. I opened the abdomen, found that it was a female and that the body cavity was dominated by a large, dilated stomach.

We wrote a brief communication reporting the phenomenon of gastric brooding which was unique in The Animal Kingdom and submitted it to 'Nature', who rejected it because it "was not of sufficient general interest to merit publication." The manuscript was therefore submitted to 'Science' that published it without alteration **(3).**

Publication of this paper was widely cited by the media and created a furore in the zoological community. Approximately one half considered the finding extremely exciting, whereas the other half refused to believe the observations which they stated were totally impossible. The vehemence of this criticism encouraged me to provide graphic proof. This was not obtained until 1981 when photographs were taken of the process of oral birth **(7).**

The gastroenterological implications of the suppression of gastric secretion were considerable. Early studies of the histological changes in the stomach **(9)** demonstrated that the acid-producing oxyntic cells had virtually disappeared. It was interpreted that if a similar response could be induced in human gastric ulcer patients, a cure might result from providing an acid-free period in which healing could take place. It was shown that the structure of the female reproductive tract was no different from the general plan in frogs **(10)**, and that the structural changes were entirely attributable to physiological behaviour.

To investigate the method of suppression of gastric secretion, and to identify any compound responsible for that suppression, I assembled a multi-disciplinary team. This group eventually demonstrated that the inhibitor was Prostaglandin E_2 (PGE_2) and that this compound occurred naturally in the jelly coating of mucopolysaccharides surrounding the ovum **(13)**. It was noted that PGE_2 was invested within the egg coating as the ovum passed down the oviducts, and that PGE_2 could be detected in oviducal homogenates of all species examined: the inhibitor was not unique to *R. silus*.

Knowledge of gastric secretion and associated physiology of frogs was very poorly known. I therefore developed a technique for continuous monitoring of pH involving the passing of a microelectrode through the skin and into the stomach via the eustachian tube and buccal cavity **(14)**. Using minced meat labelled with technicium we also examined gastric emptying and intestinal transit **(15)** and the role of pepsin **(18)**. These studies on gastric physiology were all undertaken on the pest species *Bufo marinus* because the population of *R. silus* was small. The evolutionary conservatism of the frog alimentary canal indicated that it was reasonable to extrapolate responses from one species to another.

In 1981 the population of *R. silus* disappeared for reasons that are unclear; it is now considered to be extinct. However the discovery of a new species (*R. vitellinus*) provided the opportunity to examine gastric brooding. To our surprise we found no evidence of suppression of oxyntic cells in the stomach wall, and concluded that mucus provided cytoprotection **(17)**. *Rheobatrachus vitellinus* now has disappeared and is also considered extinct, but we are left with the conclusion that the two species used different mechanisms to create a womb from a stomach.

Other biological observations leading to publications were made more on an opportunistic basis than as part of a pre-determined plan, beyond that of clarifying the nature and diversity of the fauna. An example was the chance observation that the method of foam nest production in limnodynastine myobatrachids was stereotyped, and that it was unlike the method reported in the literature of the female whipping up the foam with her legs. Instead the female trapped air bubbles with her hands and threw them into the emerging eggs and jelly. The hand movements were regular in number **(4)**. The failure of individuals of *Limnodynastes tasmaniensis* in the southeast of South Australia to produce foam nests, was found to be due to uncoordinated movements of the hands by the female **(24)**.

In 1979, acting jointly with A.A. Martin and M. Davies, a publication was produced describing the new genus and species *Megistolotis lignarius*, and providing information on its reproductive biology **(5)**. It can be claimed that this paper set a new standard of quality and detail of presentation. It followed the opportunity to explore the frog fauna of the Kimberley. Arising from this work was a study of the biology, morphology and distribution of *Cyclorana cryptotis* **(11)** that I had described from the Northern Territory with A.A. Martin in 1977.

When the Fox Report recommended that uranium mining be permitted in Australia there was the qualification that biological monitoring techniques would need to be developed, to ensure that there was no impact on the biota of the floodplains of the Northern Territory. During a visit to the area that was to become the mine site of Jabiru, I collected spawn from water that was uncontaminated and also from areas where water drained from a uranium body, and was contaminated with the daughter product Radon. When the respective tadpoles were reared to metamorphosis, it was found that significant levels of skeletal abnormalities of limbs were associated with Radon contamination. Studies of these phenomena were documented in unpublished government reports, but the

same techniques were applied at Olympic Dam in South Australia to monitor the impact of uranium over a period of several years **(20, 22)**. Because a considerable proportion of the frog fauna at Jabiru was unknown when the studies commenced, a benefit of the studies was the opportunity to explore its reproductive biology **(12)**.

For many years I have had a fruitful collaboration with my colleague Professor J.A. Bowie, exploring the peptide profiles of the skin. More than thirty publications have resulted but, because my role in the majority often has been confined to obtaining and extracting secretions, I have not included them in this submission. Exceptions are the development and characterisation of a method of electrical stimulation to extract glandular secretions, in which I played the major role **(21)**. I also contributed to studies of the impact of secretions of *Litoria caerulea* upon flies **(27)** following demonstration that that species has a mosquito repellent in its skin. Other studies ranged from the demonstration that host defence peptides occurred in tadpoles **(28)**, that male *L. splendida* had an aquatic sex pheromone that attracts females **(30**: the first record for any frog species), and that divergence in the peptide profiles of a single species reflects evolutionary trends **(31)**.

CONTRIBUTIONS TO SYSTEMATICS

(a) Extant species of New Guinea and New Britain

Following my visit to New Guinea in 1960 I commenced a revision of the members of the genus *Hyla* from a variety of sources. Some museums sent me unidentified specimens in their collections, hence the American Museum of Natural History in New York sent a species which I later described and named *Hyla multiplica* **(33)**. Progressively I examined type material of poorly known species, resulting in some of them being transferred to other genera. For example the frog *Hyla montana* in Genoa proved to be a *Nyctimystes* species **(35)** as did *Hyla obsoleta* in Stockholm **(36)**. The natural history museum at Leiden in the Netherlands forwarded over 5000 unknown specimens and I completed the generic revision in 1967. The Netherlands government provided a grant and the monograph was published in 1968 **(40)**.

R.N.H. Bulmer, Professor of Anthropology at the University of Papua New Guinea, invited me to collaborate in a project comparing the classification used by the New Guinea highlands Karam people with that of the western scientist. This work was published in 1968 **(41)**. We found limited congruence because the nomenclature of the Karam was related to the utilitarian benefit of a 'kind' (which we termed 'specieme'). No benefit or the existence of a taboo, tended to result in what we considered species of different genera being lumped together under one name. Polymorphic species were provided with names for each morph.

In conjunction with J.I. Menzies I devoted study to fossorial species **(48)** and with M. Davies redefined the increasing number of species being referred to the genus *Nyctimystes* **(55)**. Then in 1982 I worked with R.G. Zweifel in a review of the New Guinea fauna **(60)**.

My interest in New Britain commenced during my review of *Hyla*. When I examined the type of the species *Hyla brachypus* described from material taken near Rabaul, I found that it represented the genus *Oreophryne* of the family Microhylidae. This family was not known to exist east of New Guinea and the finding extended the distribution by almost 400 km. In 1967 I was funded by the South Australian Museum to undertake fieldwork in New Britain. There I found *O. brachypus* plus a second microhylid species since described as *Austrochaperina novaebritanniae* by Zweifel. I also collected four new species of the ranid genus *Platymantis* **(37)**.

(b) Extant species of Australia

My initial studies on the diversity of Australian frogs largely involved testing some of the taxonomic conclusions of Moore (1961). In this case I showed that *Hyla serrata* of Australia was a synonym of *Hyla eucnemis* of New Guinea **(36)** and that *H. latopalmata watjulumensis* of Copland (which Moore considered should be suppressed) was in fact two species: *H. watjulumensis* and a new species which I named *H. coplandi* **(39)**.

Because I was then alone in Australia in undertaking studies on the classification of frogs, I was funded by the Australian Biological Resources Study to visit all major Australian museums and identify or reidentify their collections. I examined the species *Crinia darlingtoni*, the male of which had been shown previously to carry developing young in hip pouches, whereas all other congeners had customary aquatic tadpoles. I considered that this shift in reproductive habit was of such magnitude that it destroyed the concept of a genus as a meaningful evolutionary unit. I therefore removed *darlingtoni* from *Crinia* and erected the genus *Assa* for it **(43)**. All subsequent contributors have supported this interpretation.

In the Western Australian Museum in Perth I located undescribed material which I described as the genus *Arenophrne* and the species *A. rotunda* and *Limnodynastes depressus* **(47)**.

My interests in the phylogenetic relationships of frogs led to substantial revisionary works and to novel approaches. Thus I had as early as 1972, together with R.L. Robinson, demonstrated that the predominance of different catecholamines characterised the two major families of Australian frogs **(42)**. Adrenaline predominated in the Hylidae, and Noradrenaline in the Myobatrachidae. Dopamine was present only in trace amounts. It was the systematic heritage of the taxa that mattered; ecological convergence was of no consequence.

A second example of discovering a new tool for determining phylogenetic relationships was the use of scanning electron micrographs of male nuptial pads **(65)**. The existence of distinct and extremely elaborate surface architecture was demonstrated for the first time.

Within the speciose genus *Litoria* there was evidence of lineages whose members exhibit closer morphological similarity to one another than to members of other lineages. There are various ways in which these associations can be recognised formally; in entomology for example the term sub-genus is used extensively. However in herpetology it is more popular to use a term that recognises the association of the species themselves: "species-group" or "species-complex". I selected the former **(52)** and I anticipate that ultimately each will be shown to be a distinct genus. All that is required is the elucidation of the evidence for their recognition. More recent contributors have argued only about the inclusion or exclusion of particular species within a species-group: the number of groups remains.

The relationship of the Australian hylid frogs to members of the Hylidae of South America has been a contentious issue. Some authors favoured putting this Australian species into a separate and unique family (the Pelodryadidae). My studies favoured the concept of a single family present in both of these southern continents **(51)** and I explored the relationships of the entire herpetofauna in a chapter in a book published in 1979 **(54)**.

As the opportunity arose I continued to examine the superficial mandibular musculature and vocal sac structure of various problematical species. Thus I reported the condition of *Rhinophrynus dorsalis* of Mexico **(46)**, the discoglossid *Bombina bombina* of Poland **(57)**, the sooglossid frogs confined to the Seychelles Islands of the Indian Ocean **(62)**, and the hemiphractine hylid frogs of South America **(66)**. In each case the muscle pattern contributed to an understanding of the relationships of the taxa. One of these was the sooglossid pattern that indicated an affinity to species from Africa, and not to those on the adjacent Asian mainland as some contributors asserted.

Studies on the frog fauna of the Kimberley and Northern Territory continue. Fieldwork which I have led, supplemented by my earlier laboratory-based studies have added 25 species to the known fauna of the Kimberley, being 17 new species and eight species previously only known from other States or the Northern Territory. By far the biggest impact has been upon the genus *Uperoleia* which was thought to comprise only six species, but following our efforts the total was increased to 16 **(58)**. This contribution stimulated a Ph.D. student, Ms M. Davies to examine under my supervision further populations, with the result that the total has increased further to 24 species.

In the case of the impact of my studies on the fauna of the Northern Territory, the results are more dramatic, having tripled the known fauna from 14 to 44. Of the final total 14 were new species and 16 new records. The impact of these fundamental activities cannot be underestimated because they provide a foundation for ecological studies, behavioural or physiological investigations, and are essential for the implementation of conservation management strategies.

(c) Extinct species

In the 1960s and early 1970s I asked geologists and palaeontologists why no frog fossils had been found in Australia. Most agreed that it was a puzzle and suggested that conditions simply were not suitable for fossilisation of such delicate bones. Then in early 1974 I identified a fragmented portion of a frog ilium from a deposit that had been excavated at Lake Palankarinna in the far north of South Australia. I reported it in 'Nature' as the first frog fossil from Australia **(70)**. Description took more than one year because I had to prepare a comparative collection of ilia from all families, genera and species-groups of Australian specimens, principally in the South Australian Museum.

As a result of this survey I was able to recognise features that characterised extant genera, such as the presence of dorsal flanges to the ilial shaft of *Lechriodus, Mixophyes* and *Rana* and, through the literature I was able to establish a nomenclature for the anatomical features of the pelvis. It became evident that the ilium from the assumed Miocene of Lake Palankarinna represented a new genus and species. This I named *Australobatrachus ilius* **(71)**.

These observations prompted me to search for further material amongst the debris left from Lake Palankarinna (after marsupials had been removed). I sorted through approximately 200 kg of grit and recovered six more ilial fragments which I reported. Included was a new species which I named *Limnodynastes archeri* **(73)**. At the same time I examined boxes of sievings from caves at Naracoorte in South Australia through the courtesy of R. T. Wells. In that material I located 166 ilia. The age was late Pleistocene and five species were represented, all of which were extant in the Naracoorte area **(72)**. Later studies located more Pleistocene or Holocene material from other caves in the southeast of South Australia: Tantanoola Cave **(82)** and Henschke's Cave **(87)**. I also examined material of similar age from Skull Cave and Devil's Lair at Cape Naturaliste in the southwest of Western Australia.

The overall results from the Holocene and Pleistocene sites differed substantially from the fossil record of marsupials being recovered in the same deposits. Whereas the marsupials included numerous extinct species and genera, the frogs all represented modern species that persisted in the areas near the sites. The simplest interpretation was that the frogs were extremely conservative in an evolutionary sense.

In the 1980s a major focus of Australian palaeontology was the studies of rich oligo-miocene deposits on Riversleigh Station in northwest Queensland. I was extremely fortunate to be invited by Professor Michael Archer (who was the chief investigator) to work on frogs there. As with all other material located to date, the fossilised bones were disarticulated. However almost all of the ilia recovered were in perfect condition and the majority represented an undescribed species of *Lechriodus* which I named *L. intergerivus* **(75)**.

The presence of this genus in such numbers provided an explanation to an apparent anomaly in the speciation and biogeography of the genus. *Lechriodus* is the only myobatrachid genus in which there are more species in New Guinea than in Australia. The three New Guinea species are widely distributed and there is then a vast geographic gap to the single Australian species *L. fletcheri* which extends no further north than the extreme southeast of Queensland. Clearly the genus was once more widely distributed in Australia, and it has been demonstrated that the dominance of *L. intergerivus* in the overall frog fauna diminished progressively through the Oligocene and Miocene **(77)**. More recently *Lechriodus casca* was described from an Eocene site at Murgon north of Brisbane, so partly bridging the gap between modern *L. fletcheri* and fossil *L. intergerivus*.

To date I have examined and reported at least two thousand fossils from Riversleigh including *Limnodynastes* **(76)**, *Litoria* **(78)**, *Crinia* **(79)** and *Kyarranus* **(81)**.

Pliocene fossils are rarely encountered in the Riversleigh deposits and elsewhere. From a Plio-Pleistocene site on Floraville Station, northeast of Riversleigh Station, and close to the Gulf of Carpentaria, three species have been recovered: *Cyclorana cultripes*, *C. platycephala* and *Limnodynastes* sp. cf. *L. tasmaniensis*. The extremely distinctive *Cyclorana* ilia have not been recovered at any other site in Australia, and are of special interest because it has been postulated that *Cyclorana* evolved no later than the early Oligocene. Because all members of *Cyclorana* are highly adapted for burrowing, the evolution of the group may have followed the development of seasonal aridity. The fossil evidence suggests a much more recent evolutionary history than has been proposed.

Finally in collaboration with other colleagues I have just described the first frog fossils from New Guinea **(90)**.

JOURNALS IN WHICH SUBMITTED PAPERS WERE PUBLISHED

U.K.	Proc. Zool. Soc. London/J. Zool.	3
	Nature	3
	J. Nat. Hist.	1
	Animal Behaviour	1
	The Lancet	1
	European J. Biochem	1
U.S.A.	American Mus. Novit.	1
	Comp. Gen Pharmacol.	1
	Science	2
	Occ. Pap. Mus. Nat. Hist., Kansas	1
	Herpetologica	3
	Copeia	6
	J. Herpetol.	4
	Gastroenterology	1
	Comp. Biochem. Physiol.	2
	J. Pharmacol. Toxicol.	1
	Herp. Nat. Hist.	1
	J. Morphol.	1
	J. Peptide Res.	1
	Herp. Rev.	1
	Proc. Biol. Soc. Washington	1
GERMANY	Mitt. Zool. Mus. Berlin	2
	Abh. Zool. Mus. Dresden	1
	Zool. Anzeiger	1
HOLLAND	Zool. Verhandelingen, Leiden	1
	Zool. Meded., Amsterdam	1
SWEDEN	Arkiv. Zool., Stockholm	1
BELGIUM	Bull. Environ. Contam. Toxicol.	1
	Hydrobiologia	1
RUSSIA	Russian J. Herpetol.	1
POLAND	Acta Biol., Cracov.	1

NEW ZEALAND	J. Polynesian Soc.	1
AUSTRALIA	Proc. R. Soc., Qld.	1
	Trans. R. Soc. S. Aust.	10
	Aust. J. Zool.	6
	Aust. J. Zool. Suppl.	2
	Aust. Wildlife Res.	1
	Alcheringa	2
	Rec. S. Aust. Mus.	2
	Aust. J. Exp. Biol. Med. Sci.	1
	Mem. Qld. Mus.	1
	Proc. Linn. Soc. N.S.W.	2
	Proc. R. Soc. Vic.	1
	The Beagle, N.T.	1
	Aust. J. Entomol.	1
	Rec. W. Aust. Mus.	1

M.J. TYLER: PUBLICATIONS (1958 – 2002)
SUBMITTED FOR THE DEGREE

THE BIOLOGY OF FROGS

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Curriculum Vitae
MICHAEL J. TYLER A.O.

Marital Status: Married with three independent children

Tertiary education: M.Sc. (Adel.) 1974

Occupational history:

- Associate Professor, Department of Environmental Biology, University of Adelaide, 1984 -
- Senior Lecturer, Department of Zoology, University of Adelaide, 1979 - 83
- Lecturer, Department of Zoology, University of Adelaide, 1975 - 78
- Laboratory staff, Department of Human Physiology and Pharmacology, University of Adelaide, 1961 - 74. Final position - Laboratory Manager, 1971 - 74.

Distinctions:

- Riversleigh Medal - 1998 (for contributions to Australian Palaeontology)
- Fellow, American Association for the Advancement of Science - 1998
- Michael Daley Eureka Prize for Science Communication - 1997
- Officer of the Order of Australia - 1995 (for contributions to Zoology).
- City of Adelaide, Australia Day Citizen of the Year - 1993 (for contributions to the community).
- Fellow, Australian Institute of Biology - 1988
- Australian Natural History Medallion - 1980 (for contributions to Australian Natural History)
- Sir Joseph Verco Medal - 1980 (for contributions to herpetology).

External Research Awards:

A.R.G.C.	1976 - 82	(Evolution of Australian Frogs)
A.R.G.S.	1983 - 85	(Gastric Brooding Frog: with Prof. D. Shearman *et al.*)
	1983 - 84	(Evolution of Australian frogs: with Dr M. Davies)
A.R.C.	1988 - 93	(Tertiary frogs of Queensland)
	1988 - 91	(Frog development : with Dr M. Davies)
	1993 - 95	(Systematics of Australopapuan frogs: with Dr M. Davies, Dr S. Donnellan and Dr G.F. Watson)
	1994 - 96	(Skin Secretions of frogs: with Professor J. Bowie)
	1996	(Cane Toad repellent)
A.B.R.S.	1974 - 75	(Systematics of Australian frogs)
Utah Foundation	1977	(Frogs of Kimberley)
	1979	(Frogs of Kimberley)
	1981	(Gastric Brooding Frog: joint grant with Professor D. Shearman)

Anti-Vivisection Union	1980	(Tadpoles as environmental monitoring organisms)
Dept. of Environment and Housing	1978 - 80	(Frogs and macroinvertebrates as uranium monitoring organisms: joint grant with Prof. W.D. Williams)
	1981	(Abnormality survey)
	1981 - 82	(Frog feeding study)
ANZAAS	1970&1996	(Travel grant)
Society for Study of Amphibians and Reptiles	1977	(USA travel award)
National Heart Foundation	1978	(Renin-angiotensin study in frogs: joint grant with Dr G.C. Scroop)
S.A. Museum	1965&1970	(Travel awards)
	1977	(Overseas travel grant supplement)
Kidney Foundation	1978	(Renal renin study in frogs: joint grant with Dr G.C. Scroop)
Savings Bank of SA	1982	(Gastric Brooding Frog)
Rotary Club of North Adelaide	1982	(Gastric Brooding Frog)
	1993	(Frog peptides)
Rotary Club of West Adelaide	1987	(Field studies in N.T.)
Rotary Club of East Adelaide	1993	(General studies)
Mark Mitchell Foundation	1966	(Overseas travel grant)
	1977	(Publication subsidy)
	1982	(Gastric Brooding Frog)
	1984	(Publication subsidy)
	1987	(Field studies in N.T.)
	1992	(Publication subsidy)
Pacific Express Travel Award	1983	(travel grant)
Science & Industry Endowment Fund	1970	(USA travel award)
Royal Society of S.A.	1971	(research grant)
Australian National University	1971	(travel grant)
Wildlife Fund	1989	(research grant)
Australian Conservation Foundation	1988	(travel grant)
Australian Geographic	1988	(research grant)
National Academy of Science, USA.	1990	(travel grant)

Mount Isa Mines Holdings Ltd.	1994	(field studies in N.T.)
Australian Government/ Hamilton Laboratories	1994 - 1999	(mosquito repellent)
Torrens Catchment Board	1998 - 1999	(research grant)
Environment Protection Authority	1998 - 1999	(research grant)
Rotary Club of Kidman Park	1998 - 1999	(publication subsidy)
Torrens Catchment Board	1999	(vacation scholarship)
Environment Protection Agency	1999	(research grant)

Publications:

A. Books

1. 'Frogs of South Australia.' South Australian Museum Board, 1966.
2. 'Frogs.' William Collins, 1976.
3. 'Frogs of South Australia.' (Revised Edition). South Australian Museum Board, 1977.
4. 'Amphibians of South Australia.' Handbooks Committee, Adelaide. 1978.
5. 'Frogs.' (Revised Edition). William Collins, 1982.
6. 'Frogs of Western Australia.' (with L.A. Smith & R.E. Johnstone). Western Australian Museum. 1984.
7. 'There's a frog in my stomach.' William Collins. 1984.
8. 'Frogs of the Northern Territory.' (with M. Davies). Conservation Commission of the N.T. 1986.
9. 'An introduction to frogs.' Horwitz Grahame. 1987, USA Edition 1989.
10. 'An introduction to frogs.' (Revised U.K. edition). 1989.
11. 'Australian frogs.' Viking O'Neil. 1989.
12. Encyclopedia of Australian Animals 'Frogs.' Collins, Angus & Robertson. 1992.
13. 'Earthworms.' Ashton Scholastic. 1992.
14. 'Natural History Museums. Behind the scenes.' Ashton Scholastic. 1992.
15. 'Frogs of Western Australia.' (with L.A. Smith & R.E. Johnstone). Western Australian Museum. (Revised edition). 1994.
16. 'Australian frogs. A natural history.' Reed. 1994: Cornell University Press. 1997: New Holland Publishers. 1999.

17. 'A field guide to Australian frogs.' (with J. Barker & G. Grigg). Surrey Beatty. 1995, reprinted 1999.

18. Encyclopedia of Australian Animals 'Frogs.' Revised CD-ROM edition. Webster. 1995.

19. 'Frogs as Pets. The Australian Green Tree Frog (*Litoria caerulea*).' Graphic Print Group, Adelaide. 1996.

20. 'Frogs', Mondo, New York. Revised edition. 1997.

21. 'Frogs of Western Australia'. (with L.A. Smith & R.E. Johnston) 3rd Revised Edition 1999.

B. Papers and monographs in refereed journals (350+)

C. Edited works

Editor or co-editor of nine books.

Membership of Professional Societies:

Royal Society of South Australia (Honorary Fellow)
Australian Institute of Biology (Fellow)
Australian Society of Herpetologists
Royal Zoological Society of South Australia
Society for the Study of Amphibians and Reptiles
American Association for the Advancement of Science (Fellow)
Environment Institute of Australia.

Service to Profession:

Australian Institute of Biology	President	1995 - 97
	Vice-President	1997 - 99
South Australian Museum	Chairman of Board	1982 - 92
	Honorary Associate in Herpetology	1962 -
Australian Society of Herpetologists	President	1979 - 80
	Vice-President	1973 - 74, 1980 - 81
Royal Society of South Australia	President	1985 - 86
	Vice-President	1983 - 85, 1986 - 88
	Editor	1976 - 82
	Councillor	1967 - 68, 1970 - 73
	Secretary	1964 - 67, 1968 - 70
	Programme Secretary	1962 - 64
Royal Zoological Society of SA	President and Chairman of the Board	1994 – 2001

University of Kansas Museum of Natural History	Honorary Associate	1973 - 94
SA Science House Steering Committee	Secretary	1966 - 68
Alytes	Editorial Committee	1983 - 87
California Academy of Science	Research Associate	1983 – 87
First World Congress of Herpetology	International Herpetological Committee	1983 – 89
SA Museum Redevelopment Steering Committee	Member	1982 - 86
Committee that reviewed constitution of Royal Zoological Society, Adelaide.	Chairman	1984 - 85
Interim Council of National Science & Technology Centre, Canberra	Member	1989 - 97
Second World Congress of Herpetology	Director	1990 - 94
Australian Conservation Foundation for Bicentennial Conference, Sydney	Leader of Workshop 'Wildlife'	1988
IUCN Declining Amphibian Populations Task Force	Director	1991
Australian Working Group, IUCN Task Force on Declining Amphibian Populations	Chairman	1991 - 1997
IUCN Species Survival Commission	Member	1992 -
CSIRO Cane Toad Research Advisory Committee	Member	1993 - 1996
World Congress of Herpetology	Executive Committee Secretary-General	1994 - 2002 1997 - 2002
Council, Rabbit Eradication Foundation	Member	1994 - 1996
Chemical Contaminants Group, IUCN Task Force on the Roles of Chemical Contaminants, Climate and Atmosphere	Chairman	1995 - 96
Nature Conservation Centre	Patron	1995 -
Investigator Science Centre	Patron	1993 – 2000
National Threatened Frog Working Group	Member	1997 –
Amphibia Section of Committee on Recently Extinct Organisms	Chairman	1996

Plenary Lectures and Significant Addresses:

1. Crosby Morrison Memorial Lecture, State Government Lecture Theatre, Melbourne, 1980.
2. 'Australian Geographic' magazine annual awards, Sydney Opera House, 1983.
3. Keynote Address: STAVCON (Victorian Science Teachers) Annual Conference, Melbourne, 1991.
4. Stanhope Oration, National Science Teachers Conference, Adelaide, 1991.
5. Science Commemoration Ceremony Address, The University of Adelaide, 1991.
6. Keynote Address: Enviromine Conference, Taronga Park, Sydney, 1992.
7. Master of Ceremonies, Federal Government Environmental Policy Launch by The Prime Minister of Australia, The Honourable Paul Keating, M.H.R., Adelaide, 1992.
8. Annual Lecture, Institute of Metals and Materials of Australia, Adelaide, 1992.
9. Public Lecture, Great Australian Science Show, Melbourne 1992.
10. Keynote Address: Zoos Enriching Environments, Adelaide, 1993.
11. Keynote Address: Western Australian Science Teachers Association, Perth, 1993.
12. Keynote Address: Launch of South Australian Landcare, Tumby Bay, 1993.
13. Address: Flinders University Convocation, Flinders University, 1993.
14. Address: Sir Mark Oliphant Round Table, Adelaide, 1993.
15. Keynote Address: International Conference of Science Librarians, Adelaide, 1993.
16. Public Lecture, ANZAAS, Perth, 1993.
17. Public Lecture, Great Australian Science Show, Melbourne, 1994.
18. Keynote Address: Queensland Science Teachers Conference, Townsville, 1994.
19. Keynote Address: Ohio Herpetological Conference, Cleveland, Ohio, 1994.
20. Science Oration: Royal Australian College of Pathologists, Adelaide 1994.
21. Sir Condor Laucke Oration, Nuriootpa, 1995.
22. Public Lecture, Australian Museum, Sydney, May 1996.
23. Public Lecture, University of Adelaide Alumni Association, June 1996.
24. Keynote Address: Society for the Study of Amphibians and Reptiles, Lawrence, Kansas, July 1996.
25. Keynote Address: Australian Institute of Medical Science, Adelaide, October 1996.
26. Public Lecture, ANZAAS, Canberra, October 1996.

27. Keynote Address: Australian College Occupational Health Nurses Inc., Adelaide, October 1996.

28. Keynote Address: Australian Institute of Environmental Health, Mount Gambier, March 1997.

29. Keynote Address, St. Aloysius College - Dedication of new science laboratories, Adelaide, March 1997.

30. Plenary Lecture: Third World Congress of Herpetology, Prague, Czech Republic, August 1997.

31. Address : Westminster School Speech Day, Adelaide, November 1997

32. Address : Fertility Society of Australia, Adelaide, December 1997

33. Keynote Address, Australian Institute of Engineers, Adelaide, March 1998

34. Keynote Address, ARAZPA Annual Conference, Sydney, March 1998

35. Keynote Address, PASMINCO Conference, Melbourne, March 1998

36. Keynote Address, CONASTA, Sydney, April 1998

37. Anstey Giles Memorial Lecture, Royal Australasian College of Surgeons, Adelaide, September 1998

38. Keynote Address, NSW Science Teachers Association, Sydney, September 1998

39. Deakin University Commemoration Address, Geelong, October 1998

40. Keynote Address, Environment Expo, Adelaide, November 1998

41. Inaugural Address, ANZ Lecture Theatre, Taronga Zoo, Sydney, October 1998.

42. Keynote Address, Australian Institute of Mining, Adelaide, November, 1998

43. Keynote Address, Riversleigh Society, Sydney, December 1998

44. Keynote Address, Annual Conference of National Association of Graduate Careers Advisers Services, Adelaide, December 1998

45. Keynote Address, Metamorphosis Annual Forum, Sydney, January 1999

46. Keynote Address, Sri Lanka Medical Association, Annual Conference, Kandy, Sri Lanka, March 1999

47. Keynote Address, Otorhinolaryngology Annual Conference, January 2001

Consultative Services:

1. Office of the Supervising Scientist, Alligator Rivers Region, N.T. Uranium mining project at Jabiru, N.T. Development of environmental monitoring system.
2. Amax Pty Ltd: Frog fauna at a bauxite deposit at Mitchell Plateau, W.A. Environmental management plan.
3. Gutteridge, Haskins & Davey: Amphibians and reptiles at Honeymoon Creek uranium deposit. Environmental Impact Statement.
4. Kinhill Pty Ltd: Amphibians as monitoring organisms at Roxby Downs.
5. Gutteridge, Haskins & Davey: Plan to minimise intrusion of frogs upon life at lakeside housing development at Townsville.
6. Agricultural Protection Board (W.A.) & Vermin & Noxious Weeds Board (Vic): Commission Study of Cane Toad
7. Member of Cane Toad Management Committee supervising investigation of Biological control agent. CONCOM funded. Townsville 1986-89.
8. Report on caudate amphibians and their potential effects in Australia. Prepared for wildlife organisations in all States.
9. Roxby Management Services: frogs as environmental indicator organisms.
10. Vertebrate Pests Committee: exotic frogs - requests to import received on periodic basis.
11. Saltwatch, Dept. Of the Premier, Victoria: inclusion of frogs in statewide monitoring program.
12. Australian National Parks & Wildlife Service - advice for CONCOM on endangered species.
13. Ranger Uranium Mines - pilot frog abnormality study.
14. Private consultancy - frog breeding in captivity.
15. Mount Isa Mines - consultant (1991 - 95).
16. Australian National Conservation Agency - Frog Action Plan.
17. County Estates Pty Ltd, Sydney. Advice on fauna impact statement.
18. Kinhill Pty Ltd, Sydney. Redevelopment of railway yards at Enfield - advice on endangered species.
19. Brighton City Council, Adelaide. Advice on frog population and development of natural spring.
20. CSIRO, Geelong - Creation of SPF colony of cane toads. Cane Toad Advisory Committee, Canberra. Member 1990 - 96.
21. Ardel Pty Ltd, Sydney. Advice on species of frog population on development site. Expert witness in Appeal in Land and Environment Court.
22. Hassell Pty Ltd, Adelaide - Torrens Catchment Management Plan.

23. Energy Resources of Australia - Frog abnormality study at Jabiru, N.T.

24. Federal Airports Corporation - objection to listing of Perth Airport bushland on National Estate.

25. Chanrich Properties, Sydney. Advice on population of species of frog on developments site. Expert witness in appeal in Land & Environment Court (Case I).

26. Ross Mining, Brisbane. Advice on mining impact on frog population at mine site.

27. Chanrich Properties, Sydney. Advice on population of species of frog on development site. Expert witness in appeal in Land & Environment Court (Case II).

28. Bruce Lyon Pty Ltd, Sydney. Advice on frogs on development site. Expert witness in appeal in Land & Environment Court.

29. Statewide Property Ventures, Sydney. Advice on population of species of frog on development site. Expert witness in appeal in Land and Environment Court.

30. Australia Post, Melbourne. Technical advice and promotion of frog postage stamps.

31. Resource Strategies, Brisbane. Advice on species management plan.

32. Melbourne Water. Enhancement of frog populations.

33. Melbourne Port Corporation. Advice on population of frogs on development site.

34. 'WaterCare', South Australia. Promotion of environmental care.

M.J. TYLER: PUBLICATIONS
(1958 – 2002)

Tyler, M.J. (1958). On the diet and feeding habits of the Edible Frog (*Rana esculenta* Linnaeus). *Proc. Zool. Soc. Lond.* **131**(4), 583-595.

Tyler, M.J. (1959). *Piona sp.* (Acarina, Hydrachnellae) recovered from stomachs of *Rana esculenta* L. *Ent. Mon. Mag.* **65**, 79.

Tyler, M.J. (1960). Observations on the diet and size variation of *Amphibolurus adelaidensis* (Gray) (Reptilia, Agamidae) on the Nullarbor Plain. *Trans. R. Soc. S. Aust.* **83**, 111-117.

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de la Lande, I.S., Tyler, M.J. and Pridmore, B.R. (1962). Pharmacology of the heart of *Tiliqua (Trachysaurus) rugosa* (the Sleepy Lizard). *Aust. J. exp. Biol. med. Sci.* **40**, 129-138.

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Tyler, M.J. (1963). A taxonomic study of amphibians and reptiles of the Central Highlands of New Guinea, with notes on their ecology and biology. II. Anura: Ranidae and Hylidae. *Trans. R. Soc. S. Aust.* **86**, 105-130.

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de la Lande, I.S. Tyler, M.J. and Thomas, D.W. (1965). Pharmacological analysis of the venom of the "Bulldog" ant *Myrmecia forficata*. *Recent Advances in the Pharmacology of Toxins* 71-75.

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Tyler, M.J. (1967). A new species of frog of the hylid genus *Nyctimystes* from the Highlands of New Guinea. *Trans. R. Soc. S. Aust.* **91**,191-195

Tyler, M.J. (1967). Microhylid frogs of New Britain. *Trans. R. Soc. S. Aust.* **91**, 187-190.

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