THE BIOGEOGRAPHY OF LUNGFISHES WITH A DESCRIPTION OF NEW FOSSIL TAXA FROM EAST AFRICA

By

Sifa Ephraim Ngasala

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Geological Sciences – Doctor of Philosophy

2016

ABSTRACT

THE BIOGEOGRAPHY OF LUNGFISHES WITH A DESCRIPTION OF NEW FOSSIL TAXA FROM EAST AFRICA

By

Sifa Ephraim Ngasala

The number of publications on and discoveries of new fossil lungfish species and genera has generally shown, despite some fluctuations, an increase in numbers. This is particularly the case in in Africa, Australia and South America, where lungfishes still survive as an extant group. Australian lungfishes have received the most attention, with one possible reason being the declaration that the surviving Australian lungfish is an endangered species, and the number of research expeditions and active researchers based there over a long period of time.

While Australia has received a great deal of attention, the evolution of African lungfishes, while noteworthy, has not been studied with the same level of intensity. This study focuses on newly discovered fossil lungfish specimens from Kenya and Tanzania, and then looks at Africa lungfish biogeography in a broader context.

The Cretaceous fauna of Turkana, Kenya, includes a lungfish pterygopalatine tooth plate, which is here described as Ceratodus due to the possession of multiple ceratodontid features, including six separate ridges on the occlusal surface of the tooth plate, the characteristic curvature of the tooth plate, and the specimen’s length to width ratio of almost 2:1.

Tooth plates from in the Late Oligocene fauna in the Rukwa Rift Basin (RRB) of southwestern Tanzania are here assigned to two different genera; *Ceratodus* and *Protopterus*. The *Ceratodus* from RRB is smaller in size as compared to the Cretaceous specimen from Turkana but retains features typical of ceratodontid lungfish, and it is sufficiently distinct to be described as a new species -- *Ceratodus mbedeae*.

Protopterus lungfish specimens from the RRB exhibit typical features of that genus, which survived to day in Africa, including three blade-like protruding tooth ridges and a relatively flat posterior angle in the upper jaw. The RRB *Protopterus* are not here consider sufficiently distinct to justify erection of a new species. Mapping parsimony analysis of endemism (PAE) of lungfish biogeography indicates significant changes over time. Of note are the much broader geographic distribution of lungfishes early in their history, contrasts in composition of Paleozoic versus Mesozoic assemblages, and the abrupt turnover of major groups at the end of the Devonian. Modern lungfish are today restricted to tropical regions of Africa, South America and Australia.

The similarity dendogram generated by the PAE study results in three major clusters (clades), the first cluster that constitutes Australia and Europe appears to be very distinct from the other two, namely Africa, Madagascar and South America, and Asia and North America. Madagascar is shown to be more similar to South America than to Africa within that cluster.

I, affectionately, dedicate this thesis to my beloved Dad, Mr. E. S. Ngasala who unfortunately did not live to see the end of my PhD program, in remembrance of his love, tender care and encouragement for me to go as far as I can in education journey. Rest in Peace Dear Dad!

ACKNOWLEDGEMENTS

First and foremost, I would to thank God, the Almighty, for this opportunity. I do strongly believe it is His intention to use me only as a conduit to bless and reach many more out there especially those disadvantaged kids out there in the hills, slopes and plains of Tanzania and elsewhere.

As I wrap up my PhD program here at Michigan State University, I continue to be deeply gratified by the remarkable generosity of all those people whom have supported me during my entire program. Years in years out; staff, faculty and students at MSU Department of Earth and Environmental Sciences have shown me the real reason of being happy to be part of this 'great family'. As an example, the enormous amount of support poured unto me when I lost my dad back home in Tanzania only three months after starting my studies. That will always stay in my heart – and the only thing I can say is -- Thanks! I am not confident I can describe my special appreciation to its full credit, but suffice it to say, at no other point in my life I have felt more blessed and have reached unprecedented milestones as I did during the entire time of my studies in Department of Geosciences. At one point, I had felt how lucky I was to find myself here amongst best people anyone could wish for. I did not deserve any of these but your good hearts guided you to such wonderful people to be around.

Mike, Nancy, Patrick, Robert and all the people we worked together in the Rukwa Rift Basin Project (RRBP) you are a reason of me to be here today and if you there is any way to understand the word thanks more than how it spells that is the boldest way I mean. Our colleague and my best ever mentor and friend, Said Kapilima, I believe he is looking down with widest smile and pride. I thank him and I am glad he knew he had special place in my heart.

There is that one woman, my mother, I can feel how happy you would be for pushing and encouraging me endlessly whenever you got chance to talk to me. Your words and constant reminders on the significance of finishing what I started just for the sake of your grandchildren have been power engine in my studies.

My wife, Tula, you have seen it all my struggles and deep down I believe your prayers have been answered to see the successful end of the program. My daughters, Atuganile, Rachael and Serena literally we studied together. All those trips to libraries one day you will know well that it was a true teamwork. I always pray to God you turn out to be the best well-hearted women and remember all good moments and teachings we shared.

Special thanks go to these individuals and all front-desk staff at the Office for International Students and Scholars (OISS-MSU) for advice, help and support Takhmina Maralbaeva, Brooke H.M. Stokdyk, Jessica Scott and Peter Briggs.

Finally, yet importantly, special thanks go to Mike Gottfried for the patience, discussions, and guidance throughout my program. My committee members Ralph Taggart, Danita Brandt and Bob Anstey I have no enough words to describe my appreciation to you. It is my hope you fully understand that your effort and acceptance to be in the committee I do not take for granted. Chair of Department, Dave Hyndman, Dallas, Pam and every staff in the office, you are awesome and I thank you for the advice and encouragement. Julie Libarkin and David Long, thanks for your help and advice from time to time just to see me succeed.

I really know many more people deserve a special mention here but I do not believe this space will be enough to mention all names. I thank everyone who in one way or another have been with me in this journey of my education.

PREFACE

Since the scientific discovery of first lungfish, the fascination with this unique group has never ceased. From the earliest studies, even basic classification was debatable as some lungfish were considered amphibians and some argued for placement among the fishes. Fossil remains of lungfishes have been found in different parts of the world and from geological deposits of different ages. For that reason, scientists of multiple backgrounds have shown interest in studying this group of fish, from paleontologists, geologists, taxonomists, dentists and many other fields of study.

This dissertation work is based on three major sources of information; literature review of the studies of lungfish through time as Chapter 1, description of fossil specimens from East Africa including one new species, in Chapters 2, 3, and 4, and data from different sources and databases for the broader biogeographic perspective presented in Chapter 5. The chapters describing fossil lungfish from the Rukwa Rift Basin (RRB) of Tanzania are linked to my participation as a member of the field teams exploring the RRB, and the fossil lungfish from Lake Turkana in Kenya is provided courtesy of my colleagues Patrick O'Connor and Joseph Sertich.

This dissertation aims at contributing to the body of knowledge on the evolution and fossil record of African lungfishes, which are not only intrinsically interesting due to their ability to use both lungs and gills to breathe, but also continue to play a major role as a group linked to the evolution of tetrapods – the four limbed vertebrates. In that context the fossil record of lungfishes in Africa, which is one of the three continents where the group is still extant, and the group's biogeographic history as revealed through both cluster and parsimony analysis of endemism, are of interest to an audience that reaches beyond fossil fish specialists. This study will contribute to our understanding of what was happening in Africa during and after the break-up of the supercontinent of Gondwanaland.

It is my intention to submit the individual chapters for publication to different peer-reviewed journals, including the *Journal of Vertebrate Paleontology*, *Diversity and Distributions* and *Journal of African Earth Sciences*.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

KEY TO ABBREVIATIONS

RRBP	Rukwa Rift Basin Project
RRB	Rukwa Rift Basin
KNM	Kenya National Museum
AC	anocleithrum
AN	angular
C	cartilage
CH	ceratohyal
CL	cleithrum
CLA	clavicle
CR	cranial rib
DE	dermal ethmoid
EO	exoccipital
FP	frontoparietal
OP	operculum
PR	prearticular
PRa	anterior process of the prearticular
PRan	angular process of the prearticular
PRb	middle process of the prearticular
PRc	posterior process of the prearticular
PRcor	coronoid process of the prearticular
PRsym	prearticular symphysis
PRTa	anterior ridge of the prearticular tooth plate

PRTb	middle ridge of the prearticular tooth plate
PRTc	posterior ridge of the prearticular tooth plate
PS	parasphenoid
PT	pterygoid
PTap	ascending process of the pterygoid
PTTa	anterior ridge of the pterygoid tooth plate
PTTb	middle ridge of pterygoid tooth plate
PTTc	posterior ridge of the pterygoid tooth plate
S	supraorbital
SO	suboperculum
SPR	supraangular
SQ	squamosal
V	vomerine tooth
VE	vertebra

CHAPTER I

1 INTRODUCTION

1.0 Introduction

This work intends to do three major things. Firstly, highlight further the interest and discovery history of lungfish since first described lungfish in 1862 through the intensive review and analysis of publications. Secondly, to expand our knowledge on the new geographical ranges and distribution patterns by describing systematically one new species and two genera for the first time in the new geographic range (East Africa). Thirdly, propose the new hypothesis concerning biogeography of lungfish using cluster analysis and use parsimony analysis of endemism.

1.1 Lungfish

In the geological record, lungfish appeared for the first time in the Early Devonian (Miles, 1977). The geographical ranges and diversity have fluctuated significantly through time. Today there are only three surviving genera containing six species restricted to three continents; Africa (*Protopterus* (*P. annectens, P. amphibius*, *P. aethiopicus* and *P. dolloi*), Australia (*Neoceratodus forsteri*) and South America (*Lepidesiren paradoxa*). Fossil lungfish remains include relatively complete cranial material, dental plates and their estivation burrows.

Ecologically, the habitats of lungfishes, especially African and South American species are in pools, seasonal rivers, and shallow lakes in hot regions experiencing long dry periods during which estivate in burrows covered with dried-up mucus, where they can survive several months to up to four years and until the onset of the next rainy season.

One of the characteristics which make lungfish one of the few organisms special is their ability to breath using lungs which actually is the reason they were named ‘lungfish’ make them special and able to live on land temporarily. They are capable of breathing in two different ways. They breathe using gills like any other fish but also using mouths through lungs. During aestivating time in burrows, they leave only tiny opening that is tube like leading up to fish's anterior end for breathing. In the underground, they minimize metabolism to conserve energy and avoid excretion.

1.2 Rationale

Because of wide geographical range and geological span, some records of lungfish have enjoyed more attention than the other and some regions with potential records have received less or no attention at all. In this study the publications of lungfish especially discoveries of new species or genera is reviewed. The sub-Saharan Africa region is getting more attention because of its potential record but very few studies have been conducted and published. To do so three chapters are dedicated to describing new material from the region. Most of the record in Africa is concentrated in the northern and western Africa but the living lungfish in the continent today are in south of Sahara.

1.3 Statement of the problem

The considered monophyletic group (Takezaki et al., 2004) of lungfish is widely distributed in three continents for extant lungfish and six continents for fossil remains. Several authors (e.g. Marshall, 1986; Tohyama, 2000; Takezaki et al., 2004; Shan, 2011) have done good work in studying systematically the biogeography of lungfish using different methods (e.g. morphology, molecular data). The one thing, which has been missing, is detailed mapping of all lungfish data including both extant and extinct genera. Other authors in their previous work used different methods and different number of genera. Latest is the work by Marshall, 1986 who used only 55 genera known at that time. This up to date data matrix allow for proposition of stronger biogeographical hypothesis of distribution, pattern and possible influencing forces to such patterns.

In Africa, extant lungfishes occur mainly in sub Saharan Africa, while fossil lungfish are found primarily in northern and western Africa. That may have happened either due to the amount of effort (chapter 2) i.e. number of researchers working in the region or geologic and taphonomic reason. The fieldworks were done by two major expeditions in the eastern Africa (RRBP in Tanzania and in Turkana Kenya) in region and geologic deposits have recovered fossil lungfish material ranging from isolated broken well-preserved tooth plates to articulated specimens. It is this region that previously, O'Connor et al., 2004 referred to as 'African Gap' of vertebrate fossil record in the attempt to piece together information about the role and what happened in the region during Gondwanaland breakup, we found and here in I report the new findings to 'fill the African Gap'.

1.4 Objectives

The goals of this work are as follows:

1. To review the publications of the discoveries of lungfishes in order to detect the clear pattern and general trend of the effort and discoveries in six different continents,

2. To describe three recently recovered lungfish material from eastern Africa the region previously described as ‘African Gap’ due scarcity and rarity of the vertebrate fossil record and

3. By using data matrix of genera/region (areas of endemism), to carefully use two methods of similarity and endemism method propose the hypothesis explaining the possible rationale of the observed distribution and pattern of the extinct and extant lungfish record.

1.5 Significance of the study

The clear understanding of how much effort has been put in different geographic areas especially continents for this matter and the number of findings is expected to get proper historical insight of the studies of lungfishes. Moreover, as these studies in many cases go simultaneously with other studies can give a bigger picture of what has been happening in paleontological efforts and publications. A good example for this is the 1940 - 1949 decade when most research as disrupted by WWII. The findings of this study will reopen up the efforts of more and intense paleontological and geological expeditions in regions like sub Saharan Africa where logically due to their sporadic record of extinct lungfish and availability of lungfish in most pools of water in swampy areas. Such effort is key for not only expansion of lungfish record but also other vertebrate and invertebrate, which repeatedly have been found, associated with lungfish fossils.

Many other paleontological expeditions and publications (e.g. Germany Tanganyika Tendaguru Expedition) suffered similar drop during WWI.

The biogeographic hypotheses proposed using both cluster analysis and parsimony analysis of endemicity (PAE) will shed new light of the similarity and shared areas of endemism for different lungfish genera. Such hypotheses can be further tested using extensive data matrix including phylogenetic data (morphometric and genetic) to establish more concise and robust paleobiogeographic relationships among different genera or at species level.

In addition, due to its peculiar nature of lungfish especially its place in evolution, the findings of this study can be a good addition to the body of scientific knowledge to be applied by other fields as well especially as evidence of the impact of plate tectonics in different episodes to the distribution, proliferation and extinction of major groups of different taxa.

CHAPTER II

2 BREAKTHROUGHS IN LUNGFISH STUDIES AND HISTORICAL ANALYSIS

2.0 Introduction

The first account of the dipnoan group of Sarcopterygian fish was published by (Parkinson, 1811) as the first discovery and description of the lungfish known. Ever since there has been numerous discoveries and descriptions of lungfish. Conant, 1986 and Marshall, 1986 gave detailed literature history and listing of all thus far discovered Dipnoans. There has been an extraordinary increase in our knowledge of the Dipnoan group for the past three decades since those great historical accounts with respect to the number of new forms discovered. In addition, those historical accounts did not cover the discovery trend that is the main focus of this study.

The definition of Dipnoan group proposed by (Muller, 1844) is followed in the present study. The synonyms and all naming attempts are included as an indication of effort towards the description of lungfish species both at specific and generic level.

In part, this work tries to measure the relationship between the number of species discovered over time and the effort in terms of number of active authors for each decade from the first publication to current decade. My hypothesis is that more effort put (i.e. number of active authors per decade) will result to more discoveries. The study also intends to investigate the consistency of these studies over decades, where I hypothesize to have had some fluctuations but steady increase as new findings and more researchers with interest in studying lungfish have been increasing over time.

The study explores further the contribution of each continent to the knowledge pool coming in from the discoveries and publications from all six continents where the record of lungfish either living or extinct have been found. The driving hypothesis is that; there has been similar active researches and publications in all continents.

In summary, the present study has several specific objectives. The first one is to analyze the record of known lungfish species through literature review. As it became apparent, clear that the rate of discovery of the new species is likely to have direct correlation to the amount of effort in studying lungfish at that particular time. A second objective was to statistically determine such correlation if it is due to reduced research efforts or due to reduced opportunities because the present sampling is nearing completion.

Studies of the morphological descriptions of representative lungfish and biogeographic distribution studies are found in other chapters of this thesis.

2.1 Methods

The examination of historical trends in the discovery of new species was used as an approach to access the study of the lungfish known so far. The dates of discovery of new species were taken to be the years of their first descriptions including the ones later considered as synonyms (in some cases). This approach was used in two ways. The first one was to examine historical trends in the discoveries of the lungfish species over time (in terms of decades). This was done using histogram plotting of number of new species described (named) for each decade starting with the first description in 1820. Any publication prior to that year 1820 was considered as (<1820) regardless of the decade. The second one is using MS Excel 2013 to analyze and study the relationship between active researchers over time and the number of species discovered during that decade. This aimed at using correlation coefficient (R^2) as a measure of the impact of number of findings regardless of the geological time period. The aim is to see the effectiveness of the amount of effort in scientific findings (discoveries and publications) for this particular case lungfish description (naming) of new species.

Further exploratory work was done by investigating the contribution of number of publications from six continents and African subcontinent of Madagascar by examining the number of publications from each continent over all decades.

2.2 Results

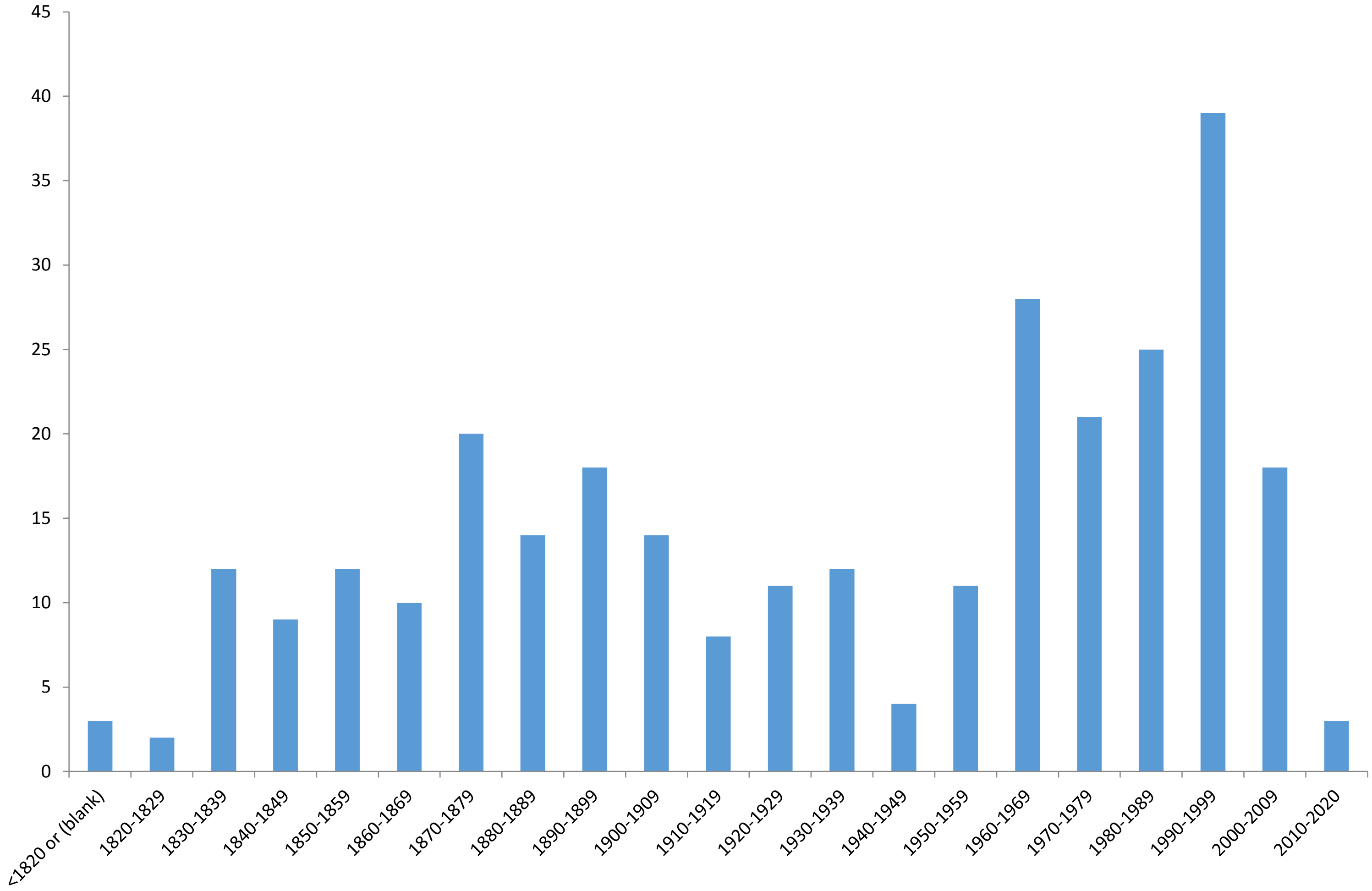

Figure 2.1: Discovery and description of new species in the family Dipnoi, 1820 – 2020, whereby x-axis are decades and y-axis number of species (disregarding all synonyms).

Table 2.1: Discovery of new species in percentage for each decade

Decade	# of Species Discovered in %
<1820	1.02
1820-1829	0.68
1830-1839	4.08
1840-1849	3.06
1850-1859	4.08
1860-1869	3.40
1870-1879	6.80
1880-1889	4.76
1890-1899	6.12
1900-1909	4.76
1910-1919	2.72
1920-1929	3.74
1930-1939	4.08
1940-1949	1.36
1950-1959	3.74
1960-1969	9.52
1970-1979	7.14
1980-1989	8.50
1990-1999	13.27
2000-2009	6.12
2010-2020	1.02

Table 2.2: Discovery through time for all six continents and Madagascar as subcontinent. The “<1820” column represents the lungfish with discoveries before that 1820 year regardless of the decade. The list includes all the synonyms.

Row Labels	Africa	Asia	Australia	Europe	Madagascar	North America	South America
<1820	0	0	1	0	0	0	1
1820-1829	0	0	0	2	0	0	0
1830-1839	19	0	0	12	0	1	14
1840-1849	8	0	0	10	0	2	0
1850-1859	18	4	0	4	0	0	0
1860-1869	0	0	0	13	0	0	0
1870-1879	0	0	10	4	0	17	0
1880-1889	0	0	1	6	0	11	0
1890-1899	0	0	2	2	0	15	3
1900-1909	12	0	4	2	0	7	2
1910-1919	6	0	9	0	0	1	1
1920-1929	0	0	14	2	2	5	0
1930-1939	0	0	2	10	0	6	0
1940-1949	2	2	0	2	0	0	0
1950-1959	5	2	0	7	0	5	0
1960-1969	33	2	0	6	0	13	2
1970-1979	8	2	4	9	0	12	1
1980-1989	12	2	12	3	1	5	3
1990-1999	18	3	44	6	0	3	0
2000-2009	7	2	9	3	2	4	1
2010-2020	2	0	1	0	0	0	1
Grand Total	150	19	113	103	5	107	29

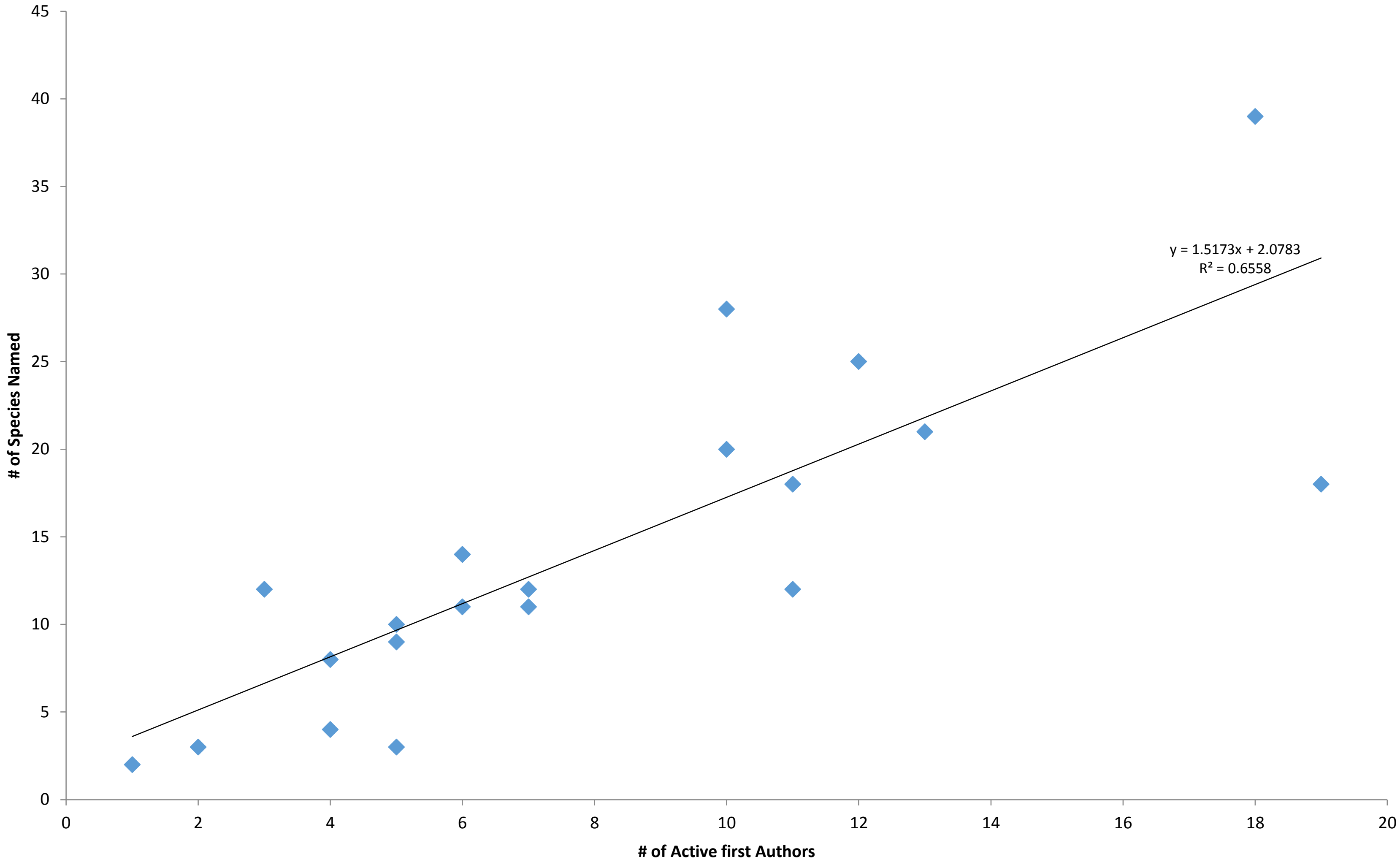

Figure 2.2: Graph showing the correlation between # of Active First authors and # of species discovered for each decade from 1820 – 2020.

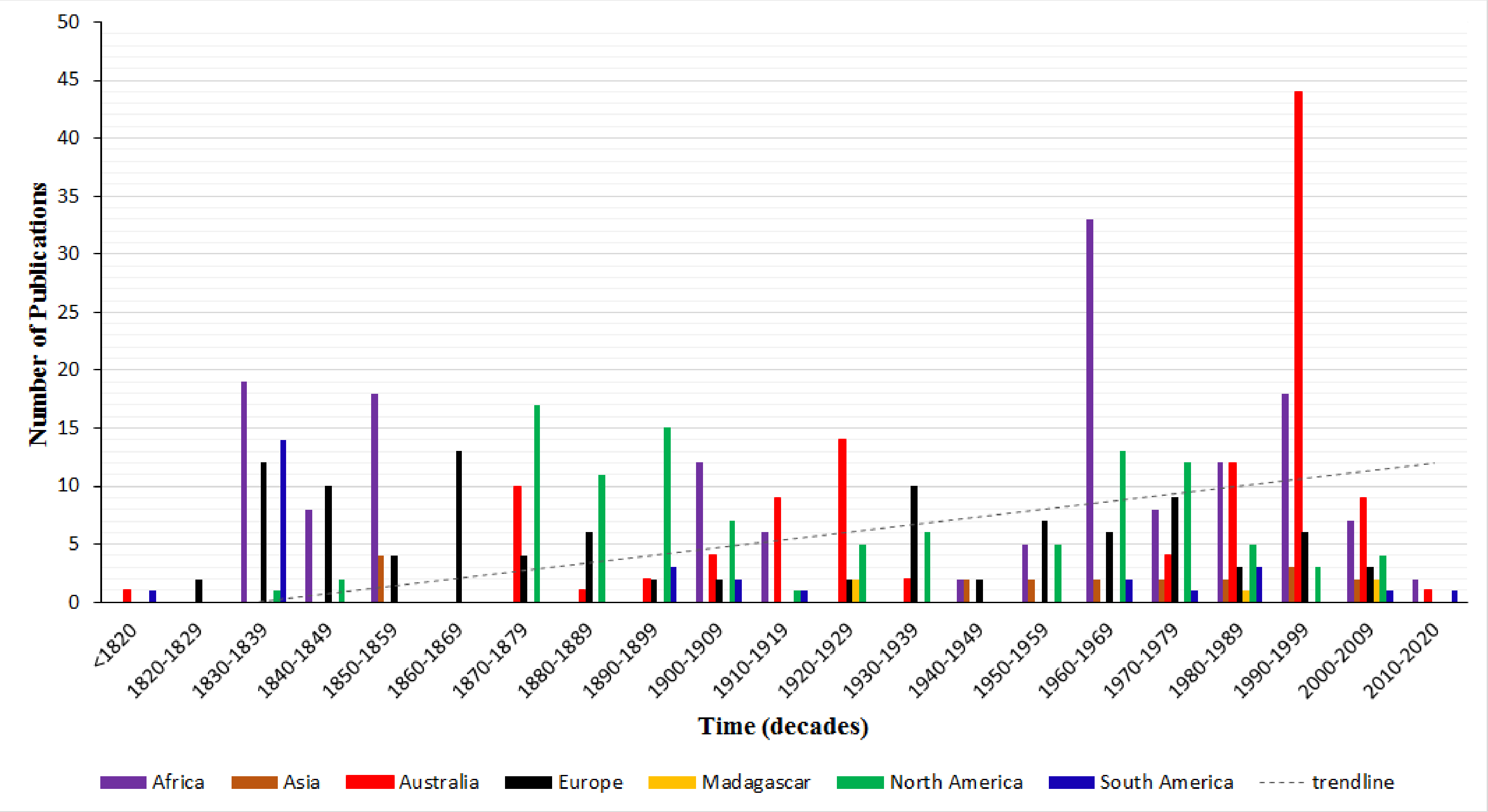

Figure 2.3: Publication rate as a measure of discovery rate of new fossils. The dotted line represent the general trend of number of publications through time.

Figure 2.1 shows the number of discoveries and description of species from the first discovery of lungfish in 1820 and some few more publications, which happened before that year. Table 2.1 lists the relative amount for each decade.

Two major bell curves can be deduced from the findings. It can clearly be seen that there has been a large increase in the number of newly described species starting third decade (1830 - 1840 forming a bell curve with the decade 1840 - 1850 (20 species) with the highest pick at the decade 1870 - 1880. The decade 1940 - 1950 witnessed the drastic drop of newly described species to less than five. The second bell shape started in the decade beginning from 1950 to 1960 before another slow discoveries or because we are at the second portion of this decade, 2010 - 2020, while figures for discoveries from 1990 to 2000 have shown an impressive spike of more than thirty-five discoveries.

Figure 2.2 intends to display the correlation between number of active authors and number of lungfish species discovered (named). There is ‘strong correlation’ of 0.6558. The worthy noted outlier is when there is about twenty active authors (which is the largest of all) and the number of named species was only 15, even less than when only 10 active authors who named more than 28 new species.

The figure 2.3 and table 2.2 show the comparison of six continents and subcontinent of Madagascar in Africa the number of distribution over period of decades in time. From this analysis, we can deduce where the effort went as means to expand the analysis done in figure 2.1. For example, that huge spike we see for discoveries in the decade 1990 to 2000 is clearly from the extreme effort in Australia (figure 2.3). During the drastic drop of the decade from 1940 to 1950 the work was done only in three continents; Asia, Europe and Africa each with only two publications. The continent of Europe has shown contribution in publications almost in all decades with the highest contribution in the decade between 1860 and 1870 when it was the only continent with contribution. From figure 2.3 we can clearly see the first publication if from lungfish from Australia followed by South America. Another drastic drop between 1910 to 1920 which can be seen in figure 2.1 are seen here to be a result of only two continents Africa and Australia contributed publications while Europe for the first time had no lungfish publications and North America and South America had one for each.

To sum up, although after a huge spike in the 1990 to 2000 decade there is significant drop in the following decade. Nevertheless, the general trend in a dotted line show the low but steady increase from the first decade to this decade.

2.3 Discussion

In this study, I investigated three major things, number and timing of lungfish discoveries; effort in terms of active authors and the regional (continents) contribution to the body of knowledge of lungfishes to review thoroughly the trend of lungfish studies.

The results show that despite the general fluctuations of these studies from decade to decade the sinusoidal curve with encompassing two major bell (normal) curves which can be deduced from the findings from the decade of 1830 - 1840 and the decade 1870 - 1880 while the second normal curve starting from the decade 1950 - 1960 to 2010 - 2020. In between there are noticeable drastic drops like that of the decade 1940 - 1950 and stand out spikes like that of decade 1990 - 2000. The first bell curve is smaller than the second one that support the hypothesis that despite these fluctuations from year to year, decade to decade and notably before WWI and WWII the studies have been relatively consistent with low but significant increase in number of species discoveries, descriptions and naming.

The findings from this study strongly support the hypothesis that the more the effort i.e. number of active researchers at certain time the higher the number of discoveries with the ‘strong correlation’ of 0.6558 which imply one of the factors contributed to more discoveries is amount of effort as a result of active ground work participation.

The results from the analysis of publications and discoveries from different continent does not support the hypothesis that similarly all continents had equal findings over time. Instead, what we see is probably only Europe can be considered to have been actively explored throughout except for the decade of 1910 - 1920 that coincidentally is during WWI which most of European countries actively participated. In addition, during the decade of 1940 - 1950 there is another huge drastic drop of lungfish researches. Another decade noteworthy is 1860 - 1870 when only Europe was active in publications and discoveries of lungfish. Gaston, 1996 suggests that it is difficult to have one generally accepted model for the long-term (speciation to extinction) temporal dynamics of species which might have contributed to the discrepancies of number of lungfishes described from different continents.

Conant, 1986 lists more than 2200 publications in the bibliography from 1811 to 1985, mostly taxonomic or reporting field studies. From 1985 to 2012 an approximate additional 200 papers on various subjects from anatomy, phylogeny, biochemistry, internal systems, behavior to reporting new discoveries. It is unlikely that the present records in this study for the years 1985-2012 are yet complete. In general, the trend in the numbers of papers published to 1939 was similar to that for new species discovered.

The balance between taxonomic papers and those on other topics within the gross statistics on publication rates has changed significantly since early 1960s when more attention has been on biochemistry, genetics and behavior. In addition, the 1970's and 1980's have seen an increase in publications on aspects of lungfish ecology and anatomy that are not oriented directly to taxonomy or distribution records. Barry, 2010 and Goudswaard et al., 2002 established that it has been recognized that lungfishes are admirable experimental animals for basic studies on predation, behavior and population dynamics to be a reason for tremendous amount of attention studies on lungfish have received.

The decline in the rates at which new species and new genera are discovered in the last two decades on a worldwide basis and in most localized geographic areas could have two possible causes. The first is that most forms already have been discovered in the well collected parts of the world especially in North America and Europe. This would be a decline in opportunity. The second is that research emphasis on the search for new forms has declined in those areas while more effort has been directed toward other parts of the world like Africa and South America. Measuring decline of opportunity is a bit more complicated and will not be discussed much in the present study. It involves the number of active people/teams engaged in research in relation to what they are able to recover. The rate at which papers on the lungfish are published is the only measure of research effort available.

Additional research needs to be conducted to determine the findings of other paleontological and geological researches how well fit in the patterns of global economic and social event impact them. Particularly for taxa whose geographical ranges and geological span is huge so that comparison of different continents and if possible regions or countries is possible.

This study raises a number of questions that are important to future studies on the biogeography, historical analysis and phylogeny of the Lungfish. The first of these is whether historical analysis of new forms can provide a sound basis for assessing the degree to which the present evaluation of the species and genera are complete and for predicting future trends in the discovery of new forms. This question can be answered at the genera level simply by examining the discovery rates of new species as a whole. However, this is too general a level to be of much value because it cannot shed light on whether present samples of the various groups of species that together comprise the family total of more than 200 nominal species are nearing completion. Before this question can be answered at levels below the family, it is necessary to establish some objective basis for organizing the species in the family into groupings that can be examined individually and on a comparative basis. At present highly disputed, full comparative data for phylogeny are available because of complexity of different recovered parts of fossils.

2.4 Conclusions

The decline in the rates at which new species and new genera are discovered in the last two decades on a worldwide basis and in most localized geographic areas could have two causes. The first one is that most forms already have been discovered in the well collected parts of the world especially in North America and Europe. This would be a decline in opportunity. The second one is that research emphasis on the search for new forms has declined in those areas while more effort has been directed toward other parts of the world like Africa and South America.

The studies and publications of lungfishes have been modestly increasing. In part, it is due to the increase of researchers and new geographical horizons and possibly the technology involved. While researches have been actively working in all continents where the lungfish record is known, over time (decades) some places have received more attention than the other. Overall recently more attention being directed to the three continents where we still have extant lungfish; Australia, Africa and South America.

It is concluded that the relative number and discoveries pattern in terms of geographical distribution are unlikely to change significantly in future as less and less effort are put in Europe and North America and Asia. Meanwhile more effort and opportunities seem to favor southern hemisphere. That is concluded so if and only if the trend of the past two decades will stay the same and that this is true with the exception of Australia, where future discoveries of new patterns are probable if past collection efforts continue.

CHAPTER III

3 A NEARLY COMPLETE CERATODONTID LUNGFISH TOOTH PLATE FROM THE UPPER CRETACEOUS LAPURR SANDSTONE, TURKANA, KENYA

3.0 Introduction and Background

The Cretaceous vertebrate fossil record from Continental Africa remains relatively poorly known, and in particular, how large-scale landform alterations (e.g., rifting, uplift) influenced biotic evolution. This bias is even more pronounced when comparing the circum-Saharan and sub-Saharan regions of the continent. Thus, virtually any identifiable fossil discovery from the sub-equatorial region of Africa is of particular interest for the value of basic paleontological data (e.g., developing ideas of species richness/diversity). The lack of diversity and scarcity of the fossil record was dubbed by O'Connor et al (2006) as the 'African Gap'. Although Lungfish from this part of Africa have been known since 19th century, represented by extant taxa – *Protopterus aethiopicus, P. amphibius, P. dolloi*, it was only recently when Gottfried et al (2009) described the ceratodontid *Lupaceratodus useviaensis* as the first dipnoan fossil from the Cretaceous of this entire region, specifically from the Rukwa Rift Basin in southwestern Tanzania. The Cenozoic fossil record of the group from the region consists of *Protopterus sp*., known from the early Pleistocene from Kanam and East Turkana, Kenya (Schwartz, 1983) and from the Late Miocene of Tanzania (Stewart, 1997).

In general, the Mesozoic fossil record of Dipnoi from the continent of Africa has been largely restricted to a few areas on the northern and western regions, with a selection of Mesozoic lungfish taxa that include: *Arganodus arganensis* from Upper Triassic (Carnian) of Morocco (Martin, 1979); *Asiatoceratodus tiguidiensis* from Tithonian age of Niger and Ethiopia

(Tabaste, 1963); *Ceratodus africanus* from Cretaceous of Egypt, Algeria, Niger, Tunisia, Morocco and from Jurassic of Algeria (Haug, 1905); *Ceratodus carinatus* from Cenomanian of Sudan (Schaal, 1984); *Ceratodus humei* from the Campanian of Egypt (Priem, 1914); *Lavocatodus humei* from Cenomanian of Morocco and Mali (Tabaste, 1963); *Lavocatodus humei* from Cenomanian of Sudan and Egypt (Schaal, 1984; Werner, 1996); *Ceratodus tuberculatus* from Campanian-Late Cretaceous of Egypt (Churcher, 1995) and from Cretaceous of Sudan (Tabaste, 1963); *Dipnotuberculus gnathodus* from Givetian of Morocco (Campbell et al, 2002); *Lavocatodus protopteroides* from Coniacian-Santonian of Mali (Martin, 1983), from the Cenomanian of Sudan (Werner, 1995) and from Turonian-Campanian of Sahara (Tabaste, 1963); *Lupaceratodus useviaensis* from Cretaceous of Tanzania (Gottfried et al., 2009); *Microceratodus angolensis* from Early Triassic of Angola (Texeira, 1947); *Protopterus sp*. from Coniacian-Santonian of Mali (Broin et al., 1974); *Protopterus sp*. from Cenomanian of Sudan (Werner, 1994); *Ptychoceratodus ornatus* from Early Triassic of South Africa (Martin, 1982) and *Ceratodus pectinatus* from Early Cretaceous of (Tabatse, 1963); *Protopterus nigeriensis* from Coniacian-Santonian of Niger (Martin, 1997); *Protopterus regulatus* from Campanian of Egypt (Schaal, 1984); *and Protopterus rhinocryptis* from of Mozambique (Gray, 1850). Also, see Claeson et al., (2014) for a review of the Late Cretaceous lungfishes from the northern Sahara.

This chapter provides the description of one of the regionally oldest fossil ceratodontid genus from the Upper Cretaceous Lapurr Sandstone, Turkana, Kenya. The firstly described taxon is assigned to the genus based on its tooth morphology.

3.1 Geographical and Geological Settings

The locality (Figure 3.1) where the described specimen was recovered (marked by a ‘star’ on the map) is located on the northwestern part of Kenya within the Turkana Basin between longitude 36^0 15’ and 36^0 20’ and latitude 4^0 20’ and 4^0 25’ in the Kenyan Rift Valley (part of eastern arm of Great East African Rift Valley) and represents an Upper Cretaceous continental sequence known as the Lapurr Sandstone. Typical of deposits of this nature, outcrops are rare (Haughton, 1963; Dingle et al., 1983; Mateer et al., 1992) and geographically restricted. The lungfish tooth plate was collected from rocks that represent a succession of fine to coarse arkosic fluvial deposits (Turkana Grits which is considered of Cretaceous age based on poorly preserved dinosaur bones (Arambourg and Wolf, 1969; Sertich et al., 2006) outcropping in Lapurr Range. The precise age of the sandstone is still indeterminate but non-comformably resting over Precambrian basement. Above the sandstones is a well-preserved layer of Oligocene basalts. The development of the Cenomanian-Paleogene Anza Rift system (Bosworth and Morley, 1994; Morley et al. 1999, Tiercelin et al. 2004) is likely related to deposition of the Lapurr sandstone, although the inference of Upper Cretaceous (Turonian-- early Campanian) is based on comparisons with subsurface geological information (Winn et al., 1993; Bosworth and Morley, 1994) and overall faunal composition.

The fossiliferous Turkana Grits has so far yielded fossils of dinosaurs (Sertich et al., 2006) and other Mesozoic reptiles (O’Connor et al., 2011).

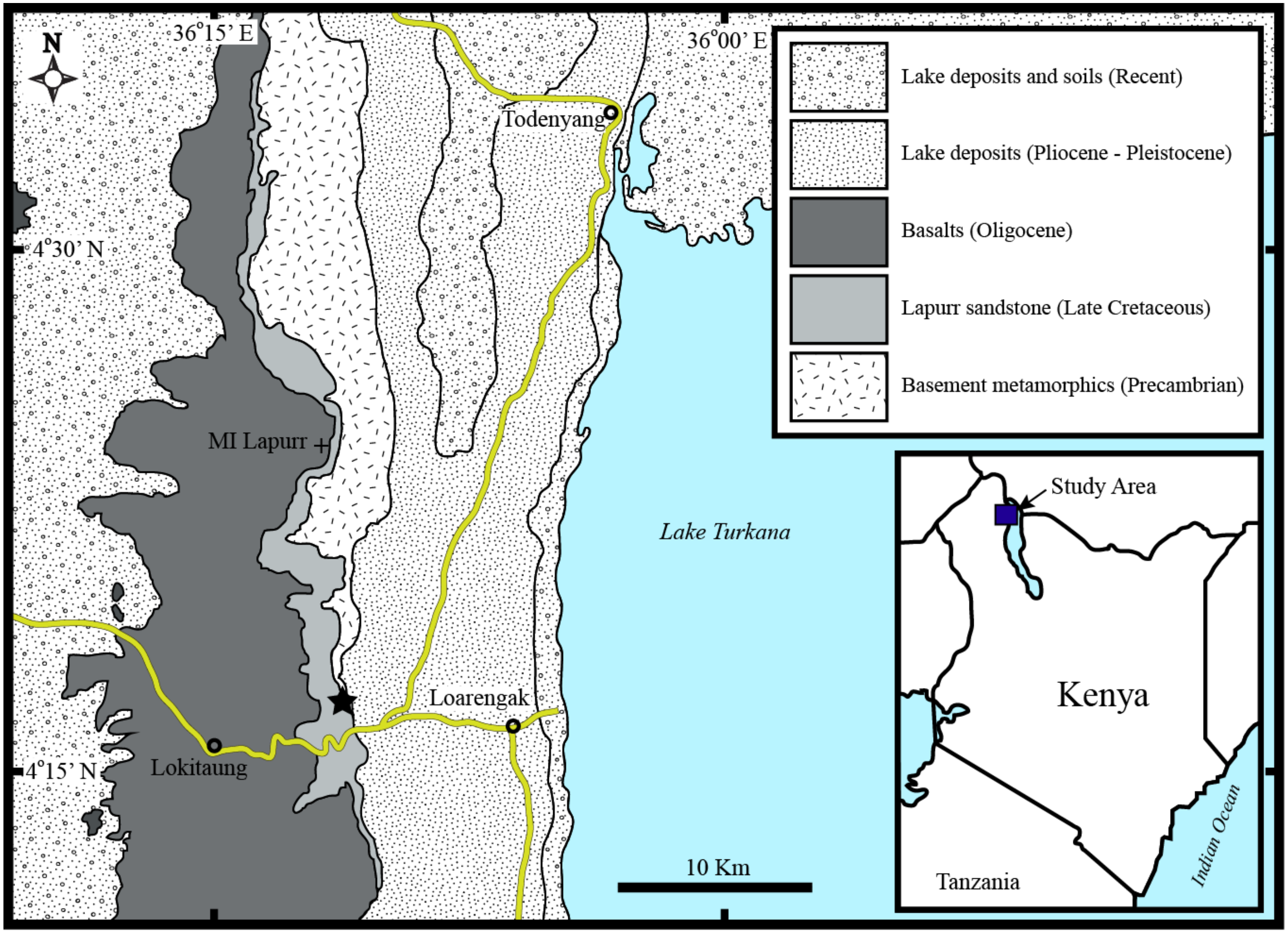

Figure 3.1: Locality map of the region of western Turkana, Kenya, where the material of Ceratodus genera was collected (modified from O'Connor et al., 2011). The star indicate the specimen recovery site.

3.2 Materials and Methods

This paper examines the partial tooth plate (KMN 8754) housed in the Kenya National Museum. A digital camera was used to capture the surface morphology of the specimen and Adobe Illustrator and Photoshop were employed for the measurements and annotation from background images. The angles and lengths of different parts of tooth plate represent standard metrics that have been used by several authors (Campbell & Barwick, 1985; Long, 1987; Kemp, 1997; Gottfried, 2009) as a way to provide ratios that are unique to different lungfish taxa.

3.2.1 Systematic Paleontology

Class SARCOPTERYGII Romer, 1955

Subclass DIPNOI Muller, 1846

Order CERATODONTIFORMES Berg, 1940

Family CERATODONTIDAE Gill, 1872

Genus *CERATODUS* Agassiz, 1838.

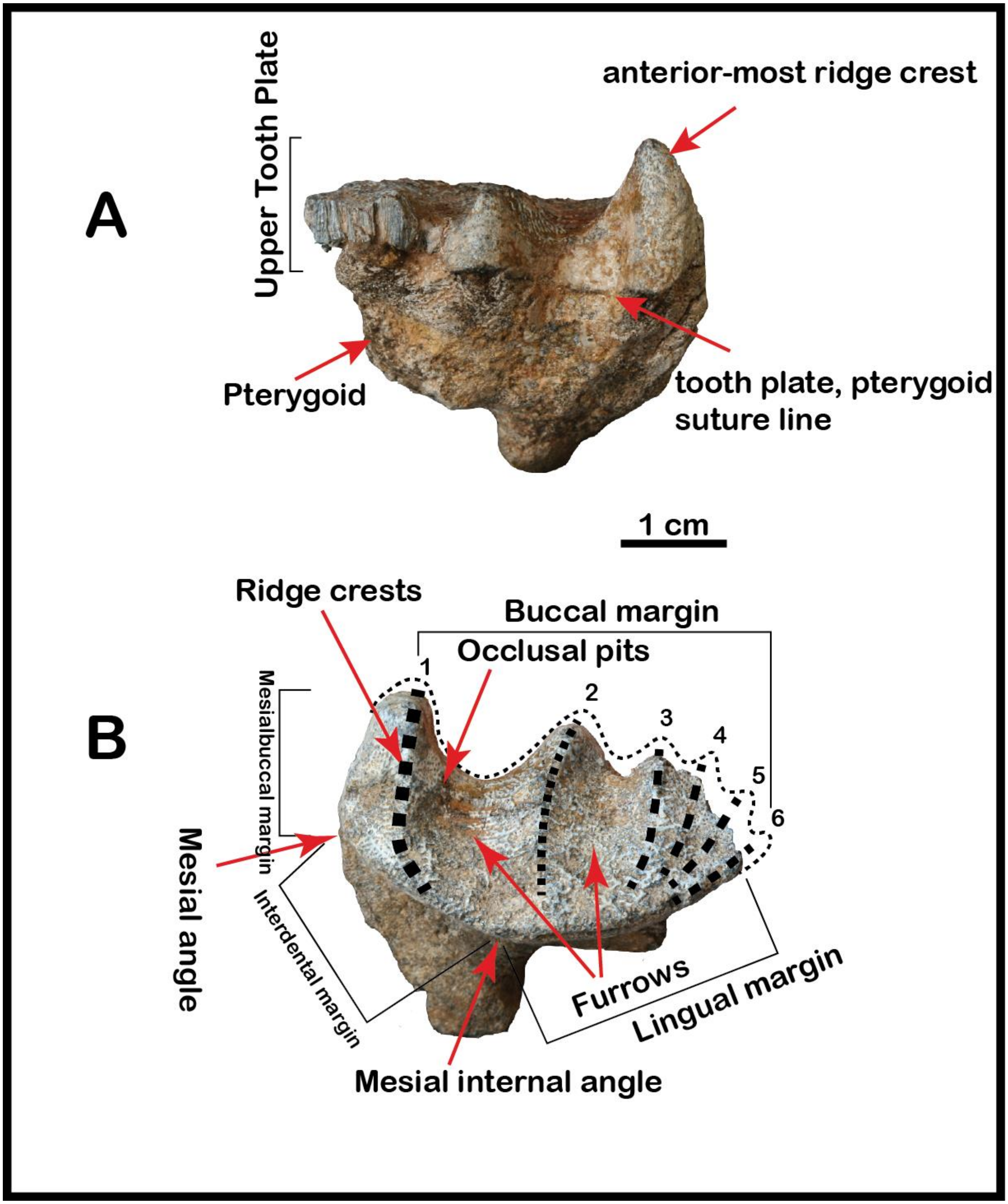

Figure 3.2: **A** lateral (buccal) view of the lungfish tooth plate specimen. **B** occlusal view of the specimen with annotations of different features and both angle and length measurements used in the study.

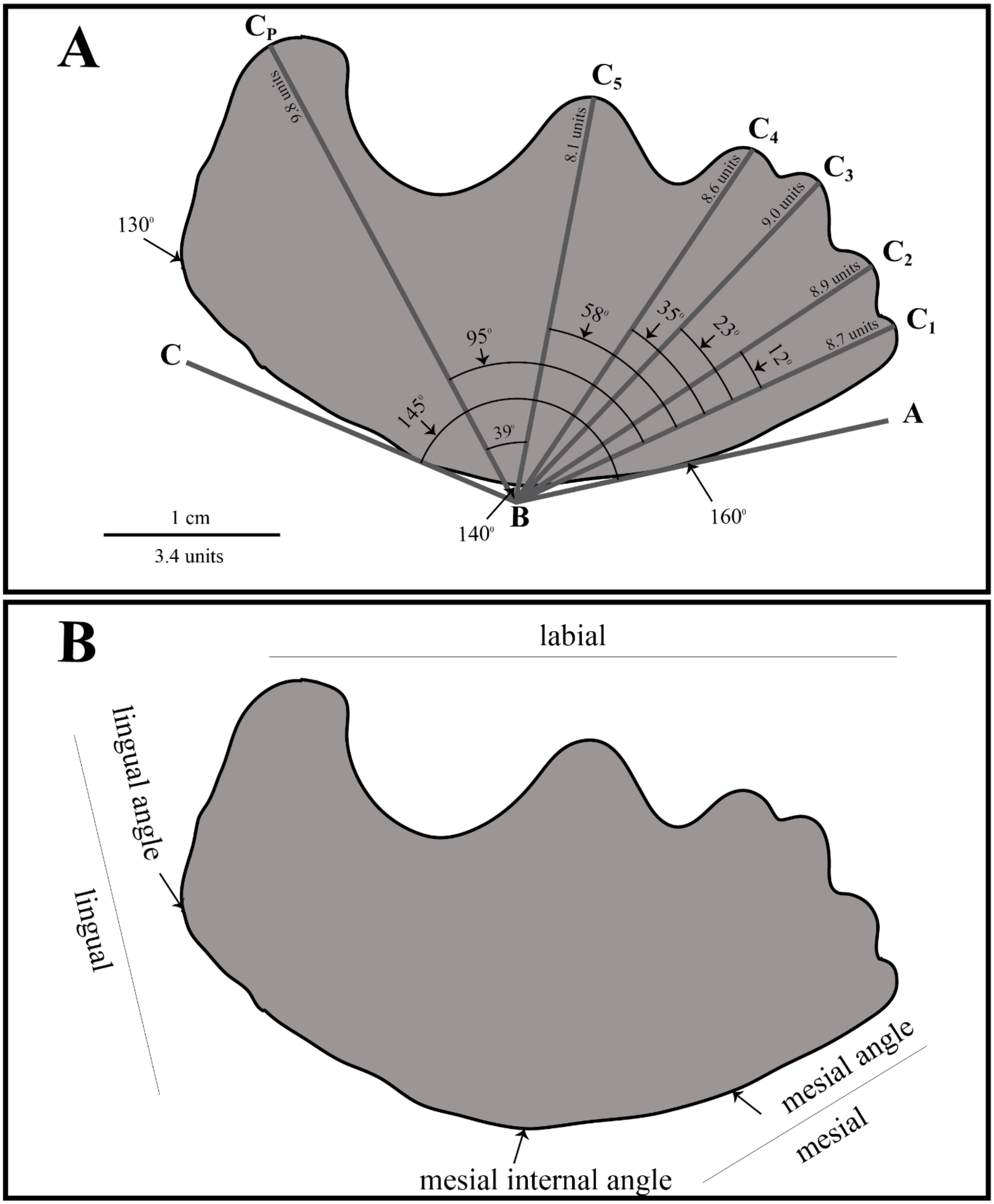

Figure 3.3: Terminology and position of measurements as used by Kirkland (1987) based on *Ceratodus stewarti* after Vorob'yeva and Minikh, 1968 and Martin, 1980. The top (**A**) illustrative drawing shows the inferred broken portion of lower part of the tooth. The lower drawing (**B**) showing orientation and reference points from which measurement in Table 3.1 were made.

Table 3.1: Measurements of *Ceratodus* specimen KMN 8754 from reference points provided in figure 3.3. Additional measurements were adapted from Milner & Kirkland (2006) for comparative purposes with *Ceratodus stewarti, C. fossanovum* (averaged from Kirkland, 1989, 1998) and *C. cf. guentheri*.

Measurement	***C. stewarti***	***C. guantheri***	***C. fossanovum***	***Turkana (KMN 8754)***
<ABC	115	100	119	140
<C_1C_P	86	77	90	95
<C_2C_P	65	51	49	58
<C_3C_P	33	24	21	35
<C_4C_P	na	na	na	23
<C_5C_P	na	na	na	12
BC_2/BC_1	82.6	94	77	82.7
BC_1/BC_P	101.7	89	96	112.6
C_1C_P/BC_P	139.2	122	128	154.1
C_1C_2/BC_1	56.5	32	61	63.3
C_1C_2/C_1C_P	41.3	44	44	46.3
C_1C_2/BC_P	57.5	39	57	71.3
C_2C_3/C_2C_P	61.2	50	60	44.6

3.3 Description

A massive left pterygopalatine tooth plate measuring 3.94 cm long (maximum length from C_P to C_1) and 2.4 cm wide (from C_2 to B) with six ridge crests and a partial pterygoid bone still attached to it. The ridge crests show consistent decrease from lingual to mesial margin with the inner obtuse angle (<ABC ~ 12^0) and right angled C_1C_P (<C_1C_P ~ 90^0). The ridges are shallow and relatively wide and flat.

Both lingual and mesial margins from obtuse angles, 130^0 and 160^0 respectively.

C_4 to C_1 angles are almost the same while the other two are the same.

C_5 is almost cutting the tooth plate in half.

The angle C_PC_5 is about 39^0

KNM 8754 is a left pterygopalatine tooth plate, preserving a small portion of the pterygoid bone. The tooth plate fragment is relatively large, measuring 4.2 cm long and 2.5 cm wide giving it a length:width ratio of 3.5:2. The tooth plate is wide and short, with six apparently non-tuberculated radial ridges of variable height from occlusal surface. In general, the apical margin of the ridges is not sharply crested. The ridges are well developed and separated by deep and wide interior furrows that become shallower posteriorly. There are four small ridges at the posterior end, all of which are very close to one another. Abraded petrodentine covers the entire occlusal surface of the tooth plate and is particularly noticeable along the ridges.

The four well-preserved posterior ridges are smoothly curvilinear and converge toward the middle of lingual margin (Figure 3.2). The posterior-most ridge (Cp) is nearly straight. By contrast, the anterior-most ridge (C1) has a distinct bend (about 130^0) at approximately two-thirds of the distance from the buccal margin. The second ridge is intermediate (C2), being curvilinear, but having the most significant bend along its course. In general, the ridges are relatively wide and flat with the exception of C1. The angle at the mesial-buccal margin is approximately 160 degrees. The very wide mesial internal angle is approximately 140 degrees, contrasting with the typically less than 120 degrees known for most species of *Ceratodus*. The largest portions of the first, second and third ridges are nearly parallel to the mesial-buccal margin, whereas the last three posterior (or distal) ridges form progressively oblique angles to the mesial-buccal margin and become increasingly parallel to the lingual margin.

3.4 Discussion

The features and biometry based on angles between ridges and length to breadth ratio within the specimen RRBP 04289 and how it compares with other previously studied lungfishes, in conclusion, is decidedly typical of the order Ceratodontiformes. In the first place of support for this is the possession of features like; presence of four well-preserved posterior ridges that are smoothly curvilinear and converge toward the middle of lingual margin while the second ridge is intermediate, being curvilinear, but having the most significant bend along its course. In the second place of support for this is the, it is how the measurements fit in well within the genus; the curvature of ridges from the mesial to lingual side of the tooth plate angles are slightly obtuse to very acute while length ratios display constancy almost throughout with the exception.

Martin, 1982a uses sharpness of tooth plate crests to differentiate Ptychoceratodontidae, with high cutting crests from Ceratodontidae which have low, broad crushing crests. The specimen RRBP 04289 described herein is characterized with relatively broad, flat crests and very shallow furrows which would indicate a family association with the Ceratodontidae with three genera, *Ceratodus*, *Neoceratodus* (the surviving monotypic extant Australian genus) and *Metaceratodus* (Schultze, 1992). Previously (Chapman, 1914) considered it as a subgenus because the features appeared to be between the two.

Despite having some slight damage on edges, broken pterygoid bone from beginning to the end of the tooth plate, due to wear the key features (Kemp, 1997) such as: broad and flat tooth plates; robust ridges that originate medially; and presence of occlusal pits and preservation of the suture line which shows how firmly they were attached, and suggests the specimen belongs to the genus *Ceratodus*. This fits well in Agassiz (1838) original description of the genus *Ceratodus,* characterized by having a convex margin directed inward (i.e., lingually), with the prongs (ridges) facing outward.

The differences between the specimen and *Lupaceratodus* and another ceratodus described in “Chapter 4” in this work. This tooth plate clearly differs from *Lupaceratodus* in lacking curved ridges (only the first-preserved ridge in RRBP 04289, KNM 8754 is curved). The specimen also differs from another African Cretaceous fossil, *Ceratodus tuberculatus* (Churcher et al., 2006) origionally *Retodus tuberculatus* (Tabaste, 1963) from Kharga Oasis, Egypt, by the lack of large oval punctuations and especially by the absence of a line of tubercles along the apical margin of each ridge. Finally, KNM 8754 differs from *Metaceratodus* (Chapman, 1914; Schultze, 1992; Kemp, 1997) from Australia and South America in southern hemisphere by the shape of the ridges, which are larger and less robust than those of *Metaceratodus*.

Cretaceous lungfish (Martin, 1995) are readily distinguishable from Triassic and Jurassic by having mostly six and in few cases five or seven different number of ridge crests. Their tooth plates are broad (with ratio almost 2:1 for breadth:width) and relatively low ridge crests (Milner & Kirkland, 2006). The ratio of breadth to width for this specimen is 3.5:2. The lingual margin is near straight (>160 degree) while the mesial internal angle is about 110 degrees. Like most typical Cretaceous *Ceratodus,* a line from second ridge tip to mesial internal bend, appear to divide the tooth plate into two halves.

Despite of the minor differences, it is clear that this material resembles the general shape, form of the ridges and ornamentation of the *Ceratodus africanus* tooth plates (Cunha and Ferreira, 1980) and those of *Ceratodus humei* (Toledo, 2006). That said, there is no enough biometric or distinctive features evidence to place in one of the species or erect new species for the moment.

Of the very significant interest is that this specimen from Turkana is the first representative of ceratodontid lungfish in the region and age which highlight the closing geographical gap from what previously restricted in the northern and western Africa. However, since this specimen is only partially preserved, it is not possible to refer it to any of the nominal species of the genus Ceratodus, nor to erect a novel species based on the preserved morphology (Vorob'eva, 1967).

Systematic interpretation based on tooth plates must be approached cautiously because of intraspecific and ontogenetic variability, which can hinder both quantitative and qualitative analyses (Alves, 2012). Kemp, 1996, 1997 recognizes the intraspecific and ontogenetic variability among the genus *Ceratodus* and *Neoceratodus* which further complicates the possibility of pinpointing confidently for now based on the pterygopalatine specimen we have regardless of its uniqueness to name it as a separate new species. Smith & Krupina, 2009 point out the easier way to differentiate adult from juvenile lungfish is by observing on their tooth plate the presence or absence of conical bumps (denticles). The presence or indication of gradient size change of denticles imply the plate is from juvenile lungfish.

To my knowledge this represents the second described Cretaceous lungfish fossil from the eastern part of Africa, following (Gottfried et al., 2009) description of *Lupaceratodus useviaensis* from middle Cretaceous Galula Formation (Roberts et al., 2010) exposed in the Rukwa Rift Basin of Tanzania.

The assigning of the Lapurr Grits, Turkana, Kenya to the upper Cretaceous based on the remains of preserved fragmented dinosaur bone (Arambourg and Wolf, 1969; Sertich et al., 2006) and later description of pterodactyloid pterosaur (O'Connor et al., 2011) get new evidencing support from the description of *Ceratodus* lungfish, which were not only present during this period but also have had known occurrence in fossil record to the north, from the Kharga Oasis, Egypt.

In overall tooth plate structure and biometry, the specimen in the present study mostly resembles the genus Ceratodus described by Agassiz, 1838 in his description of *Ceratodus* *diutinus*, especially in the robustness of the ridges and its characteristic obtuse to acute curvature and angles formed in between. This study adds evidence to previous knowledge that Lapurr (Grits) Sandstone in the northwestern part of Kenya, Turkana is appropriately assigned to the upper Cretaceous.

CHAPTER IV

4 A NEW SPECIES OF THE LUNGFISH CERATODUS (DIPNOI) FROM THE LATE PALEOGENE OF THE RUKWA RIFT BASIN IN SOUTHWESTERN TANZANIA

4.0 Introduction

Lungfish species of the extinct genus of *Ceratodus* have been found from all continents with the exception of Antarctica (where the only record is from the Triassic of Antarctica (Young, 1991)) in geological deposits of Mesozoic age (Cavin et al., 2015). During this time, they were widespread and diverse. In this part of Africa there is no single record of *Ceratodus* in Cenozoic geological deposits, instead *Protopterus* genus is the only one previously described.

Several authors (e.g. Marchalonis, 1969; Kemp, 1977; Shuler, 2000) suggested the very close relationship between *Ceratodus* genus and the extant Australian lungfish *Neoceratodus forsteri* that in turn share same Ceratodontidae family. The other two surviving lungfish genera are *Protopterus* from Africa and *Lepidesiren* from South America.

Ceratodus is recognizable by its unique tooth plate with grooves and ridges morphological features for both upper and lower plate. Despite change of number of ridges over time (Martin, 1995), but principally they look morphologically the same. In some cases, skull roof has reliably been used to identify *Ceratodus* (Kemp, 1998) despite the variation in the number and arrangement of bones composing the skull roof.

Following the recent discoveries by two major expeditions, the Rukwa Rift Basin Project (RRBP) and Turkana Project in East Africa, of several vertebrates including lungfishes in a region that previously termed as “African Gap” by O’Connor et al., 2011 due to the evolutionary history of the fossil vertebrate taxa being poorly documented have sparked more research work to be done.

In this work using well-preserved pterygoid palatine tooth plate, I report a new species of a *Ceratodus* genus from the Late Paleogene of the Rukwa Rift Basin (RRB) in Southwestern Tanzania.

4.1 Geographical and Geological Context

The Nsungwe Formation is exposed at the Songwe area in Mbeya region, southwest of Tanzania (Figure 4.1) between ($8^o30'$, $8^o40'$S, $33^o00'$, $33^o10'$E) latitude and longitude respectively.

It consists of a succession of two members, the lower Utengule Member and upper Songwe Member of about 400 meters thick, spanning much of the Lower Paleogene especially Oligocene period.

The sediments in the lower member, that overlying purple and red sandstones of the Galula Formation, are dominantly coarse-grained and provide the best exposures in the Formation and can stand out white sandstone/conglomerate unit and composed mainly of well-rounded quartz pebbles.

The top sequence of Songwe member is almost four times thicker than and distinct from Utengule Member below it by the composition of finer grains varying from a thin, green cross-bedded/ripple-laminated sandstone to a series of richly fossiliferous red, orange, and gray–green siltstones, mudstones, laminated claystones, lenticular sandstones, and devitrified bentonitic tuffs (Roberts et al., 2010).

This specimen and other vertebrate fossils in locality are from within same fluvial facies at localities *TZ-01, TZ-01S, TZP-2,* and *Nsungwe 2,* four of the richest localities of the Songwe Member of the Nsungwe Formation.

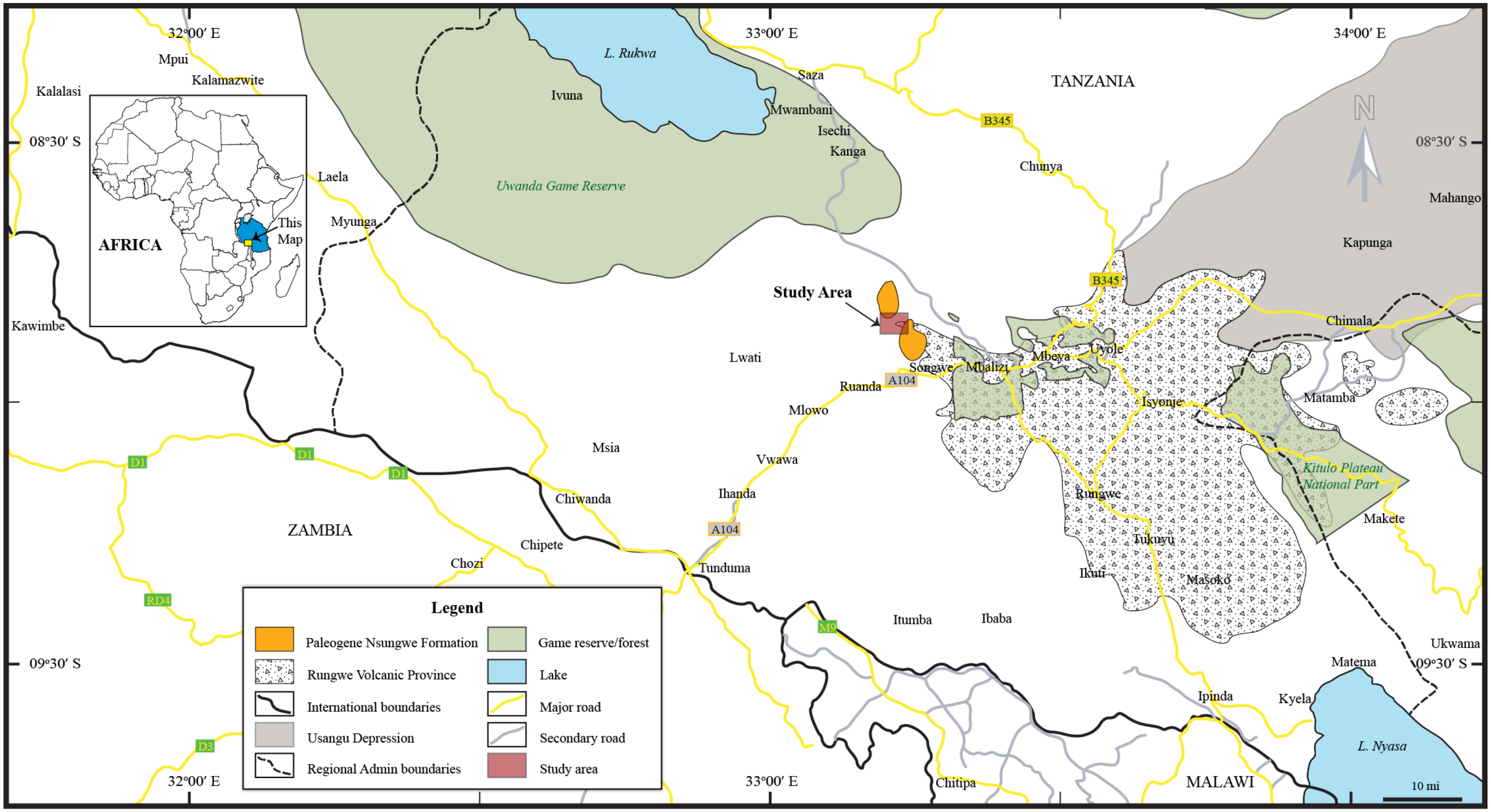

Figure 4.1: Geographical area and outcrop area of the Nsungwe Formation where the specimen described herein was recovered in the Rukwa Rift Basin, southwestern Tanzania. The inset Africa map showing Tanzania (shaded black), study area depicted as a grey box.

4.2 Materials and Methodology

The fossil material (specimen RRBP 04289) described in this work was collected during field campaigns by the ongoing Rukwa Rift Basin Project (RRBP) from the late Oligocene Nsungwe Formation in the Rukwa Rift Basin of southwestern Tanzania conducted since 2001. It is a single well-preserved pterygopalatine tooth plate currently held at Ohio University and available for study upon request; the fossil is the property of the Tanzania Antiquities Division.

Lungfish fossils were mechanically prepared by K. Whitman. Comparative materials included Fig. 3 of RRBP 04289 (*Lupaceratodus useviaensis*) and from different literature including comparisons of rarer forms were made with specimens figured in the literature (Kirkland, 1987; Milner & Kirkland, 2006).

Specimens were magnified on a Nikon stereomicroscope bundled with Spot Advanced software (version 3.5.8), and photographed using a Spot Insight QE Color camera (model 4.2, image resolution 2048 by 2048) at different focal points, creating image stacks of 4-9 pictures per specimen. Focused photomontages were then assembled from stacks of images using the program Helicon Focus (version 5.3.4) to generate the figure plates. For each specimen, the angular and length measurements were made using Adobe Illustrator and Photoshop CS 6. Most Nsungwe lungfish specimens are incomplete, although some allow for precise measurements of some aspects of their morphology.

Specimens were assigned to lungfish taxon based on shape and configuration of the ridges of the tooth plates. Tooth plate characteristics have previously been used in differentiation and description of lungfishes (e.g. Martin, 1980, 1982). Morphological descriptions in the following sections follow terminology used on extant *Protopterus aethiopicus* from Tanzania (*Figure 4.2*).

4.3 Systematic Paleontology

Class SARCOPTERYGII Romer, 1955

Subclass DIPNOI Muller, 1846

Order CERATODONTIFORMES Berg, 1940

Family CERATODONTIDAE Gill, 1872

Genus *CERATODUS* Agassiz, 1838

Species *CERATODUS MBEDEAE,* sp. nov (Figure 4.2)

4.4 Specimen

Rukwa Rift Basin Project (RRBP) 09247, incomplete left pterygopalatine tooth plate.

4.5 Diagnosis

Unlike other typical *Ceratodus,* there are five distinctive features/reasons that seem to be unique to this specimen. The first one is crests C2 and C3 are more cylindrical (Figure 4.2) in nature with conical (marked by blue stroke on Figure 4.2) like feature (cusps) developing on the mesial-internal side. The furrow between the two is smallest and deepest of the rest. Secondly, the buccal margin displays unusual closure between the consecutive ridges. That make them when stood upright look more like prearticular (upper) tooth plate of *Protopterus* with the exception of more than three ridges that is the normal state for *Protopterus*. Also for that reason show no much difference in the crests end as typical Ceratodus would have that as a consequence makes it impossible to use measurements as used by Kirkland, 1987 based on *Ceratodus stewarti*, after Vorob'yeva and Minikh, 1968 and Martin, 1980 to do comparative analysis with other Ceratodus. Thirdly, C4 and C5 remarkable flattening toward each other leaving huge furrow on either side. Both ridges have developed a line of weakness (marked by red stroke in Figure 4.2) as if would be shed or knocked off somehow later. That feature is unique to this specimen only among *Ceratodus*. The broken ridge 1 or C1 seem to be flat with little bump (ridge) than continuation of flat furrow between C1 and C2 which is more like PRTc in *Protopterus*. Fourthly, the relative curvature (bending) as seen in Figure 4.2 from C1 to Cp is like a bend in *Protopterus* to the prearticular symphysis (PRsymp).

4.6 Locality and Age

The studied specimens were recovered from Rukwa Rift Basin (RRB) within East African Rift Valley System which began forming in the Miocene (22 – 25 Ma.), on the north of Lake Nyasa and southwest of Lake Tanganyika. The deposits are mainly a sequence of fossiliferous continental rift-fill.

4.7 Etymology

The species is named *Ceratodus mbedeae*, sp. Nov. in recognition of prominent Tanzanian sedimentologist, Prof. Evelyne Mbede, who has worked extensively in the region.

4.8 Description

A small (about 12 mm C_1Cp long and 6 mm BC_4 wide ceratodontid lungfish tooth plate with six ridge crests. In between the ridges are relatively wide well-like furrows. The furrows do not cut-across the edges of the crown. They are partially filled with grayish medium to coarse-grained sediment.

The tooth plate crown is ornamented with straight ridges in the middle and curved ridges on the lingual and mesial sides. From the labial viewpoint ridges, appear to be relatively flat with smooth round corners. The five furrows decrease outwardly in size from the largest in the middle.

With the exception of C_1C_P being slightly acute the rest of the ridges form sharp angles, the sharpest being C_5C_P - 20 degrees.

This single known specimen of *Ceratodus mbedeae* sp. nov. (RRBP 09247) is a moderately well-preserved pterygopalatine tooth plate with broken terminal ridges (C1 & Cp). Due to wear, the buccal margin which exhibits unusual features is partially broken. On the mesial margin, the crest of the ridge C1 is partially broken but appears to be low and well joined above the furrow between C1 and C2. The occlusal surface is worn and smooth with a pointed mesial internal end and multiple ridges within an interdentenal mass of flattened lake-like furrows in occlusal view (Figure 4.5). The occlusal surface for C4 and C5 closes in while C6 is flatter anteriorly on the lingual margin.

The pterygopalatine specimen is about 12 mm long and 6 mm wide with the typical *Ceratodus* length:width ratio of 2:1. The specimen is completely disarticulated from the pterygoid with unusual bending at its anterior end instead of a more concave to flat shape. Overall, the specimen is morphologically unique for its time interval relative to temporal availability from that seen in other *Ceratodus* species from Africa and other continents.

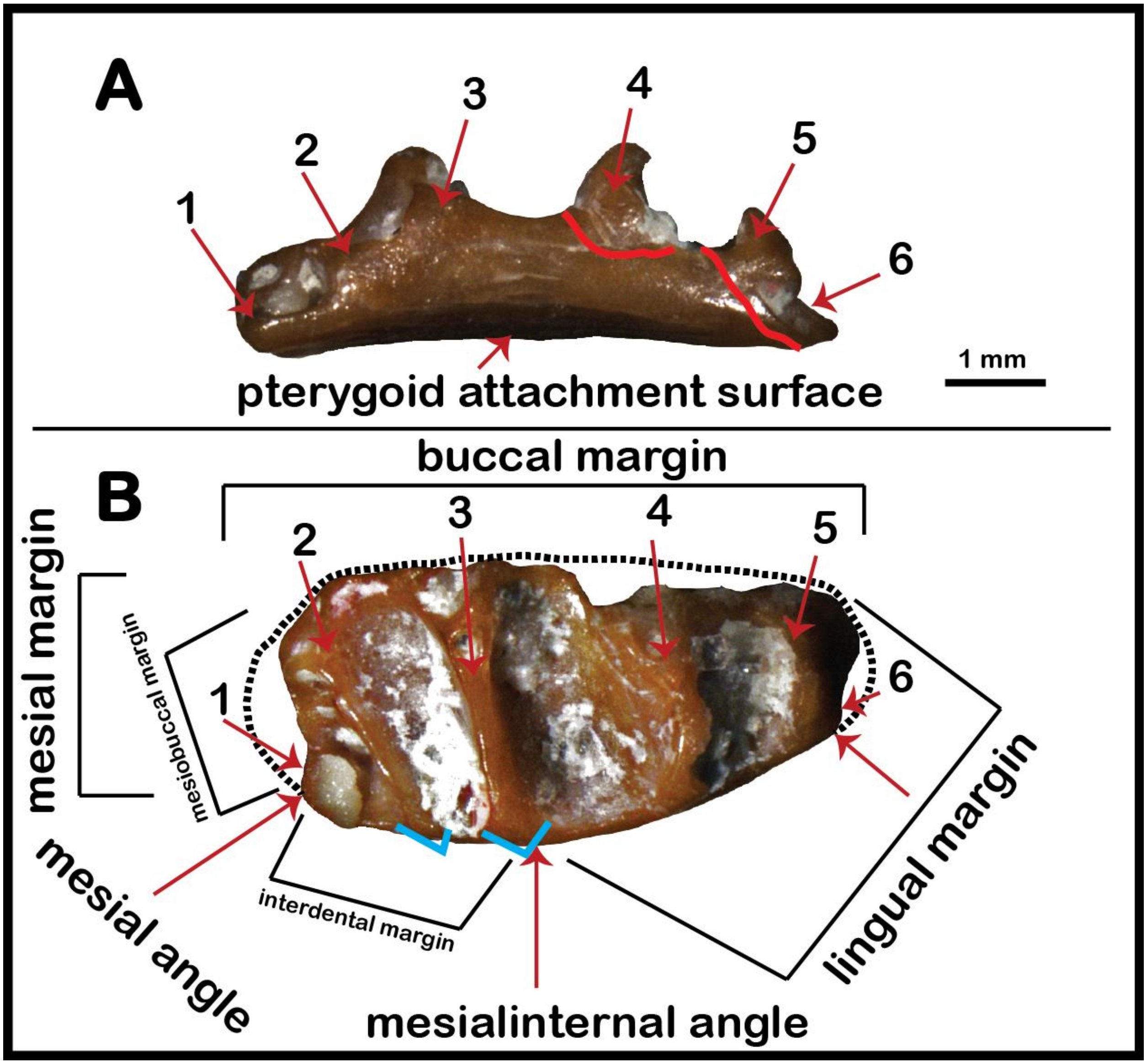

Figure 4.2: Illustration of the RRBP 09247 lungfish specimen ceratodontid (*Ceratodus mbedeae* sp. nov.) tooth plate material showing morphological terms used in this study **A**. is lateral posterior (buccal) view and **B**. is occlusal top view with sediment partially filling furrows.

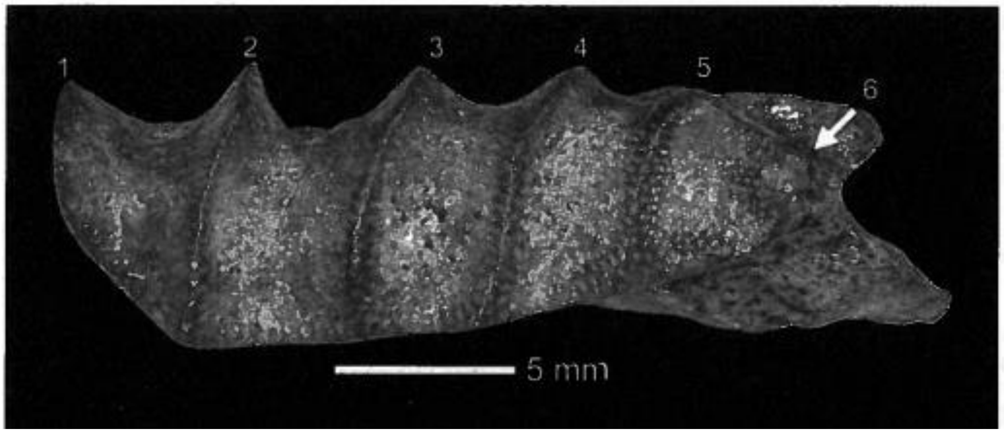

Figure 4.3: For comparison purpose *Lupaceratodus useviaensis* upper left tooth plate and a portion of the pterygoid element (RRBP 04289), from the Cretaceous Galula Formation (Red Sandstone Group), Rukwa region, southwestern Tanzania (Gottfried et al., 2009)

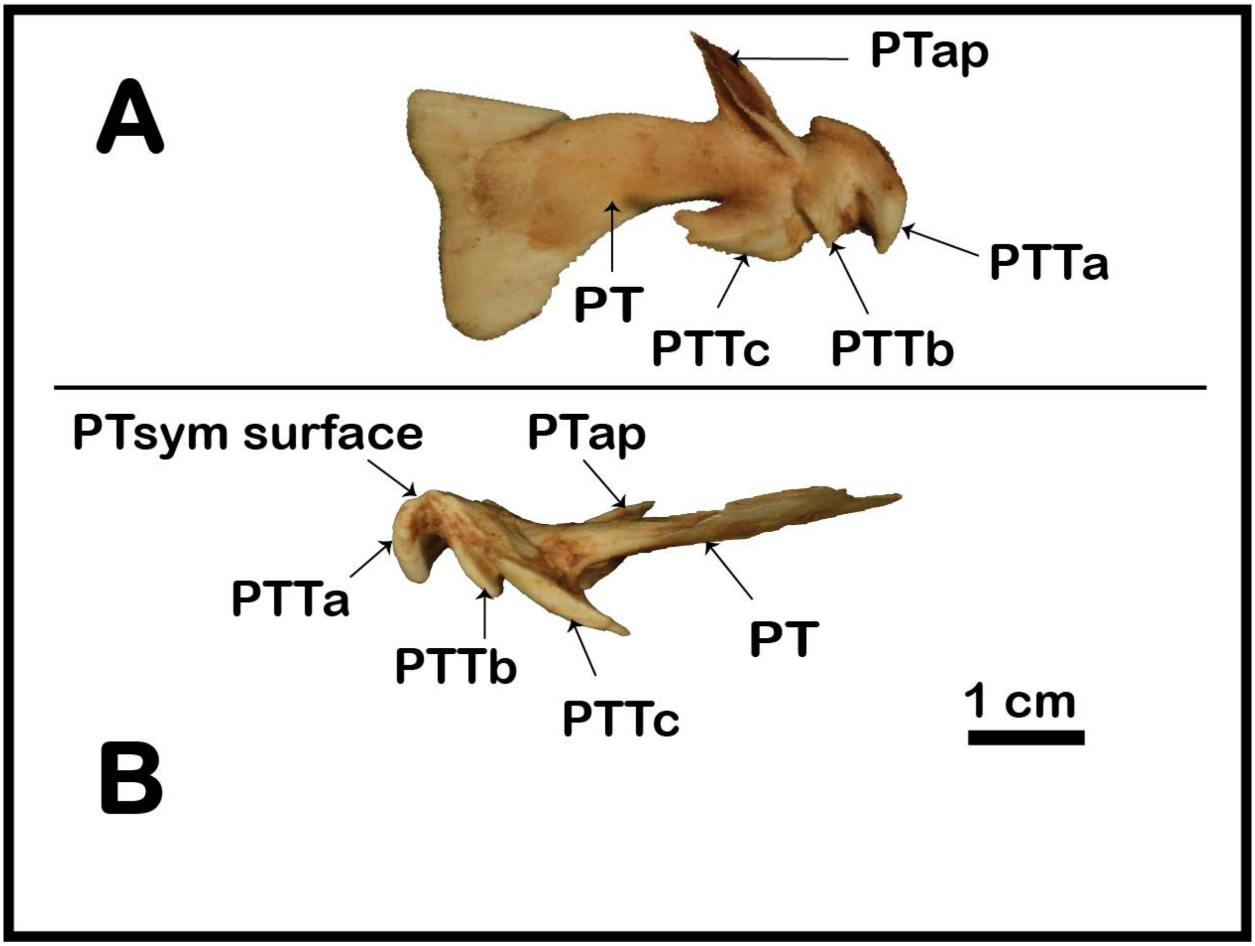

Figure 4.4: For comparison is modern lungfish *P. aethiopicus* from L. Victoria Tanzania. A is the occlusal lateral view and B is dorsal lateral view.

4.9 Discussion and Conclusion

Despite the wear and partial tear at the edge portion of ridge 1 and 6, the state of preservation and the morphological clarity of important features of the single specimen RRBP 04289 allow to confidently assigning it to the *Ceratodus* genus and new species. The proposed new species is *Ceratodus mbedeae* sp. nov. The specimen described herein is characterized with relatively broad, flat crests and very shallow furrows.

In Africa, there are three major lungfish genera in fossil record, *Lavocatodus, Protopterus* and *Ceratodus*. The tooth plate for the genus *Protopterus* has one columnar anterior most blade with cusp and the other two without cusps pointing backward (Otero, 2010) while the *Lavocatodus* genus is identified by the absence of a distinct suture between the pre-angular and pre-articular in the tooth plates (Martin, 1995). On the other hand, this specimen RRBP 04289 like the typical *Ceratodus* defined originally by Agassiz, (1838) is mainly characterized by having a convex margin directed inward (i.e. lingually) with the prongs (ridges) facing outward.

The number of ridges on the *Ceratodus* has been associated with the evolution of the taxa by gradual increase of the ridges as part of their adaptation in new ecological habitats. Teller, 1891 documented when reporting *Ceratodus sturii* that Triassic *Ceratodus* exhibited more than five crests on the upper/lower tooth plates, noting that all members of the genus before the Triassic exhibited four or less crests. Cope, 1876 suggested that *Ceratodus* specimens exhibiting more than five crests were rare and that those found in Cretaceous deposits exhibited six ridges. The ridges in the Cretaceous forms were weak, flat and transversal and backwardly directed crests like that of *C. sturii* from Triassic. Churcher & deIuliis, 2001 interpreted the morphology on *C. humei* from the Baris Formation in the Kharga Oasis of Egypt to exhibit five radiating ridges and crests with a tiny sixth denticulation. Cretaceous *Ceratodus* generally exhibit distinctive four bowed shearing ridges that are subparallel and at a right angle to both the lingual and buccal borders of the element (Churcher et al., 2006). Tabaste, 1963 suggested the typical occlusal pattern for Cretaceous *Ceratodus* to be six ridges, or alternatively five ridges with additional one or two reduced lingually. The closest modern form to the Ceratodus specimens described herein thought to be the extant Australian lungfish, preserving at maximum seven ridges directed forwardly, with the seventh small or sometimes absent (Kemp, 1977).

The lungfish tooth plate (RRBP 04289) from the Nsungwe Formation is found alongside other Cenozoic taxa including invertebrates (Feldmann, 2007), anurans (Blackburn et al., 2015) crocodylians (Stevens et al., 2016), snakes (McCartney et al., 2014), and mammals (Stevens et al, 2005, 2006, 2008, 2013).

Elsewhere in the region (East Africa) we find only *Protopterus* genus fossil lungfish which belong to the Lepidosirenidae. Other lungfish material from Cretaceous deposits in the region include a *Ceratodus* lungfish tooth plate (Chapter 3 of this work) from Lupurr, Turkana Kenya and *Lupaceratodus useviensis* (Gottfried, 2009) from Usevia, in western Tanzania.

The tooth plate described in this study is representative of one of the scarce and sparse record of lungfish record in Africa and first from Paleogene geological deposits in Africa. Previously, most lungfish tooth plate are from the Early Cretaceous and have been assigned either to the genus *Ceratodus* or *Lavocatodus* while the lungfish material assigned to the genus *Protopterus* mostly of Cenozoic age and from sub-Saharan Africa. Consequently, for the first time introduce a new species, *Ceratodus mbedeae* from the Late Paleogene of the Rukwa Rift Basin in Southwestern Tanzania.

CHAPTER V

5 A NEW PROTOPTERUS ASSEMBLAGE RECORD OF CENOZOIC LUNGFISHES FROM TANZANIA

5.0 Introduction

Lungfish are one of living lobe-finned fish whose records date back to the Devonian, distinctively can tolerate low-oxygen environments associated with seasonal drying. Today there are three genera of extant lungfish: *Protopterus* (Africa), *Lepidosiren* (South America), and *Neocerotadus* (Australia). In Africa, lungfish are represented by four species all of them belonging to the genus *Protopterus*.

The Cenozoic record of African lungfishes is more geographically and phylogenetically diverse. Of over 50 publications documenting Cenozoic fossil lungfish, less than 5% derive from south of the Sahara (Table 5.1). Yet it is the sub-Saharan region that hosts all modern African lungfish (Table 5.2). The eastern African Cenozoic lungfish record documents *Protopterus* sp. from a number of sites in Kenya, including Rusinga, Loperet, Ombo, Kirium, Lothagam, Omo River and East Turkana. Pleistocene deposits in Manonga Valley in central Tanzania have long been the only Cenozoic lungfish record in that country. Given the sparse record of the Dipnoan clade in the African Cenozoic fossil record, any new materials are important for understanding the diversification of the clade.

In this chapter, I describe recently collected lungfish fossils from the late Oligocene Nsungwe Formation in the Rukwa Rift Basin (RRB) of southwestern Tanzania (Figure 5.1).

Table 5.1: The Cenozoic fossil record of African lungfishes (adapted from Otero, 2010)

Species	Locality	Country	Age	Reference
P. sp.cf aethiopicus	Ishango	RDC	Middle Pleistocene	Greenwood, 1959
Protopterus sp.	Katanga	RDC	Middle Pleistocene	Brooks et al., 1995
Protopterus sp.	Ishango	RDC	Middle Pleistocene	Greenwood, 1959
Protopterus sp.	East Turkana	Kenya	Early Pleistocene	Schwartz, 1983
Protopterus sp.	Kanam	Kenya	Early Pleistocene	Schwartz, 1983
Protopterus sp.	Upper Semliki	RDC	Early Pleistocene	Greenwood, 1959
Protopterus sp.	Lake Malawi	Malawi	Early Pleistocene	Coryndon, 1966
Protopterus sp.	East Turkana	Kenya	Late Pliocene	Schwartz, 1983
Protopterus sp.	Lothagam	Kenya	Late Pliocene	Stewart, 2003
Protopterus sp.	Omo River	Kenya	Late Pliocene	Schwartz, 1983
P. sp. cf. annectens	Wadi Natrun	Egypt	Late Pliocene	Stromer, 1914
Protopterus sp.	Lake	Uganda	Early Pliocene	Van Neer, 1994
Protopterus sp.	Lothagam	Kenya	Early Pliocene	Stewart, 2003;
Protopterus sp.	Sinda Mohari	RDC	Early Pliocene	Greenwood and Howes, 1975
Protopterus sp.	Manonga	Tanzania	Early Pliocene	Stewart, 1997
Protopterus sp.	Lake	Uganda	Late Miocene	Van Neer, 1994
Protopterus sp.	Lothagam	Kenya	Late Miocene	Stewart, 2003
Protopterus sp.	Sinda Mohari	RDC	Late Miocene	Greenwood and Howes, 1975
Protopterus sp.	Manonga	Tanzania	Late Miocene	Stewart, 1997
Protopterus sp.	Kirimun	Kenya	Middle Miocene	Van Couvering 1972, 1977
Protopterus sp.	Ombo	Kenya	Middle Miocene	Schwartz, 1983
Protopterus polli	Malembe Cabinda	RDC	Early Miocene	Dartevelle and Casier, 1949
Protopterus sp.	Loperot	Kenya	Early Miocene	Van Couvering 1972; 1982, Mead, 1975
Protopterus sp.	Rusinga	Kenya	Early Miocene	Greenwood 1951; Van Couvering 1972, 1977, Schwartz, 1983
Lepidosiren paradoxa	Fayoum	Egypt	Early Oligocene	Stromer, 1910
Protopterus aethiopicus	Fayoum	Egypt	Early Oligocene	Stromer, 1911
Protopterus annectens	Fayoum	Egypt	Early Oligocene	Stromer, 1912
Protopterus libycus	Fayoum	Egypt	Early Oligocene	Stromer, 1913
Protopterus sp.	Dur At Talha	Libya	Late Eocene (Priabonian)	Otero et al. in review
Protopterus sp. cf. elongus	Birket Qarun	Egypt	Late Eocene (Priabonian)	Murray et al., 2010
Lavocatodus sp.	Bir el Ater	Algeria	Middle Eocene	Martin, 1995
Protopterus elongus	Tilemsi	Mali	Middle Eocene	Martin, 1996
Lavocatodus humei	Tamaguilelt	Niger	Middle Eocene	Martin 1983; Patterson and Longbottom, 1989
Lavocatodus sp.	Tamaguilelt	Niger	Middle Eocene	Lavocat, 1955
Protopterus sp.	Glib Zegdou	Algeria	Middle Eocene	Adaci et al., 2007
Protopterus sp.	El Kohol	Algeria	Early Eocene	Martin, 1995
Lavocatodus casieri	Iullemeden	Niger	Paleocene (Thanetian)	Cappetta, 1972
Lavocatodus giganteus	In Farghas	Mali	Paleocene (Thanetian)	Martin, 1995
Protopterus sp.	Ilimzi	Morocco	Paleocene (Thanetian)	Martin, 1995
Protopterus sp.	Adrar Mgorn	Morocco	Paleocene (Thanetian)	Martin, 1995
?Protopterus crassidens	Dakhlel Oasis	Egypt	Campanian	Churcher and De Iuliis, 2001
?Protopterus regulatus	Bahariya and Kharga	Egypt	Campanian	Schaal, 1984
Lavocatodus protopteroides	Several localities	Sahara	Turonian-Campanian	Tabaste 1963; Martin, 1984a
Lavocatodus protopteroides	In Beceten	Mali	Coniacian-Santonian	Martin, 1983
Protopterus nigeriensis	In Beceten	Niger	Coniacian-Santonian	Martin, 1997
Protopterus sp.	In Beceten	Mali	Coniacian-Santonian	Broin et al., 1974
Protopterus sp.	Wadi Milk	Sudan	Cenomanian	Werner, 1994
Lavocatodus protopteroides	Wadi Milk	Sudan	Cenomanian	Werner, 1995
Lavocatodus humei	Wadi Milk	Sudan	Cenomanian	Werner, 1996
Lavocatodus humei	Djoua Valley	Egypt	Cenomanian	Haug, 1905
Lavocatodus humei	Bahariya and Kharga	Egypt	Cenomanian	Schaal, 1984
Lavocatodus humei	Kem Kem beds	Morocco	Cenomanian	Tabaste 1963; Dutheil, 1999
Lavocatodus humei	Tafilalet	Mali	Cenomanian	Tabaste, 1963

This chapter follows description of *Lupaceratodus useviaensis* (Gottfried et al., 2009) from Cretaceous Usevia Formation deposits in the region, and represents the first Late Oligocene lungfish from the Rukwa Rift Basin (Gottfried, 2006). Importantly, recovery of dipnoan materials from the Paleogene of Africa below the equator helps to address a sizable gap in the fossil record of lungfishes, adding breadth to the Nsungwe Formation fauna and deepening paleoecological insights into the late Oligocene record of the continental African interior (Roberts et al., 2010, 2012). This study builds upon on the late Oligocene Nsungwe Formation faunal record of fossil invertebrates (e.g., Feldmann et al., 2007), alestid fishes (Stevens et al., in press), ptychadenid anurans (Gottfried, 2007, Blackburn et al., 2015), crocodylians (O'Connor et al., 2012.), boid and colubroid snakes (McCartney et al, 2014), and several clades of mammals (Stevens et al, 2005, 2006, 2008, 2009a & b, 2013).

5.1 Geological and Geographical Setting

The Nsungwe formation represents the outcropping eroded sedimentary rocks of the sequence of continental rift-fill deposits of the Songwe sub-basin of the Rukwa Rift Basin (RRB), that is further subdivided into the lower Utengule and upper Songwe member (Roberts et al., 2010, 12). The Nsungwe sediments, overlaying the Galula Formation, were accumulated in the Early Paleogene.

All lungfish material described in this chapter were recovered from the Songwe Member, assigned a Late Oligocene (24.95 MY) age based on biostratigraphy, dated ash beds, and detrital zircon geochronology (Stevens et al., 2005, 2006, 2008, 2009, 2013; Roberts et al., 2010, 2012). The Fossil-bearing sediments apart from lungfish recently other aquatic taxa such as alestid fishes, frogs, crustaceans and mollusks have been recovered.

The specimen described herein was recovered by a team of the Rukwa Rift Basin Project (RRBP) Expedition (2001 - to date) working in Mbeya Region in southwestern Tanzania about 20 kilometers from the regional capital between ($8^0$30’, $8^0$40’S, $33^0$00’, $33^0$10’E) latitude and longitude respectively (Figure 5.1). Specimens were collected from three fossil localities along the river banks of the Songwe and Nsungwe rivers, each about one quarter mile from the Zambia-Tanzania highway.

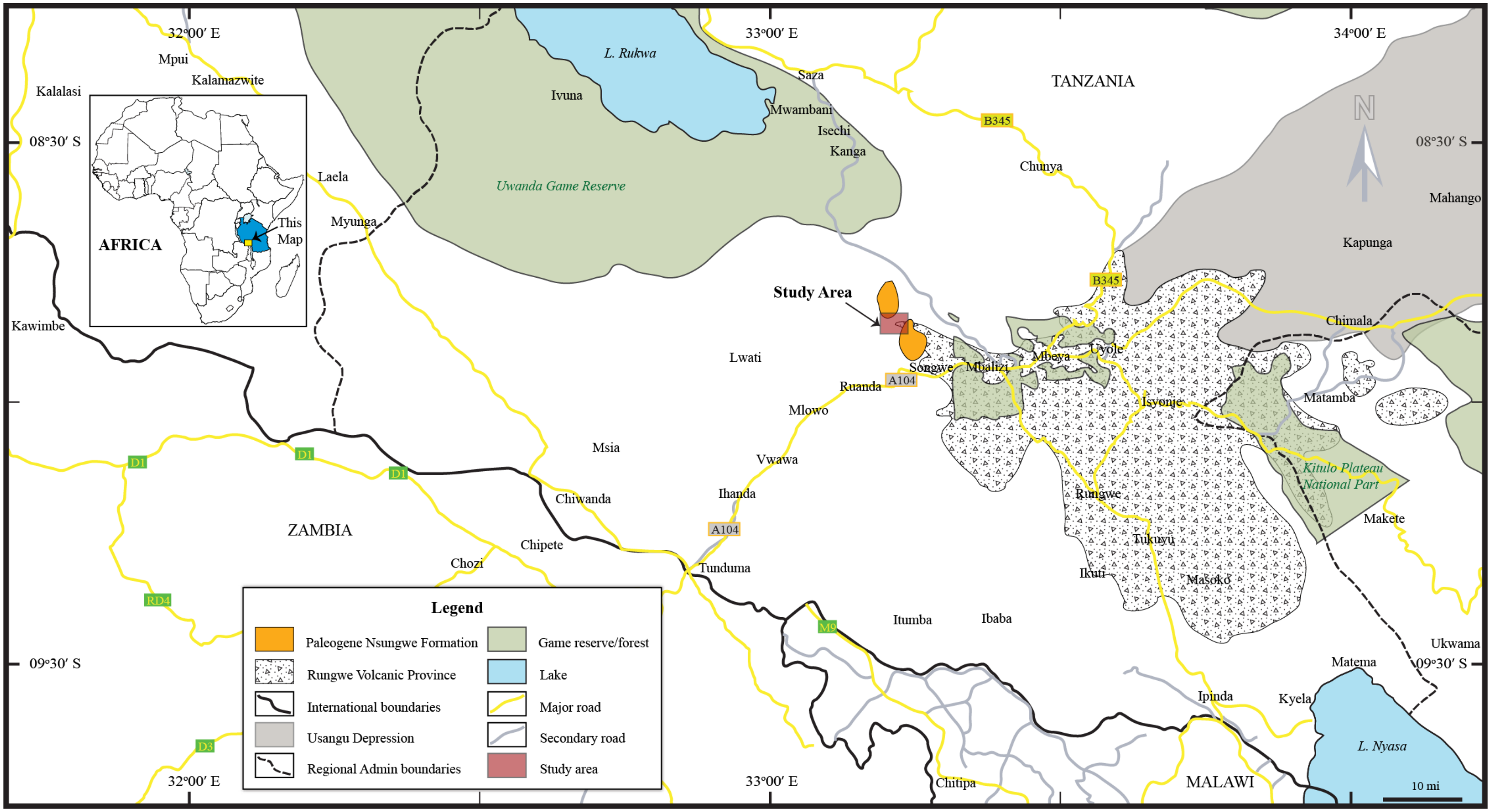

Figure 5.1: A map showing the research area in the Rukwa Rift Basin (RRB) of southwestern Tanzania where all lungfish specimen studied herein were recovered from.

5.2 Materials and Methods

All fossil lungfish specimens described in this chapter were collected from the late Oligocene Nsungwe Formation in the Rukwa Rift Basin of southwestern Tanzania. Five isolated specimens were collected from 3 localities: TZP-2, *Nsungwe 2* and *Nsungwe 2B*. Casts of the fossils are held at Ohio University and are available for study upon request; original fossils are the property of the Tanzania Antiquities Division. Lungfish fossils were mechanically prepared by K. Whitman. Comparative materials included: RRBP 09247; RRBP 04147; RRBP 08314; RRBP 05429 and RRBP 09059 all actual specimen numbers). Additional comparisons of rarer forms were made with specimens figured in the literature (Kirkland, 1987; Milner & Kirkland, 2006).

Specimens were magnified on a Nikon stereomicroscope bundled with Spot Advanced software (version 3.5.8), and photographed using a Spot Insight QE Color camera (model 4.2, image resolution 2048 by 2048) at different focal points, creating image stacks of 4-9 pictures per specimen. Focused photomontages were then assembled from stacks of images using the program Helicon Focus (version 5.3.4) to generate the figure plates. For each specimen, the following measurements were made using Adobe Illustrator and Photoshop CS 6. Most of Nsungwe lungfish specimens are incomplete, although some dimensions allow for precise measurements.

Specimens were assigned to lungfish taxon based on shape and configuration and morphometric measurements of the ridges of tooth plate. Tooth plate characteristics have previously been used in differentiation and description of lungfishes (e.g. Martin, 1980, 1982). Morphological descriptions in the following sections follow terminology as labeled on modern *Protopterus aethiopicus* from Tanzania (Figure 5.2).

Table 5.2: Showing all abbreviations used in the photos and illustrative drawings

AC	anocleithrum
AN	angular
C	cartilage
CH	ceratohyal
CL	cleithrum
CLA	clavicle
CR	cranial rib
DE	dermal ethmoid
EO	exoccipital
FP	frontoparietal
OP	operculum
PR	prearticular
PRa	anterior process of the prearticular
PRan	angular process of the prearticular
PRb	middle process of the prearticular
PRc	posterior process of the prearticular
PRcor	coronoid process of the prearticular
PRsym	prearticular symphysis
PRTa	anterior ridge of the prearticular tooth plate
PRTb	middle ridge of the prearticular tooth plate
PRTc	posterior ridge of the prearticular tooth plate

Table 5.2 (cont'd)

PS	parasphenoid
PT	pterygoid
PTap	ascending process of the pterygoid
PTTa	anterior ridge of the pterygoid tooth plate
PTTb	middle ridge of pterygoid tooth plate
PTTc	posterior ridge of the pterygoid tooth plate
S	supraorbital
SO	suboperculum
SPR	supraangular
SQ	squamosal
V	vomerine tooth
VE	vertebra

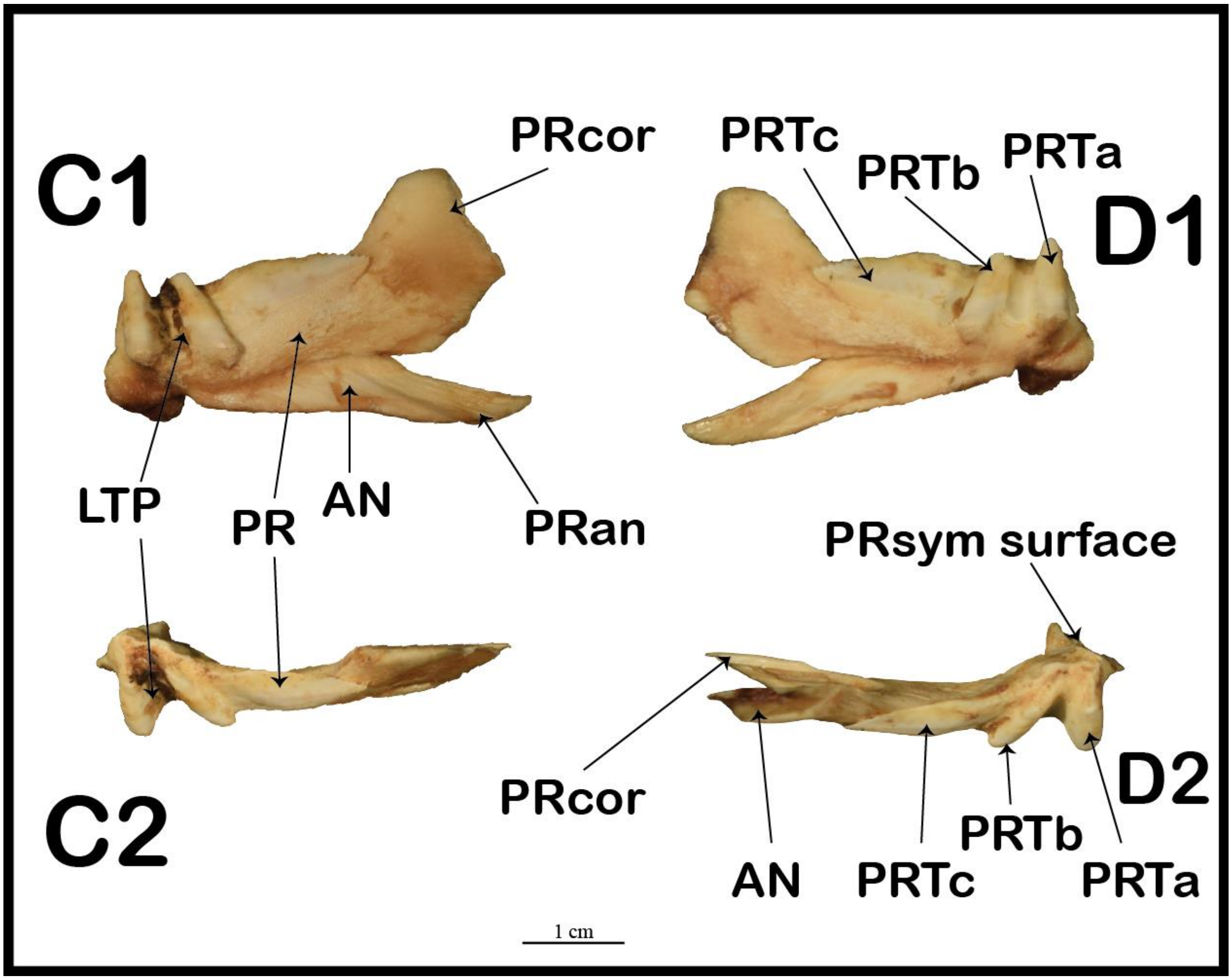

Figure 5.2: Modern lungfish with annotations and labeled mandible features C1; C2; D1; D2 where, C2 is side view of left lower tooth plate articulated to prearticular; D2 is side view of right lower tooth plate articulated to prearticular; C1 is lateral of the occlusal view of left lower tooth plate articulated to prearticular; D1 is lateral of the occlusal view of right lower tooth plate articulated to prearticular. For abbreviations see Table 5.2.

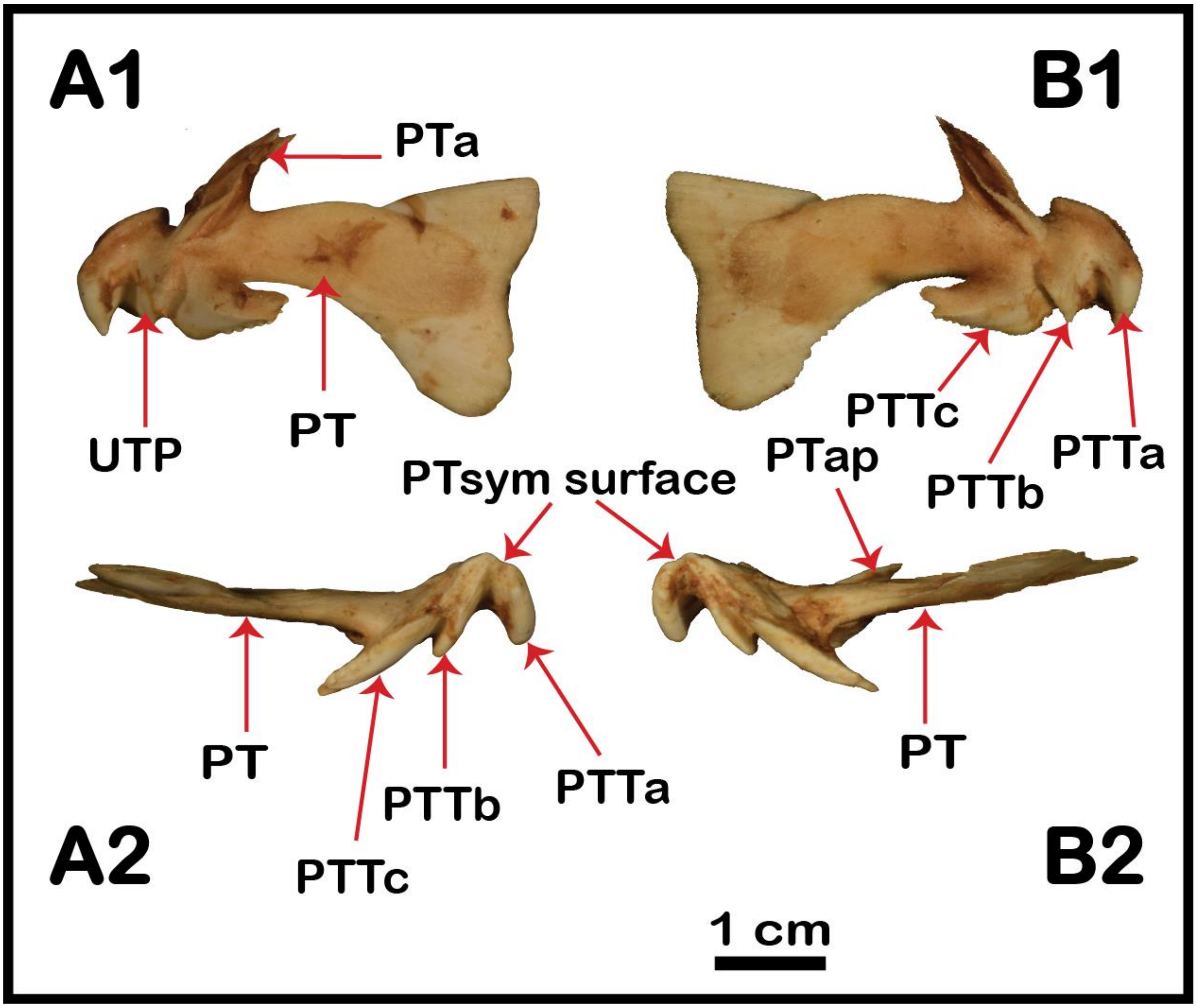

Figure 5.3: Modern lungfish with annotations and labeled maxilla features A1; A2; B1; B2 where, B2 is side view of left upper tooth plate articulated to pterygoid; A2 is side view of right upper tooth plate articulated to pterygoid; A1 is lateral of the occlusal view of left upper tooth plate articulated to pterygoid; B1 is lateral of the occlusal view of right upper tooth plate articulated to pterygoid. For abbreviations see Table 5.2.

5.2.1 Systematic Paleontology

Superclass OSTEICHTHYES Huxley, 1880

Class SARCOPTERYGII Romer, 1955

Subclass DIPNOI Müller, 1845

Family PROTOPTERIDAE (Owen, 1839)

Genus *PROTOPTERUS* (Owen, 1839)

Species *Protopterus* sp.

5.2.2 Modern Lungfish

Today, there are only two families of lungfish surviving, namely, Lepidosirenidae and Ceratodontidae. The *Lepidosiren* in South America, *Protopterus* in Africa, and *Neoceratodus* in Australia. In the genus *Protopterus*, largely confined to tropical Africa, four species; *P. annectens*, *P. amphibius*, *P. aethiopicus* and *P. Dolloi* exist (Maina, 1987). Lungfish taxonomy and classification has mainly based on two things, either the tooth plate (anatomy and morphology) or skull roof bones (number and pattern of arrangement). Herein we mostly study the mouth (buccal) bones i.e. teeth and their attachment.

In order to do so, I will be comparing, especially for *Protopterus* fossil bones with a total of eight buccal recently prepared specimens available at Ohio University of *Protopterus aethiopicus* from Lake Victoria in northern Tanzania (Figure 5.2) were used.

5.3 Background: Description of Modern *Protopterus* Specimen

5.3.1 Mandibles - Prearticular

The prearticular is important integral part of the mandible that bear a pair of dense whitish lower tooth plate anteriorly (Figure 5.2). As for pterygoid the left and right pair of prearticular are joined at prearticular symphysis (PRsymp surface). The prearticular is a robust, paired bone that forms a large part of the anterior portion of the mandible (Figure 5.2). The prearticular robustically at the dorsal surface fuses the upper tooth plate with three ridges, each with specific shape and function.

The angular (A), paired bone that sits on the lateral surface and posterior end of the prearticular in a groove, gradually projects dorsally at about 40 degrees from prearticular bone which at posterior-most position it has another less dense process project upward (PRcor).

There are three ridges present in the prearticular tooth plate with the two anterior-most ones (PRTa and PRTb) forming pointed cusp-cylindrical shape and the last one (PRTc) flattening posteriorly. Between the two anterior ridges there is deeper furrow compared to the next one between PRTb (the longest) and PRTc which is shallower and decreasing backwardly.

While the two anterior ridges form the conical cusps in occlusion, the posterior ridge extends much farther than the other two ridges and forms a serrated blade-like structure running posteriorly along the prearticular bone. The two anterior ridges of the lower tooth plates from both sides of prearticular fit between the anterior and middle ridges of the pterygoid tooth plate while the posterior ridge of the prearticular tooth plate sits posterior to all of the ridges in the pterygoid tooth plate when in occlusion.

Here is a list of specimen used for comparison figure 5.2: C2 is side view of left lower tooth plate articulated to prearticular; D2 is side view of right lower tooth plate articulated to prearticular; C1 is lateral of the occlusal view of left lower tooth plate articulated to prearticular and D1 is lateral of the occlusal view of right lower tooth plate articulated to prearticular.

5.3.2 Maxilla - Pterygoid

The pterygoid is a large, maxilla paired bone that bear essential front upper tooth plate in lungfish. The pterygoid has three major blade-like that are fused tightly to it, but relatively thicker sniping teeth, namely, anterior ridge of the pterygoid tooth plate (PTTa), middle ridge of pterygoid tooth plate (PTTb) and posterior ridge of the pterygoid tooth plate (PTTc).

They are dense, and in ridges with sinusoidal furrows widening backward with its first (PTTa) forming acute angle with PTTb.

The pterygoid articulates at its anterodorsal surface with the supraorbital that fits into a groove that extends along the ascending process (PTap). The elements of a pair of pterygoid are fused in adults at the pterygoid symphysis (PTsym surface from Figure 5.2B).

The bone is in same level as the top of anterior tooth plate when placed laterally as in Fig 2B. A1 with its ventral posterior-most process descending and ascending dorsal process extends upward. In addition to ascending process there are also other three additional tooth plate ridges processes that extend anteriorly and laterally.

The modern lungfish used herein for comparison (*P. aethiopicus*) pterygoid (Figure 5.2B) is widens and its posterior-most process projects posterolaterally. The posterior-most processes which flare out dorsoventrally to form a flattened wing-shaped structure are less dense and slightly translucent.

Here is a list of specimen used for comparison figure 5.2: B2 is side view of left upper tooth plate articulated to pterygoid, A2 is side view of right upper tooth plate articulated to pterygoid, A1 is lateral of the occlusal view of left upper tooth plate articulated to pterygoid and B1 is lateral of the occlusal view of right upper tooth plate articulated to pterygoid.

5.3.3 Systematic Paleontology

Superclass OSTEICHTHYES Huxley, 1880

Class SARCOPTERYGII Romer, 1955

Subclass DIPNOI Müller, 1845

Family PROTOPTERIDAE (Owen, 1839)

Genus *PROTOPTERUS* (Owen, 1839)

Species *Protopterus sp.*

5.3.3.1 Specimen RRBP 05429 - *Protopterus* Right Maxilla

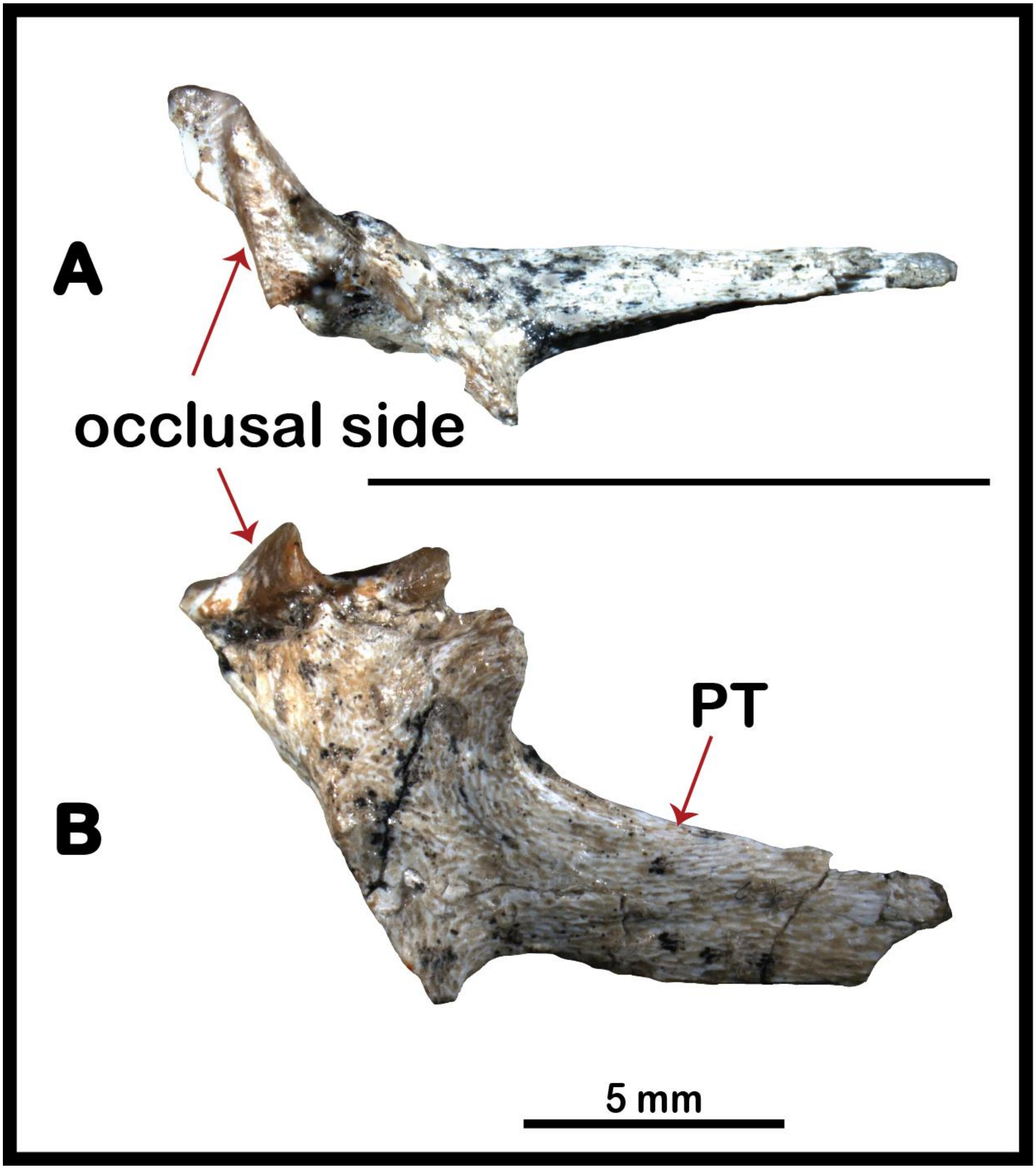

Figure 5.4: RRBP 05429: *Protopterus* right maxilla; A is latitudinal side view and B is exterior lateral view

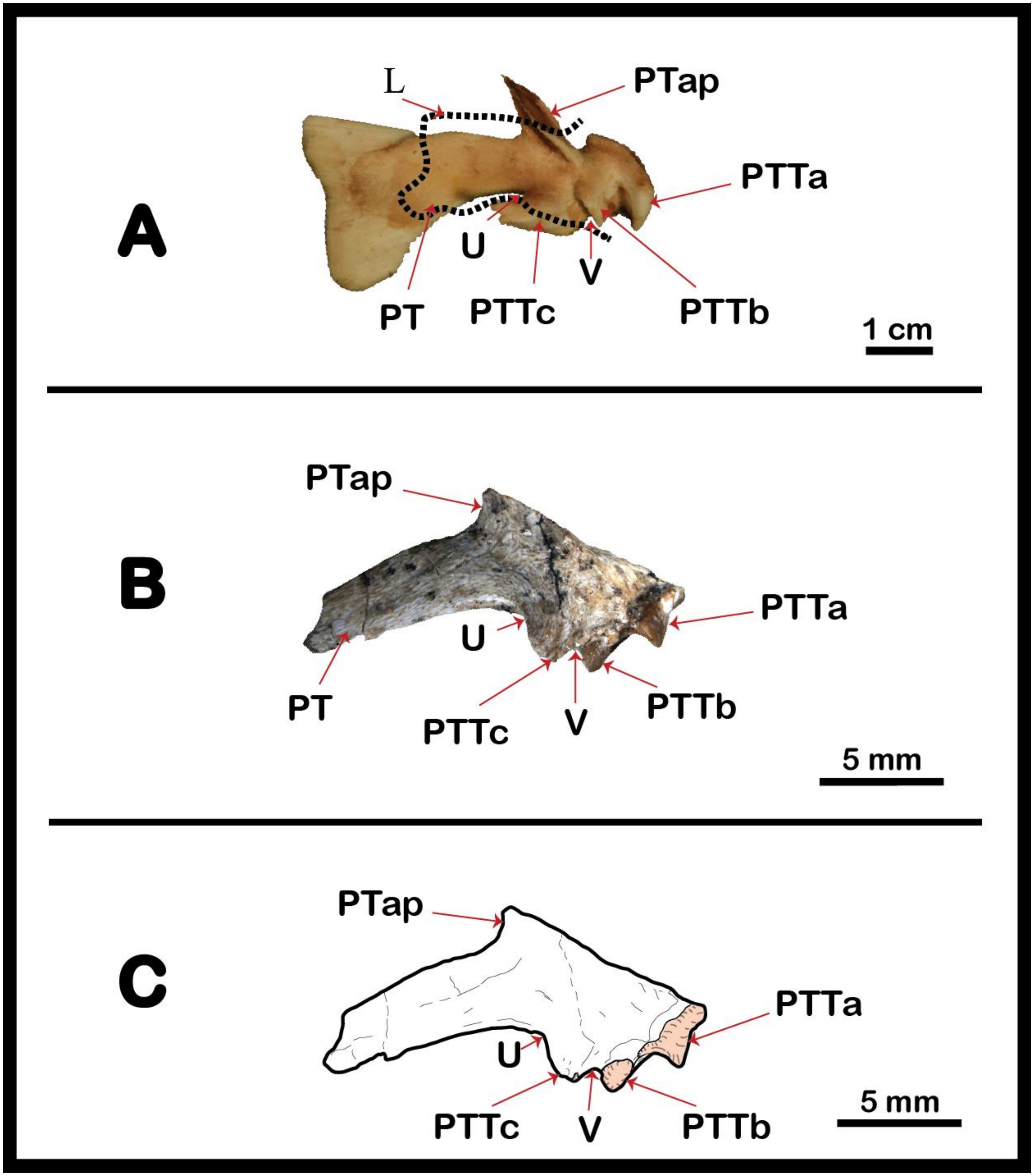

Figure 5.5: RRBP 05429: *Protopterus aethiopicus* from L. Victoria Tanzania right maxilla (A) comparable to the specimen in photo B and in drawing C. The abbreviations meaning are found in Table 2. U and V shows corresponding curvature features between fossil and modern lungfish. L is for possible line of breakage in the fossil.

5.3.3.2 PRBP 05429 Description

The specimen PRBP 05429 is a pterygopalatine with broken (missing) posterior most process and pterygoid ascending process (PTap) and PTTc. It displays signs of compression due to multiple cracks running through the bone, while the occlusal part of the tooth plate remain well in place attached to the pterygoid

The remarkable distinguishing features from the modern *P. aethiopicus* include the considerable huge distance between the beginning of the PTap and anterior end occlusal of the tooth plate. In modern lungfish (*P. aethiopicus*) as can be seen in fig 3B, the base of the PTap is just next to the intersection of PTa and PTb. That means the petrodentine portion is well reduced in the specimen or in other words has increased significantly over time.

Second notable feature is the massive portion of the pterygoid bone. The bone form an angle of about right angle with the PTTc process while in modern lungfish is very acute of less than 10 degrees.

The pterygoid bone itself even with the absence of posterior most process appear to be thing posteriorly and bent ventrally when placed standing laterally as opposed to *P. aethiopicus* which displays general horizontal orientation.

The three tooth plate ridges and two sulci in between is the critical characteristic for *Protopterus* is well preserved in place despite all other differences from modern lungfish.

It is safe to say this is definitely *Protopterus* but also it is not *P. aethiopicus* not the other two described specimens. Meantime we refrain to suggest species level as there is no reliable reference to naming *Protopterus* species when entirely relying on the tooth plate and jaw bone data alone. Poll, 1961 uses only meristic characters to classify modern African lungfish. Other researchers have not been able to full use teeth as criteria for distinguishing *Protopterus*. For that reason, we can only confidently say the genus level but not get into suggesting species name for now.

5.3.4 Systematic Paleontology

Superclass OSTEICHTHYES Huxley, 1880

Class SARCOPTERYGII Romer, 1955

Subclass DIPNOI Müller, 1845

Family PROTOPTERIDAE (Owen, 1839)

Genus *PROTOPTERUS* (Owen, 1839)

Species *Protopterus sp*.

5.3.4.1 Specimen RRBP 08314 - *Protopterus* Left Maxilla

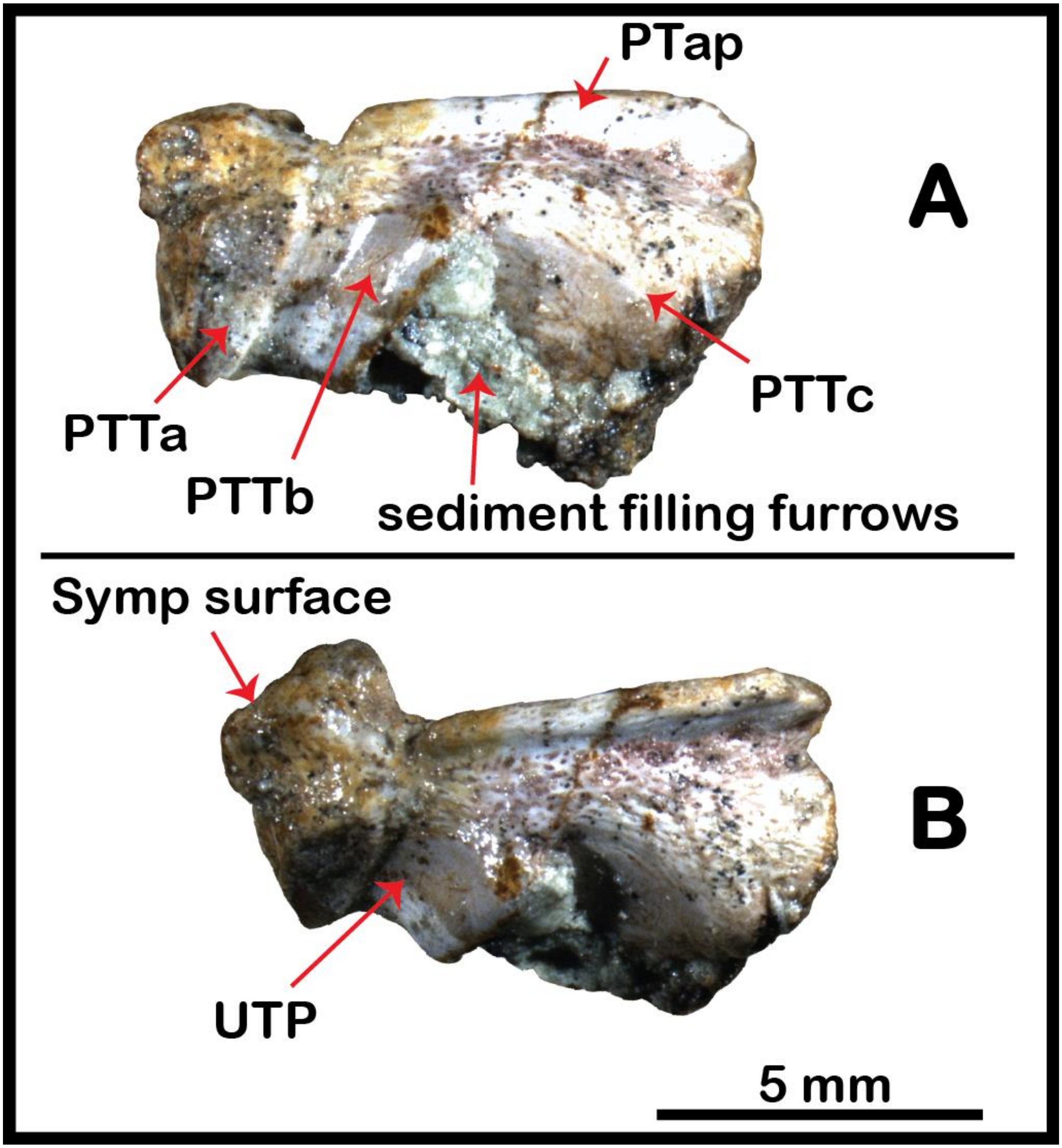

Figure 5.6: RRBP 08314: *Protopterus* left maxilla with A. lateral occlusal view and B. oblique top view.

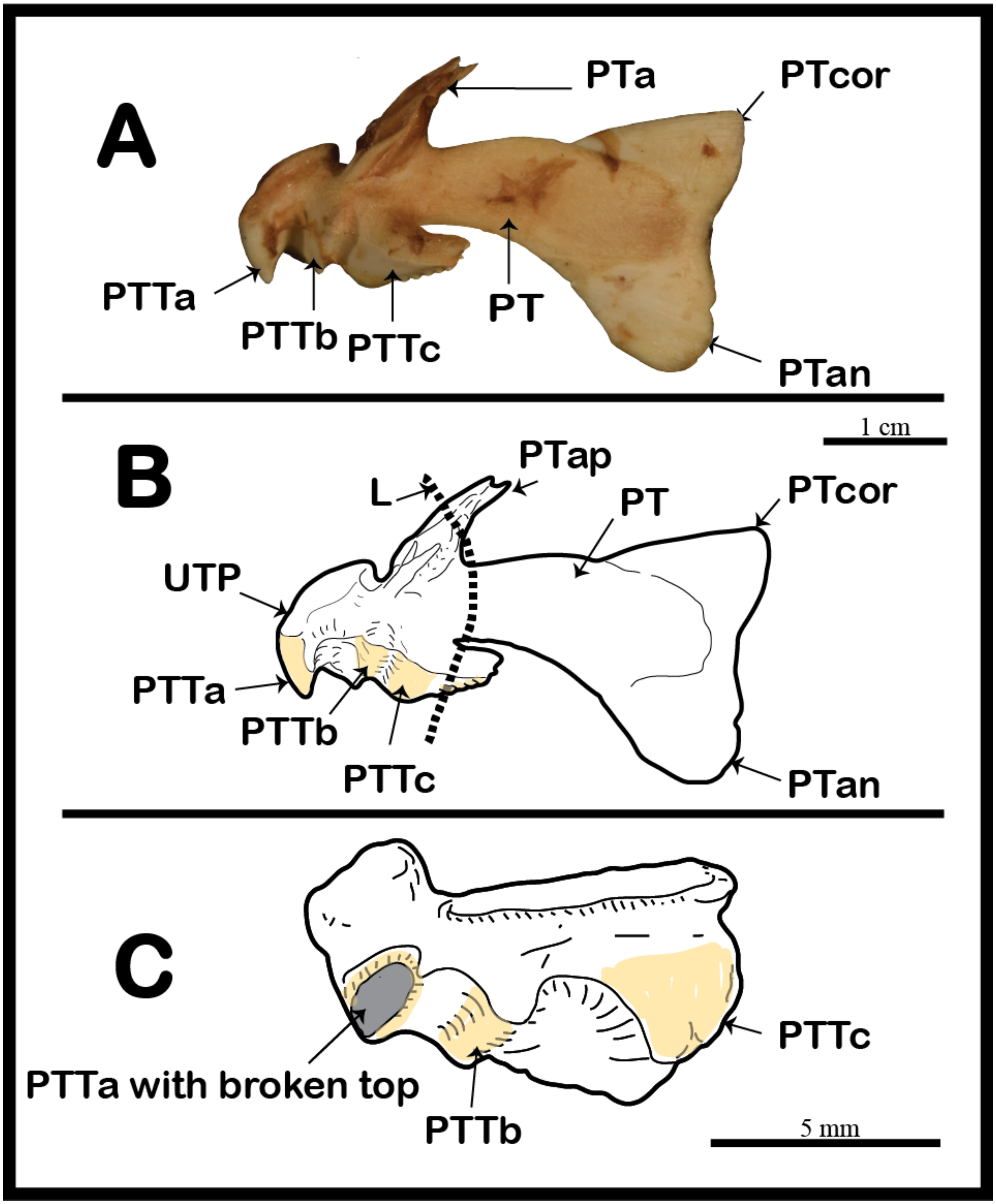

Figure 5.7: Fig Interpretive Drawing of RRBP 08314: *Protopterus* top left maxilla (B) and interpretive drawing of modern lungfish from Fig. 2. A1 upper left maxilla. The dotted line, L, represent the possible broken location of RRBP 08314, while numbers 1 – 3 are ridges of the tooth plate.

5.3.4.2 Material, Horizon, Locality, and Age

This one particular specimen is a near complete and well preserved tooth plate (Fig. 7, 7A, 7B) well isolated from the prearticular and missing proper edges due to wear. It has been catalogued RRBP 05429 and housed in Ohio University Museum is from the locality *TZP 2* near the confluence of Nsungwe and Songwe river, in Mbeya Region, Tanzania (Fig. 1). The locality is in the RRB as part of the EARS. It is fluvial facies assigned a Late Oligocene (24.95 MY) age of the Songwe Member of the Nsungwe Formation.

5.3.4.3 PRBP 08314 Description

The well-preserved specimen PRBP 08314 is a left maxilla bone (pterygopalatine) attached to the massive portion of an upper tooth plate. The noticeable wear on the plate are the occlusal (top) portion of anterior tooth (PTTa) and on the flat part pointing backward (Fig. 4A) and its serrations of posterior tooth plate (PTTc). The specimen is very small, approximately 10 mm long and 5 mm deep.

The symphysis surface (symp surface) where this left pterygoid bone come into contact with the right counterpart is more or less vertical and straight from PTTa as opposed to modern lungfish, *P. aethiopicus,* where there is strong convex bend.

Another important feature which distinguishes this specimen from *P. aethiopicus* is the PTap bone. Despite its base being very similar in terms of where it starts but is hardly ascending at all. It is horizontal laterally and in full contact with the pterygoid bone although they are not fused together.

In the specimen the sulcus between PTTa and PTTb is deep and form an acute angle. The sulcus can be seen in Fig 4a filled with graying sediment. In the modern lungfish (Fig. 3B) it is in V-shape, and very shallow especially compared to angle between PTTa and PTTb.

It is very difficult to tell apart for certain the shape and concavity of the pterygoid bone as the specimen does not extend that far, is broken right at the beginning of the bone. But taking the PTap orientation as a guide of the extension then suggests the very horizontal and tight to the pterygoid bone.

The shape, angle sizes and orientation of the tooth plate ridges and sulci show no any congruence to either modern or the other specimen, PRBP 04147 described above. That brings us to similar situation where we evidently place the specimen in the *Protopterus* genus but cannot conclusively determine the species level.

5.3.5 Systematic Paleontology

Superclass OSTEICHTHYES Huxley, 1880

Class SARCOPTERYGII Romer, 1955

Subclass DIPNOI Müller, 1845

Family PROTOPTERIDAE (Owen, 1839)

Genus *PROTOPTERUS* (Owen, 1839)

Species *Protopterus sp*.

5.3.5.1 Specimen RRBP 04147: *Protopterus* Mandible

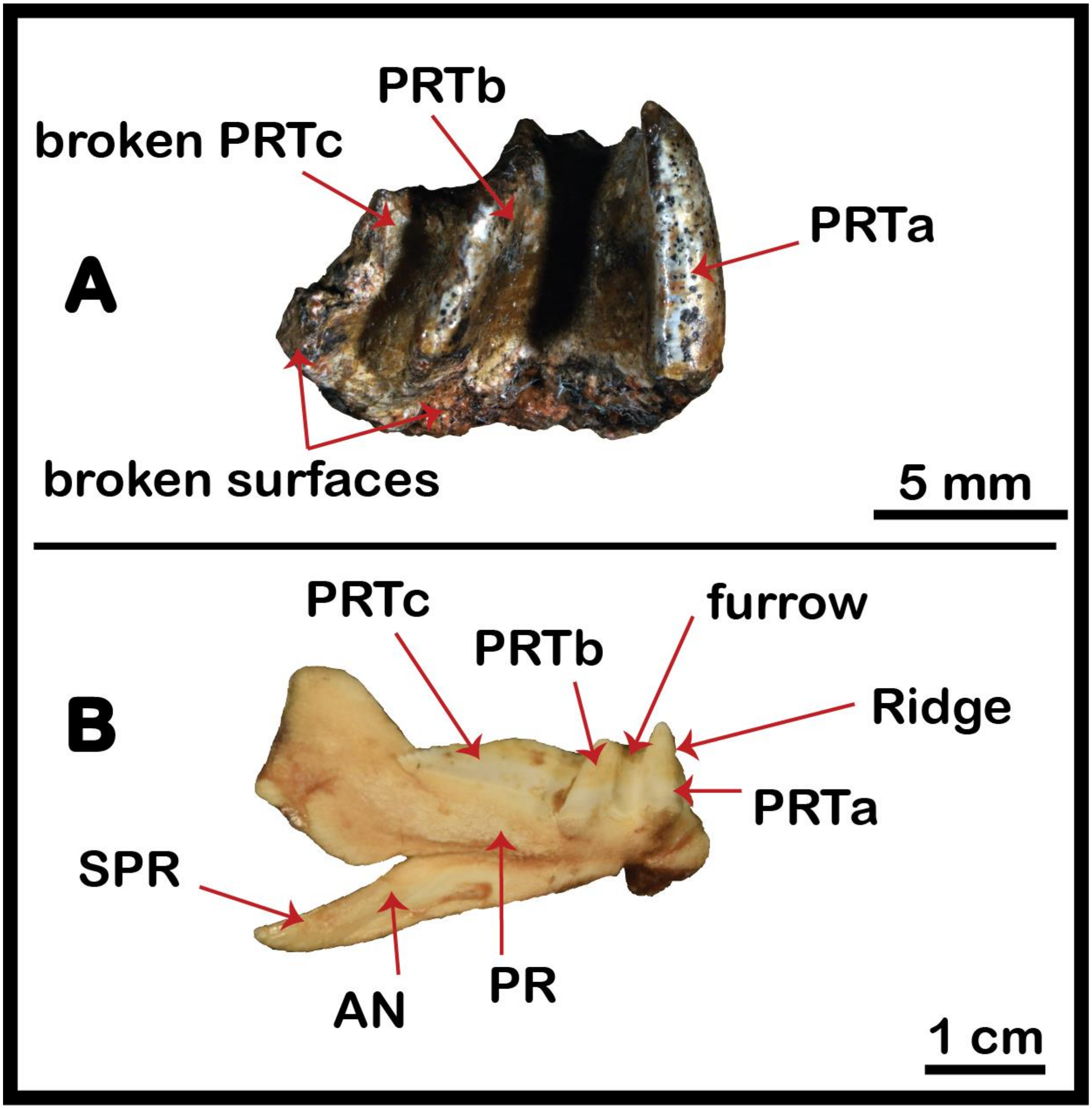

Figure 5.8: RRBP 04147: *Protopterus* mandible. A is fossil specimen and B is extant specimen for comparison.

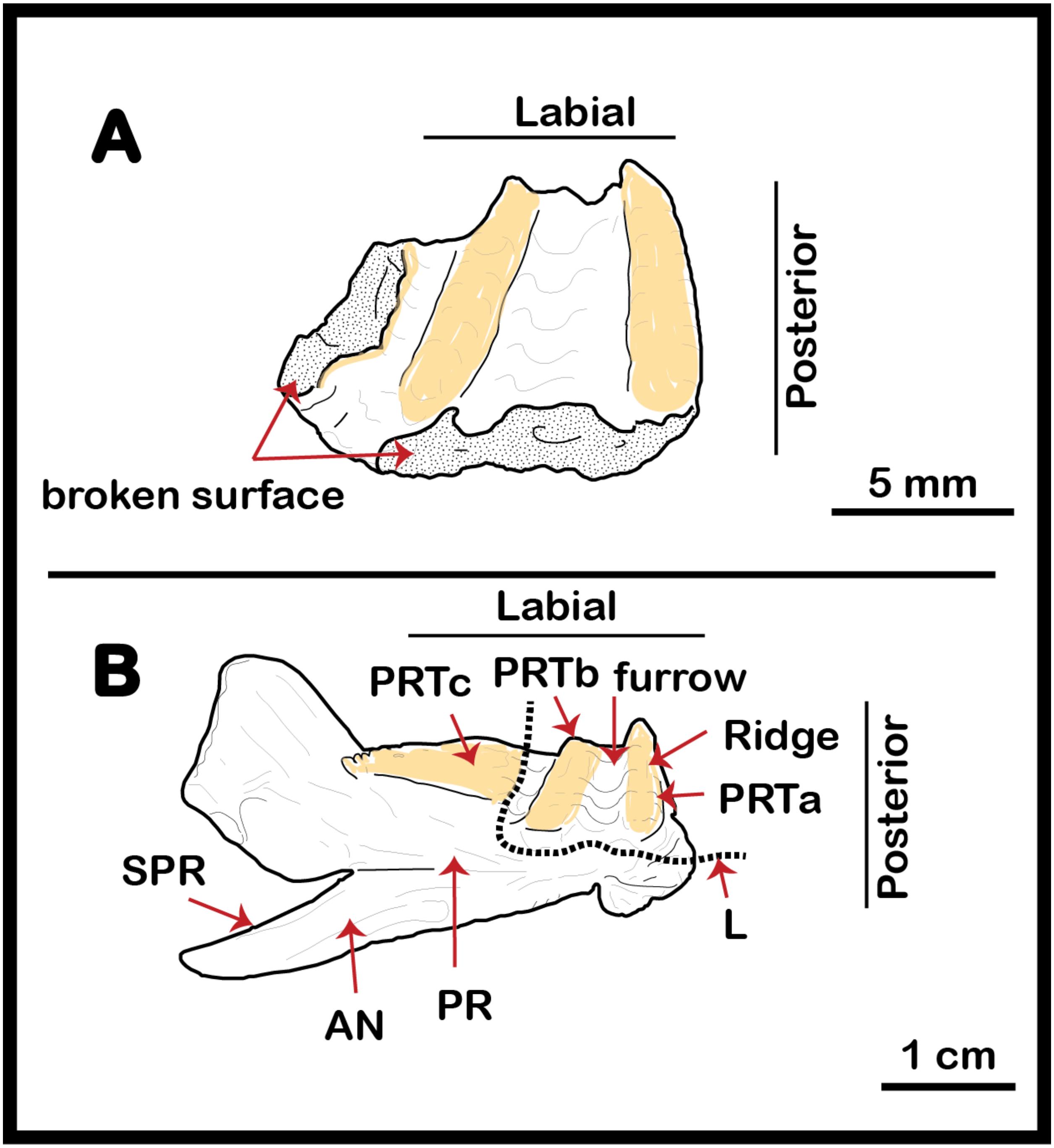

Figure 5.9: Interpretive Drawing of RRBP 04147: A is interpretive drawing of genus *Protopterus* right lower tooth plate specimen and B is interpretive drawing of lower tooth plate of the *P. aethiopicus* from Lake Victoria, Tanzania. The dotted line, L, represent the possible broken location of RRBP 04147 at the end of dentine-like hard material, and numbers 1 – 4 are ridges of the tooth plate.

5.3.5.2 Material, Horizon, Locality, and Age

This one particular specimen is a near complete and well preserved tooth plate (Fig. 7, 7A, 7B) well isolated from the prearticular and missing proper edges due to wear. It has been catalogued RRBP 04147 and housed in Ohio University Museum is from the locality *TZP 2* near the confluence of Nsungwe and Songwe river, in Mbeya Region, Tanzania (Fig. 1). The locality is in the RRB as part of the EARS. It is fluvial facies assigned a Late Oligocene (24.95 MY) age of the Songwe Member of the Nsungwe Formation.

5.3.5.3 PRBP 04147 Description

This is an incomplete massive right lower tooth plate (LTP) of *Protopterus*. Although partially broken posteriorly and ventrally leaving only a few but very essential and recognizable evidence. There are characteristic PTTa and PTTb *Protopterus* tooth ridges on the plate. The two ridges have conical-shaped cusps, columnar (cylindrical to triangular prism) blade like crests on the occlusal with wide gaps in between which fit well with pterygopalatine tooth plate (*Figure 5.5*).

At the posterior breaking surface, you can extrapolate easily the extension of the PRTc to being flat pointing posteriorly parallel to angular (A). On the ventral breaking surface there is clear indication to be along the angular suture line which defines *Protopterus* (Martin, 1995). That removes *Lavacatodus*, which is characteristically closest to *Protopterus* as a possible consideration.

The angles between ridges and sulci depth and orientation set this apart from modern lungfish, *P. aethiopicus* (*Figure 5.6*), whose angles are very sinusoidal in nature. The angle between PRTa and PRTb is dipping backward in PRTb sulcus and in general very wide at the base on the other hand in *P. aethiopicus* angle between PRTa and PRTb is in U shape as a part of continuum of sinusoidal wave like all the way from PRTc to the anterior most end of the lower tooth plate.

The angle formed by the sulcus between PRTb and PRTc is well sloping toward PRTc in more V-shape pointing backward displaying the forward leaning sinusoidal curve.

The middle ridge, PRTb, is wide and at base two ridge like structure twining converges at the top with pointy cusp. That is different from the modern PRTb which is basically singular column throughout with only conical cusp at the top.

The two ridges PRTa and PRTb in the specimen curve backward and thinning in screwdriver shape a little bit as you move from base to the cusps' top. In the *P. aethiopicus* no bending but uniform diameter, straight and parallel to each other from base to cusps with their conical cusps small and start almost near the top.

This is one specimen with features typical of *Protopterus* and the presence of suture line between prearticular (PR) and angular (A) along the ventral breaking surface further isolate the possibility to be genus *Lavacatodus* par Martin (1995) definition. Three strong vertical and almost parallel blade-like ridges make it non confusable with *Ceratodus* genus another close clade of African fossil lungfish.

5.3.6 Systematic Paleontology

Superclass OSTEICHTHYES Huxley, 1880

Class SARCOPTERYGII Romer, 1955

Subclass DIPNOI Müller, 1845

Family PROTOPTERIDAE (Owen, 1839)

Genus *PROTOPTERUS* (Owen, 1839)

Species *Protopterus sp.*

5.4 Discussion

Morphologically, many typical features such as; the distinctive tooth plate with three crests are columnar petrodentine; the pterygoid, bearing an ascending process (PTap) in the posterior position with a broad groove; first two crests (PTTc and PTTb) of the tooth plates short, with no cusps and pointing backward, and the third crest (PTTa) long and with cusps of the specimen RRBP 05429 studied herein suggest that it belonged to *Protopterus* genus of lungfish.

Temporally and geographically for Africa, this is a new addition to already known fossil record of lungfish of *Protopterus* genus such as *Protopterus libycus* from Fayoum, Egypt (Early Oligocene) Stromer, 1910; *Protopterus sp*. from Dur At Talha, Libya (Late Eocene (Priabonian)) Otero et al., 2015; *Protopterus sp. cf. elongus* from Birket Qarun, Egypt (late Eocene (Priabonian)) Murray et al., 2010; *Protopterus sp.* from Glib Zegdou, Algeria (middle Eocene) Adaci et al., 2007; *Protopterus sp*. from El Kohol, Algeria (Early Eocene) Martin, 1995; *Protopterus sp*. from Ilimzi, Morocco (Paleocene (Thanetian)) Martin, 1995 and *Protopterus sp.* from Adrar Mgorn, Morocco (Paleocene (Thanetian)) Martin, 1995. And for this part of Africa, in southwest Tanzania, is a new and first described *Protopterus* record to be reported. This finding expand the horizon of the Cenozoic lungfish from Africa.

Despite the fact that some authors (e.g. Schultze, 2004; Cavin et al., 2007) in their analyses found most of these families to be paraphyletic, other taxonomists (e.g. Martin, 1982, 1984; Kemp, 1998) recognize Ceratodontidae, Neoceratodontidae, Asiatoceratodontidae, Ptychoceratodontidae and Lepidosirenidae. In the debate one thing agreed by almost unanimously is the clear distinction of the family Lepidesirenidae, in the order Lepidosireniformes with three (Martin, 1995) genera *Lavocatodus*, *Protopterus* and *Lepidosiren*, from the rest for their distinctive columnar petrodentine is present in the tooth plates (Lison, 1941; Denison, 1974; Miles, 1977); angular and pre-articular firmly sutured in the lower jaw, with a tall ascending coronoid process and a wide pulp cavity (Martin, 1983; Kemp, 1998); upper jaw composed of the pterygoid, bearing an ascending process in the posterior position with a broad groove (Martin, 1983; Bemis, 1986; Kemp, 1998); tooth plates with three crests; first two crests of the tooth plates short, with no cusps, and the third crest long and with cusps (Kemp, 2003); upper and lower plates contiguous in the mid-line (Kemp, 1998).

This is definitely not the first *Protopterus* to be described from Africa. Other *Protopterus,* in the fossil record, are *Protopterus libycus* (Stromer, 1910), *Protopterus polli* (Dartevelle & Casier, 1949), *Protopterus elongus* (Martin, 1995) and *Protopterus nigeriensis* (Martin 1997). The rest just like this specimen are not that definitive to be placed in specific species. The erecting of these four nominative species each used features and method which in turn raise problems of its own to naming *Protopterus* just based on isolated jaw or tooth plate before you end up with multiplication of fossil species (Martin, 1983). *Protopterus libycus* was described based on the height of the crests and the fusion of the ridges; *Protopterus polli* is based on an angle between the tooth plate crests that differ from that in the modern specimens, and some specimens have four crests; *Protopterus nigeriensis* based on number and size of the crests on tooth plate and *Protopterus elongus* based on its inferred size compared to modern specimen.

For lungfish, in this case *Protopterus*, when specimen of jaw with tooth plate is broken or disarticulated like this one adds even more complications to identifying of the species. On the other hand, it is quite easy to tell apart the genus level as it has been possible from distinctive features.

It is imperative to develop some form of standard method for identifying common features among *Protopterus* and from there being able to differentiate taxa. Otherwise it is safe to stop at *Protopterus sp*. (Greenwood, 1959). In the classification of modern African lungfish (Poll, 1961) relied solely on meristic measurements which provide no help to suggest the fossil material like specimen RRBP 05429 belong to one of the modern lungfish only with intraspecific different features or it completely different because there are no shared traits for their pterygopalatine tooth plates.

The finding of this *Protopterus*, also allows speculation of their existence and survival in the region where we still find similar living genus to be attributed to not only their ability to estivate but also to employ a variety of other strategies, including moving into marginal swampy habitats, to survive the prolonged dry seasons characteristic of African continental climates.

In general, the reporting of this first record of *Protopterus* from the Nsungwe Paleogene Formation in southwest Tanzania adds to our knowledge, about the diversity, temporal and geographical range of *Protopterus* during Paleogene and as previous authors it is very difficult to assign this *Protopterus* into a specific new species just based on the jaw fragments which are commonly preserved.

CHAPTER VI

6 PARSIMONY ANALYSIS OF ENDEMICITY (PAE) OF LUNGFISH GENERA

6.0 Introduction

6.0.1 Lungfish

Lungfishes or famously known as dipnoan, due to their `dual breathing behavior' are considered as a bridging creature which moved onto the land from water (Maina, 1987) as they are one of the closest living group of fish to the tetrapods. They are characterized by the possession of a 'lung' opening off the ventral side of the esophagus (Chew et al., 2004).

The geological record of three genera of living lungfishes; *Lepidosiren* from South America, *Protopterus* from Africa and *Neoceratodus* from Australia dates back to as far as early Devonian (Berman, 1976; Bemis, 1986) when their ancestors were more massive and widespread (Romer, 1955; Qiao & Zhu, 2015). The earliest record of fossil lungfish is *Rhinodipterus* found from early Devonian marine deposits of the Gogo formation of Western Australia (Clement & Long, 2010) followed by fossils found from almost all continents and freshwater deposits of various geological times (e.g. Schultze & Chorn, 1997; Günther, 1871). One of the most characteristic biological properties of the lungfish, is their ability to estivate - survive in turbid environment by hibernating in burrows for up to a year until dry season ends (Wilkie et al., 2006). That has enabled lungfish to survive in a wide range of aquatic habitats from lakes e.g. Lake Victoria (Goudswaard et al., 2002) and Lake Baringo in Kenya (Baer et al., 1992); river amazon basin (Wake, 1986), rivers in west Africa e.g. Anambra river in Anambra State, Nigeria (Ikechukwu & Obinnaya 2010), River Congo Basin (Trewavas, 1954); also in swampy areas like in Central Africa (Greenwood 1986), Permian Texas (Berman, 1968). Second outstanding feature of lungfish is their dentition, which includes strong tooth plates which are preserved as fossils (Gunther, 1871), and unique skull fragments (Clement, 2009). In general fossil lungfish are essentially known from isolated teeth and skull fragments and estivation burrows (Carlson, 1968).

Despite the amount of both historical and taxonomic record which include geological and geographical data, very few biogeographical studies have been done thus far (e.g. Marshall, 1986; Clement, 2012) With the availability of different biogeographical method, none of the previous studies have employed PAE analysis, cluster analysis and in depth geographical distribution of lungfish to study biogeographical distribution of lungfish that start from Devonian to present taxa from different location.

6.0.2 Cluster Analysis

The type of clustering that is used in this study is similarity clustering that is concerned with creating groups of individuals on the basis of similarity (Chatfield and Collins, 1980; Everitt, 1980; Gordon, 1981; Dillon and Goldstein, 1984; Romesburg, 1984; James and McCulloch, 1990; van Tongeren 1995).

Clustering, as many other biogeography statistical techniques has its own limitations (Everitt, 1980). Despite those limitations similarity analysis as a method of clustering analysis should be used as an exploratory step in the analysis. Johnston, 1976 suggests that while clustering creates groups, one needs to discover if the criteria are better met by the dismantling of existing groups, thus requiring further analysis than a simple clustering procedure. The second test does not necessarily need to be a completely different and in this case PAE is used.

6.0.3 Parsimony Analysis of Endemicity (PAE)

Parsimony analysis of endemicity (PAE) (Rosen, 1988) or parsimony analysis of distributions (PAD) (Trejo-Torres & Ackerman, 2001) – uses a parsimony algorithm in order to obtain an area cladogram, based on the taxa inhabiting the areas (Rosen, 1988; Rosen & Smith, 1988; Morrone & Crisci, 1995). PAE has been applied by several authors to establish relationships among different biogeographical units, e.g. localities, quadrats, areas of endemism, continents, islands, etc. (Craw, 1989; Cracraft, 1991; Myers, 1991; Morrone, 1994a,b, 1998; Fernandes et al., 1995; Morrone et al., 1997, 1999; Posadas et al., 1997; Geraads, 1998; Sfenthourakis & Giokas, 1998; Watanabe, 1998; Glasby & Álvarez, 1999; Luna-Vega et al., 1999, 2000; Espinosa-Organista et al., 2000; Ron, 2000; Bisconti et al., 2001; Ippi & Flores, 2001; Morrone & Márquez, 2001; Trejo-Torres & Ackerman, 2001; García-Barros et al., 2002).

The present study in the bigger picture aim at generating useful information on the distributional patterns of lungfish and assist in detecting and proposing areas that are important from a biogeographic viewpoint for these widely distributed fishes covering almost all geographic ranges of the world. This is done by analyzing the distributional patterns and to detect areas of richness and endemism of lungfish by applying endemism indices to grid-cells, and biogeographic analyses applying a parsimony analysis of endemicity (PAE) method. While other earlier phylogenetic and biogeography studies of the lungfish have covered either some genera or species and some just specific zoogeographical regions in this study will expand the taxa and zoogeographical regions data to further investigate the biogeographical distribution through time.

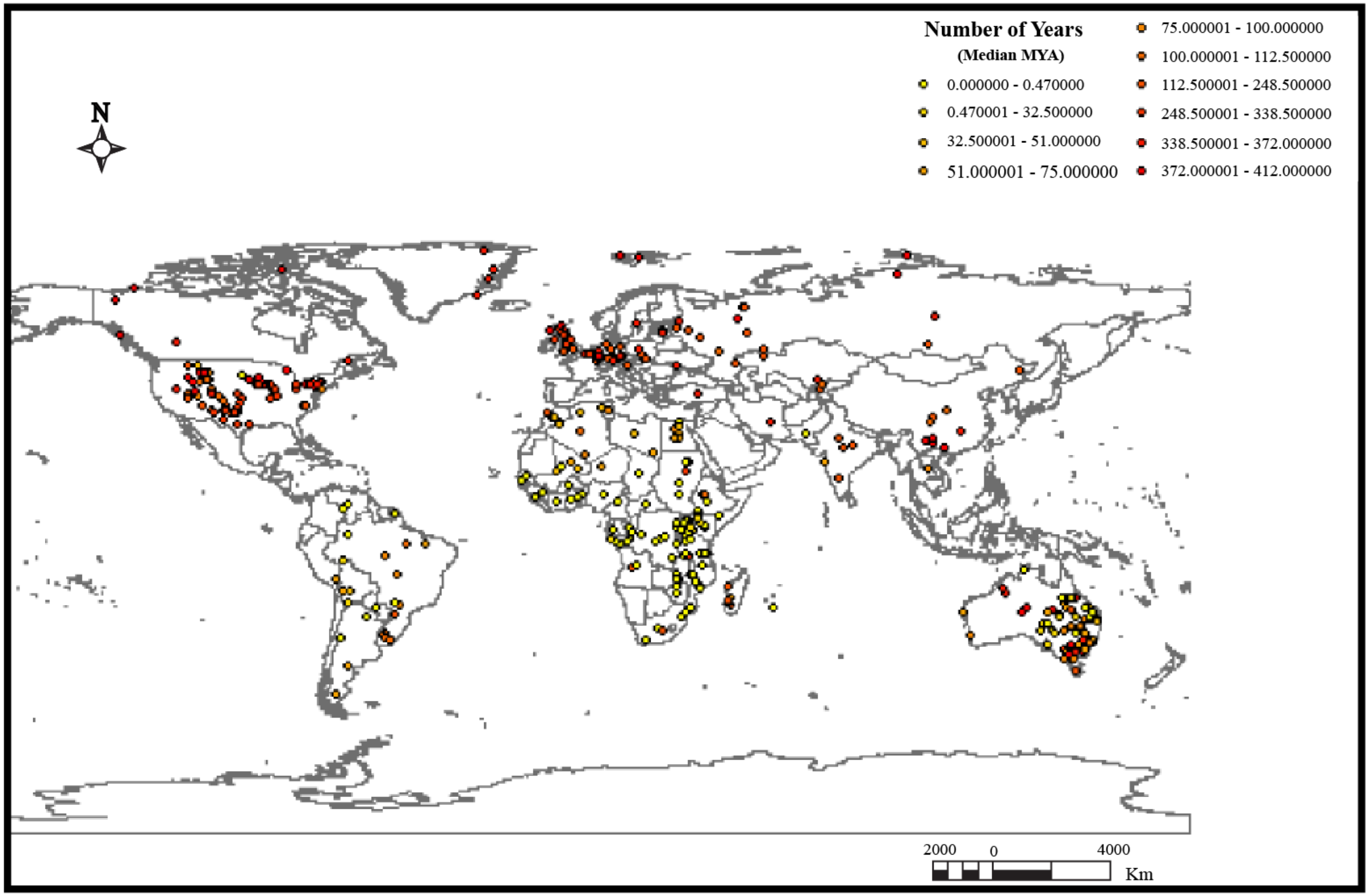

Figure 6.1: Geographic distribution of species of lungfish in the fossil record with numbers of known genera. Noteworthy are the contrast in composition of Paleozoic and Mesozoic assemblages, abrupt change of great groups at top of the Devonian and restriction of pre-Devonian lungfish to a relatively single superfamily (*Dipnorhynchus*).

6.1 Methodology

Distributional data were obtained from the review of more than 100 published articles, books and with this information; I constructed a georeferenciated records database. From distributional data, geographic distribution map of each taxon were obtained using ArcView GIS (ESRI, 1999).

Then a presence-absence matrix was generated for the compilation of lungfish genera accross all continents. Binary cluster analysis was applied to the data, and the biogeographic relationships of lungfish genera were examined using Ward similarity coefficient (Rice & Bellarnd 1982, Birks 1987) using R software (Hornik, 2011). Ward similarity measures the degree of overlap among continents in terms of their taxa occurance. The same data were subjected to parsimony analysis of endemicity (PAE; Rosen 1988, Morrone and Crisci 1995 using PAUP 4.0 Swafford, 2000 with hypothetical ancestral continent consisting of all absences as outgroup, heuristic searches employing TBR branch swapping.

This procedure yielded a systematic matrix of distances among biogeographic units (continents) for rough comparison to the similarity in degree of overlap among the fauna done by Ward dendogram of similarity. Basic steps of PAE, as modified by Morrone (1994a) for identifying areas of endemism, are as follows:

- Identifying zoological regions on a global map to be used in the analysis, considering continents only where at least one locality of one genus exists.
- Construct a data matrix where columns represent the taxa and rows represent the areas (quadrats, provinces, etc.). If a taxon is present in the area, the entry is '1' and if it is absent, the entry is '0'. A hypothetical area coded with '0' for all columns is added to root the cladogram.

- Undertake a parsimony analysis of the data matrix. In case several cladograms result, obtain a strict consensus cladogram.
- Identify in the cladogram the groups of areas defined by at least two taxa.

6.2 Results

6.2.1 Parsimony Analysis of Endemicity (PAE)

This Parsimony Analysis of Endemicity (PAE) analysis aim to present a hypothesis for the sequence of branching within lineages by examining the distributions of shared-derived character states (synapomorphies). The relationships between genera of lungfishes were evaluated using PAUP version 4.0b4a (Swofford, 2000). The hypothetical region was used as the outgroup which is hypothetical ancestor for rooting phylogenetic trees as it basically has the most primitive character states lacking in the rest of the lungfishes.

In the parsimony analysis of endemicity (PAE) of the widespread record of lungfishes six continents, Europe, Australia, North America, Africa, South America and Asia clade and the African subcontinent (Madagascar) were included together with hypothetical area coded with all ‘0’ as an outgroup. The data matrix (Table 6) had in total 87 lungfish genera x 7 regions of endemism.

The PAE yielded a single most parsimonious area cladogram, with 103 steps, consistency index of 0.60, and retention index of 0.64 (Figure 6.2); taxa diagnosing the nodes in the cladogram are detailed in Table 6). Seven nested monophyletic groups were distinguished within the cladogram.

Table 6.1: Part 1 of the Genera x areas (continents) Data matrix for Cluster Analysis and Parsimony Analysis of Endemism

Genus	**Africa**	**Asia**	**Australia**	**Europe**	**Madagascar**	**North America**	**South America**
Adelargo	0	0	1	0	0	0	0
Adololopas	0	0	1	0	0	0	0
Amadeodipterus	0	0	1	0	0	0	0
Andreyeichthys	0	0	0	1	0	0	0
Apatorhynchus	0	0	0	0	0	1	0
Aphelodus	0	0	1	0	0	0	0
Archaeceratodus	0	0	1	1	0	0	0
Arganodus	1	0	0	1	0	1	0
Ariguna	0	0	0	0	0	0	0
Asiatoceratodus	1	1	0	0	0	0	1
Atlantoceratodus	0	0	1	0	0	0	1
Beltanodus	0	0	0	0	1	0	0
Cathlorhynchus	0	0	1	0	0	0	0
Ceratodus	1	1	1	1	1	1	1
Chaoceratodus	0	0	0	0	0	0	1
Chirodipterus	0	1	1	0	0	1	1
Conchodus	0	1	0	0	0	1	0
Conchopoma	0	0	1	1	0	1	0
Ctenodus	0	0	1	1	0	1	0
Delatitia	0	0	1	0	0	0	0
Diabolepis	0	1	0	0	0	0	0
Dipnorhynchus	0	0	1	1	0	0	0
Dipnotuberculus	1	0	0	0	0	0	0
Dipterus	0	0	0	1	0	1	0
Dongshanodus	0	1	0	0	0	0	0
Eoctenodus	0	0	1	0	0	0	0
Epiceratodus	0	0	1	1	0	0	0
Equinoxiodus	0	0	0	0	0	0	1
Erikia	0	1	0	0	0	0	0
Ferganoceratodus	0	1	0	0	0	0	0
Fleurantia	0	0	0	0	0	1	0
Ganopristodus	0	0	0	1	0	0	0
Ganorhynchus	0	0	1	1	0	1	0

Table 6.2: Part 2 of the Genera x areas (continents) Data matrix for Cluster Analysis and Parsimony Analysis of Endemism

Genus	Africa	Asia	Australia	Europe	Madagascar	North America	South America
Gnathorhiza	0	0	0	1	0	1	0
Gosfordia	0	0	1	0	0	0	0
Griphognathus	0	0	1	1	0	1	0
Grossipterus	0	0	0	1	0	1	0
Harajicadipterus	0	0	1	0	0	0	0
Holodipterus	0	0	1	1	0	0	0
Ichnomylax	0	0	1	1	0	0	0
Iowadipterus	0	0	0	0	0	1	0
Iranorhynchus	0	0	0	0	0	1	0
Jarvikia	0	0	0	0	0	1	0
Lavocatodus	1	0	0	0	0	1	0
Lepidosiren	1	0	0	0	0	0	1
Lupaceratodus	1	0	0	0	0	0	0
Megapleuron	0	0	0	0	0	1	0
Melanognathus	0	0	0	0	0	1	0
Metaceratodus	0	0	1	0	0	0	0
Microceratodus	1	0	0	0	0	0	0
Mioceratodus	0	0	1	0	0	0	0
Namatozodia	0	0	0	0	0	0	0
Neoceratodus	1	0	1	0	0	0	0
Nielsenia	0	0	0	1	0	0	0
Oervigia	0	0	0	1	0	0	0
Orlovichthys	0	0	0	1	0	0	0
Osteoplax	0	0	0	1	0	0	0
Palaeodaphus	0	0	0	1	0	0	0
Palaeospondylus	0	0	0	1	0	0	0
Paleophicthys	0	0	0	0	0	1	0

Table 6.3: Part 3 of the Genera x areas (continents) Data matrix for Cluster Analysis and Parsimony Analysis of Endemism

Genus	**Africa**	**Asia**	**Australia**	**Europe**	**Madagascar**	**North America**	**South America**
Paraceratodus	0	0	0	0	1	0	0
Pentlandia	0	0	0	1	0	0	0
Phaneropleuron	0	0	0	1	0	0	0
Pillararhynchus	0	0	1	0	0	0	0
Pinnalongus	0	0	0	1	0	0	0
Powichthys	0	0	0	1	0	1	0
Proceratodus	0	0	0	0	0	1	0
Protopterus	1	0	0	0	0	0	0
Ptychoceratodus	1	0	1	1	1	0	1
Retodus	1	0	0	0	0	0	0
Rhinodipterus	0	0	1	1	0	0	0
Rhynchodipterus	0	0	0	1	0	0	0
Sagenodus	0	0	0	1	0	1	0
Scaumenacia	0	0	0	0	0	1	0
Sinodipterus	0	1	0	0	0	0	0
Soederberghia	0	0	1	1	0	1	0
Sorbitorhynchus	0	1	0	0	0	0	0
Speonesydrion	0	0	1	1	0	0	0
Stomiahykus	0	0	0	0	0	1	0
Straitonia	0	0	0	0	0	0	0
Sunwapta	0	0	0	0	0	1	0
Tarachomylax	0	1	0	1	0	0	0
Tranodis	0	0	0	0	0	1	0
Uranolophus	0	0	0	0	0	1	0
Uronemus	0	0	0	1	0	0	0
Westollrhynchus	0	0	0	0	0	1	0
Xeradipterus	0	0	1	0	0	0	0

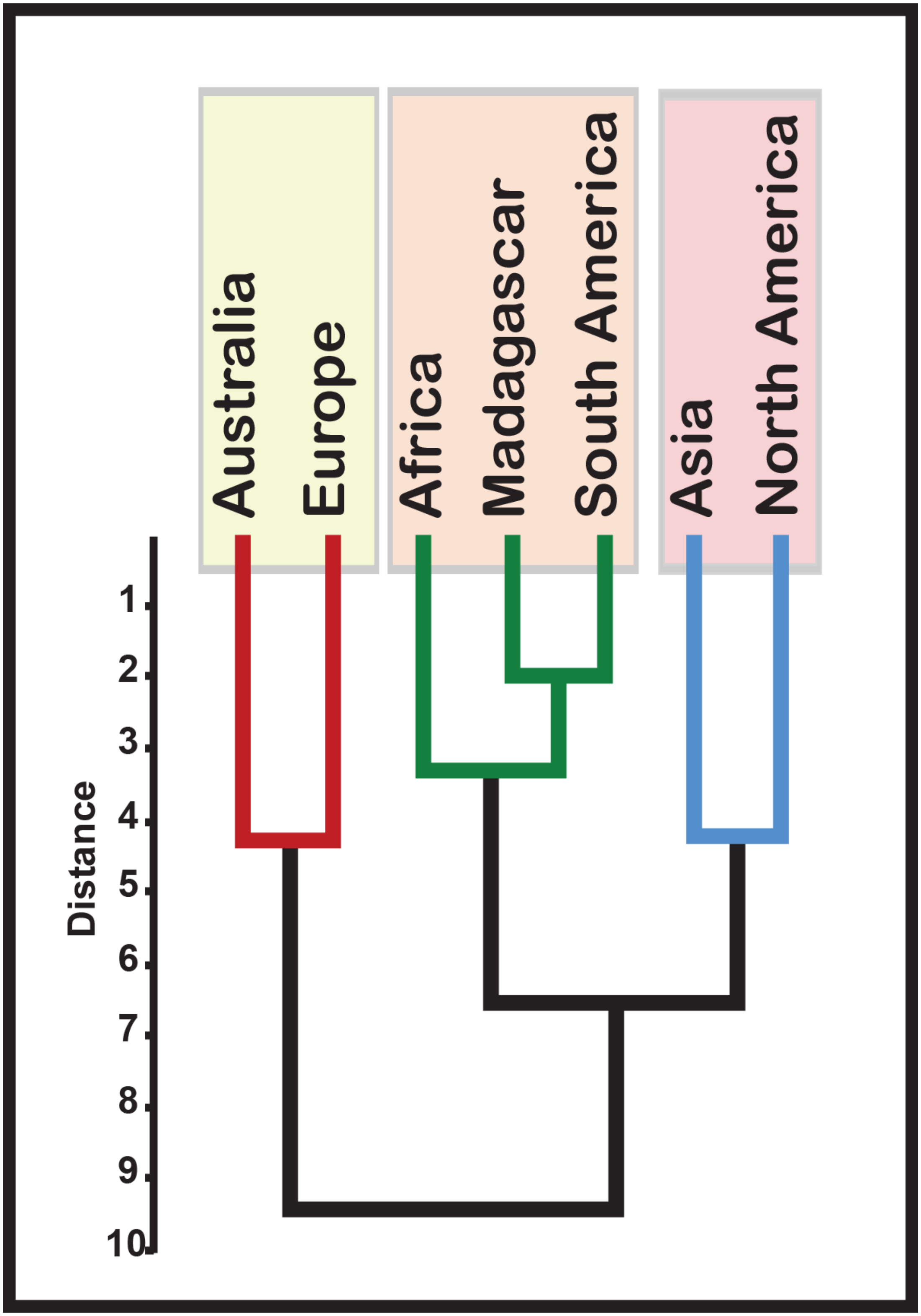

Figure 6.2: Dendrogram summarizing the overall similarity among the area units (continents). In this instance the UPGMA procedure was used based on the square matrix of similarities derived from Ward's (1963) similarity index with the concentration ellipse level of 95%.

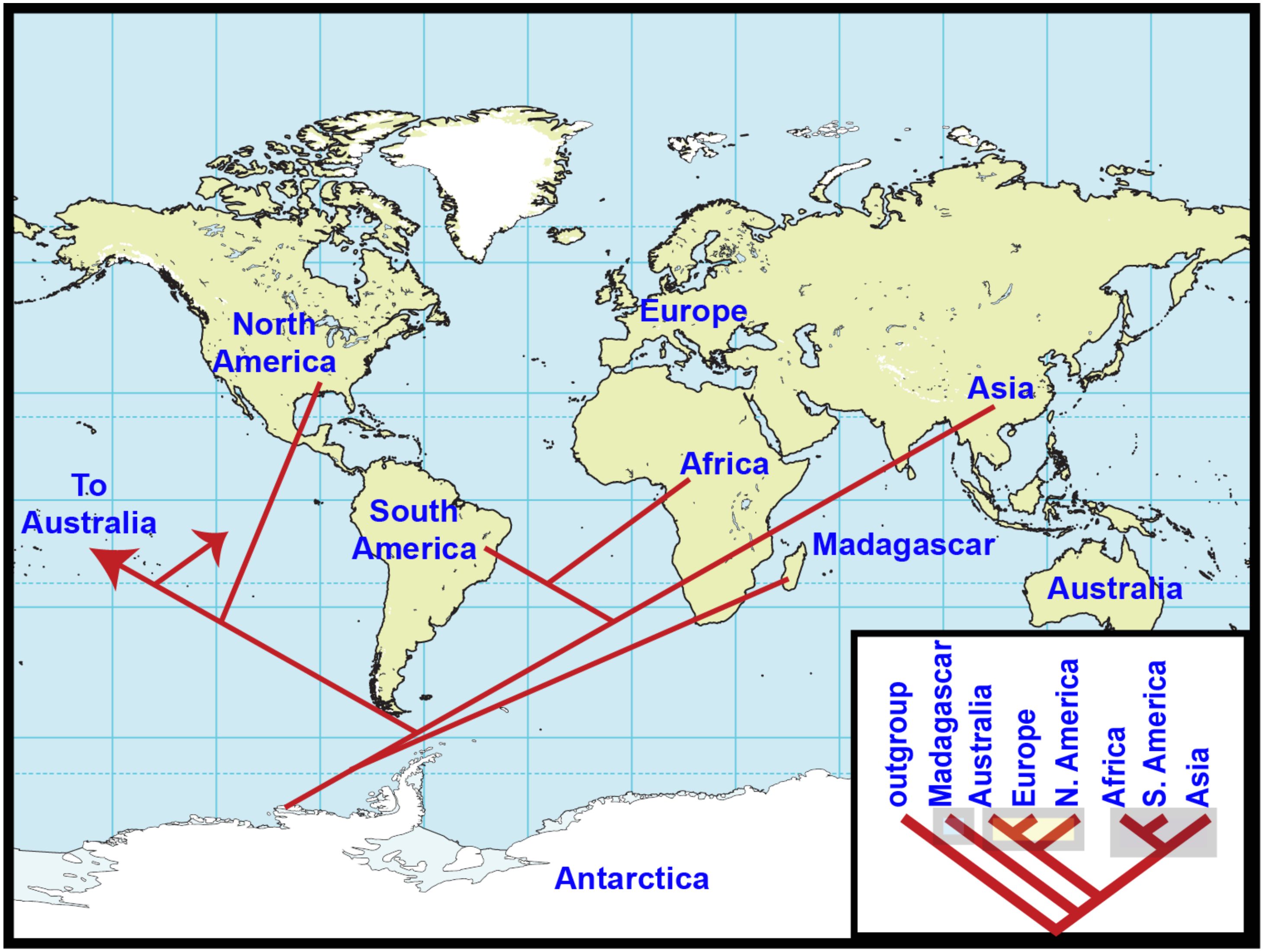

Figure 6.3: PAE strict consensus cladogram of 54 most parsimonious area cladograms showing three main clades: the African subcontinent (Madagascar); the Europe, Australia and North America; and the Africa, South America and Asia clade. The inset is a cladogram as produced by PAUP 4.0.

6.3 Discussion

A total of 87 (Table 6.1-3) genera of lungfish, both fossils and living were included in the analyses for geographical distribution, PAE analysis (cladogram) and similarity (dendrogram). The different geological periods with different numbers of representative (six extant genera and the rest extinct genera) and geographical ranges throughout time were considered.

6.3.1 Distribution Pattern (Geographic ranges)

For the living lungfish we find them (Figure 6.1) on three continents; South America (*Lepidesiren* genus), Australia (1 *Neoceratodus* genus) and Africa (1 *Protopterus* genus – *P. dolloi, P. aethiopicus, P. amphibious* and *P. annectens*).

Lepidesiren of South America which has only one species (Bishop, 1968) are mainly found in the amazon basin in Brazil and bordering countries like Bolivia, Paraguay and Uruguay in rivers like Parana River, Iguazu River and Tapajos River.

African *Protopterus* is represented by four species (Bemis, 1986) and found in Western Africa in countries like Nigeria (Anambra river), Cameroon in Mbakaou river and Lake Bankim; in east Africa in lakes Victoria in Tanzania and Baringo in Kenya and rivers like Victoria Nile; while in northern Africa are found in Sudan (e.g. river Nile, Egypt (river Nile and Ethiopia (river Omo) and Central Africa found mainly in Congo river basin in DRC and Congo in rivers like Congo river.

In Australia there is only one extant taxon, *Neoceratodus forsteri*, the closest living relative to the ancient *Ceratodus* (Kemp, 1997) in rivers St Mary and Bunnett in Queensland in eastern Australia (Kemp, 2001). Due to their small number and significance in evolution are designated in special group of endangered species (Kemp, 2000).

Such distribution of extant lungfishes whereby the African and south American being very close – both of them in same family of lepidesirenformes is very interesting. The two genera are sharing aestivating (Greenwood, 1986) behavior and both can use two methods in breathing either by lungs or gills (Kemp, 1999). The Australian lungfish seem to have retained most of primitive lungfish characters like being obligatory gill breathers, massive tooth plates, larger and tougher scales and inability to estivate.

For the fossil lungfish through time we see changes of endemism and geographic ranges. In the early Devonian, they are mostly pan African. In Jurassic they are mostly restricted to northern hemisphere especially in Europe and North America. In general, over time the richness and abundance have been dying out from 87 genera for Mesozoic to less than 40 during Cenozoic and now only 3 genera surviving.

Africa is the only continent with a fossil record from the Devonian to present extant lungfish. On the island of Madagascar, which fragmented away from the mainland Africa during the Mid-Jurassic (Eagles and Konig, 2008; Konig and Jokat, 2010; Royer and Coffin, 1992), the only two lungfish recorded are early Triassic *Beltanodus ambilobensis* from Ambilobe, northern Madagascar (Schultze, 1981); Cretaceous (Campanian) *Ceratodus madagascariensis* from central Madagascar (Agassiz, 1838; Priem, 1924); Triassic *Paraceratodus germaini* from Sakamena Medio Formation, southwest Madagascar Sakamena Medio Formation

Madagascar (Marshall, 1986) and Late Triassic (Carnian) *Ptychoceratodus acutus* from Isalo Group, Isalo II beds, Madagascar (Priem, 1924; Jaekel, 1926 and Martin et al., 1999)

Recently five (5) genera have been reported from Triassic of China *Ceratodus heshanggouensis* from Watang, Xingxian, Shanxi Province Heshanggou Formation, China (Liu and Yah, 1957); Middle Jurassic *Ceratodus minor* from Shung-ya-kou, Hai-t'ang-pu, Kiangyou, Szechuan-China (Liu and Yah, 1957); *Ceratodus szechuanensis* from Shung-ya-kou, Hai-t'ang-pu, Kiangyou, Szechuan-China (Agassiz, 1838; Young, 1942); Lower Jurassic *Ceratodus* youngi from Weiyuan, West Szechuan-China (Agassiz, 1838; Liu et Yah, 1957); Late Devonian *Chirodipterus liangchengi* from Hunan, China (Gross, 1933; Campbell and Barwick, 1990a); Early Devonian (Lochkovian) *Diabolepis speratus* from Xitun Formation of Yunnan, China (Chang and Yu, 1984); Early Devonian (Lochkovian) *Diabolepis speratus* from Formation of Yunnan, China (Chang and Yu, 1984); Devonian (early Emsian) Erikia jarviki Erikia from Gumu of Wenshan, Yunnan; Guangnan, Yunnan, China Pojiao Formation; late Jurassic *Ferganaceratodus szechuanensis* from Thailand, Asia; late Eifelian (Middle Devonian) *Sinodipterus beibei* from Qingmen in the suburb of Zhaotong, Yunnan, China Qujing Formation (Qiao, T. and Zhu, M., 2009); Lower Devonian (Late Emsian) *Sorbitorhynchus deleaskitus* from Zhongping Village, Xiangzhou County, Guangxi Zhuang Autonomous Region, China the Liuhui Member of the Dale (formerly Sipai) Formation (Campbell & Barwick, 1990) and late Emsian, Lower Devonian *Tarachomylax multicostatus* from Zhanyi, eastern Yunnan Province, South China making a total of 8 genera from Asia alone. In general Asia provide scares and sparse record of lungfish both in terms of quantity and geographical distribution.

The key highlight of the general distribution pattern of the timing of geographic ranges and the timing of geologic and climatic events do give very little information but somehow interesting. Africa and SA etc. Phylogenetic analyses (Marshall, 1986) like PBA, cladistics analysis etc. tied to these events would be the best way to conclusively make sound statement (theory) on the general pattern. For now, it is suffice to say distribution pattern of lungfish genera through time at least mirrors the timing of some major geologic and climatic events.

6.3.2 Cluster Analysis

The dendogram (Figure 6.3) from the similarity cluster analysis aims at first to summarize data to help detect patterns and relationships of lungfishes both living and extinct which would help to predict and secondly devise hypothesis (Gordon, 1981) about the patterns and relationships for their basic distribution. The dendogram in conjunction with the parsimony analysis of endemicity together may suggest the possible pattern with the biogeographical distribution of lungfish.

A cluster analysis performed using Ward's matrix on the biogeographical data of lungfishes produced the resulting dendrogram illustrated in Figure 6.3. A cluster analysis performed using Ward's matrix on the biogeographical data of lungfishes produced the resulting dendrogram illustrated in Figure 6.3.

The dendogram form three major clusters (clades). The first cluster which constitute Australia and Europe appear to be very distinct in terms of similarity from the other two. The other two clusters are the cluster of Africa, Madagascar and South America and the cluster of Asia and North America. In the second cluster it shows Madagascar to be more similar to South America than Africa in that big cluster.

The link suggesting Africa, Madagascar and South America to have more similarities is the most significant one for this study because it clearly identifies the close relationship of even modern lungfish in those continents especially Africa and South America. Further investigations of these results reveal that, once again, plate tectonics (and possibly climate) is the major force causing the clustering at this point. On the other hand, the clustering of Asia and North America and their proximity through times during breaking up and joining of continents lends more evidence to the idea that plate tectonics is the primary clustering influence. The cluster formed by the continents of Australia and Europe prior to joining with the other two continents very likely is not based on simple explanation of plate tectonics but rather homoplasy (convergent evolution) due to similar environmental pressures.

6.3.3 PAE Cladogram

The second analysis following the cluster analysis in Parsimony Analysis of Endemicity (PAE) using areas of endemism. Six continents and the sub African continent of Madagascar were used as areas of endemism. In using presence/absence data only, there is an implicit assumption that taxa found at a particular area are sufficiently abundant to ensure their representation for other similar taxa endemic to that area. Dipnoi are a widespread and diverse clade ideally suited for biogeographic studies as they relatively abundant and distinct in different continents.

The three clades generated in PAE corroborates the three clusters found in similarity cluster analysis with some differences in groupings. In PAE the African subcontinent of Madagascar appear to form a clade of its own and South America which in cluster analysis is closest is in the second degree of closeness. Australia and Europe clade are still in the same cluster although the North America in the cluster analysis is associated with Asia.

In general, there is still some similarity of the clustering like number of clades and basic member compositions of each clade. There is also a notable shifting and rearrangements of some members of these clusters.

6.4 Conclusion

The geographical distribution analysis, cluster analysis and Parsimony Analysis of Endemicity (PAE) have been employed to study the patterns and possible influences of the distribution of lungfish 87 genera.

The distribution map (Figure 1) shows throughout historical records of lungfish from extinct record to modern lungfish record they have been widely distributed. Especially for extinct record it indicates the occupancy of this group of sarcopterygians to have been found in all continents with the exception of Antarctica where we ye to find their remains. Modern lungfish with three genera are only restricted in three continents, Africa, South America and Australia.

The cluster analysis and Parsimony Analysis of Endemicity (PAE) both generate three clusters of areas of similar patterns of distribution (Figure 2) and areas of endemism (Figure 3) respectively. The clustering appears to mirror the formation and break ups of the continents which suggests the plate tectonics to have played important role in the distribution patterns of lungfishes. In some cases, like closeness (similarity) of Australia and Europe might be due to parallel evolution due to environmental pressure.

LITERATURE CITED

LITERATURE CITED

Aanyu, K., and D. Koehn. “Influence of Pre-Existing Fabrics on Fault Kinematics and Rift Geometry of Interacting Segments: Analogue Models Based on the Albertine Rift (Uganda), Western Branch-East African Rift System.” *Journal of African Earth Sciences* 59, no. 2 (2011): 168–184.

Adaci, Mohammed, Rodolphe Tabuce, Fateh Mebrouk, Mustapha Bensalah, Pierre-Henri Fabre, Lionel Hautier, Jean-Jacques Jaeger, et al. “Nouveaux Sites À Vertébrés Paléogènes Dans La Région Des Gour Lazib (Sahara Nord-Occidental, Algérie).” *Comptes Rendus Palevol* 6, no. 8 (December 2007): 535–44. doi:10.1016/j.crpv.2007.09.001.

Agassiz, L. *Recherches Sur Les Poissons Fossiles 3 318 Petitpierre, Neufchatel*. Vol. 5, 1838.

Alves, Yuri Modesto, Lúcio Paulo Machado, Lílian Paglarelli Bergqvist, and Paulo M. Brito. “Redescription of Two Lungfish (Sarcopterygii: Dipnoi) Tooth Plates from the Late Cretaceous Bauru Group, Brazil.” *Cretaceous Research* 40 (2013): 243–50. doi:10.1016/j.cretres.2012.07.007.

Arambourg, Camille, and R. G. Wolff. “Nouvelles Données Paléontologique Sur L’âge Des ‘Gres Du Lubur’ (Turkana Grits) Al’ouest Du Lac Rodolphe.” *Comptes Rendus Société Géologique de France* 6 (1969): 190–202.

Arthington, Angela H. “Australian Lungfish, *Neoceratodus forsteri*, Threatened by a New Dam.” *Environmental Biology of Fishes* 84, no. 2 (2009): 211–221.

Baer, S., R. D. Haller, and T. A. Freyvogel. “Growth of the African Lungfish, *Protopterus amphibious* Peter, in Aquaculture.” *Aquaculture Research* 23, no. 2 (1992): 265–267.

Bellan, G., and D. Bellan-Santini. “Utilizzazione Delle Analisi Di Parsimonia (Cladistica) in Sinecologia Bentonica: Esempi in Una Zona Inquinata.” *Societá Italiana Di Ecologia Atti* 18 (1997): 247–250.

Bemis, William E. “Feeding Systems of Living Dipnoi: Anatomy and Function.” *Journal of Morphology* 190, no. S1 (1986): 249–275.

BERG, LS. “Classification of Recent and Fossil Agnatha and Fish.” *Trudy Zoologicheskogo Instituta*, 1940.

Berman, David S. “Cranial Morphology of the Lower Permian Lungfish *Gnathorhiza* (Osteichthyes: Dipnoi).” *Journal of Paleontology*, 1976, 1020–1033.

———. “Lungfish from the Lueders Formation (Lower Permian, Texas) and the Gnathorhiza-Lepidosirenid Ancestry Questioned.” *Journal of Paleontology*, 1968, 827–835.

Birks, H. John B. “Recent Methodological Developments in Quantitative Descriptive Biogeography.” In *Annales Zoologici Fennici*, 165–177. JSTOR, 1987. http://www.jstor.org/stable/23734493.

Bisconti, M., W. Landini, G. Bianucci, G. Cantalamessa, G. Carnevale, L. Ragaini, and G. Valleri. “Biogeographic Relationships of the Galapagos Terrestrial Biota: Parsimony Analyses of Endemicity Based on Reptiles, Land Birds and Scalesia Land Plants.” *Journal of Biogeography* 28, no. 4 (2001): 495–510.

Bishop, I. R., and G. E. H. Foxon. “The Mechanism of Breathing in the South Asmerican Lungfish, *Lepidosiren paradoxa*; Radiological Study.” *Journal of Zoology* 154, no. 3 (1968): 263–71. doi:10.1111/j.1469-7998. 1968.tb01663.x.

Blackburn, David C., Eric M. Roberts, and Nancy J. Stevens. “The Earliest Record of the Endemic African Frog Family Ptychadenidae from the Oligocene Nsungwe Formation of Tanzania.” *Journal of Vertebrate Paleontology* 35, no. 2 (March 4, 2015): e907174. doi:10.1080/02724634.2014.907174.

Bosworth, William, and Chris K. Morley. “Structural and Stratigraphic Evolution of the Anza Rift, Kenya.” *Tectonophysics* 236, no. 1 (1994): 93–115.

Brooks, A. S., D. M. Helgren, J. S. Cramer, A. Franklin, W. Hornyak, J. M. Keating, R. G. Klein, W. J. Rink, H. Schwarcz, and J. N. Smith. “Dating and Context of Three Middle Stone Age Sites with Bone Points in the Upper Semliki Valley, Zaire.” *Science (New York, N.Y.)* 268, no. 5210 (April 28, 1995): 548–53.

Brooks, Dr. “Historical Ecology - a New Approach to Studying the Evolution of Ecological Associations.” *Annals of the Missouri Botanical Garden* 72, no. 4 (1985): 660–80. doi:10.2307/2399219.

Campbell, K. S. W., and R. E. Barwick. “A New Devonian Lungfish, *Pillararhynchus longi* n. Gen. n. sp., from Gogo, Australia.” *Paleobiology* 16 (1990a): 168.

———. “An Advanced Massive Dipnorhynchid Lungfish from the Early Devonian of New South Wales, Australia.” *Records of the Australian Museum* 37 (1985): 301–316.

———. “The Axial Postcranial Structure of *Griphognathus whitei* from Gogo; Comparisons with Other Devonian Dipnoans.” *Records of the Western Australian Museum* 21, no. 1 (2002): 67–201.

Campbell, K. S. W., R. E. Barwick, and T. J. Senden. “Development of the Posterior Endocranium of the Devonian Dipnoan *Griphognathus whitei*.” *Journal of Vertebrate Paleontology* 32, no. 4 (2012): 781–798.

Cappetta, Henri. *Les Poissons Crétacés et Tertiaires Du Bassin Des Iullemmenden (République Du Niger)*. Société méridionale pour l’expansion de la recherche scientifique, 1972.

Carlson, Keith J. "The Skull Morphology and Estivation Burrows of the Permian Lungfish, *Gnathorhiza serrata*." *The Journal of Geology*, 1968, 641–663.

Case, Ermine Cowles. *A New Species of Ceratodus from the Upper Triassic of Western Texas*, 1921.

Cavin, Lionel, Larbi Boudad, Haiyan Tong, Emilie Läng, Jérôme Tabouelle, and Romain Vullo. "Taxonomic Composition and Trophic Structure of the Continental Bony Fish Assemblage from the Early Late Cretaceous of Southeastern Morocco." *PLOS ONE* 10, no. 5 (2015): e0125786. doi:10.1371/journal.pone.0125786.

Cavin, Lionel, Varavudh Suteethorn, Eric Buffetaut, and Haiyan Tong. "A New Thai Mesozoic Lungfish (Sarcopterygii, Dipnoi) with an Insight into Post-Palaeozoic Dipnoan Evolution." *Zoological Journal of the Linnean Society* 149, no. 2 (February 1, 2007): 141–77. doi:10.1111/j.1096-3642.2007.00238.x.

Chang, M. M., and X. B. Yu. "Structure and Phyogenetic Significance of *Diabolepis speratus* gen. et sp. nov., a New Dipnoan-like Form from the Lower Devonian of Eastern Yunnan, China." *Proc. Linn. Soc. N.S.W.* 107 (1984): 171–84.

Chapman, A. "On a New Species of *Ceratodus* from the Upper Triassic of Western Texas." *Occasional Papers of the Museum of Zoology, University of Michigan*, 1914, 1–2.

Chatfield, Christopher, and Alexander J. Collins. "Introduction." In *Introduction to Multivariate Analysis*, 3–17. Springer, 1980. http://link.springer.com/chapter/10.1007/978-1-4899-3184-9_1.

Chelius, Chad, and Angie Taylor. *Adobe Illustrator CS6: Learn by Video*. 1st ed. Berkeley, CA, USA: Peachpit Press, 2012.

Chew, Shit F., Lilian Ho, Tan F. Ong, Wai P. Wong, and Yuen K. Ip. "The African Lungfish, *Protopterus dolloi*, Detoxifies Ammonia to Urea during Environmental Ammonia Exposure." *Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches* 78, no. 1 (2004): 31–39. doi:10.1086/422771.

Churcher, C. S. "Giant Cretaceous Lungfish *Neoceratodus tuberculatus* from a Deltaic Environment in the Quseir (=Baris) Formation of Kharga Oasis, Western Desert of Egypt." *Journal of Vertebrate Paleontology* 15, no. 4 (December 27, 1995): 845–49. doi:10.1080/02724634.1995.10011267.

Churcher, C. S., and G. De iuliis. "A New Species of *Protopterus* and a Revision of *Ceratodus humei* (Dipnoi: Ceratodontiformes) from the Late Cretaceous Mut Formation of Eastern Dakhleh Oasis, Western Desert of Egypt." *Palaeontology* 44, no. 2 (March 1, 2001): 305–23. doi:10.1111/1475-4983.00181.

Churcher, Charles S., Gerardo De Iuliis, and Maxine R. Kleindienst. "A New Genus for the Dipnoan Species *Ceratodus tuberculatus* Tabaste, 1963." *Geodiversitas* 28, no. 4 (2006): 635–647.

Claeson, Kerin M., Hesham M. Sallam, Patrick M. O’Connor, and Joseph JW Sertich. “A Revision of the Upper Cretaceous Lepidosirenid Lungfishes from the Quseir Formation, Western Desert, Central Egypt.” *Journal of Vertebrate Paleontology* 34, no. 4 (2014): 760–766.

Clement, Alice M. “A New Genus of Lungfish from the Givetian (Middle Devonian) of Central Australia.” *Acta Palaeontologica Polonica* 54, no. 4 (2009): 615–626.

———. “A New Species of Long-Snouted Lungfish from the Late Devonian of Australia, and Its Functional and Biogeographical Implications.” *Palaeontology* 55, no. 1 (2012): 51–71.

Clement, Alice M., and John A. Long. “Air-Breathing Adaptation in a Marine Devonian Lungfish.” *Biology Letters* 6, no. 4 (2010): 509–512.

Conant, Elizabeth Babbott. “An Historical Overview of the Literature of Dipnoi: Introduction to the Bibliography of Lungfishes.” *Journal of Morphology* 190, no. S1 (1986): 5–13.

Cope, E. D. *Zittel’s Manual of Palaeontology. American Naturalist*. Vol. 21, 1887.

Coryndon, S. C. “Preliminary Report on Some Fossils from the Chiwondo Beds of the Karonga District, Malawi.” *American Anthropologist* 68, no. 2 (1966): 59–66. doi:10.1525/aa.1966.68.2.02a00980.

Cox, C. Barry, and Peter D. Moore. *Biogeography: An Ecological and Evolutionary Approach*. 8th ed. Blackwell Publishing, 2010. http://www.cell.com/partod/pdf/S0169-4758(00)01737-3.pdf.

Cracraft, John. “Patterns of Diversification within Continental Biotas: Hierarchical Congruence among the Areas of Endemism of Australian Vertebrates.” *Australian Systematic Botany* 4, no. 1 (1991): 211–227.

Craw, Robin. “New Zealand Biogeography: A Panbiogeographic Approach.” *New Zealand Journal of Zoology* 16, no. 4 (1989): 527–547.

Cunha, F. L. S., and C. S. Ferreira. “Um Dipnoi Na Formação Itapecuru (Cenomaniano), Maranhão, Brasil.” In *CONGRESO ARGENTINO DE PALEONTOLOGIA Y BIO-ESTRATIGRAFIA*, 2:1–9, 1980.

Dartevelle, E., and E. Casier. “Poissons Fossiles Du Congo (*Protopterus polli* nov. sp.).” *Annales Du Museum Du Congo Belge* 3 (1949): 201–256.

De Broin, F., E. Buffetaut, J.-Cl Koeniguer, J.-Cl Rage, D. Russell, Ph Taquet, C. Vergnaud-Grazzini, and S. Wenz. “La Faune de Vertébrés Continentaux Du Gisement d’In Beceten (Sénonien Du Niger).” *Comptes Rendus de l’Académie Des Sciences, Paris* 279 (1974): 469–472.

Denison, Robert Howland. *The Structure and Evolution of Teeth in Lungfishes*. Field Museum of National History, 1974.

Dillon, William R. Goldstein, Matthew William R. Dillon, and Matthew Goldstein. *Multivariate Analysismethods and Applications*. 519.535 D5. New York: John Wiley and Sons, 1984. http://www.sidalc.net/cgi-bin/wxis.exe/?IsisScript=sibe01.xis&method=post&formato=2&cantidad=1&expresion=mfn=000315.

Dingle, Regina V., William G. Siesser, and A. R. Newton. *Mesozoic and Tertiary Geology of Southern Africa*. Balkema Rotterdam, 1983.

Dutheil, Didier B. “An Overview of the Freshwater Fish Fauna from the Kem Kem Beds (Late Cretaceous: Cenomanian) of Southeastern Morocco.” *Mesozoic Fishes* 2 (1999): 553–563.

Eagles, Graeme, and Matthias König. “A Model of Plate Kinematics in Gondwana Breakup.” *Geophysical Journal International* 173, no. 2 (2008): 703–717.

Espinosa-Organista, D., Juan J. Morrone, C. Aguilar, and J. Llorente. “Regionalización Biogeográfica de México: Provincias Bióticas.” *Biodiversidad, Taxonomía Y Biogeografía de Artrópodos de México: Hacia Una Síntesis de Su Conocimiento* 2 (2000): 61–94.

ESRI (Environmental Systems Research Institute). *ArcView GIS Version 3.1.1. ESRI.* 3.1.1., 1999.

Everitt, Brian. *Cluster Analysis*. Second edition. Reviews of Current Research 11. London: New York: published on behalf of the Social Science Research Council by Heinemann Educational Books; Halsted Press, 1980.

Feldmann, Rodney M., Patrick M. O’Connor, Nancy J. Stevens, Michael D. Gottfried, Eric M. Roberts, Sifa Ngasala, Erin L. Rasmusson, and Saidi Kapilima. “A New Freshwater Crab (Decapoda: Brachyura: Potamonautidae) from the Paleogene of Tanzania, Africa.” *Neues Jahrbuch F??r Geologie Und Pal??ontologie - Abhandlungen* 244, no. 1 (2007): 71–78. doi:10.1127/0077-7749/2007/0244-0071.

Fernandes, M. E. B., J. M. Cardoso da Silva, and J. DE S E SILVA JUNIOR. “The Monkeys of the Islands of the Amazon Estuary, Brazil: A Biogeographic Analysis.” *Mammalia* 59, no. 2 (1995): 213–222.

García-Barros, Enrique, Pilar Gurrea, María José Luciáñez, José Martin Cano, Miguel L. Munguira, Juan Carlos Moreno, Helios Sainz, María José Sanz, and J. Carlos Simón. “Parsimony Analysis of Endemicity and Its Application to Animal and Plant Geographical Distributions in the Ibero-Balearic Region (Western Mediterranean).” *Journal of Biogeography* 29, no. 1 (2002): 109–124.

Gaston, Kevin J. “Species-Range-Size Distributions: Patterns, Mechanisms and Implications.” *Trends in Ecology & Evolution* 11, no. 5 (1996): 197–201.

Geraads, Denis. “Biogeography of Circum-Mediterranean Miocene-Pliocene Rodents; a Revision Using Factor Analysis and Parsimony Analysis of Endemicity.” *Palaeogeography, Palaeoclimatology, Palaeoecology* 137, no. 3 (1998): 273–288.

Gill, Theodore. *Arrangement of the Families of Fishes or Classes Pisces, Marsipobranchii, and Leptocardii Prepared for the Smithsonian Institution by Theodore Gill*. Smithsonian Institution, 1872. https://books.google.com/books?hl=en&lr=&id=u8I9sU7wr-oC&oi=fnd&pg=PR7&dq=Arrangement+of+the+families+of+fishes,+or+classes+Pisces,+Marsipobranchii,+and+Leptocardii&ots=sUqCtrAlBo&sig=9KWofbXdzZbmCWz01-HW6Of65qU.

Glasby, Christopher J., and Belinda Alvarez. "Distribution Patterns and Biogeographic Analysis of Austral Polychaeta (Annelida)." *Journal of Biogeography* 26, no. 3 (1999): 507–533.

Gordon, Andrew D. *Classification: Methods for the Exploratory Analysis and Multivariate*. Chapman and Hall, 1981.

Gottfried, Michael D., Patrick M. O'connor, Frankie D. Jackson, Eric M. Roberts, and Remegius Chami. "Dinosaur Eggshell from the Red Sandstone Group of Tanzania." *ResearchGate* 24, no. Jun 2004 (January 24, 2009): 494–97. doi:10.1671/0272-4634(2004)024[0494:DEFTRS]2.0.CO;2.

Gottfried, Michael D., Nancy J. Stevens, Eric M. Roberts, Patrick M. O. Connor Chami, and Remigius Chami. "A New Cretaceous Lungfish (Dipnoi, Ceratodontidae) from the Rukwa Rift Basin, Tanzania." *African Natural History* 5, no. 1 (2009): 31–36.

Gottfried, Michael, Nancy Stevens, Patrick O'Connor, Eric Roberts, and Sifa Ngasala. "A New Fossil Record for the African Lungfish *Protopterus* from the Paleogene of Tanzania." In *Journal of Vertebrate Paleontology*, 27:83A–83A. SOC VERTEBRATE PALEONTOLOGY 60 REVERE DR, STE 500, NORTHBROOK, IL 60062 USA, 2007.

Goudswaard, Kees PC, Frans Witte, and Lauren J. Chapman. "Decline of the African Lungfish (*Protopterus aethiopicus*) in Lake Victoria (East Africa)." *African Journal of Ecology* 40, no. 1 (2002): 42–52.

Goudswaard, P. C., F. Witte, and E. F. B. Katunzi. "The Tilapiine Fish Stock of Lake Victoria before and after the Nile Perch Upsurge." *Journal of Fish Biology* 60, no. 4 (April 1, 2002): 838–56. doi:10.1111/j.1095-8649.2002.tb02413.x.

Gray, Maria-Emma. *Figures of Molluscous Animals, Selected from Various Authors*. Vol. 4. Longman, 1850. https://books.google.com/books?hl=en&lr=&id=LYo-AAAAcAAJ&oi=fnd&pg=PA1&dq=gray+1850&ots=brsOk7EnFp&sig=yFL90xy6sjOnQzMDgaNh0J8FkV8.

Greenwood, P. H. "CXI.—Fish Remains from Miocene Deposits of Rusinga Island and Kavirondo Province, Kenya." *Journal of Natural History* 4, no. 48 (1951): 1192–1201.

Greenwood, P. Humphry. "The Natural History of African Lungfishes." *Journal of Morphology* 190, no. S1 (1986): 163–179.

Greenwood, Peter Humphry. *Quaternary Fish Fossils*. Vol. 4. Hayez, 1959.

Greenwood, Peter Humphry, and Gordon Jon Howes. *Neogene Fossil Fishes from the Lake Albert-Lake Edward Rift (Zaire).* British museum (natural history) geology, 1975.

Gross, WALTER. “Die Unterdevonischen Fische Und Gigantostraken von Overath.” *Abhandlungen Der Preu\s Sischen Geologischen Landesanstalt (NF)* 145 (1933): 41–77.

Günther, Albert. “Description of *Ceratodus*, a Genus of Ganoid Fishes, Recently Discovered in Rivers of Queensland, Australia.” *Philosophical Transactions of the Royal Society of London* 161 (1871): 511–71.

Haug, Emile. *Paléontologie*. Publication de la Société de géographie. Paris: Documents scientifiques de la Mission saharienne (Mission Foureau-Lamy), 1905.

Haughton, Sidney Henry. *The Stratigraphic History of Africa South of the Sahara*. Hafner Publishing Company, 1963.

Huxley, Prof, and others. “8. Contributions to Morphology. Ichthyopsida.—No. 1. On *Ceratodus* Forsteri, with Observations on the Classification of Fishes.” In *Proceedings of the Zoological Society of London*, 44:24–59. Wiley Online Library, 1876. http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.1876.tb02541.x/full.

Ikechukwu, Okafor Anthony, and Chukwu Lucian Obinnaya. “Haematological Profile of the African Lungfish, *Protopterus annectens* (Owen) of Anambra River, Nigeria.” *Journal of American Science* 6, no. 2 (2010): 123–130.

Ippi, Silvina, and Verónica Flores. “Las Tortugas Neotropicales Y Sus Áreas de Endemismo.” *Acta Zoológica Mexicana*, no. 84 (2001): 49–63.

Jaekel, Otto. *Zur Morphologie Der Gebisse Und Zähne*, 1926.

James, Frances C., and Charles E. McCulloch. “Multivariate Analysis in Ecology and Systematics: Panacea or Pandora’s Box?” *Annual Review of Ecology and Systematics*, 1990, 129–166.

Johansen, Kjell, and Ragnar Hol. “A Radiological Study of the Central Circulation in the Lungfish, *Protopterus aethiopicus*.” *Journal of Morphology* 126, no. 3 (1968): 333–348.

Johansen, Kjell, Claude Lenfant, and Gordon C Grigg. “Respiratory Control in the Lungfish, *Neoceratodus forsteri* (Krefft).” *Comparative Biochemistry and Physiology* 20, no. 3 (1967): 835–54. doi:10.1016/0010-406X (67)90057-6.

Johnston, R. J. “Classification in Geography (Concepts and Techniques in Modern Geography 6).” In *Geo Abstracts*, 1976.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren. “Data Analysis in Community and Landscape Ecology,” 1995. http://agris.fao.org/agris-search/search.do?recordID=NL2012065194.

Kemp, A. “A Revision of Australian Mesozoic and Cenozoic Lungfish of the Family Neoceratodontidae (Osteichthyes: Dipnoi), with a Description of Four New Species.” *Journal of Paleontology*, 1997, 713–733.

———. “Early Development of Neural Tissues and Mesenchyme in the Australian Lungfish *Neoceratodus forsteri* (Osteichthyes: Dipnoi).” *Journal of Zoology* 250, no. 3 (2000): 347–372.

———. “Ontogeny of the Skull of the Australian Lungfish *Neoceratodus forsteri* (Osteichthyes: Dipnoi).” *Journal of Zoology* 248, no. 1 (May 1, 1999): 97–137. doi:10.1111/j.1469-7998.1999.tb01027.x.

———. “Role of Epidermal Cilia in Development of the Australian Lungfish, *Neoceratodus forsteri* (Osteichthyes: Dipnoi).” *Journal of Morphology* 228, no. 2 (1996): 203–221.

———. “Skull Structure in Post-Paleozoic Lungfish.” *Journal of Vertebrate Paleontology* 18, no. 1 (1998): 43–63.

———. “The Biology of the Australian Lungfish, *Neoceratodus forsteri* (Krefft 1870).” *Journal of Morphology* 190, no. Supplement No. 1 (1986): 181–198.

———. “The Pattern of Tooth Plate Formation in the Australian Lungfish, *Neoceratodus forsteri* Krefft.” *Zoological Journal of the Linnean Society* 60, no. 3 (1977): 223–258.

Kemp, Anne. “Chirodipterus Potteri, a New Devonian Lungfish from New South Wales, Australia: And the Ontogeny of Chirodipterid Tooth Plates.” *Journal of Vertebrate Paleontology* 20, no. 4 (2001): 665–674.

———. “Dental and Skeletal Pathology in Lungfish Jaws and Tooth Plates.” *Alcheringa: An Australasian Journal of Palaeontology* 27, no. 2 (January 1, 2003): 155–70. doi:10.1080/03115510308619555.

Kirkland, J. I. “Fossil Elasmobranchs from the Mid-Cretaceous (Middle Cenomanian Middle Turonian) Greenhorn Cyclothem of Eastern Nebraska.” *Proceedings of the Nebraska Academy of Science* 99 (1989): 52.

Kirkland, JAMES I. “Morrison Fishes.” *Modern Geology* 22, no. 1 (1998): 1–4.

Kirkland, James Ian. *Upper Jurassic and Cretaceous Lungfish Tooth Plates from the Western Interior: The Last Dipnoan Faunas of North America*, 1987.

Kitzan, Sonja M., and Phillip R. Sweeny. “A Light and Electron Microscope Study of the Structure of *Protopterus annectens* Epidermis. I. Mucus Production.” *Canadian Journal of Zoology* 46, no. 4 (1968): 767–772.

Klika, E., and A. Lelek. “A Contribution to the Study of the Lungs of the *Protopterus annectens* and *Polypterus senegalensis*.” *Folia Morphologica* 15, no. 2 (1966): 168–175.

König, Matthias, and Wilfried Jokat. “Advanced Insights into Magmatism and Volcanism of the Mozambique Ridge and Mozambique Basin in the View of New Potential Field Data.” *Geophysical Journal International* 180, no. 1 (2010): 158–180.

Lavocat, R. “Découverte de Dipneustes Du Genre *Protopterus* Dans Le Tertiaire Ancien de Tamaguilelt (Soudan Français).” *COMPTES RENDUS HEBDOMADAIRES DES SEANCES DE L ACADEMIE DES SCIENCES* 240, no. 19 (1955): 1915–1917.

Lehman, Jean-Pierre. *A Propos de Ceratodus Sturii Teller. 1891*, 1975.

Lison, L. “Recherches Sur La Structure et L’histogenese Des Dents Des Poissons Dipneustes.” *Archives de Biologie, Paris* 52 (1941): 279–320.

Liu, H., and H. Yeh. “Two New Species of *Ceratodus* from Szechuan, China.” *Vertebrata Palasiatica* 1, no. 4 (1957): 305–309.

Long, J. A. “A Redescription of the Lungfish Eoctenodus Hills 1929, with Reassessment of Other Australian Records of the Genus *Dipterus*, Sedgwick and Murchison 1828.” *Records of the Western Australian Mu- Seum* 13 (1987): 297–314.

Luna Vega, Isolda, Othón Alcántara Ayala, David Espinosa Organista, and Juan J. Morrone. “Historical Relationships of the Mexican Cloud Forests: A Preliminary Vicariance Model Applying Parsimony Analysis of Endemicity to Vascular Plant Taxa.” *Journal of Biogeography* 26, no. 6 (1999): 1299–1305.

Maina, J. N. “The Morphology of the Lung of the African Lungfish, *Protopterus aethiopicus*.” *Cell and Tissue Research* 250, no. 1 (October 1, 1987): 191–96. doi:10.1007/BF00214671.

Marchalonis, J.J. “Immunology and Cell Biology - Abstract of Article: Isolation and Characterization of Immunoclobulin-Like Proteins of the Australian Lungfish (*Neoceratodus forsteri*).” *Aust J Exp Biol Med* 47, no. 4 (1969): 405–19.

Marshall, Charles R. “A List of Fossil and Extant Dipnoans.” *Journal of Morphology* 190, no. S1 (1986): 15–23.

Martin, M. “*Arganodus atlantis* et *Ceratodus arganensis*, Deux Nouveaux Dipneustes Du Trias Supérieur Continental Marocain.” *Comptes Rendus Academie Des Sciences, Paris, Sciences de La Terre et Des Planetes Ser. D* 289 (1979): 89–92.

———. “Nouvelles Données Sur La Phylogénie et La Systématique Des Dipneustes Postpaléozoïques.” *Comptes Rendus de l’Académie Des Sciences, Paris, Série II* 294 (1982): 611–614.

Martin, Michel. “Deux Lepidosirenidae (Dipnoi) Crétacés Du Sahara, *Protopterus humei* (Priem) et *Protopterus protopteroides* (Tabaste).” *Paläontologische Zeitschrift* 58, no. 3–4 (1984): 265–277.

———. “*Dipteronotus gibbosus* (Actinopterygi, Chondrostei) Nouveau Colobodontide Du Trias Superieur Continental Marocain.” *Geobios* 13, no. 3 (1980): 445–449.

———. “Nouveaux Lepidosirenides (Dipnoi)du Tertiaire Africain.” *Geobios*, Premiers Vertandébrandés et Vertandébrandés Infandérieurs, 28 (1995): 275–80. doi:10.1016/S0016-6995(95)80126-X.

———. “Nouvelles Données Sur La Phylogénie et La Systématique Des Dipneustes Postpaléozoiques, Conséquences Stratigraphiques et Paléogéographiques.” *Geobios* 15 (1982): 53–64.

———. “Phylogénie et Systématique Des Cératodontiformes(Dipnoi), Paléoécologie et Paléobiogéographie,” 1983. http://cat.inist.fr/?aModele=afficheN&cpsidt=9429900.

———. “Protopterus nigeriensis Nov. Sp., L’un Des Plusanciens *Protoptères* — DIPNOI — (In Beceten, Sénonien Du Niger).” *Comptes Rendus de l’Académie Des Sciences - Series IIA - Earth and Planetary Science* 325, no. 8 (1997): 635–38. doi:10.1016/S1251-8050(97)89466-9.

———. *Revision of Ceratodus Concinnus PLIENINGER*. Staatliches Museum für Naturkunde, 1980.

Martin, Michel, Laurent Barbieri, and Gilles Cuny. “The Madagascan Mesozoic Ptychoceratodontids (Dipnoi) Systematic Relationships and Paleobiogeographical Significance.” *Oryctos* 2 (1999): 3–16.

McCartney, Jacob A., Nancy J. Stevens, and Patrick M. O’Connor. “The Earliest Colubroid-Dominated Snake Fauna from Africa: Perspectives from the Late Oligocene Nsungwe Formation of Southwestern Tanzania.” *PloS One* 9, no. 3 (2014): e90415.

Mcmahon, B. R. “A Functional Analysis of the Aquatic and Aerial Respiratory Movements of an African Lungfish, *Protopterus aethiopicus*, With Reference to the Evolution of the Lung-Ventilation Mechanism in Vertebrates.” *Journal of Experimental Biology* 51, no. 2 (1969): 407–30.

Mead, James G. “A Fossil Beaked Whale (Cetacea: Ziphiidae) from the Miocene of Kenya.” *Journal of Paleontology*, 1975, 745–751.

Miles, R. S. “Dipnoan (Lungfish) Skulls and the Relationships of the Group: A Study Based on New Species from the Devonian of Australia.” *Zoological Journal of the Linnean Society* 61, no. 1–3 (August 1, 1977): 1–328. doi:10.1111/j.1096-3642. 1977.tb01031.x.

Milner, Andrew R.C., and James I. Kirkland. “Preliminary Review of the Early Jurassic (Hettangian) Freshwater Lake Dixie Fish Fauna in the Whitmore Point Member, Moenave Formation in Southwest Utah.” *Southwest Utah. New Mexico Museum of Natural History and Science Bulletin* 37 (2006): 510–521.

Morronc, Juan J., Liliana Katinas, and Jorge V. Crisci. “A Cladistic Biogeographic Analysis of Centrai. Chile.” *Journal of Comparative Biology* 2 (1997): 25–41.

Morrone, J. J., M. del C. Coscarón, and others. “Distributional Patterns of the American Peiratinae (Heteroptera: Reduviidae).” *Zoologische Mededeelingen* 70 (1996): 1–15.

Morrone, J. J., and E. C. Lopretto. “Parsimony Analysis of Endemicity of Freshwater Decapoda (Crustacea: *Malacostraca*) from Southern South America.” *Neotropica* 41 (1995): 3–8.

Morrone, Juan. “On Udvardy’s Insulantarctica Province: A Test from the Weevils (Coleoptera: Curculionoidea).” *Journal of Biogeography* 25, no. 5 (1998): 947–955.

Morrone, Juan J. “Distributional Patterns of Species of Rhytirrhinini (Coleoptera: Curculionidae) and the Historical Relationships of the Andean Provinces.” *Global Ecology and Biogeography Letters*, 1994b, 188–194.

———. “On the Identification of Areas of Endemism.” *Systematic Biology* 43, no. 3 (1994a): 438–441.

Morrone, Juan J., and Jorge V. Crisci. “Historical Biogeography: Introduction to Methods.” *Annual Review of Ecology and Systematics*, 1995, 373–401.

Morrone, Juan J., and Juan Márquez. “Halffter’s Mexican Transition Zone, Beetle Generalized Tracks, and Geographical Homology.” *Journal of Biogeography* 28, no. 5 (2001): 635–650.

Morrone, Juan J., David Espinosa Organista, Claudia Aguilar Zúñiga, and Jorge Llorente Bousquets. “Preliminary Classification of the Mexican Biogeographic Provinces: A Parsimony Analysis of Endemicity Based on Plant, Insect, and Bird Taxa.” *The Southwestern Naturalist* 44, no. 4 (1999): 507–514.

Müller, J. *Mémoire Sur Les Ganoides et Sur La Classification Naturelle Des Poissons*, 1845.

Müller, Johannes. *Über Den Bau Und Die Grenzen Der Ganoiden Und Über Das Natürliche System Der Fische*. Gedruckt in der Druckerei der Königlichen Akademie der Wissenschaften, 1846. https://books.google.com/books?hl=en&lr=&id=1pJ9fnBYOSgC&oi=fnd&pg=PA1&dq=%C3%9Cber+den+Bau+und+die+Grenzen+der+ganoiden+und+%C3%BCber+das+nat%C3%BCrliche+System+der+Fische&ots=SkOZoT-CS5&sig=6-nBY0xiTRsDIMFZWAzQkNoKTtw.

Murray, Alison M., Todd D. Cook, Yousry S. Attia, Prithijit Chatrath, and Elwyn L. Simons. “A Freshwater Ichthyofauna from the Late Eocene Birket Qarun Formation, Fayum, Egypt.” *Journal of Vertebrate Paleontology* 30, no. 3 (2010): 665–680.

Myers, A. A. “How Did Hawaii Accumulate Its Biota? A Test from the Amphipoda.” *Global Ecology and Biogeography Letters* 1 (1991): 24–29.

O'Connor, Patrick, Michael Gottfried, Eric Roberts, Nancy J. Stevens, Frankie Jackson, and Erin Rasmusson. "Closing the African Gap: A New Cretaceous Vertebrate Fauna from Tanzania." In *Journal of Vertebrate Paleontology*, 23:84A–84A. Taylor & Francis Inc 530 Chestnut Street, STE 850, Philadelphia, PA 19106 USA, 2003.

O'Connor, Patrick M., Michael D. Gottfried, Nancy J. Stevens, Eric M. Roberts, Sifa Ngasala, Saidi Kapilima, and Remigius Chami. "A New Vertebrate Fauna from the Cretaceous Red Sandstone Group, Rukwa Rift Basin, Southwestern Tanzania." *Journal of African Earth Sciences* 44, no. 3 (2006): 277–288.

O'Connor, Patrick M., Joseph J.W. Sertich, and Fredrick K. Manthi. "A Pterodactyloid Pterosaur from the Upper Cretaceous Lapurr Sandstone, West Turkana, Kenya." *Anais Da Academia Brasileira de Ciências* 83, no. 1 (2011): 309–315.

Otero, Olga. "Current Knowledge and New Assumptions on the Evolutionary History of the African Lungfish, *Protopterus*, Based on a Review of Its Fossil Record." *Fish and Fisheries* 34, no. 1 (2010): 93–113.

Otero, Olga, Aurélie Pinton, Henri Cappetta, Sylvain Adnet, Xavier Valentin, Mustapha Salem, and Jean-Jacques Jaeger. "A Fish Assemblage from the Middle Eocene from Libya (Dur At-Talah) and the Earliest Record of Modern African Fish Genera." *PloS One* 10, no. 12 (2015): e0144358.

Parkinson, J. *Organic Remains*. Vol. III. Landon: Sherwood, Neely, and Jones, 1811. http://za2uf4ps7f.search.serialssolutions.com/?url_ver=Z39.88-2004&rft_val_fmt=info%3Aofi%2Ffmt%3Akev%3Amtx%3Abook&rft.genre=bookitem&rft.btitle=Organic%20Remains&rft.spage=269&rft.date=1811&rft.aulast=Parkinson&rft.aufirst=J.&rfr_id=info%3Asid%2Fwiley.com%3AOnlineLibrary.

Patterson, Colin, and A. E. Longbottom. "An Eocene Amiid Fish from Mali, West Africa." *Copeia*, 1989, 827–836.

Poll, M. *Revision Systkmatic et Raciation Geographique Des Protopteridae de 1'Afrique Centrale*. Vol. Zool. 103. Ann. Mus. R. Congo Belge 8, 1961.

Posadas, P., J. M. Estevez, and J. J. Morrone. "Distributional Patterns and Endemism Areas of Vascular Plants in the Andean Subregion." *Fontqueria* 48 (1997): 1–10.

Posadas, Paula. "Distributional Patterns of Vascular Plants in Tierra Del Fuego: A Study Applying Parsimony Analysis of Endemicity (PAE)." *Biogeographica* 72, no. 4 (1996): 161–177.

Priem, Fernand. *Paléontologie de Madagascar: XII-Les Poissons Fossiles*. Masson, 1924.

———. *Sur Des Poissons Fossiles et En Particulier Des Siluridés Du Tertiaire Supérieur et Des Couches Récentes d'Afrique: Suivi de: Sur Des Poissons Fossiles Des Terrains Tertiaires*

D'eau Douce et D'eau Saumâtre de France et de Suisse. Société géologique de France, 1914.

Qiao, Tuo, and Min Zhu. "A New Early Devonian Lungfish from Guangxi, China, and Its Palaeogeographic Significance." *Alcheringa: An Australasian Journal of Palaeontology* 39, no. 3 (2015): 428–437.

———. "A New Early Devonian Lungfish from Guangxi, China, and Its Palaeogeographic Significance." *Alcheringa: An Australasian Journal of Palaeontology* 39, no. 3 (2015): 428–37. doi:10.1080/03115518.2015.1015819.

———. "A New Tooth-Plated Lungfish from the Middle Devonian of Yunnan, China, and Its Phylogenetic Relationships." *Acta Zoologica* 90, no. s1 (2009): 236–252.

Rice, Jake, and Rene J. Belland. "A Simulation Study of Moss Floras Using Jaccard's Coefficient of Similarity." *Journal of Biogeography*, 1982, 411–419.

Richter, M., and C. E. V. Toledo. "The First Triassic Lungfish from South America (Santa Maria Formation, Paraná Basin) and Its Bearing on Geological Correlations within Pangaea." *Geological Society, London, Special Publications* 295, no. 1 (2008): 43–54.

Roberts, Eric M., Patrick M. O'Connor, Michael D. Gottfried, Nancy Stevens, Saidi Kapalima, and Sifa Ngasala. "Revised Stratigraphy and Age of the Red Sandstone Group in the Rukwa Rift Basin, Tanzania." *Cretaceous Research* 25, no. 5 (2004): 749–759.

Roberts, Eric M., Patrick M. O'Connor, Nancy J. Stevens, Michael D. Gottfried, Zubair A. Jinnah, Sifael Ngasala, Adeline M. Choh, and Richard A. Armstrong. "Sedimentology and Depositional Environments of the Red Sandstone Group, Rukwa Rift Basin, Southwestern Tanzania: New Insight into Cretaceous and Paleogene Terrestrial Ecosystems and Tectonics in Sub-Equatorial Africa." *Journal of African Earth Sciences* 57, no. 3 (2010): 179–212.

Roberts, Eric M., N. J. Stevens, P. M. O'Connor, P.H.G.M. Dirks, Michael D. Gottfried, W. C. Clyde, R. A. Armstrong, A. I. S. Kemp, and S. Hemming. "Initiation of the Western Branch of the East African Rift Coeval with the Eastern Branch." *Nature Geoscience* 5, no. 4 (2012): 289–294.

Romer, Alfred Sherwood. "Herpetichthyes, Amphibioidei, Choanichthyes or Sarcopterygii?" *Nature* 176 (1955): 126.

Romesburg, H. Charles. *Cluster Analysis for Researchers*. Belmont, California: Lifetime Learning Publications, 1984.

Ron, Santiago R. "Biogeographic Area Relationships of Lowland Neotropical Rainforest Based on Raw Distributions of Vertebrate Groups." *Biological Journal of the Linnean Society* 71, no. 3 (2000): 379–402.

Rosen, Brian R. “From Fossils to Earth History: Applied Historical Biogeography.” In *Analytical Biogeography*, 437–481. Springer, 1988. http://link.springer.com/chapter/10.1007/978-94-009-1199-4_17.

Rosen, Brian R., and Andrew B. Smith. “Tectonics from Fossils? Analysis of Reef-Coral and Sea-Urchin Distributions from Late Cretaceous to Recent, Using a New Method.” *Geological Society, London, Special Publications* 37, no. 1 (1988): 275–306.

Royer, J. Y., and M. F. Coffin. “Jurassic to Eocene Plate Tectonic Reconstructions in the Kerguelen Plateau Region.” In *Proceedings of the Ocean Drilling Program, Scientific Results*, 120:917–930. Texas: College Station, TX, Ocean Drilling Program, Texas A&M University, 1992. http://ecite.utas.edu.au/73818.

Royer, Jean-Yves, and Millard F. Coffin. “50. Jurassic to Eocene Plate Tectonic Reconstructions in The Kerguelen Plateau Region1.” In *Proceedings of the Ocean Drilling Program: Scientific Results*, 917. The Program, 1988. http://www-odp.tamu.edu/Publications/120_SR/VOLUME/CHAPTERS/sr120_50.pdf.

Schaal, Stephan. *Oberkretazische Osteichthyes, Knochenfische, Aus Dem Bereich von Bahariya Und Kharga, Ägypten, Und Ihre Aussagen Zur Palökologie Und Stratigraphie*. Reimer, 1984.

Schultze, Hans-Peter. “A Comparison of Controversial Hypotheses on the Origin of Tetrapods.” *Origin of the Higher Groups of Tetrapods. Comstock, Ithaca*, 1991, 29–67.

———. “A Dipnoan Tooth Plate from the Lower Cretaceous of Kansas, USA.” *Transactions of the Kansas Academy of Science (1903)*, 1981, 187–195.

———. *Fossilium Catalogus: Animalia*. 131. W. Junk, 1992.

———. “Mesozoic Sarcopterygians.” *Mesozoic Fishes* 3 (2004): 463–492.

Schultze, H.-P., and J. Chorn. “The Permo-Carboniferous Genus *Sagenodus* and the Beginning of Modern Lungfish.” *Contributions to Zoology* 67, no. 1 (1997): 9–70.

Schwartz, Hilde Lisa. “Paleoecology of Late Cenozoic Fishes from the Turkana Basin, Northern Kenya,” 1983.

Sertich, Joseph, Frederick Kyalo Manthi, Scott Sampson, Mark Loewen, and Mike Getty. “Rift Valley Dinosaurs: A New Late Cretaceous Vertebrate Fauna from Kenya.” In *Journal of Vertebrate Paleontology*, 26:124A–124A. SOC VERTEBRATE PALEONTOLOGY 60 REVERE DR, STE 500, NORTHBROOK, IL 60062 USA, 2006.

Sfenthourakis, Spyros, and Sinos Giokas. “A Biogeographical Analysis of Greek Oniscidean Endemism.” *Israel Journal of Zoology* 44, no. 3–4 (1998): 273–282.

Shah, S. C., and P. P. Satsangi. “A New Ceratodus Species from the Maleri Beds, Andhra Pradesh.” *Records of the Geological Survey of India* 98 (1969): 175–178.

Silva, José Maria Cardoso da, and David Conway Oren. “Application of Parsimony Analysis of Endemicity in Amazonian Biogeography: An Example with Primates.” *Biological Journal of the Linnean Society* 59, no. 4 (1996): 427–437.

Smith, Lindsay I. “A Tutorial on Principal Components Analysis.” *Cornell University, USA* 51 (2002): 52.

Starks, Joy L., and Alec Fehl. *Adobe Photoshop CS6: Comprehensive*. 1st ed. Boston, MA, United States: Course Technology Press, 2012.

Stevens, Nancy, Michael Gottfried, Patrick O’Connor, and Eric Roberts. “Macroscelideans from the Oligocene of Southwestern Tanzania.” In *Journal of Vertebrate Paleontology*, 26:128A–128A. SOC Vertebrate Paleontology 60 Revere Dr, STE 500, Northbrook, IL 60062 USA, 2006.

Stevens, Nancy J., Michael D. Gottfried, Eric M. Roberts, Saidi Kapilima, Sifa Ngasala, and Patrick M. O’Connor. “Paleontological Exploration in Africa: A View from the Rukwa Rift Basin of Tanzania.” In *Elwyn Simons: A Search for Origins*, 159–180. Springer, 2008. http://link.springer.com/chapter/10.1007/978-0-387-73896-3_12.

Stevens, Nancy J., Patricia A. Holroyd, Eric M. Roberts, Patrick M. O’Connor, and Michael D. Gottfried. “*Kahawamys mbeyaensis* (n. gen., n. sp.) (Rodentia: Thryonomyoidea) from the Late Oligocene Rukwa Rift Basin, Tanzania.” *Journal of Vertebrate Paleontology* 29, no. 2 (2009a): 631–634.

Stevens, Nancy J., Patrick M. O’Connor, Michael D. Gottfried, Eric M. Roberts, and Sifa Ngasala. “An Anthropoid Primate Humerus from the Rukwa Rift Basin, Paleogene of Southwestern Tanzania.” *Journal of Vertebrate Paleontology* 25, no. 4 (2005): 986–989.

Stevens, Nancy J., Patrick M. O’Connor, Michael D. Gottfried, Eric M. Roberts, Sifael Ngasala, and Mary R. Dawson. “Metaphiomys (Rodentia: Phiomyidae) from the Paleogene of Southwestern Tanzania.” *Journal of Paleontology* 80, no. 2 (2006): 407–410.

Stevens, Nancy J., Patrick M. O’Connor, Eric M. Roberts, and Michael D. Gottfried. “A Hyracoid from the Late Oligocene Red Sandstone Group of Tanzania, *Rukwalorax jinokitana* (gen. and sp. nov.).” *Journal of Vertebrate Paleontology* 29, no. 3 (2009b): 972–975.

Stevens, Nancy J., Erik R. Seiffert, Patrick M. O’Connor, Eric M. Roberts, Mark D. Schmitz, Cornelia Krause, Eric Gorscak, Sifa Ngasala, Tobin L. Hieronymus, and Joseph Temu. “Palaeontological Evidence for an Oligocene Divergence between Old World Monkeys and Apes.” *Nature* 497, no. 7451 (2013): 611–614.

Stevens, William N., Kerin M. Claeson, and Nancy J. Stevens. “Alestid (Characiformes: Alestidae) Fishes from the Late Oligocene Nsungwe Formation, Rukwa Rift Basin, of Tanzania.” *Journal of Vertebrate Paleontology* 36, no. 5 (September 2, 2016): e1180299. doi:10.1080/02724634.2016.1180299.

Stewart, Kathlyn M. “A New Species of *Sindacharax* (Teleostei: Characidae) from Lothagam, Kenya, and Some Implications for the Genus.” *Journal of Vertebrate Paleontology* 17, no. 1 (1997): 34–38.

———. “Fossil Fish Remains from Mio-Pliocene Deposits at Lothagam, Kenya.” *Lothagam, the Dawn of Humanity in Eastern Africa* 3 (2003): 76–111.

Stromer, E. v. “Über Das Gebiss Der Lepidosirenidae Und Die Verbreitung Tertiärer Und Mesozoischer Lungenfische.” *Festschrift Zum 60 Geburtstage Der R. Hertwigs* 2 (1910): 612–614.

———. “Wirbeltierreste Der Baharije-Stufe. 1. Einleitung. 2.” *Libycosuchus. Abhandl. Math.-Phys. Kl. K. Bayr. Ak. Wiss. XXVII*, 1914.

Swofford, D. L. “PAUP* Version 4.0 b10. Phylogenetic Analysis Using Parsimony (* and Other Methods).” *Sinauer, Sunderland, MA*, 2002.

Tabaste, Nicole. “Étude de Restes de Poissons Du Crétacé Saharien.” *Mémoire IFAN, Mélanges Ichthyologiques* 68 (1963): 437–485.

Takezaki, Naoko, Felipe Figueroa, Zofia Zaleska-Rutczynska, Naoyuki Takahata, and Jan Klein. “The Phylogenetic Relationship of Tetrapod, Coelacanth, and Lungfish Revealed by the Sequences of Forty-Four Nuclear Genes.” *Molecular Biology and Evolution* 21, no. 8 (2004): 1512–1524.

Teixeira, Carlos. “Nouvelles Recherches et Revision de La Flore de Cercal (Portugal).” *Brotéria, Ci. Nat* 16 (1947): 5–13.

Teller, Friedrich Joseph. *Über Den Schädel Eines Fossilen Dipnoërs Ceratodus Sturii Nov. Spec. Aus Den Schichten Der Oberen Trias Der Nordalpen: Mit 4 Lithographirten Tafeln Und 8 Zinkotypien Im Text*. A. Hölder, 1891.

Tiercelin, J. -J, J. -L Potdevin, C. K Morley, M. R Talbot, H Bellon, A Rio, B Le Gall, and W Vétel. “Hydrocarbon Potential of the Meso-Cenozoic Turkana Depression, Northern Kenya. I. Reservoirs: Depositional Environments, Diagenetic Characteristics, and Source Rock–reservoir Relationships.” *Marine and Petroleum Geology* 21, no. 1 (January 2004): 41–62. doi:10.1016/j.marpetgeo.2003.11.007.

Tohyama, Yoko, Tomomi Ichimiya, Hiromi Kasama-Yoshida, Ying Cao, Masami Hasegawa, Hisako Kojima, Yoichi Tamai, and Tadashi Kurihara. “Phylogenetic Relation of Lungfish Indicated by the Amino Acid Sequence of Myelin DM20.” *Molecular Brain Research* 80, no. 2 (2000): 256–59. doi:10.1016/S0169-328X(00)00143-1.

Trejo-Torres, J. Carlos, and James D. Ackerman. “Biogeography of the Antilles Based on a Parsimony Analysis of Orchid Distributions.” *Journal of Biogeography* 28, no. 6 (2001): 775–794.

Trewavas, Eth. "The Presence in Africa East of the Rift Valley of Two Species of *Protopterus, P. annectens and P. amphibius.*" *Ann. Mus. Congo Belge Ser. Quarto Zool* 1 (1954): 83–100.

Van Couvering, John A. "Geology of Rusinga Island and Correlation of the Kenya Mid-Tertiary Fauna." University of Cambridge, 1972. http://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.452369.

Van Couvering, Judith Anne Harris. "Early Records of Freshwater Fishes in Africa." *Copeia*, 1977, 163–166.

———. *Fossil Cichlid Fish of Africa*. 29. Palaeontological Association, 1982.

Van Neer, Wim. "Geology and Palaeontology of the Albertine Rift Valley, Uganda- Zaire, II: Paleobiology," 1994, 89–127.

Vega, Isolda Luna, Othon Alcantara Ayala, Juan Morrone, David Espinosa Organista, and others. "Track Analysis and Conservation Priorities in the Cloud Forests of Hidalgo, Mexico." *Diversity and Distributions* 6, no. 3 (2000): 137–143.

Vorobyeva, E. I. "A Triassic Ceratod from South Fergana and Remarks on the Systematics and Phylogeny of Ceratodontids." *Paleontologicheskii Zhurnal* 1967 (1967): 102–111.

Vorobyeva, E. I., and M. G. Minikh. "Experimental Application of Biometry to the Study of Ceratodontid Dental Plates." *Paleontological Journal* 2 (1968): 217–227.

Wake, Marvalee H. "Urogenital Morphology of Dipnoans, with Comparisons to Other Fishes and to Amphibians." *Journal of Morphology* 190, no. S1 (1986): 199–216.

Ward Jr, Joe H. "Hierarchical Grouping to Optimize an Objective Function." *Journal of the American Statistical Association* 58, no. 301 (1963): 236–244.

Wasawo, D. P. S. "A Dry Season Burrow of *Protopterus aethiopicus* Heckel." *Revue de Zoologie et de Botanique Africaines* 60 (1959): 65–70.

Watanabe, Katsutoshi. "Parsimony Analysis of the Distribution Pattern of Japanese Primary Freshwater Fishes, and Its Application to the Distribution of the Bagrid Catfishes." *Ichthyological Research* 45, no. 3 (1998): 259–270.

Werner, C. "Der Erste Nachweis von Gymnophionen (Armphibia) in Der Kreide (Wadi-Milk-Formation, Sudan). Mit 3 Abbildungen Im Text." *Neues Jahrbuch Fur Geologie Und Palaontologie-Monatshefte*, no. 10 (1994): 633.

White, Joseph D. "Brown, J. H., and M. V. Lomolino. 1998. Biogeography. 2nd Ed. Sinauer Associates, Inc., Sunderland, Massachusetts, Xii + 691 Pp. ISBN 0-87893-073-6, Price (Hardcover), $68.00." *Journal of Mammalogy* 80, no. 4 (December 6, 1999): 1385–89. doi:10.2307/1383194.

Whitmore Jr, F. C. “A Paleocene Lungfish, *Ceratodus humei* Priem, 1914, from Jabal Umm Himar, Kingdom of Saudi Arabia.” *United States Geological Survey Bulletin* 2093 (1995): 1–5.

Wilkie, Michael P., Tammie P. Morgan, Fernando Galvez, Richard W. Smith, Makiko Kajimura, Yuen K. Ip, and Chris M. Wood. “The African Lungfish (*Protopterus dolloi*): Ionoregulation and Osmoregulation in a Fish out of Water.” *Physiological and Biochemical Zoology* 80, no. 1 (2006): 99–112.

Winn Jr, Robert D., John C. Steinmetz, and William L. Kerekgyarto. “Stratigraphy and Rifting History of the Mesozoic-Cenozoic Anza Rift, Kenya.” *AAPG Bulletin* 77, no. 11 (1993): 1989–2005.

Young, C. G. “On Two New Fossil Fishes from Southwestern China*.” *Bulletin of the Geological Society of China* 21, no. 1 (1941): 91–96. doi:10.1111/j.1755-6724. 1941.mp21001007. x.

Young, G. C. “Fossil Fishes from Antarctica.” *The Geology of Antarctica. Oxford Monographs on Geology and Geophysics* 17 (1991): 538–567.