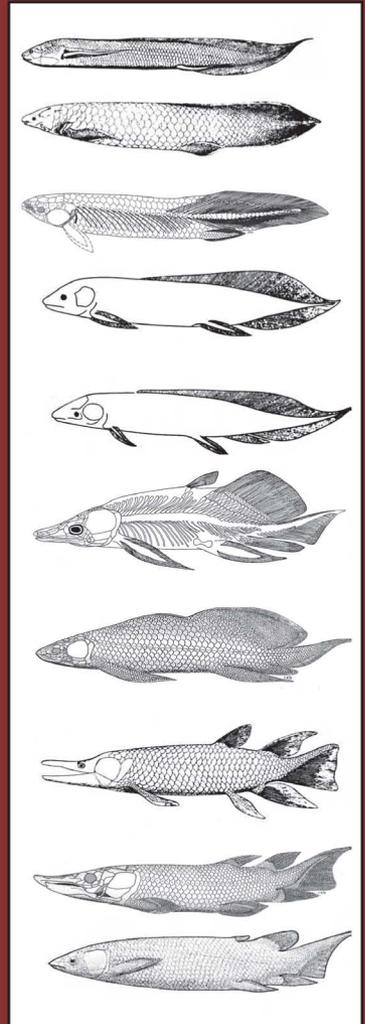
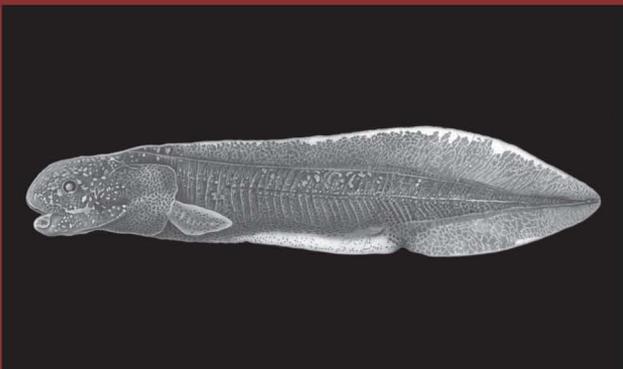


The Biology of Lungfishes

Editors

Jørgen Mørup Jørgensen

Jean Joss



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Preface

Since the last comprehensive monograph on lungfishes appeared in 1987, edited by Bemis, Burggren and Kemp, much new information has appeared concerning this little clade (Nelson 2006). This is the main reason for the present collection of reviews on some of the most important aspects of lungfish biology. We believe that the unique position between fishes and tetrapods will make this book of interest not only to scientists but also to the general reader with an interest in evolution and biology of the vertebrates.

It is a pleasure to thank the contributors of the chapters for devoting their time to create a treatise like this to share their knowledge with everyone. We are also indebted to the reviewers who committed time and talent to ensure the excellent quality of each contribution.

Jean Joss and Jørgen Mørup Jørgensen

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Introduction

The first modern book devoted to the biology of lungfishes was published in 1987 as a result of a conference held in 1985. This conference was primarily inspired by the seminal publication of Donn Rosen, Peter Forey, Brian Gardner and Colin Patterson (1981), which reanalysed the morphological characters of lungfish for comparison with other sarcopterygians, both living and fossil, using cladistic analyses of rigorously selected synapomorphies to the exclusion of any pleisomorphic characters. These four eminent fish systematists/evolutionary biologists concluded that lungfish and not “rhipidistian” fish, were the direct ancestors of tetrapods. Moreover, they exposed the rhipidistians as being a paraphyletic clade, requiring the separate consideration of the groups contained within such as the porolepiformes and osteolepiformes. These conclusions were greeted with horror from most researchers in the area of the fish-tetrapod transition but they did stimulate renewed interest in the Dipnoi (lungfishes) from a phylogenetic point of view. The first section of the 1987 book was entirely given over to consideration of the phylogenetic position of lungfish.

At about the same time new molecular techniques were beginning to be applied to phylogenetic questions, including those of the fish-tetrapod transition. Of course these techniques could only consider the relationships between living species, of which there are only 7-8 – six lungfish and two coelacanth. As it became more and more apparent that the lungfish grouped with tetrapod species to the exclusion of all others, there began a considerable resurgence of interest in study of the extant lungfishes. This interest was fuelled a decade or so later by increased access to living lungfish from a Facility for breeding the Australian lungfish, which was established at Macquarie University in 1993. This species of lungfish was and still is protected by CITES, which requires all lungfish material being sent to researchers outside Australia to be justified as legitimate research by purchase of an appropriate permit from the CITES-registered Authority. This requirement has helped to filter out the more frivolous interests in lungfish from those seriously investigating how fish ancestors transformed into the first tetrapods, during the mid to Late Devonian.

As it is now more than 20 years since the publication of “The Biology and Evolution of Lungfishes” and areas of study such as physiology, development, and behaviour of lungfish have variably flourished during this time, a book bringing most of this new data together is over due. Living lungfishes comprise a small group of sarcopterygian fishes of just three genera, each genus being confined to a

separate continent in the Southern Hemisphere. As had been noted in 1987, they combine many features from both fishes and tetrapods. In our invitations to authors we have put emphasis on research fields that have progressed most in the last 20 years, but also we have tried to find authors in areas, which have not been covered extensively in recent reviews. So, all authors in the present book are different from the authors in the 1987 treatise “The Biology and Evolution of Lungfishes” with the exception of Dr. R Glenn Northcutt. His expertise in neural and sensory structures and his broad knowledge of lobe finned fishes (sarcopterygian fishes) made him the most appropriate author to present recent progress in this area.

The first part of the present book is an updated account of the fossil record by Prof Jenny Clack and colleagues, followed by a chapter on the current phylogeny of lungfishes by Dr Zerina Johanson and Prof Per Ahlberg. The next three chapters concern the natural history of the three genera: the Australian *Neoceratodus* by Dr Peter Kind, the four African *Protopterus* species by Dr Christom Mlewa and colleagues and the South American *Lepidosiren* by Dr Vera Almeida-Val and her colleagues. The rest of the book contains chapters that describe morphology or physiology of various organ systems. These primarily cover areas that were not covered in the first book, such as the skin by Dr Lorenzo Alibardi and colleagues, head muscles by Dr Rui Diogo and Virginia Abdala, development of the head by Dr Rolf Ericsson, Prof Jean Joss and Prof Lennart Olsson, the teeth by Prof Moya Meredith Smith and Dr Zerina Johanson. We have not included some active areas of current research such as the “evo-devo” projects, that we expect will be very informative in the next few years and should comprise the raw material for a further update in much less than 20 years!

Also, we have not included a bibliography as in the first book, which gave us access to Babs Conant’s magnificent bibliography of all published works on lungfish prior to 1986. The reference lists at the end of each chapter in this volume are intended to at least partially update this bibliography for readers.

We hope that the widespread interest in these fantastic and highly significant fishes will lead to even more research investigations as well as intensified protection. Most of the lungfishes are vulnerable and if this book can contribute to more understanding of the uniqueness and importance of these fishes resulting in intensified protection of their environments, to the benefit of coming generations of human beings, our most sincere hopes will have been fulfilled.

Bemis W.E., Burggren W.W., Kemp N.E. eds. (1987) “The Biology and Evolution of Lungfishes” AR Liss.

Rosen D., Forey P., Gardner B., Patterson C. (1981) Lungfishes, tetrapods, paleontology, plesiomorphy. Bulletin of the American Museum of Natural History 167: 159-276.

Jean Joss and Jørgen Mørup Jørgensen

The Fossil Record of Lungfishes

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ABSTRACT

The fossil record of lungfish is reviewed. Some of their unique characteristics are explained and illustrated, including some less well-known anatomical elements that are often misidentified or unidentified in museum collections of Paleozoic vertebrates. Lungfish records from the Early Devonian to the Late Mesozoic are illustrated and described chronologically. Their major diversification occurred during the Devonian Period, with more than 70 named species. Subsequently they declined in diversity during the Carboniferous and Permian to a low of three genera at the present day. Some Carboniferous and Permian forms show intermediate morphologies between the Late Devonian and Mesozoic forms. Some of the intriguing questions of lungfish biology that can be addressed from the fossil record are outlined, such as the modification of their skeletons from a more or less primitive sarcopterygian pattern to their specialised form with loss of cosmine on bones and scales, few dermal skull bones, continuous mid-line fins and reduction of the paired fins to narrow, whip-like appendages. Late Devonian and Carboniferous lungfish are frequently found associated with tetrapods, and several lungfish anatomical elements are sometimes mistaken for those of tetrapods. The reduction in ossification of lungfish skeletons creates problems for understanding their fossil record: it may be explicable in terms of retention of a juvenile state. Reduction

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in ossification takes place alongside increase in the genome size: it has been suggested that these two phenomena may be related. Their varied patterns of dentition may be explicable by the interaction of only a few developmental processes, but the present pattern had been established by the Devonian. The evolution of air-breathing, aestivation, biogeographical distribution and change in habitat from fully marine during the Early Devonian to entirely freshwater at present are reviewed.

Keywords: evolutionary history, anatomy, Devonian, Palaeozoic, Mesozoic, Cenozoic.

INTRODUCTION

Lungfish have left some of the most characteristic as well as some of the most baffling elements in the fossil record. In part because of the richness of detail found in their Devonian fossil record they have been the subjects of deep disagreements concerning their relationships and functional morphology, whereas because of the paucity of their post-Devonian record, they have been, for the most part, neglected or misidentified in studies of more recent faunas. This chapter aims to present an overview of their diversity, anatomy and evolutionary history in the hope of promoting wider interest in the story they can tell us.

Lungfish first appear in the Early Devonian and are one of only three sarcopterygian groups to survive to the present day (the others being coelacanth and tetrapods), thus they have a range of about 400 million years. From their beginnings in the Early Devonian, their diversity in terms of morphology and species richness increased to reach its acme in the Late Devonian. More than seventy species are described, exemplified in particular by faunas in Australia. Subsequent to the Devonian, though they were distributed more or less worldwide throughout the Late Paleozoic, their fossil record declined. This may to a large extent be unconnected with their actual diversity and distribution, and more to do with the fact that the animals themselves became less amenable to preservation in the fossil record. Lungfish show a gradual reduction of ossification of both the internal and external skeletons, beginning in the Late Devonian and continuing through the Carboniferous, meaning not only that skeletal material becomes correspondingly less well represented, but that which does remain is usually disarticulated, making attribution to genus or species difficult or impossible in many cases.

The most durable and characteristic elements of the post-Devonian lungfish anatomy are their unique tooth plates (Figure 1), commonly found in isolation in many fossil localities representative of freshwater environments from the Carboniferous onward. In Devonian forms, and in Carboniferous ones where they are associated with other skeletal elements, it is evident that tooth plate morphology can be diagnostic to genus or species, and the same is assumed for later examples in which little or no skeletal material is available (Kemp 1997; Cavin *et al.* 2007).

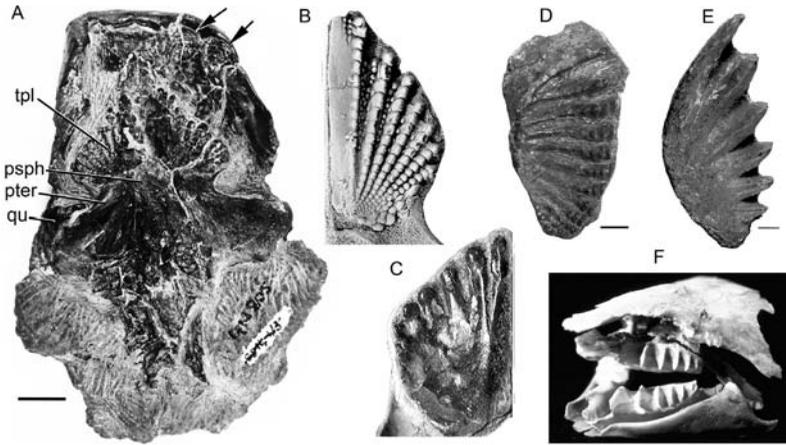


Fig. 1 Lungfish tooth plates. A. Palate of *Dipterus valenciennesi*, showing tooth plates (tpl), pterygoids (pter), parasphenoid (psph), quadrates (qu) and notches for the nares (arrows). Middle Devonian, UMZC (University Museum of Zoology, Cambridge) GN.805 (Photograph J. A. Clack). B. *Andreveyichthys epitomus*, a ridged tooth plated form. PIN (Palaeontological Institute, Moscow) 2921/1976. Late Devonian). C. Tooth plate of *Chirodipterus australis*, a dentine-plated form. AMF (Australian Museum, Sydney) 120082, Late Devonian. D. Tooth plate of *Ctenodus interruptus*, mid-Carboniferous, specimen MM (Manchester Museum) L10412 (from Sharp 2007). E. Tooth plate of *Sagenodus inaequalis*, Late Carboniferous, specimen NEWHM (Hancock Museum, Newcastle upon Tyne) G172.32. F. Skull of *Neoceratodus forsteri* showing tooth plates in lateral view, Recent (Photograph, J. A. Long). B, C from Ahlberg *et al.* (2006), scale not given; A, D, E. Scale bars 10 mm. D, E. from Sharp (2007).

Thus apart from a few instances, tooth plates alone are our guide to Mesozoic and Cenozoic lungfishes.

As well as their external morphology that is widely used in their systematics (e.g. Kemp 1993, 1994a, 1997), lungfish tooth plates have been subjected to detailed microstructural and histological analyses, to examine their growth patterns, to compare them with modern forms, and to try to assess the primitive condition (e.g. Denison 1974; Campbell and Barwick 1995, 1998, 1999, 2000; Campbell and Smith 1987; Campbell *et al.* 2002, Kemp 1995, 2002a; Reisz *et al.* 2004). To summarize this extensive literature is beyond the scope of this review.

In addition to tooth plates, a number of unique cranial features distinguish lungfish from any other osteichthyan groups. Rather than a symmetrical series of paired bones along the midline of the skull, fossil lungfish show what is best described as a 'hopsotch' pattern, in which pairs alternate with single midline bones (Figure 2). So difficult have these proved to be to equate to those in either actinopterygians or sarcopterygians that Forster-Cooper (1937) proposed a

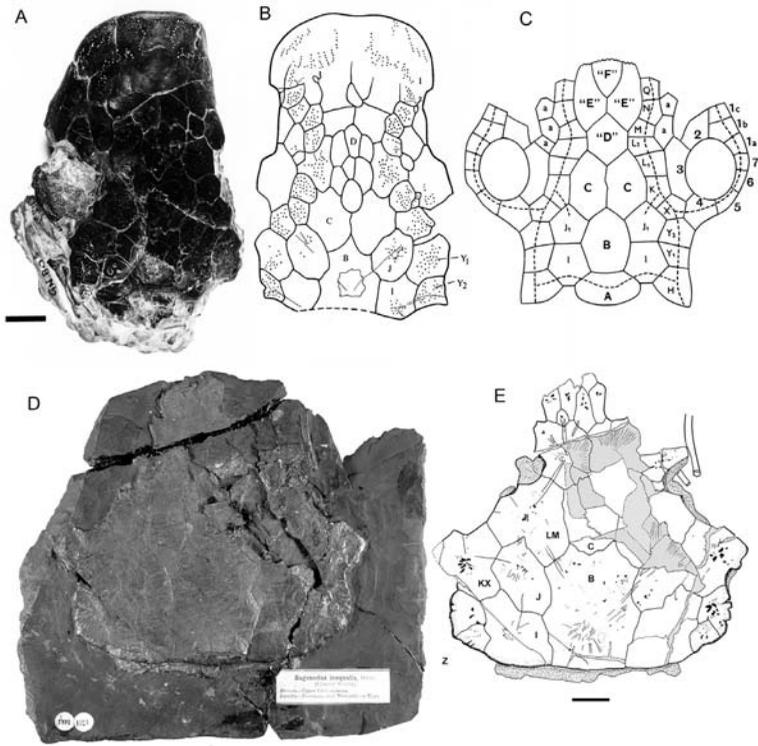


Fig. 2 Lungfish skull roofs. A. *Dipterus valenciennesi*, Middle Devonian, specimen UMZC GN.805 (Photograph J. A. Clack). Scale bar 10 mm. B. Skull roofing bones of *D. valenciennesi*, with lettering system on some bones (from Jarvik 1980). C. Forster-Cooper's alpha-numerical system of bone identification in an idealized skull roof (from Forster-Cooper 1937). D, E. *Sagenodus inaequalis* skull roof. NMS (National Museum of Scotland) 1878.45.7, Late Carboniferous (Photograph and specimen drawing respectively from Sharp 2007). Scale bar for D and E, 20 mm

system of letters and numbers to facilitate discussion of patterns among lungfishes (Figure 2C). Though he intended this to be a temporary measure, it is still in use today. However, even this scheme is difficult to apply to more derived forms from the Mesozoic (Cavin *et al.* 2007), though several workers have proposed schemes (e.g. Schultze 1981; Kemp 1998a).

In primitive forms like *Dipterus* the skull roof is inrolled along the snout margins, where there are two embayments for the anterior and posterior nostrils on each side (Figure 1, arrows). Other unique characters include the loss of both the premaxilla and maxilla of other osteichthyans, and all but the most primitive have lost the dentary. The dentary is still present in hatchling *Neoceratodus*, but is

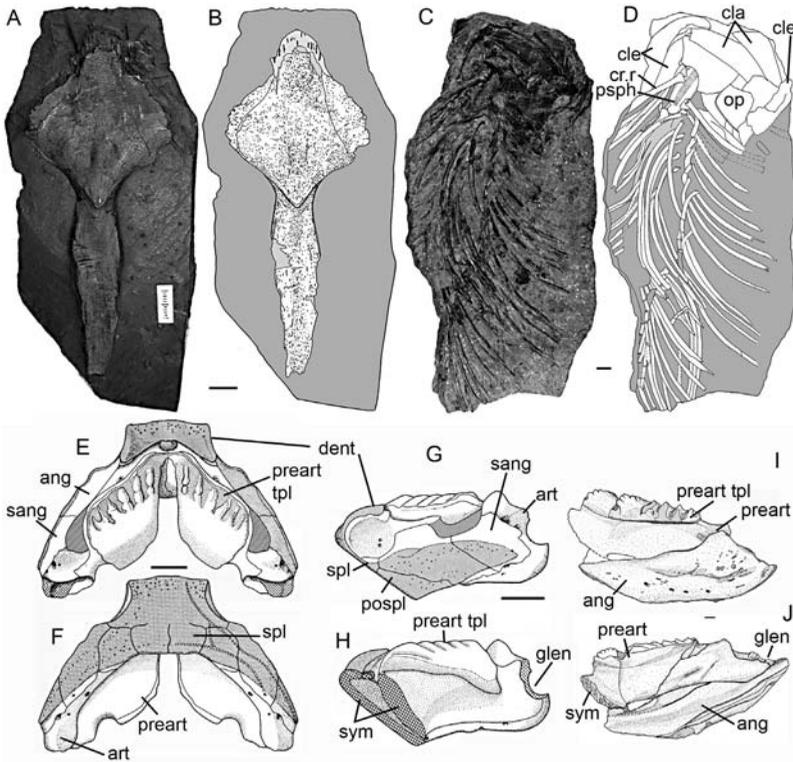


Fig. 3 Lungfish anatomy. A, B. *Sagenodus inaequalis*, isolated parasphenoid. NMS 1878.45.13, Late Carboniferous, photograph and specimen drawing respectively. C, D. Partial skeleton of *Ctenodus* sp., Early Carboniferous showing ribs and other elements. NMS 1906.108, photograph and specimen drawing respectively. E, F. Jaws of *Chirodipterus australis* in dorsal and ventral views respectively. G, H. Lower jaw of *C. australis* in external and internal views respectively. I, J. Lower jaw of *S. inaequalis* in external and internal views respectively. External view reversed for ease of comparison. Note that some bones are missing from the external surface. A–D and I–J from Sharp (2007). Grey fill, matrix; hatching, broken bone. E–H from Miles (1977). Close grey stipple in E–H cosmine-covered regions; coarse cross-hatch, unfinished bone; fine cross-hatch, Meckelian fenestra; coarse stipple, articular surface. Scale bars, 10 mm. Abbreviations: ang, angular; art, articular; cla, clavicle; cle, cleithra; cr.r, cranial rib; dent, dentary; glen, glenoid; op, operculum; psph, parasphenoid; pospl, postsplenial; preart, prearticular; tpl, tooth plate; sang, surangular; spl, splenial.

resorbed during early development (Smith and Krupina 2001; Kemp 1995, 2002b). Dentitions are carried on the pterygoid (and sometimes the vomers) in the upper jaw, and on the prearticular and dentary (where present) in the lower jaw (Figure 3E–J). Most lungfish have a characteristically shaped parasphenoid lying between the pterygoids (Figures 1, 3A, B), though in earlier forms, such as *Diabolepis*

(Chang 1995) or *Uranolophus* (Schultze 1992a; Denison 1968), it was situated more posteriorly, separating only the posterior parts of the pterygoids. It has a lozenge-shaped anterior portion with a stem posteriorly (and is not infrequently mistaken for a tetrapod interclavicle, even by knowledgeable vertebrate paleontologists eg. Jarvik (1996, Plate 52, Fig 3)). The palatal bones are firmly attached to the braincase producing an 'autostylic' skull in which the hyomandibula is not involved with jaw suspension. In lungfish the hyomandibula is reduced as a result. The operculum is a conspicuous bone, usually almost circular in outline, and the subopercular an almost featureless elongate oval (Figure 4). Also recognizably lungfish are characters of the hyobranchial system such as the robust ceratohyal, and the shoulder girdle bones such as the anocleithrum, cleithrum and clavicle (Figure 4). These bones are often found in isolation especially in Carboniferous rocks, and are not always identifiable by other than fossil lungfish specialists (as also are isolated lower jaws that have lost their tooth plates). Lungfish skulls are highly modified from the usual sarcopterygian pattern in response to the unique mechanism of air-breathing and suction feeding employed by lungfish, as is the existence of cranial ribs attached to the occipital portion of the braincase (Figure 3C, D). The hyoid arch is anchored to the shoulder girdle and the cranial ribs are used to help the animal raise its head out of water to gulp air (Bishop and Foxon 1968; Long 1993).

Among the most commonly found postcranial remains of lungfish, especially from Carboniferous deposits, are the ribs (Figure 3C, D). These are robust, with a single head bearing a comma-shaped articular facet, and a shaft that is strongly curved, parallel-sided, and with longitudinal grooves along its entire length. The latter gives the ribs either a figure-of-eight or comma-shaped cross-section. The length and curvature of these ribs indicate that they almost completely encircled the body, which would have had an almost cylindrical cross-section as a result. These ribs are not infrequently mistaken for those of tetrapods. In addition, the well ossified centra of some Devonian lungfishes could be mistaken for those of tetrapods, and closely resemble the pleurocentra of Carboniferous embolomeres (see for example figure 5, Campbell and Barwick 2002).

From what can be seen of their early fossil record, lungfish evolution underwent a number of parallel anatomical changes, most of which ended with a gradual reduction of morphological and ecological diversity. These will be illustrated in more detail below, but briefly they are: reduction of the skull roofing bones and dermal scale cover; a loss of diversity in dental patterning and tissue modelling; restriction of their midline fin morphology; the reduction of both cranial and postcranial endoskeletons; restriction of freshwater habitats from a base of marine and marginal marine origins; and elaboration of their air-breathing adaptations.

Lungfish as a group have only recently been subjected to strict cladistic analyses (eg. Schultze and Marshall 1993; Schultze 2001; Schultze and Chorn 1997; Friedman 2007a, b; Sharp 2007), with some of the most prolific researchers on the group explicitly rejecting this methodology (eg. Campbell and Barwick 1988, 1990).

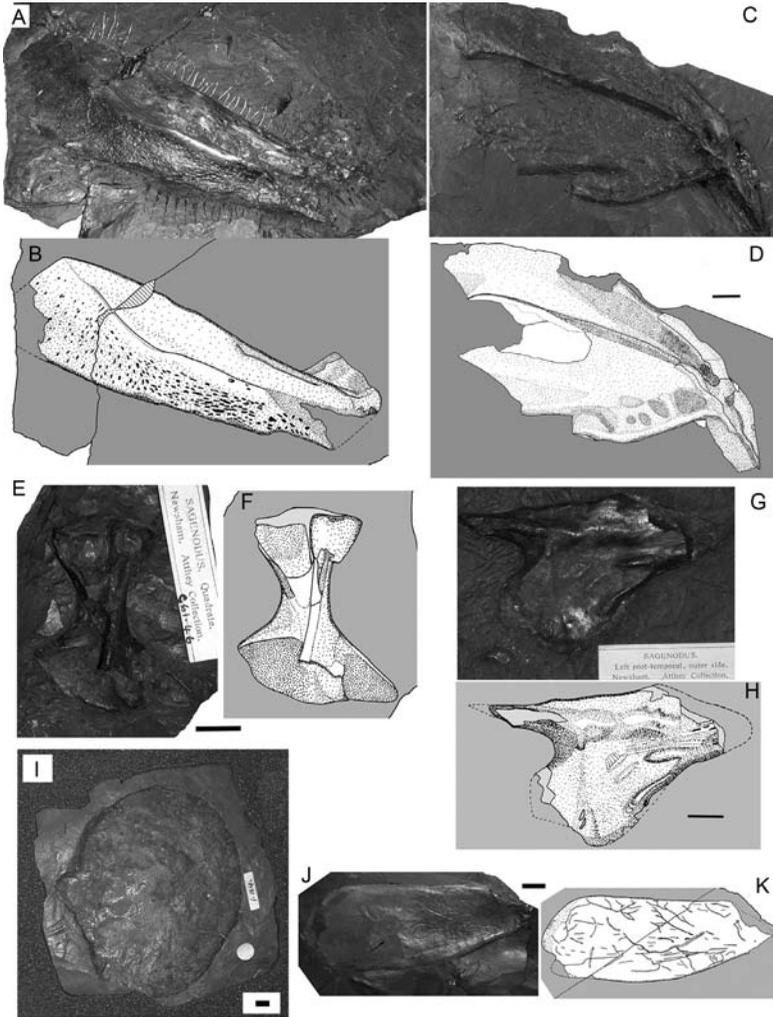


Fig. 4 Isolated elements of *Ctenodus* and *Sagenodus*. A, B. *Ctenodus* sp., right clavicle. MM unregistered, photograph and specimen drawing respectively. Size about 90 mm. C, D. *Ctenodus* sp. left cleithrum in external view, NMS 1968.17.47, photograph and specimen drawing respectively. E, F. *Sagenodus inaequalis*, left ceratohyal in lateral view. NEWHM G61.46, photograph and specimen drawing respectively. G, H. *Sagenodus inaequalis*, left anocleithrum in external view. NEWHM G61.64, photograph and specimen drawing respectively. I. *Ctenodus* sp., operculum in external view. NEWHM G40.97, photograph. J, K. *Ctenodus* sp., suboperculum. CAMSM (Cambridge, Sedgwick Museum) E4524, photograph and specimen drawing. All from Sharp (2007).

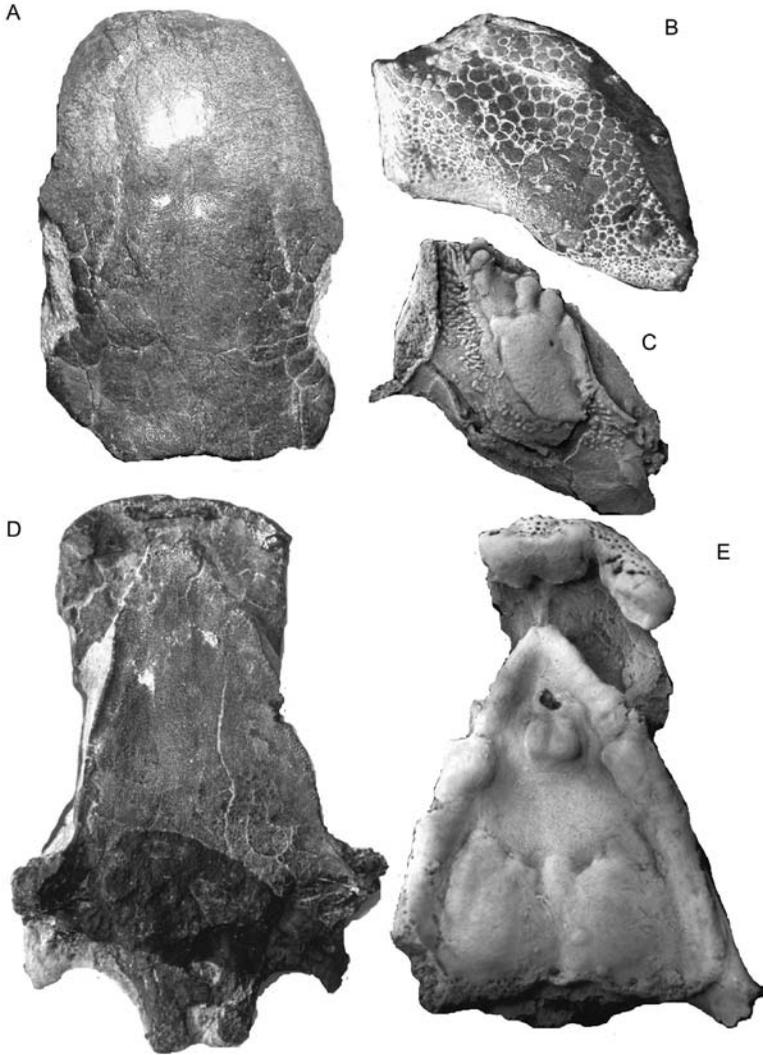


Fig. 5 Early Devonian lungfishes. A. *Diabolepis speratus* skull and B. lower jaw, Lochkovian, China. IVPP (Institute of Vertebrate Palaeontology, Beijing) V7238, length of specimen about 16 mm. C. *Ichnomyx kurnai* lower jaw, Pragian, Australia. NMV (Museum Victoria) P188479, maximum width of jaw about 30 mm. D. *Uranolophus wyomingensis* palate, Pragian, USA. Field Museum PF3792, length of specimen 195 mm. E. *Dipnorhynchus kurikae* palate, Emsian, Australia. ANU (Australian National University) 48676, length of specimen 94 mm. A–E, photographs by J.A. Long.

Thus their internal relationships have been controversial. Though not the main focus of this chapter, it is inevitable that some discussion of relationships will be necessary, for without this, discussion of topics such as their palaeobiogeography and directions of morphological evolution are very difficult to understand. For a more in depth discussion of lungfish phylogenetic relationships, readers should consult Chapter 2.

Their relationship to other sarcopterygian groups is also debated, though many researchers on the subject now accept them as belonging to a group known as 'Dipnomorpha' that also includes the Devonian Porolepiformes. Sister group to the Dipnomorpha in this scheme is the Tetrapodomorpha, making dipnoans the closest living relatives to tetrapods to the exclusion of coelacanths (Ahlberg 1991; Cloutier and Ahlberg 1996; Ahlberg and Johanson 1998). Not all paleoichthyologists accept this scheme (Zhu and Schultze 2001), and furthermore, molecular studies are equivocal, with some studies placing coelacanths and dipnoans as sister groups to the exclusion of tetrapods (Zardoya and Meyer 2001).

Marshall (1986) and Schultze (1992b) gave almost comprehensive lists of fossil and extant taxa of lungfish up to those dates. After a brief and not exhaustive chronological review of fossil lungfishes this chapter will address some issues of current interest in their biology and ecology.

EARLY DEVONIAN LUNGFISHES

Some controversy surrounds the deep relationships of lungfish, with two taxa central to the debate. *Youngolepis* and *Diabolepis* (Figure 5A, B) are two taxa from Yunnan, China that lived during the Early Devonian, and consist of disarticulated skull elements. There is a fairly widely held consensus that *Diabolepis* is basal to other dipnoans, but whether *Youngolepis* is a stem member of the Dipnoi, or is closer to the porolepiforms is not clear (eg. Cloutier and Ahlberg 1996; Smith and Chang 1990; Zhu *et al.* 1999; Zhu and Schultze 2001; Zhu and Yu 2002). *Diabolepis* shares some unique features of the structure of the lower jaw and dentition with dipnoans, including radiating rows of rounded teeth of similar structure to those of true lungfish, and reduction of the lower jaw bones. It shows the beginnings of the modern dipnoan structure of the skull roof, palate and braincase that so clearly characterize later lungfish (Chang 1992). It also shows more general characters such as a median parallel-sided and denticulate parasphenoid, pierced by a hypophyseal foramen. On the other hand, some characters of *Diabolepis* are shared with porolepiforms, corroborating the suggestion of a relationship between dipnoans and porolepiforms (Chang 1995). Campbell and Barwick (2001) contested the relationship between *Diabolepis* and Dipnoi on the grounds that the morphological and structural similarities between them were not genuine homologues, but had evolved in parallel. This view is not widely accepted.

As well as typical tooth plates, in the Devonian there were also two other forms of dentition found among lungfishes: those with more or less solid dentine plates

with or without tubercles, and those with sheets of denticles only. Among the earliest of lungfish in the fossil record is *Dipnorhynchus*, a tooth plated form found in Pragian and Emsian age deposits (Middle and Late Early Devonian) of Australia (Figure 5E). Several species have been recognized, from a range of localities including Wee Jasper and Taemas (Campbell and Barwick 1982a, b, 1999, 2000). This primitive form shows the mosaic pattern of skull bones that characterizes lungfish throughout their history, though in this genus, there are more and smaller bones, particularly around the snout region. It shows that the tooth plates grew by addition of new dentine around the margins of the pterygoids. Campbell and Barwick (2000) gave a reconstruction of the skull in lateral view showing a very high, deep skull, based on a very well preserved large specimen. *D. kurikae* from Wee Jasper has a well preserved braincase, that will be helpful in elucidating the relationships of the genus, but unfortunately, no postcranial remains are known from the genus.

Speonesydrion is another tooth plated form from Wee Jasper in Australia (Emsian), that shows teeth in radial rows and a mosaic of bones on the snout. It is known from exceptionally well preserved material but which is limited to skull and jaw elements (Campbell and Barwick 1984). However, both juvenile and larger specimens are known, that shed some light on the growth of the teeth. *Ichnomyxax*, from the Pragian of Australia (Long *et al.* 1994) and Emsian of Siberia (Reisz *et al.* 2004), is a form closely-related to *Speonesydrion* with well-defined radial rows of teeth coalescing onto a thick dentine heel on the lower jaw (Figure 5C). *Tarachomyxax* from the Emsian of Russia is another tooth plated form with a combination of primitive and derived characters (Barwick *et al.* 1997). It was cosmine covered, with a mosaic of small bones in the skull roof. Barwick *et al.* (1977) suggested that it was more derived than *Speonesydrion*, but could not place it exactly in a phylogeny.

Both *Sorbitorhynchus* and *Erikiia* from Emsian age deposits in China show cosmine on all their dermal bones. Cosmine is a composite tissue, formed by dentine, a pore-canal system, and an enameloid cover, found in most primitive lungfishes and in other primitive sarcopterygians such as osteolepidids (basal tetrapodomorphs). It has been considered to house a sensory system, and especially so in the snouts of lungfish (see below). The palatal dentition consisted of flat, heavy dental plates, and in the mandible, between these plates is a depression that has been interpreted as housing a soft tissue pad on the tongue, used in an elaborate suction feeding mechanism. Wang *et al.* (1993) also suggested several other explanations for the purpose of this depression, including that it was a pathology, a position supported by Kemp (1994a). Much of the hyobranchial system of *Sorbitorhynchus* is unknown, so whether or not it was modified in concert with that aspect of the mandible cannot be judged (Wang *et al.* 1993). *Erikiia* from Yunnan Province is a dipnorhynchid related to the Australian forms (Chang and Wang 1995), whereas *Sorbitorhynchus* has thick dentine plates and is allied to the chirodipterid lineage (Wang *et al.* 1993).

Uranolophus from the Pragian of Wyoming, USA, and *Melanognathus* (Schultze 2001) from the Emsian of arctic Canada are both of the denticulated type. *Uranolophus* has some claim to being the most primitive lungfish known from well-preserved material (Campbell and Barwick 1995) (Figure 5D). Both these forms had short jaws and a short snout, and in *Uranolophus* the jaws met in a strong contact zone, suggesting the capability of a powerful bite (Long 1995).

MIDDLE DEVONIAN LUNGFISHES

Probably the best known Middle Devonian lungfish, certainly the one most widely distributed in world museum collections is *Dipterus valenciennesi* (Figures 1A, 2A, 6). This species is found most commonly in the Caithness and Moray deposits in Scotland and Orkney — the Scottish Old Red Sandstone. Many other species are known from Russia, the USA and other parts of the world, for example, *D. oervigi* from the Bergisch Gladbach region of Germany (see Marshall 1986; Schultze 1992a). *Dipterus* was first discovered in the early 19th century, though it was not until 1871 that Günther first realised that it was related to the modern lungfishes, (Günther 1871), thus it was the first fossil lungfish to be recognized as such.

Its skull is very well known from numerous specimens and it carries cosmine on all dermal bones, including scales and fin rays (lepidotrichia), though at least on the skull, this is variable in its expression. In some specimens, the snout is completely covered with cosmine, whereas in others, individual bones of the snout mosaic are obvious. Periodic resorption of cosmine, perhaps seasonally or annually, has been inferred to explain the series of concentric lines running round each skull bone, called ‘Westoll lines’ (Westoll 1936; Thomson 1975) in those specimens in which individual bones are visible. These contrasts originally caused confusion as to how many species actually existed. Forster-Cooper’s study (1937) showed that there was only one present in Scotland, and his alphanumeric system of bone identification was formulated on the basis of this species (Figure 2C). In many ways *Dipterus* is a fairly primitive genus, and is often used to provide a picture of primitive lungfish postcranial anatomy.

The pectoral fin skeleton was long, consisting of 7-9 mesomeres, with jointed radials either side. The pelvic fin skeleton is poorly known, but was probably of a similar type to the pectoral. The anterior dorsal and anal midline fins were fairly conventional compared with those of other primitive sarcopterygians: the anterior dorsal fin consisted of a basal plate with unjointed radials and lepidotrichia; the anal fin had a basal plate and four jointed radials and lepidotrichia. The second dorsal fin is of interest because this is the one which first begins to show modifications through lungfish evolution. In *Dipterus*, it was of a primitive form and consisted of a basal plate and several branching and jointed radials. The tail was conventionally heterocercal as in other primitive sarcopterygians (Ahlberg and Trewin 1995) (Figure 6).

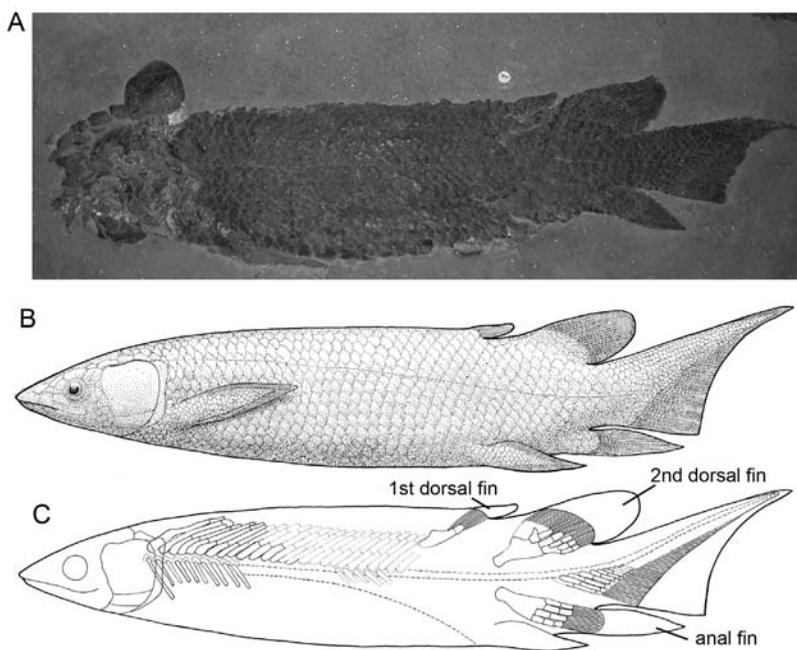


Fig. 6 *Dipterus valenciennesi*. A. Specimen photograph UMZC GN.804, 265 mm snout to tail length (Photograph, J. A. Clack). B. Life reconstruction. C. Skeletal reconstruction. B and C from Ahlberg and Trewin (1995).

Much of the postcranial skeleton was poorly ossified even in large individuals, showing the beginning of a trend through lungfish evolution towards less and less ossification. In *Dipterus*, though the anterior parts of the vertebral column including the supraneural spines that sat above each centrum, were reasonably well ossified, the posterior parts were not, and neither were the paired fin skeletons (Figure 6). The vertebral centra retained a large central hole for passage of the notochord, a primitive osteichthyan state also seen in most other Paleozoic lungfishes. There were short ribs on the vertebrae, but, contrary to some earlier assessments, it probably had no cranial ribs. Growth series for *Dipterus* from Caithness show changes to body proportions during ontogeny, showing how the head became relatively shorter compared with the length of the body (Ahlberg and Trewin 1995).

The skull had a bluntly rounded snout, exhibiting the typical embayments for the nostrils (Figure 1A). The palate and lower jaw tooth plates bore radiating rows of bluntly rounded teeth. The jaw hinge, as in other lungfish, lay far forward in the skull, in contrast to its posterior position in other osteichthyans (Figure 1A). The lower jaw was somewhat 'underslung' suggesting that *Dipterus* was a bottom-feeder. The opercular bone was large and round suggesting a substantial

orobranchial chamber and that *Dipterus* was still reliant on gill breathing. Moreover, the distribution of *Dipterus* through the sediments of the Caithness Old Red Sandstone at Achanarras show that it was the first fish to become established in the locality, and was the last to disappear (Trewin 1986), corroborating the idea that it was the fish most tolerant of adverse (i.e. oxygen-depleted) conditions. Possibly it could breathe air when necessary.

There has been some suggestion that a small enigmatic fossil creature known as *Palaeospondylus gunni*, found only in deposits at Achanarras and on Orkney, can be identified as the 'larval' form of *Dipterus* (sic, Thomson *et al.* 2003). (Since lungfish do not truly metamorphose, hatchlings should strictly not be referred to as 'larvae' (A. Kemp pers. comm. 2008).) However, work on *Dipterus* itself, and on the ontogeny of the modern lungfish *Neoceratodus*, has shown that this cannot be the case (Miller 1930; Joss and Johanson 2006). Features that led to the original suggestion included the absence of teeth and the possession of a cranial rib. However, specimens of *Dipterus* as small as those of *Palaeospondylus* have been found that do not show the odd characteristics of that curious animal. These specimens, as well as fossils of very small juveniles of the Devonian lungfish *Andreyevichthys* (Krupina and Reisz 1999), and hatchling *Neoceratodus* (Kemp 1999), do carry full dentitions. Furthermore, *Dipterus* almost certainly did not possess cranial ribs and did not have fully ossified ring centra, as *Palaeospondylus* clearly does (Joss and Johanson 2006).

Another Middle Devonian lungfish from the Caithness and Orkney basin is *Pentlandia*, and though its dental anatomy is much less well known, its body morphology was more like that of the Late Devonian *Fleurantia* in having a separate but small first dorsal fin and an elongated second dorsal (pers. obs. JAC, National Museum of Scotland specimen NMS 1995.4.121).

Iowadipterus is a Middle Devonian lungfish from the USA (Schultze 1992a). This was a fairly primitive form retaining cosmine, with a relatively long head, but not a long snout, contrasting with long snouted forms commoner in the Late Devonian. In the single specimen, the end of the snout is completely cosmine-covered, but further back a bone mosaic is retained. The dentition is not visible. Schultze (1992a) reconstructed the musculature that might have operated its short lower jaw in combination with its long and deep skull roof, to provide powerful adductors. The dentition of this form is unfortunately unknown, but Schultze (1992a) suggested that in operation, it fell between the long snouted, denticle bearing forms that probably used suction feeding and rasping, and the short snouted tooth plated forms that used suction feeding and crushing mechanisms.

Stomiahykus from the Eifelian of Canada was a form with flat, dentine-covered tooth plates. *Dipnotuberculus*, from the Givetian of Morocco, had dental plates bearing a few large rounded tuberosities: a palate, a partial mandible and a dental plate are all that are preserved of this genus (Campbell *et al.* 2002).

Mount Howitt, in Victoria, is a Givetian age site preserving complete body fossils of lungfish in all stages of growth. Here are found *Howidipterus* and

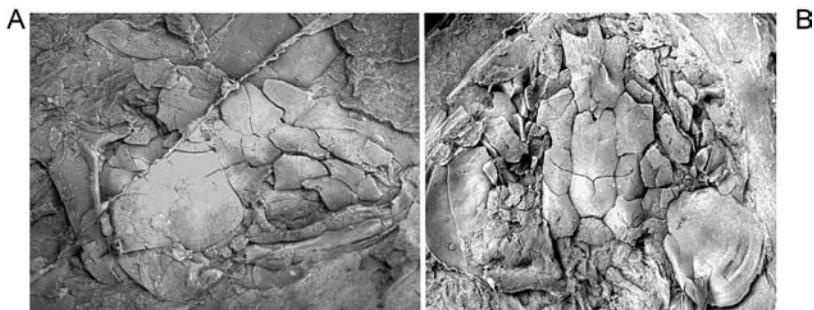


Fig. 7 Middle Devonian lungfishes. A. *Barwickia downunda* MV P181782, width of operculum, 20 mm. B. *Howidipterus donnae* NMV P118790, length of skull roof from posterior of A bone to tip of fused DE bones is 30 mm. Both casts whitened with ammonium choride. Photographs by J. A. Long.

Barwickia (Figure 7). *Howidipterus* had unusual tooth plates with well-developed teeth along the margins of each plate, coupled with smooth crushing denticulated surfaces more centrally. *Barwickia* was a denticulated form, but had an almost identical body form to *Howidipterus*. On closer comparison, it emerged that their dentitions were part of a spectrum of possibilities: in *Barwickia* there were fewer rows of teeth and more denticles compared with *Howidipterus* that had more rows of teeth and fewer denticles (Long 1992, 1993; Long and Clement 2009).

Eoetenodus from the Givetian of Victoria, Australia is known from several isolated bones and tooth plates. It had a long stalked parasphenoid, *Dipterus*-like tooth-plates and robust shoulder girdle (Long 1987). The oldest lungfish record from South America is a *Dipterus*-like toothplate and some scales from the Givetian-Frasnian of Venezuela (Young and Moody 1992).

LATE DEVONIAN LUNGFISHES

This is the time when lungfishes reached their peak of diversity. Several localities have yielded extensive material of a variety of genera, perhaps the richest being the Frasnian locality of Gogo in Australia. At least eight genera are present there, within the very narrow stratigraphic range represented by this locality. The rocks in which the lungfish are found are fully marine, and represent a community dwelling either on and around a limestone reef or in deep water between reefs. The fish were buried rapidly and limestone accumulated around the specimens, preserving them in three dimensions and often in complete states of skeletal articulation. In some instances, for example some placoderms, even soft tissue was replaced in detail allowing study of muscle structure (Trinajstic *et al.* 2007).

The two commonest genera are *Chirodipterus* and *Griphognathus*, exemplifying two ends of the spectrum of morphologies of skull shape and dentition seen in Devonian lungfish (Figures 8A, 9A). They have been described in minute detail

by Miles (1977) and Campbell and Barwick (1999, 2002), including neurocrania and postcrania. *Chirodipterus* is a short snouted form, bearing massive dentine-covered plates on its palate and lower jaw, whereas *Griphognathus* is a long snouted, form bearing sheets of denticles on those surfaces (Figure 9A). *Griphognathus* had a massively ossified branchial and postcranial skeleton with complete ring centra. It may have been a bottom-dweller searching the sediment with a suction-feeding technique, or using its plier-like beak to snap off branching corals and stromatoporoids and rasp them away with the denticle-covered palate. *Griphognathus* is also found in other parts of the world during this time, including the USA and Europe, and in deposits that may not all have been fully marine. *Chirodipterus* was originally named for a form from Europe, and recent work suggests that the Australian form may in fact belong to a different genus (Long 2005; Friedman 2007b). *Holodipterus* is less common, but includes several species at first put into several subgenera by Pridmore *et al.* (1994), but later some of these were erected as separate genera by Long (in press) (Figure 8B). This genus had the deepest head profile of any Late Devonian lungfish, which combined with its long lower jaw symphysis and massive adductor muscle fossae, testifies to its ability as a powerful crusher of hard-shelled food items. Some *Holodipterus* species had tooth plates carrying bulbous crushing surfaces (*H. gogoensis*, Miles 1977), but others seem to show mainly a denticulated plate with toothlike projections along the margins (new genus A, Long in press) (Figure 8D). *Holodipterus* continually remodelled its dentition by resorption and new growth at the labial margins. *Robinsondipterus* shows the elongated snout similar to *Griphognathus*, but with tooth-like blebs of dentine along the biting margins. New genus B had powerful crushing surfaces but retained sharp teeth on separate dentaries on the lower jaws (Long in press) (Figure 8C).

Other Gogo taxa include the chirodipterids *Gogodipterus*, a form with tooth plates carrying strongly developed ridges and grooves, and *Pillalarhynchus*, a long, deep headed form with narrow concave tooth plates (Figure 8F, G). *Adololophas* is another tooth plated form, in this case the material includes an almost complete body with articulated scale cover. Interestingly, this shows a diminution of scale thickness and cosmine cover from front to back of the animal (Campbell and Barwick 1998). A strong case has been made that all these genera were marine, bottom dwelling, and did not breathe air on a regular basis, based on having a full complement of functional gill-arches (Campbell and Barwick 1988; Long 1993). However, *Griphognathus* also occurs in shallow water, marginal marine environments in Europe (Schultze and Chorn 1997). Recent work has shown that the Gogo *Griphognathus* might be considerably different from the type material and should be placed in a different genus (Long 2005; Friedman, 2007a, b).

Another Frasnian locality that has yielded fossil lungfish is Miguasha in Canada. Here, two genera are described, *Fleurantia* and *Scaumenacia*, the latter named after an anglicized version of Escuminac Bay, in which Miguasha is situated (Figure 9D, E). These two genera show the beginnings of a trend seen in lungfish

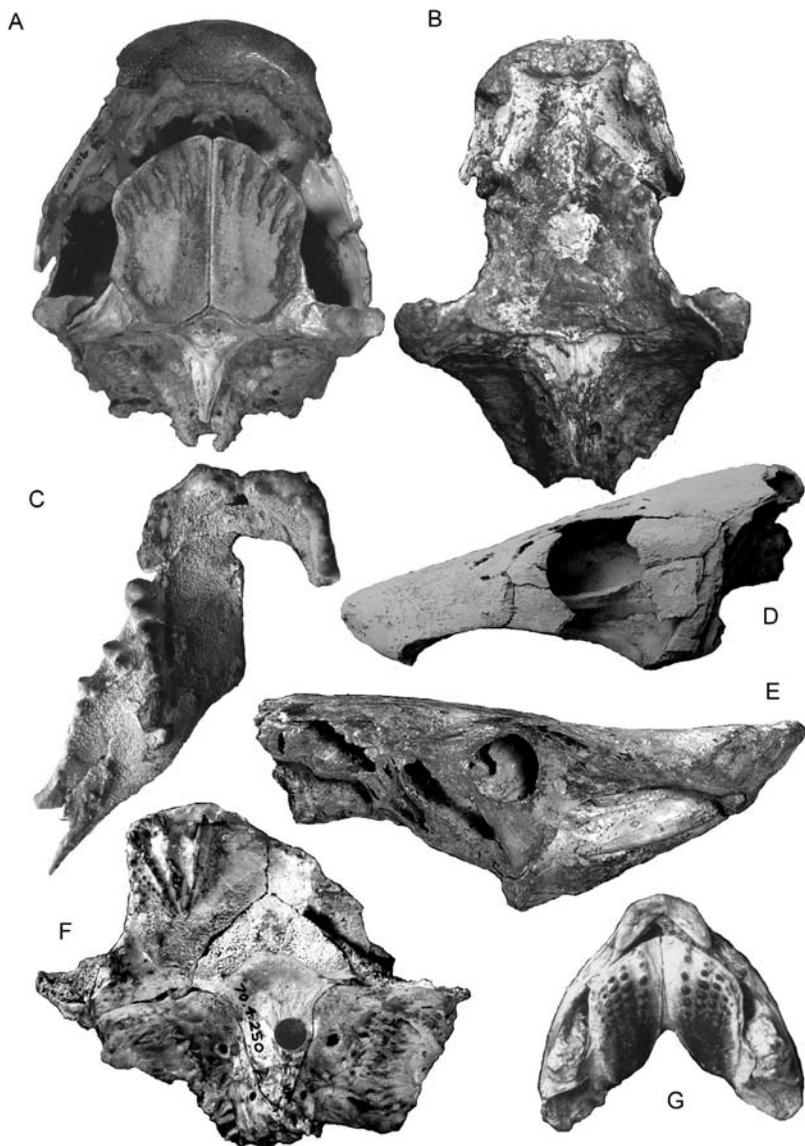


Fig. 8 Late Devonian lungfishes. A. *Chirodipterus australis* WAM (Western Australian Museum) 90.10.8, skull length 70 mm. B. *Holodipterus gogoensis* ANU 49102, length of skull 130 mm. C. new genus B (Long in press), lower jaw. ANU 49103, width across base of postdentaries 30 mm. D. new genus A (Long in press). MV P221813, length of skull 115 mm. E. *Grippognathus whitei* WAM 86.9.651 length of skull 160 mm. F. *Gogodipterus paddyensis* WAM 70.4.250 maximum width of preserved palate 71 mm. G. *Pillararhynchus longi* lower jaw. ANU 49196 maximum width across jaws 30 mm. All photographs by J.A. Long.

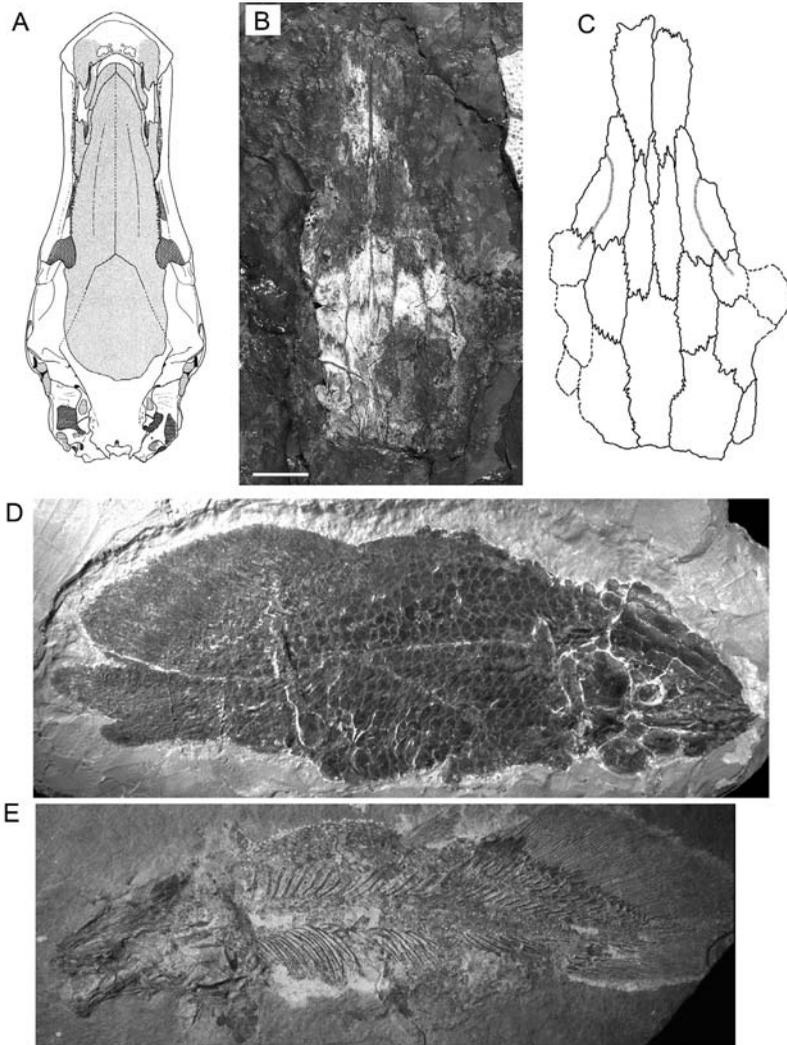


Fig. 9 Late Devonian lungfishes. A. Palate of *Griphognathus whitei*, a denticulated form (from Miles 1977). B, C. *Soederberghia groenlandica*, specimen ANSP (Academy of Natural Sciences, Philadelphia) 20902, photograph and interpretive drawing respectively. (Photograph, E. B. Daeschler). Scale bar 10 mm. D. *Scaumenacia curta*. Specimen number not traced. E. *Fleurantia denticulata* BMNH P.24745-P24736 length of specimen 215 mm. D, E, Photographs M. Arsenault, Parc de Miguasha, from Long 1995).

evolution towards enlargement of the second dorsal fin and its amalgamation with the caudal fin. *Fleurantia* still had a separate first dorsal, with an elongate second dorsal, whereas in *Scaumenacia* the first dorsal, though separate from the elongate

second, was long and low and appears to lack any supports from the vertebral column (Cloutier 1996). The situation seems to have been comparable to that at Mount Howitt: *Scaumenacia* was a tooth plated form, whereas *Fleurantia* was a denticulated form, but the two genera had similar body plans. A detailed bed-by-bed study of the deposits at Miguasha was made by Cloutier *et al.* (1996), who showed that *Scaumenacia* occurs throughout the whole sequence of the Escuminac Formation, and is one of the commonest taxa at the locality. By contrast, *Fleurantia* occurs only in the lower parts of the sequence and is relatively rare. There appear to be no obvious correlations between the faunal assemblages and the lithostratigraphic units found there: the entire sequence may represent a brackish or marginal marine environment (Cloutier *et al.* 1996). These two genera may have had specific requirements that are not reflected in the preserved environment.

Devonian lungfishes were first found in East Greenland, in Famennian age deposits, in many cases alongside fossils of Devonian tetrapods. Four genera are known: *Soederberghia*, *Nielsenia*, *Jarvikia* and *Oervigia* (Bendix-Almgreen 1976). *Soederberghia* is the best known, and has congeners widely distributed throughout the world in similar age deposits (Figure 9B, C). For example, it is also known from the Catskill formation in Pennsylvania USA (Friedman and Daeschler 2006), from Belgium (Clement and Boisvert 2006), and from two localities in Australia: the spectacular fossil fish locality of Canowindra (Ahlberg *et al.* 2001), and the Jemalong Quarry that has also yielded tetrapod remains (Campbell and Bell 1982). Thus this genus is one associated with tetrapods in Greenland, Pennsylvania and Australia. It was a long snouted, denticulate form that could grow to a large size, and is one of the youngest genera to be represented by ossifications of the braincase region, though even it shows some aspects in which reduction has begun. It is known from postcranial remains that were quite well ossified, including long, curved ribs and substantial ring-centra in which the notochordal pit was sometimes completely obliterated. *Soederberghia* shows adaptations of the palate and postcranium interpreted as being associated with air-breathing — a cranial rib and a parasphenoid with a long posterior stem (Ahlberg *et al.* 2001).

Of the other Greenland genera, the tooth plated *Oervigia* and the denticulated *Jarvikia* were both long snouted, and resembled *Scaumenacia* and *Fleurantia* respectively. The short snouted *Nielsenia* is known from only a single specimen.

Other Famennian localities have yielded lungfish specimens, one of the most prolific being the Andreyevka-2 locality near Tula in Russia. Here, thousands of disarticulated bones especially of tooth plates of juvenile lungfish have been recovered by acid-digestion of the limestone, allowing growth series to be reconstructed from the great size-range of specimens available (Krupina and Reisz 1999). This genus, *Andreyvichthys*, is another lungfish found in association with tetrapod material (Figure 1B).

Orlovichthys, also from the Famennian of Russia, the Orel region, is known on the basis of an almost complete skull with dentition. It had a relatively narrow skull,

with dentition organised into tooth plates (Krupina *et al.* 2001). *Adelargo* from the late Famennian of Australia is known from isolated elements, tooth plates, bones and scales, and a partial skull roof (Johanson and Ritchie 2000).

Two Famennian genera from Scotland are worth a mention. *Rhynchodipterus* from Rosebrae Quarry near Elgin has been considered a close relative of *Griphognathus* and *Soederberghia*, but this remains to be adequately tested. It has a fairly primitive appearance in terms of fin morphology, and is long snouted with a somewhat duck-like skull profile. Recently, the single specimen has been CT scanned, and work in progress by Friedman and Coates should help clarify its anatomy and relationships. *Phaneropleuron* from Dura Den has not been fully described. Huxley (1861) gave lithographs of a number of specimens, and Westoll (1949) suggested that it was like *Scaumenacia*. Thomson (1969a) reconstructed the body outline as having combined dorsal and caudal fins, more like *Uronemus*. Both *Rhynchodipterus* and *Phaneropleuron* require redescription, and could throw important light on lungfish postcranial evolution.

CARBONIFEROUS AND PERMIAN LUNGFISHES

After the Late Devonian, the taxonomic diversity of the lungfishes went into a significant decline, and there are many fewer genera known from the Carboniferous to the Recent than there are in the Devonian. However the timing of this decline is not altogether clear: the Early Carboniferous record is particularly sparse but this may represent a taphonomic artefact. The marked by a drop in the morphological diversity shown by the dipnoans in the Carboniferous is characterized by the loss of all long-snouted lungfish, and all lungfish without ridged tooth plates except one, *Conchopoma*. Thus it may be that some ecological niche previously occupied by long-snouted lungfish became unavailable at the Devonian–Carboniferous boundary. Similarly, by the Carboniferous, there seems to be an almost complete loss of endoskeletal ossification, and there are no known fossil lungfish from the post-Devonian which preserve the braincase or more than a few elements of the endoskeleton. This transition from morphological diversity to conservatism is still poorly understood.

For the Carboniferous, much of the lungfish record is known from the United Kingdom and, as for most freshwater and terrestrial fauna, the fossil record is sparse in the earliest parts of the era. Only isolated bones are known from the Tournaisian (eg. a rib from Dumbartonshire, Clack and Finney 2005)). The oldest Carboniferous taxon is probably *Ctenodus romeri* from the Viséan (Arundian) of Berwickshire (Thomson 1965). It is a tooth plated lungfish known only from its dentition, although there is some isolated cranial material probably attributable to this species (T. R. Smithson, pers. comm.).

Ctenodus is the most common Early Carboniferous (= Mississippian) genus known (Figure 4), and is distributed throughout the Carboniferous, although

there does not seem to be any temporal overlap between the five apparently valid species. *Ctenodus romeri* from the Viséan, and *Ctenodus interruptus* (Barkas 1869) from the Viséan/Namurian boundary, are only known from tooth plates (Figure 1). *Ctenodus murchisoni* (Ward 1890), from the Westphalian C of the Staffordshire coal fields, has a single skull roof associated with it. *Ctenodus cristatus* (Agassiz 1838), from the Westphalian, and an un-named species from the Early Carboniferous (Sharp 2007) both have a not inconsiderable amount of skeletal material preserved, although little of it is articulated.

Ctenodus is an interesting genus because there is a progressive change from tooth plates which are similar in size to those of *Dipterus*, to being of extremely large size in the Late Carboniferous species, implying an increase in overall body size. Tooth plates of *C. murchisoni* reach up to 10cm in length, and have up to 23 tooth ridges, making them some of the largest tooth plates known. *Ctenodus* exhibits a variety of morphologies of tooth plate, within the framework of the ridged plate, that is quite striking. Were articulated specimens to be found in association with all these tooth plate morphologies, it is uncertain that they would be retained within the same genus.

Also from the Early Carboniferous are the genera *Straitonia* (Thomson 1965) and *Uronemus* (*Ganopristodus* of Schultze 1992a), both genera found in Scotland. *Straitonia* is a monospecific taxon from the Asbian (D1) of the Viséan, and is an almost complete specimen preserved in a nodule. It is the most completely preserved British Carboniferous lungfish and shows a postcranial skeleton that seems to demonstrate a dorsal fin fused with a diphyrcal caudal fin, and no independent anal fin. *U. splendens* is known from remains of the skull roof and exhibits a unique form of dermal ornament, more akin to that of tetrapods than lungfish. There seems to be relatively little support for the union of this with another species, *U. lobatus*, within the same genus and it is desirable that the taxonomy of this genus be addressed.

The genus *Tranodis* is known from several localities in the late Mississippian of North America (Thomson 1965; Schultze and Bolt 1996). Recently numerous specimens of a *Tranodis*-like lungfish have been recovered from a site in Hancock County, Kentucky, also of late Mississippian age (Garcia *et al.* 2006a, b). This locality is also notable for the variety of the tetrapods that are preserved there. Many of the lungfish specimens are preserved in situ in carbonate concretions representing burrows at the top of a shale horizon in the upper part of the exposure, and are the oldest known such burrows. They are considered to be aestivation burrows by the authors. This part of the sequence at Hancock is interpreted as representing a small ox-bow lake in a floodplain environment, with intermitant connection to a larger lake or river.

Another Early Carboniferous form is *Delatitia* from the Mansfield Basin in Australia. It consists of a partial skull roof and tooth plates and bears some resemblance to *Ctenodus*, though it retains some primitive features of the skull bone pattern (Long and Campbell 1985).

The most well known and widespread Late Carboniferous (= Pennsylvanian) taxon, *Sagenodus*, is found in the United Kingdom as well as the Permian of the United States and the Czech Republic. A tooth plated genus, *Sagenodus* (Owen 1867) has a stratigraphic distribution of around 60 million years and is widespread in Europe and North America (Figure 4). The British species of *Sagenodus*, *S. inaequalis*, was well described by Watson and Gill (1923) and the American taxa were comprehensively addressed by Schultze and Chorn (1997). Almost all of the morphology of *S. copeanus* is known, from many disarticulated elements and a single articulated specimen, from the Hamilton Quarry in Kansas (Figure 10).

Sagenodus is found, along with *Ctenodus*, at the well known tetrapod locality of Newsham in Northumberland, UK, and its remains exist there in abundance. Schultze and Chorn (1997) have described *Sagenodus* as ‘The beginning of modern lungfish’, noting that it appears structurally intermediate between Devonian and post-Paleozoic lungfish. In addition they noted that the genus must be tolerant of a range of salinities because it is known from shallow marine to freshwater deposits. While *Sagenodus* is only known from one species in the UK, there are a number of species present in North American deposits and its range extends to the end of the Early Permian.

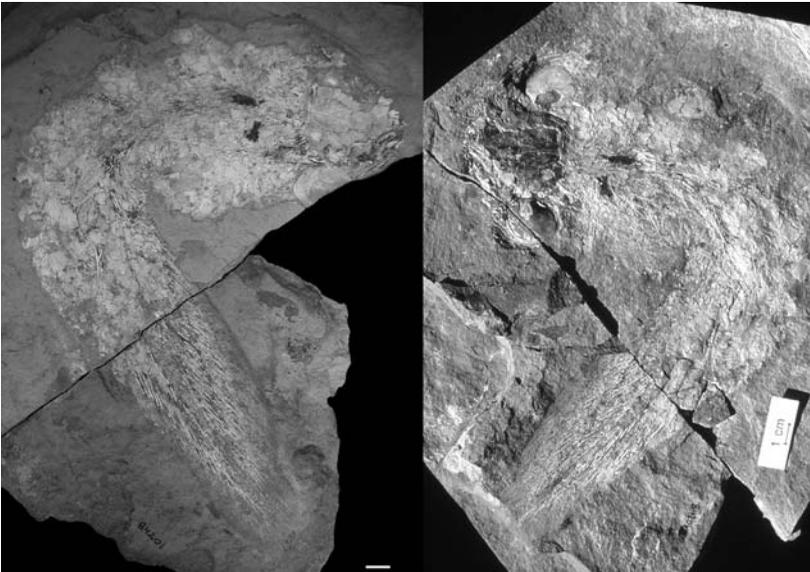


Fig. 10 *Sagenodus copeanus* Specimen KUVP (Kansas University Vertebrate Paleontology) 84201 part and counterpart. (Photographs, E. L Sharp, H.-P. Schultze). Scale bar 10 mm.

The generic diversity of lungfishes in the Permian is rather sparse, but two genera are known from many species. *Conchopoma* first appeared in the Late Carboniferous, with several species named from that Period, but species have also been described from the Early Permian. *C. gadiforme* from Europe is the best known of these (Schultze 1975). *Conchopoma* is the last-surviving genus of non-tooth plated lungfishes, and has cone-shaped individual teeth on the palate (Marshall 1988). It is best known from the Late Carboniferous of Mazon Creek, where almost complete skeletons have been found. It occurs alongside three other genera of lungfish including *Megapleuron*, that also persisted into the Early Permian.

Gnathorhiza is by far the most speciose of the Permian lungfish and is known from many localities in the United States, some preserving skeletal material and some only tooth plates (Olson and Daly 1972). *G. bothrotretus* is known from quite well preserved skeletons discovered within burrow-infills from a locality in New Mexico. This locality actually preserved large numbers of burrow-infills, although only four contained skeletal material. Two inferences were drawn from this. First, the burrows had been made by aestivating animals, indicating that the climate experienced seasonal drought. Secondly, that the mortality rate among those animals was quite low, given that only four skeletons remained among hundreds of burrow-infills (how many of these burrows were investigated is not stated (Berman 1976)). It stands in contrast to the discovery of the *Tranodis* specimens, many of which were found in articulation within their burrows. *Monongahela* is another genus named from the Permian (Marshall 1986), though it is only known from tooth plates and partial lower jaws and has been synonymized with *Palaeophichthys*, a genus known from the Middle Pennsylvanian (Schultze 1994). The synonymy was disputed by Kemp (1998b).

Figure 11 shows the distribution of genera of lungfishes, mentioned in the text, throughout the Devonian and Carboniferous arranged by stage, to illustrate the fall in diversity at the end of the Devonian. Readers should note that some genera survived through more than one stage and that the positions of genera within stages are not indicated.

MESOZOIC AND CENOZOIC LUNGFISHES

Subsequent to the end of the Paleozoic, remains of lungfishes decline in abundance. They consist largely of tooth plates, though about a dozen are known from skull roofs and a few from more complete remains. These include *Ariguna* and *Gosfordia* from the Early Triassic of Australia, two of the few post-Paleozoic forms known from complete fish (Kemp 1994b; Ritchie 1981). Mesozoic and Cenozoic lungfishes were reviewed by Schultze (2004), to whose work the reader is referred, and from which the summary presented here is largely drawn. More recently the most significant find has been of articulated skull remains and a limited amount

C A R B O N I F E R O U S	Late Carboniferous 323mya	<i>Conchopoma, Gnathorhiza</i> <i>Ctenodus, Sagenodus</i>
	Early Carboniferous 354mya	<i>Ctenodus, Uronemus, Straitonia</i>
D E V O N I A N	Late Famennian	<i>Soederberghia</i> , other Greenland forms <i>Orlovichthys, Andreyevichthys</i> <i>Rhynchodipterus, Phaneropleuron</i>
	Frasnian 370mya	<i>Fleurantia, Scaumenacia</i> <i>Chirodipterus, Griphognathus,</i> <i>Holodipterus</i> , other Gogo forms
M I D D L E	Givetian	<i>Howidipterus, Barwickia</i> <i>Dipnotuberculus, Eoctenodus</i> <i>Dipterus, Pentlandia</i>
	Eifelian 391mya	<i>Stomiahykus, lowadipterus</i>
E A R L Y	Emsian	<i>Sorbitorhynchus, Tarachomyx</i> <i>Speonesydrium</i> <i>Dipnorhynchus</i>
	Pragian	<i>Uranolophus, Melanognathus</i> <i>Ichnomyx</i> <i>Diabolepis, Youngolepis</i>
	Lockhovian 416mya	

Fig. 11 Devonian and Carboniferous timescale showing distribution of lungfish genera. (Note that position within stages does not necessarily indicate exact stratigraphic level of the taxon within that stage.)

of postcranial material from the genus *Ferganoceratodus* in Late Jurassic deposits in Thailand (Cavin *et al.* 2007) (Figure 12). This has added to the discussion of lungfish biology and relationships. It retains a bony snout, the only post-Devonian genus known to do so.

By the Mesozoic, lungfish dentitions had stabilized to the typical ridged tooth plates seen in modern genera, though they varied in the number and proportions of the ridges. These are often diagnostic as to genera and species, and show that there was quite a large array of genera and species during these later periods, but their morphological diversity was much more limited than in the Paleozoic (eg. Kemp 1993, 1994b, 1997, 1998a). Cavin *et al.* (2007) illustrated some of the variability to be found among them. Postcranial skeletons had stabilized to the long combined dorsal and caudal fins seen first among Carboniferous genera such as *Sagenodus*, and paired fins were long and narrow. Reduction of the ossification of the skull and postcranial skeleton also proceeded apace. The morphology is exemplified by the Triassic genus *Gosfordia* (Ritchie 1981) (Figure 12).

Taking their diversity as measured by the number of named taxa, there seems to be no obvious trend towards reduction. Taking that information at face value, there have been peaks during the Early and mid-Triassic, the Early and mid-Cretaceous, and the Late Cenozoic. Schultze (2004) has interpreted at least part of this pattern as attributable to the presence of extensive freshwater sequences from the Triassic compared to the prevalence of marine deposits from the Jurassic. At the Cretaceous/Tertiary (K/T) boundary, the number of taxa was cut by half, but five genera persist into the Cenozoic.

Most post-Paleozoic lungfish are from freshwater deposits, though not all: Schultze (2004) noted marine occurrences in Middle Triassic deposits, though possible Cretaceous marine records may be reworked (Kemp 1993; Cavin *et al.* 2007). Global distribution shows a trend towards restriction into southern continents. Triassic genera are found in Europe, Asia, southern Africa, Australia, and South America, though not, so far, in North America, despite being fairly common there in the Paleozoic. Asian and North American Jurassic deposits have yielded lungfish remains, though surprisingly, Australian ones have not. This may be a taphonomic effect in that the sediments are too acidic to preserve the remains (A. Kemp pers. comm. 2008). The last record of a European lungfish comes from the Middle Jurassic of England. In the Cretaceous they are found in South America, northern Africa, Madagascar, and once more, and most abundantly, in Australia. Cenozoic examples have been found in northern Africa, but otherwise they seem to have been restricted to South America and Australia, which is more or less their modern distribution. Cavin *et al.* (2007) explored this pattern based on their new phylogenetic analysis that suggested a deep split between lepidosirenids and *Neoceratodus*, inferring that vicariant events better explained the known distributions than did dispersal events.

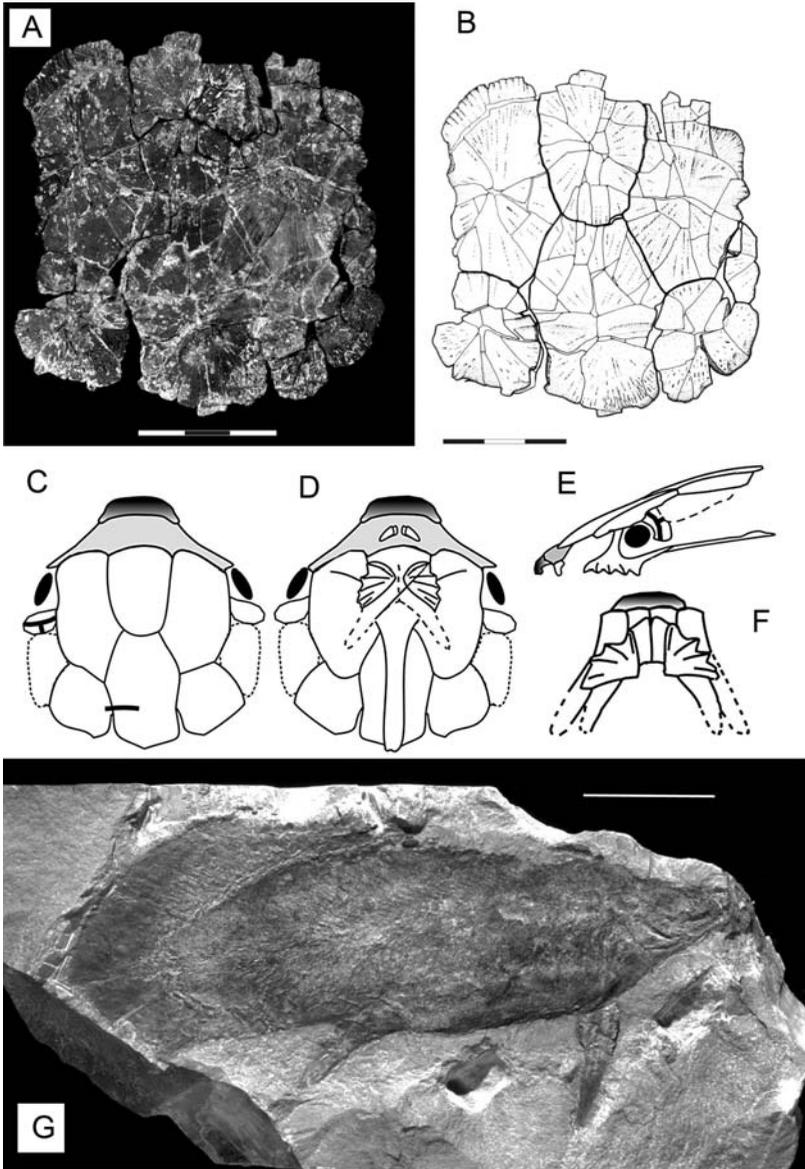


Fig. 12 Mesozoic lungfishes. A–F. *Ferganoceratodus martini*. A. Photograph and interpretive drawing respectively TF (Thai Fossils, Sahat Sakhan Dinosaurs Research Centre) 7712. Scale bars 30 mm. C, D. Reconstruction of skull in dorsal and ventral view respectively. E. Skull reconstruction in left lateral view. F. Lower jaw in dorsal view. A–F from Cavin *et al.* (2007). G. *Gosfordia truncata*, AMF 60621. (Photograph, J. A. Long). Scale bar 100 mm.

The extant Australian lungfish was initially named *Ceratodus*, on the basis of the similarity of its tooth plates to fossil forms from the Triassic. The extant form was given its present name in 1876 (de Castelnau 1876). As more '*Ceratodus*' tooth plates were found, discrimination between morphologies became more precise. Many '*Ceratodus*' tooth plates were assigned to new genera such as *Ptychoceratodus*, *Asioceratodus*, *Microceratodus* and *Archaeoceratodus* (Schultze 1981; Kemp 1992, 1993, 1997, 1998a). Despite this, *Ceratodus* itself still appears to be the longest-surviving form, with Early Triassic to end-Paleogene species being recognized. Neither Schultze (2004) nor Cavin *et al.* (2007) consider *Ceratodus* to be particularly closely related to *Neoceratodus*. *Neoceratodus* as a genus, in fact the species *N. forsteri*, is now traced back to the Early Cretaceous (Kemp 1997; Kemp and Molnar 1981), *Protopterus* back to the mid-Cretaceous, and *Lepidosiren* back to the Late Cretaceous (Schultze 2004).

Evolutionary History of Lungfishes

Fossil lungfishes, especially the rich Paleozoic records, throw light on the evolutionary history, biology and ecology of the group that would otherwise be impossible to infer. Despite the fragility of our understanding of their phylogeny, several significant 'trends' can be seen. Many of these were first noted in detail by Westoll (1949), but have been brought up to date over subsequent decades. Many areas of interest are not without their controversy, and many issues remain unresolved today.

Among the more consistent and striking observations is the reduction of ossification of both the dermal and endochondral skeleton through their geological record, though this is paralleled in other groups such as coelacanth. Early lungfishes retained a heavy cosmine covering over skulls and scales, a feature in common with other early sarcopterygians. It may have been resorbed periodically in several Devonian forms, and was lost completely by all post-Devonian taxa. The number of skull bones themselves became reduced, from the complex mosaic in *Dipnorhynchus* to the remnants seen in modern forms, with reduction progressing from front to back. Lateral lines came to run within the skin rather than through the skull bones. With few exceptions, *Ferganoceratodus* being one such, only the more posterior skull bones are retained in post-Paleozoic lungfish. Scales too not only lost their cosmine, but also their bone, causing Huxley (1861) to comment of the Famennian *Phaneropleuron* that they were 'exceedingly thin', 'containing very little bony matter'. That condition is not so different from *Neoceratodus* today, though even in *Protopterus*, some mineralization is retained in the scales (Zylberberg 1988). Other changes to the skull have been observed: enlargement of the orbit, shortening of the cheek, and reduction then loss of ossification of the braincase. These, along with other changes to the postcranial skeleton, such as loss of lepidotrichia, restriction of midline fins to the continuous dorsal and caudal fin, and reduction in ossification of the vertebral column have been suggested as

resulting from heterochronic processes such as paedomorphosis (Bemis 1984; Joss and Johanson 2006). This may explain some of these observed sequential changes, but does not explain the gradual but complete limitation towards the ridged tooth plate pattern from the varied dental morphologies seen in early forms. The presence of substantially ossified ribs in many Carboniferous lungfish taxa suggests a delay in the trend towards reduction in ossification seen in the rest of the postcranial skeleton.

Loss of cosmine presents interesting problems of its own. Cosmine has been interpreted as intimately linked with an electrosensory or lateralis-derived system housed within the pore canals characteristic of that tissue (Thomson 1975; Northcutt and Gans 1983; Gans and Northcutt 1983; Cheng 1989). It has been shown fairly convincingly that comparable structures are seen in the snout of *Neoceratodus*, though the relationship to a sensory system has been disputed. Bemis and Northcutt (1992) interpreted the pore canal system as associated with a complex cutaneous vascular system involved in the deposition of mineralized tissues. Cavin *et al.* (2007) showed that *Ferganoceratodus*, the only post-Devonian lungfish with a 'hard snout' (though it lacked cosmine) nonetheless showed bony structures comparable to those of Devonian forms, and suggested it as an intermediate stage between Devonian forms and *Neoceratodus*. They agreed with Bemis and Northcutt (1992) that the system was not sensory, but was a system for deposition of mineralized tissue: this raises the question of why it was retained in *Neoceratodus*, which is poorly ossified throughout its skeleton.

The evolution of the postcranial skeleton has elicited comments from many authors, from Westoll (1949) onwards (eg. Long 1993, 1995; Ahlberg and Trewin 1995) (Figure 13). It is a manifest fact that whereas early lungfishes show a primitive sarcopterygian pattern, exemplified by *Dipterus*, at the other end of the spectrum from *Sagenodus* in the Carboniferous to the modern forms, the second dorsal, caudal and possibly anal fins amalgamate, the tail becomes symmetrical rather than heterocercal, and the paired fins elongate. Intermediate morphologies are shown by genera like *Fleurantia* and *Scaumenacia*. Further studies of genera such as *Pentlandia* or *Ctenodus* may help to understand aspects of postcranial evolution, though, until the phylogeny of early lungfish is sufficiently well understood, such questions will remain hard to answer. Why this derived morphology became established at the expense of more flexible patterns is speculative, but may be linked to paedomorphic processes (Bemis 1984; Long 1990), and/or environmental influences that also encouraged air-breathing (Long 1993). Recently discovered hatchlings from Devonian lungfish may go some way to illuminating this question (Newman and den Blaauwen 2008).

There has also been discussion about the inflation in genome size seen in modern lungfishes in comparison with almost all other osteichthyans (salamanders have acquired a similar feature, thought by most researchers today to be convergently derived). Increase in genome size is reflected in cell size, and so is amenable in a limited way to study in fossils. Thomson (1972) was the first to discuss this idea,

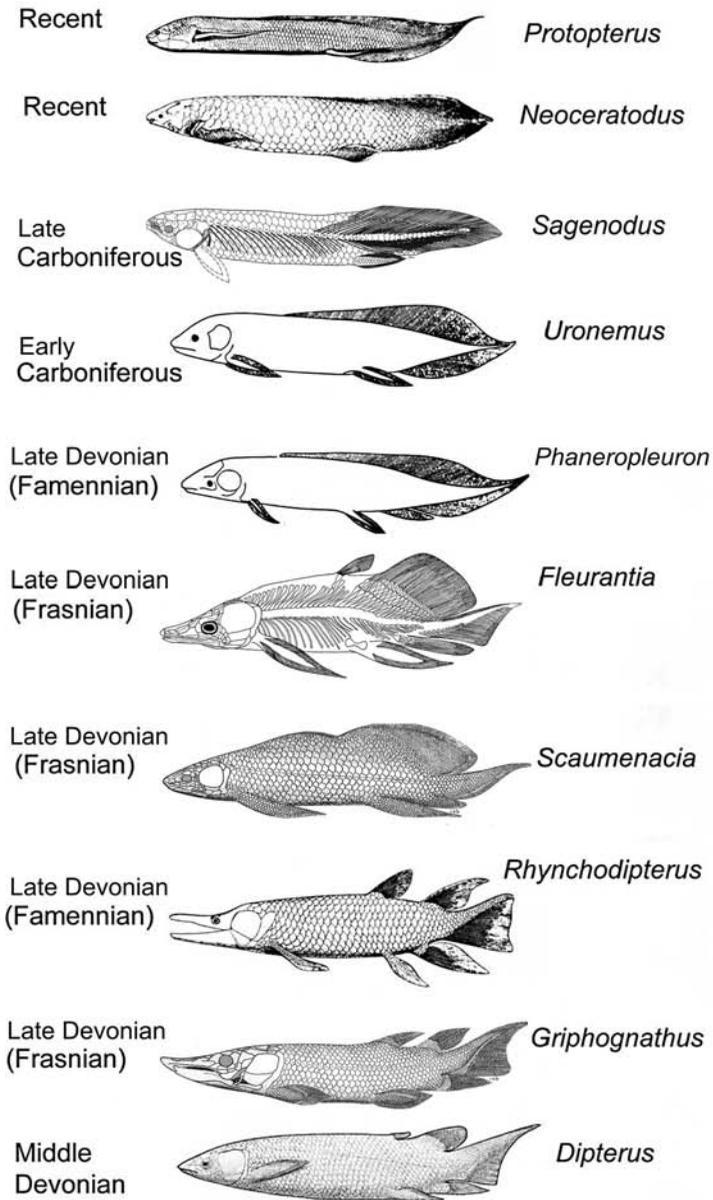


Fig. 13 Evolution of lungfish body form. *Dipterus* from Ahlberg and Trewin (1995); *Griphognathus* from Campbell and Barwick (1988); *Rhynchodipterus* from Jarvik (1980); *Fleurantia* from Cloutier (1996); *Scaumenacia* from Campbell and Barwick (1988); *Phaneropleuron* from Jarvik (1980); *Uronemus* from Jarvik (1980); *Sagenodus* from Schultz and Chorn (1997); *Neoceratodus* from Jarvik (1980); *Protopterus* from Jarvik (1980).

showing that cell size (ie. volume) was smallest in Devonian taxa, increased in Carboniferous taxa, again in Permian ones, and further again in Mesozoic forms. Thus the increase was not a sudden one-off event. Bemis (1984) pointed out that in salamanders, increase in genome size was linked to paedomorphosis (specifically, neoteny), and inferred that the same may be true for lungfish. Cell size is related to the rate of cell division, so that growth is retarded, and may result in neotenic species. Joss and Johanson (2006) pointed out that small cell size is characteristic of vertebrates showing both metamorphosis and direct development, and suggested that cell size increase might be related to loss of metamorphosis in post-Devonian lungfish, with retention of a *Neoceratodus*-type hatchling morphology into the adult. Unfortunately, since the hatchlings or juveniles of post-Devonian lungfish are rarely found in the fossil record, the existence or not of metamorphosis in these taxa is unlikely to be testable. Thomson (1972) further suggested that increase in cell-size may be linked to loss of diversity through the history of lungfishes. Though accepting the general principle of paedomorphism in lungfishes, Ahlberg and Trewin (1995) were skeptical that all the apparently paedomorphic changes seen in the morphology of the group were causally linked, noting that a robust phylogeny was the first requirement to test the hypothesis.

Another area of long-standing controversy concerns the morphology of the dentition in the Devonian forms. One view of the phylogeny divides the taxa into three separate lineages: denticulate forms, dentine plated forms, and those with true tooth plates, each of the dental types evolving as separate radiations (eg. Campbell and Barwick 1988, 1990). Other views of the phylogeny suggest that this scheme is unparsimonious when other skeletal information is taken into account, and the contrasting dentitions are seen as having arisen multiple times in several different lineages (eg. Schultze and Marshall 1993).

The radiating pattern of ridges on the tooth plates of post-Devonian forms grows by addition at the lateral ends of the ridges, without any shedding of teeth such as is found in other osteichthyans (Smith and Krupina 2001). In forms such as *Dipterus*, individual protuberances (teeth) can be identified, as they can in juveniles of *Neoceratodus*. In adults of *Neoceratodus*, they have become amalgamated into continuous ridges. Studies of growth series of both *Neoceratodus* and *Andrejevichthys* have shown that the same developmental pattern is observed in both showing that it is a very ancient mechanism, virtually unchanged since the Late Devonian (Krupina and Reisz 1999; Reisz and Smith 2001; Smith and Krupina 2001, Kemp 2002a). Work on the development of lungfish dentition has tended to suggest that, though it shows unique features compared to other osteichthyans, once established, only a limited number of processes are required to produce the varying patterns. Ahlberg *et al.* (2006) proposed a scheme whereby four different pterygoid dentitions could be generated by manipulating just two ontogenetic processes: tooth addition and tooth resorption (Figure 14A). They assumed that sheet dentine is added at the lateral pterygoid margin and that resorption is followed by the deposition of a denticle field. The idea that the dental

morphologies fall along spectra of types is suggested for example by the differing morphologies seen within *Holodipterus*, and the fact that denticles lie between the toothed ridges in *Andrejevichthys* (Ahlberg *et al.* 2006) (Figure 1).

Little work has addressed questions of the functional significance of Paleozoic lungfish tooth plate morphology. Questions concerning the significance of numbers and spacing of ridges, or presence or absence of cusps would be hard to address because of the limited availability of modern analogues. Study of microwear might prove difficult because most Carboniferous tooth plates have been prepared using mechanical means which damage the surface of the enamel. However, tooth plate wear patterns and pathologies from Cenozoic forms have been shown to record environmental conditions, with increased numbers and types of pathologies occurring in populations under climatic or other stress. Different populations of lungfishes from the Cenozoic of Australia show some that were healthy, some that were aging and showed no recruitment, and some in which attrition or disease were prevalent (Kemp 2005).

Because of the exceptional preservation of some Devonian lungfishes, some unexpected aspects of their biology can be ascertained. For example, braincases of Gogo species, such as *Chirodipterus*, allow details of the vestibular system to be described (Miles 1977). Semicircular canals and their ampullae have perichondrally lined walls, and though the saccular region is less well ossified, the utricular region is discernible. It shows a derived character of lungfish, seen also in *Protopterus* (Retzius 1881) and *Lepidosiren* (J.M. Jørgensen pers. comm., see Chapter 19): a relatively enlarged utricular sac (Figure 14B). This character

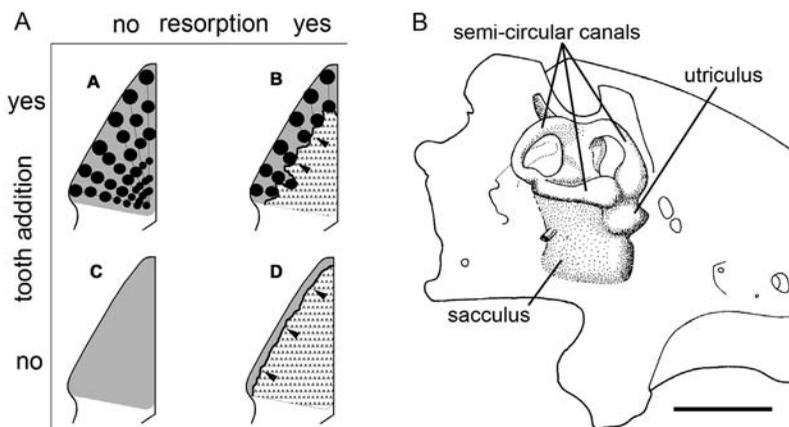


Fig. 14 A. Processes governing tooth plate development (from Ahlberg *et al.* 2006). B. Reconstruction of inner ear of *Chirodipterus australis* showing large utricular chamber (from Miles 1977). Scale bar 10 mm.

may therefore date back to an early stage in their evolutionary history, though its significance is uncertain.

Details of the nasal capsules, blood vessels of the snout, and of the lower jaw have been reconstructed in detail for some taxa such as *Griphognathus* (Miles 1977), *Dipnorhynchus* (Campbell and Barwick 1982b, 2000), *Speonesydrion* (Campbell and Barwick 1984) and *Holodipterus* (Pridmore *et al.* 1994). Dental caries has been reported in Paleozoic lungfish (Kemp 1991) and many other pathologies, such as abrasion, attrition, spur and step wear, malocclusion, hyperplasia and abscesses are seen in Cenozoic examples (Kemp 2005).

The shift in palaeoenvironments of fossil lungfish from essentially marine to exclusively freshwater through their history is well documented, though details are not without their controversies. The earliest forms such as *Diabolepis* (Chang 1995) and *Dipnorhynchus* (Campbell and Barwick 1999), as well as all the Gogo lungfishes, are found in marine limestones. Through the Devonian, lungfishes seem progressively to invade marginal marine, estuarine and even fully freshwater environments. For example, in the mid-Devonian, *Dipterus* occurs in the Orcadie basin, basically a lake environment, though with occasional marine incursions (Trewin 1986). The Givetian forms *Howidipterus* and *Barwickia* are amongst the earliest forms found in fully freshwater environments (an intermontane lake). The Late Devonian *Soederberghia* occurs in freshwater flood-plain pond environments in the Catskill Formation of Pennsylvania, East Greenland and Australia (Ahlberg *et al.* 2001; Cressler 2006), though Ahlberg *et al.* (2001) suggest some continuity of the flood-plain habitat with marginal marine environments. The type of environment represented at Miguasha has been controversial. Prichonnet *et al.* (1996) suggested that it varied from fully marine, through marginal marine to freshwater at different times, and included horizons that reflect periods of stagnant conditions, whereas Cloutier *et al.* (1996) interpreted it as brackish to marginal marine throughout.

By the Carboniferous, most lungfishes are thought to have been freshwater, inhabiting coal swamp environments. However, there is some controversy over whether all coal swamp facies represent freshwater environments or whether some may have been under periodic marine influence (Schultze 1995). Recent work by one of the authors (ELS) has shown that among British Carboniferous lungfishes, *Ctenodus* seems to have been marine-intolerant. This contrasts with *Sagenodus* which is found from deltaic to more fully marine environments, and may have been euryhaline (Schultze and Chorn 1997). By the Permian the majority of lungfish were freshwater dwellers, but the environment inhabited by *Gnathorhiza* is disputed. Schultze and Chorn (1997) claim that it was tolerant of marine conditions and found in nearshore deposits. Evidence of marine dwelling lungfishes diminishes steadily through the Mesozoic, and by the Cenozoic, lungfishes were exclusively freshwater animals.

During the latter part of the Late Devonian and the Carboniferous, lungfish remains are often found associated with deposits that yield tetrapods, suggesting that they inhabited similar environments. In fact the presence of lungfish elements has been used to provide potential clues to the presence of Paleozoic tetrapods (T.R. Smithson, S.P. Wood, pers. comm. 2007).

Interpretation of their environment impinges on another topic of lungfish biology, that of aestivation (see below). Specimens of *Gnathorhiza* have been found embedded in burrows, which has often been taken to imply that they were aestivating. Schultze and Chorn (1998) suggest on the other hand that they burrowed to avoid high tides in a marginal marine situation, however this seems an unlikely explanation for the Hancock specimens of *Tranodis*. An alternative explanation of the 'burrows' might be as breeding nests. Modern *Protopterus* is known to build tubular or blind-ending burrows in which males, or less usually females, guard the eggs (Greenwood 1987; Mlewa *et al.*, this volume). Some types of nests resemble, though are smaller than, dry season aestivation burrows in *P. aethiopicus* (Greenwood 1987). The burrows of *Tranodis* are orientated sub-vertically to the bedding planes (Garcia *et al.* 2006b) and are described as 'banana-shaped' (G. Storrs, pers. comm. 2008).

Another topic of great interest is the development of air-breathing within the lungfish lineage. The earliest lungfishes were marine, and did not show any of the specializations for air breathing that are found in post-Devonian forms. The assumption was that marine forms are unlikely to have required any air-breathing facility, and that deep water dwellers are unlikely to have exploited it. However, it has recently been shown that even Gogo underwent periodic anoxic events (Trinajstic *et al.* 2007), though the relationship between them and where the lungfishes were found has not been established. The fact that *Griphognathus* was not exclusively a deep-water marine form is telling. Some air-breathing capacity is generally accepted among many paleoichthyologists as well as physiologists as being an ancient trait of osteichthyans (Schultze and Chorn 1997; Perry *et al.* 2001), so that even the earliest lungfishes probably had some capability in that respect.

Air-breathing adaptations in lungfish have been studied by Campbell and Barwick (1988) and Long (1993) based on well-preserved cranial and postcranial elements of the Gogo and Mount Howitt (Frasnian) lungfishes respectively. Campbell and Barwick (1988) showed how the buccopharyngeal chamber increased in size by the forward movement of the quadrates relative to the back of the skull, accompanied by a corresponding increase in length of the posterior parasphenoid stalk. They also showed how the posterior margins of the tooth plates and the region of the parasphenoid between them allowed the tongue to form a buccal seal in modern forms, reflected in fossil ones with similar palatal morphologies. They pointed out modifications of the hyobranchial system and shoulder girdle that developed enhanced capacity for rotation in association with enlargement of the gape for air-gulping. These observations were augmented by Long (1993), who

added a cranial rib to the above list of features: this structure helps to anchor the pectoral girdle during air-gulping (Bishop and Foxon 1968). He found no evidence of a cranial rib in Gogo lungfishes, but did so in *Howidipterus* and *Barwickia*, from which he inferred some degree of air-breathing to be present. *Dipterus* was once thought to have had a cranial rib (Ahlberg and Trewin 1995), though this is no longer considered to be the case. However, den Blaauwen *et al.* (2005) suggested that nevertheless it showed some of the features of the palate suggesting that it was capable of some degree of air breathing though it did not have the complete suite of features found in later forms. Many of these features, including a cranial rib, have recently been described in the Gogo lungfish *Rhinodipterus* (Clement and Long 2010), suggesting that even some marine forms were air breathing.

It should also be borne in mind that the same adaptations as are used in air-gulping in lungfishes are also employed in their suction feeding mechanisms. It would be hard to disentangle evolution of the adaptations for these functions from each other. Early lungfish may have developed them first in connection with suction feeding, only later to co-opt them into air-gulping, so it may not be valid to infer air-breathing in the earliest forms (Sharp 2007).

The association of many later Devonian lungfishes with tetrapods has also been taken to suggest that both groups may have lived in relatively anoxic waters in which air-breathing might have been an advantage. It has been noted that during this time, it was the long-snouted denticulate forms that were more closely associated with tetrapods. Some of these, such as *Soederberghia*, possessed cranial ribs and an elongate parasphenoid stalk (Ahlberg *et al.* 2001), suggesting that they were air-breathers.

The similarity of the long curved trunk ribs of Carboniferous lungfish to those of tetrapods might lead to speculation that they may have been involved in costal ventilation, as they are in amniotes and their stem group. However, experiments on lungfish breathing suggests that they gulp air using the orobranchial and parabronchial chambers (Thomson 1969). They do not use hypaxial muscles for expiration, though they do have three hypaxial muscle layers, in contrast to two as found in actinopterygians and four as in tetrapods. Apparently, the additional layer is used in locomotion but not in breathing, at least in modern forms (Brainerd *et al.* 1993). Modern lungfish have very reduced ribs, along with general reduction of the ossified endoskeleton, which leaves open the possibility that the strongly ossified and cylindrical rib-cage of fossil forms was used differently from that in recent ones, though was most likely used in locomotion. By the Carboniferous, most of the air-breathing adaptations seen in modern lungfishes were in place, and the co-occurrence of tetrapods and lungfish is continued.

Supposed lungfish burrows noted in the Devonian of the Catskills have been suggested as early evidence of aestivation in lungfishes. However, the burrows were probably misidentified (Friedman and Daeschler 2006), and could be tree-stump infills, to judge from the published photographs. The earliest hard evidence for burrows are thus probably those of *Tranodis* from the Mississippian of Kentucky.

Neither Schultze and Chorn (1997) nor Cavin *et al.* (2007) were convinced that the burrows containing *Gnathorhiza* necessarily implied a capacity to aestivate. Part of the reason for this is that among modern lungfish, only *Protopterus* and *Lepidosiren* are certainly known to aestivate in totally dry conditions, and *Gnathorhiza* is remote phylogenetically from these taxa. Thus they argue that aestivation could be i) a character that evolved among Paleozoic lungfish and was lost by *Neoceratodus*, or ii) evolved in parallel within several lineages, or iii) was absent in *Gnathorhiza*. Cavin *et al.* (2007) did allow the possibility that *Gnathorhiza* could burrow to survive short dry spells but perhaps not whole seasons. The inferences are challenged by the occurrence of the *Tranodis* burrows, assuming they were associated with aestivation. Cavin *et al.* (2007) also admit that even a robust phylogeny may not satisfactorily answer this question. There are many aspects of lungfish evolution and biology that may be answerable with future finds, though there will probably be others that remain a mystery.

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References

- Agassiz, L. (1838). *Recherches sur les poissons fossiles, 1833-1844*, Neuchatel, Imprimerie de Petitpierre et Prince.
- Ahlberg, P.E. (1991). A re-examination of sarcopterygian interrelationships, with special reference to the Porolepiformes. *Zoological Journal of the Linnean Society of London* 103: 241-287.
- Ahlberg, P.E. and Trewin, N. (1995). The postcranial skeleton of the Middle Devonian lungfish *Dipterus valenciennesi*. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 85: 159-175.
- Ahlberg, P.E. and Johanson, Z. (1998). Osteolepiforms and the ancestry of tetrapods. *Nature* 395: 792-794.
- Ahlberg, P.E., Johanson, Z. and Daescher, E.B. (2001). The Late Devonian lungfish *Soederberghia* (Sarcopterygii, Dipnoi) from Australia and North America, and its biogeographical implications. *Journal of Vertebrate Paleontology* 21: 1-12.
- Ahlberg, P.E., Smith, M.M. and Johanson, Z. (2006). Developmental plasticity and disparity in early dipnoan (lungfish) dentitions. *Evolution and Development* 8: 331-349.
- Barkas, T.P. (1868). *Ctenodus interruptus*. *Scientific Opinion* 2: 113-114.

- Barwick, R.E., Campbell, K.S.W. and Mark-Kurik, E. (1997). *Tarachomyx*: A new Early Devonian dipnoan from Severnaya Zemlya, and its place in the evolution of the Dipnoi. *Geobios* 30: 45-73.
- Bemis, W.E. (1984). Paedomorphosis and the evolution of the Dipnoi. *Paleobiology* 10: 293-307.
- Bemis, W.E. and Northcutt, R.G. (1992). Skin and blood vessels of the snout of the Australian lungfish *Neoceratodus forsteri*, and their significance for interpreting the cosmine of Devonian lungfishes. *Acta Zoologica* 73: 115-139.
- Bendix-Almgreen, S.E. (1976). Palaeovertebrate faunas of Greenland. In: A. Escher and W.S. Watt (eds). *Geology of Greenland. Gronlands Geologiske Undersøgelse*. Copenhagen, Denmark. pp. 536-573.
- Berman, D.S. (1976). Occurrence of *Gnathorhiza* (Osteichthyes: Dipnoi) in aestivation burrows in the Lower Permian of New Mexico with a description of a new species. *Journal of Paleontology* 50: 1034-1039.
- Bishop, I.R. and Foxon, G.E.H. (1968). The mechanism of air-breathing in the South American lungfish *Lepidosiren paradoxa*. *Journal of Zoology* 154: 263-271.
- Brainerd, E.L., Ditelberg, J.S. and Bramble, D.M. (1993). Lung ventilation in salamanders and the evolution of vertebrate air-breathing mechanisms. *Biological Journal of the Linnean Society* 49: 16-183.
- Campbell, K.S.W. and Barwick, R.E. (1982a). A new species of the lungfish *Dipnorhynchus* from New South Wales. *Palaeontology* 25: 509-527.
- Campbell, K.S.W. and Barwick, R.E. (1982b). The neurocranium of the primitive dipnoan *Dipnorhynchus sussmilchi* (Etheridge). *Journal of Vertebrate Paleontology* 2: 286-327.
- Campbell, K.S.W. and Bell, M.W. (1982). *Soederberghia* (Dipnoi) from the Late Devonian of New South Wales. *Alcheringa* 6: 143-149
- Campbell, K.S.W. and Barwick, R.E. (1984). *Speonesydron*, an Early Devonian dipnoan with primitive tooth plates. *Palaeo Ichthyologica* 2: 1-48.
- Campbell, K.S.W. and Barwick, R.E. (1988). Geological and palaeontological information and phylogenetic hypotheses. *Geological Magazine* 125: 207-227.
- Campbell, K.S.W. and Barwick, R.E. (1990). Paleozoic dipnoan phylogeny: Functional complexes and evolution without parsimony. *Paleobiology* 16: 143-169.
- Campbell, K.S.W. and Barwick, R.E. (1995). The primitive dipnoan palate. *Journal of Vertebrate Paleontology* 15: 13-27.
- Campbell, K.S.W. and Barwick, R.E. (1998). A new tooth-plated dipnoan from the Upper Devonian Gogo Formation and its relationships. *Memoirs of the Queensland Museum* 42: 403-437.
- Campbell, K.S.W. and Barwick, R.E. (1999). Dipnoan fishes from the Late Devonian Gogo Formation of Western Australia. *Records of the Australian Museum* 57: 107-138.
- Campbell, K.S.W. and Barwick, R.E. (2000). The braincase, mandible and dental structures of the Early Devonian lungfish *Dipnorhynchus kurikae* from Wee Jasper, New South Wales. *Records of the Australian Museum* 52: 103-128.
- Campbell, K.S.W. and Barwick, R.E. (2001). *Diabolepis* and its relationship to the Dipnoi. *Journal of Vertebrate Paleontology* 21: 227-241.
- Campbell, K.S.W. and Barwick, R.E. (2002). The axial postcranial structure of *Griphognathus whitei* from the Upper Devonian Gogo Formation of Western Australia: Comparisons with other dipnoans. *Records of the Australian Museum* 21: 167-201.

- Campbell, K.S.W. and Smith, M.M. (1987). The Devonian dipnoan *Holodipterus*: dental form variation and remodelling growth mechanisms. *Records of the Australian Museum* 39: 131-167.
- Campbell, K.S.W., Barwick, R.E., Chatterton, B.D.E. and Smithson, T.R. (2002). A new Middle Devonian dipnoan from Morocco: Structure and histology of the tooth plates. *Records of the Australian Museum* 21: 39-61.
- Cavin, L., Suteethorn, V., Buffetaut, E. and Tong, H. (2007). A new Thai Mesozoic lungfish (Sarcopterygii, Dipnoi) with an insight into post-Palaeozoic dipnoan evolution. *Zoological Journal of the Linnean Society* 149: 141-177.
- Chang, M.M. (1995). *Diabolepis* and its bearing on the relationships between porolepiforms and dipnoans. In: M. Arsenault, H. Lelièvre and P. Janvier (eds). *Studies on Early Vertebrates*. Miguasha, Quebec: Bulletin du Muséum National d'Histoire Naturelle, Paris, France. pp. 235-268.
- Chang, M.-M. and Wang, J.-Q. (1995). A new Emsian dipnorhynchid (Dipnoi) from Guangnan, southeastern Yunnan, China. *Geobios* 19: 233-239.
- Cheng, H. (1989). On the tubuli in Devonian lungfishes. *Alcheringa* 13: 153-166.
- Clack, J.A. and Finney, S.M. (2005). *Pederpes finneyae*, an articulated tetrapod from the Tournaisian of western Scotland. *Journal of Systematic Palaeontology* 2: 311-346.
- Clement, G. and Boisvert, C.A. (2006). Lohest's true and false 'Devonian amphibians': Evidence for the rhynchodipterid lungfish *Soederberghia* in the Famennian of Belgium. *Journal of Vertebrate Paleontology* 26: 276-283.
- Clement, A.M. and Long, J.A. (2010). Air-breathing adaptation in a marine Devonian Lungfish. *Biology Letters* (Published online doi:10.1098/rsbl.2009.1033).
- Cloutier, R. (1996). Dipnoi (Akinetia: Sarcopterygii). In: H.-P. Schultze and R. Cloutier (eds). *Devonian Fishes and Plants of Miguasha*, Quebec, Canada. Verlag Dr Friedrich Pfeil. Munich, Germany. pp. 198-226.
- Cloutier, R. and Ahlberg, P.E. (1996). Morphology, characters and the interrelationships of basal sarcopterygians. In: M.L.J. Stiassny and L. Parenti (eds). *Interrelationships of Fishes II*. Academic Press, London, UK. pp. 445-479.
- Cloutier, R., Loboziak, S., Candilier, A.M. and Blicek, A. (1996). Biostratigraphy of the Upper Devonian Escuminac Formation, eastern Québec, Canada: A comparative study based on miospores and fish. *Review of Palaeobotany and Palynology* 93: 191-215.
- Cressler, W.L. (2006). Plant paleoecology of the Late Devonian Red Hill locality north-central Pennsylvania, and *Archaeopteris*-dominated wetland plant community and early tetrapod site. In: S.F. Greb and W.A. DiMichele (eds). *Wetlands through Time*. Boulder, CO, USA: Geological Society of America Special Paper, 79-102.
- Den Blaauwen, J.L., Barwick, R.E. and Campbell, K.S.W. (2005). Structure and function of the tooth plates of the Devonian lungfish *Dipterus valenncienesi* from Caithness and the Orkney islands. *Records of the Australian Museum* 23: 91-113.
- De Castelnau, F. (1876). Remarques au sujet du genre *Neoceratodus*. *Journale de Zoologie* 5: 342-343.
- Denison, R.H. (1968). Early Devonian lungfishes from Wyoming. *Fieldiana, Geology* 17: 353-413.
- Denison, R. H. (1974). The structure and evolution of teeth in lungfishes. *Fieldiana Geology* 33: 31-58.

- Forster-Cooper, C. (1937). The Middle Devonian fish fauna of Achanarras. Transactions of the Royal Society of Edinburgh 59: 223-239.
- Friedman, M. (2007a). Cranial structure in the Devonian lungfish *Soederberghia groenlandica* and its implications for the interrelationships of 'rynchodipterids'. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 98: 1-20.
- Friedman, M. (2007b). The interrelationships of Devonian lungfishes (Sarcopterygii: Dipnoi) as inferred from neurocranial evidence and new data from the genus *Soederberghia* Lehman 1959. Zoological Journal of the Linnean Society 151: 115-171.
- Friedman, M. and Daeschler, E.B. (2006). Late Devonian (Famennian) lungfishes from the Catskill Formation of Pennsylvania, USA. Palaeontology 49: 1167-1183.
- Gans, C. and Northcutt, R.G. (1983). Neural crest and the origin of vertebrates: A new head. Science 120: 268-274.
- Garcia, W.J., Storrs, G.W. and Greb, S.F. (2006a). The Hancock County tetrapod locality: a new Mississippian (Chesterian) wetlands fauna from western Kentucky (USA). In: S.F. Greb and W.A. DiMichele (eds). Wetlands through Time. Geological Society of America Special Papers 399: 155-167.
- Garcia, W.J., Storrs, G.W. and Greb, S.F. (2006b). Lungfish burrows from the Mississippian (Chesterian) of north-western Kentucky. Journal of Vertebrate Paleontology 26: 65A.
- Graham Smith W. and Westoll, T.S. (1937). On a new long-headed dipnoan fish from the Upper Devonian of Scaumenac Bay, P.Q. Canada. Transactions of the Royal Society of Edinburgh 59: 241-268.
- Greenwood, P.H. (1987). The natural history of African lungfishes. In: W.E. Bemis, W.W. Burggren and N.E. Kemp (eds). The Biology and Evolution of Lungfishes. Journal of Morphology, supplement 1 for 1986. pp. 163-180
- Günther, C.A.L.G. (1871). Description of *Ceratodus*, a genus of ganoid fishes, recently discovered in rivers of Queensland, Australia. Transactions of the Royal Society of London 161: 377-379.
- Huxley, T.H. (1861). Preliminary essay upon the systematic arrangement of the fishes of the Devonian epoch. Memoirs of the Geological Survey of the UK. Figures and descriptions illustrative of British organic remains: Scientific Memoirs 2: 421-460.
- Jarvik, E. (1980). Basic Structure and Evolution of Vertebrates, Volume 1. Academic Press, London, UK.
- Jarvik, E. (1996) The Devonian tetrapod *Ichthyostega*. Fossils and Strata 40: 1-206.
- Johanson, Z. and Ritchie, A. (2000). A new Famennian lungfish from New South Wales, Australia, and its bearing on Australian-Asian terranes. Alcheringa 24: 99-118.
- Joss, J. and Johanson, Z. (2006). Is *Palaeospondylus gunni* a fossil larval lungfish? Insights from *Neoceratodus forsteri* development. Journal of Experimental Zoology (Mol. Dev. Evol.) 306B: 1-9.
- Kemp, A. (1991). Palaeopathology and lungfish tooth plates. In: M.M. Chang, Y. Liu and G. Zhang (eds). Early Vertebrates and Related Problems of Evolutionary Biology. Science Press, Beijing, China. pp. 441-464.
- Kemp, A. (1992). New neoceratodont cranial remains from the Late Oligocene-Middle Miocene of Northern Australia with comments on generic characters for Cenozoic lungfish. Journal of Vertebrate Paleontology 12: 284-293.

- Kemp, A. (1993). *Ceratodus diutinus*, a new fossil ceratodont from Cretaceous and Tertiary Deposits in Australia. *Journal of Paleontology* 67: 883-886.
- Kemp, A. (1994a). Possible pathology in the snout and lower jaw of a Chinese Devonian dipnoan, *Sorbitorhynchus deleaskitus* (Osteichthyes: Dipnoi). *Journal of Vertebrate Paleontology* 14: 453-458.
- Kemp, A. (1994b). Australian Triassic lungfish skulls. *Journal of Paleontology* 68: 647-654.
- Kemp, A. (1995). Marginal tooth bearing bones in the lower jaw of the Recent Australian lungfish, *Neoceratodus forsteri* (Osteichthyes: Dipnoi). *Journal of Morphology* 225: 345-355.
- Kemp, A. (1997). A revision of Australian Mesozoic and Cenozoic lungfish of the family Neoceratodontidae (Osteichthyes: Dipnoi) with a description of four new species. *Journal of Paleontology* 71: 713-733.
- Kemp, A. (1998a). Skull structure in post-Paleozoic lungfish. *Journal of Vertebrate Paleontology* 18: 43-63.
- Kemp, A. (1998b). On the generic status of *Palaeophichthys parvulus* Eastman 1908 and *Monongahela stenodonta* Lund 1970 (Osteichthyes: Dipnoi). *Annals of the Carnegie Museum* 67: 225-243.
- Kemp, A. (1999). Ontogeny of the skull of the Australian lungfish, *Neoceratodus forsteri* (Osteichthyes: Dipnoi). *Journal of Zoology* 248: 97-137.
- Kemp, A. (2002a). Growth and hard tissue remodeling in the dentition of the Australian lungfish, *Neoceratodus forsteri* (Osteichthyes: Dipnoi). *Journal of Zoology* 257: 219-235.
- Kemp, A. (2002b). The marginal dentition of the Australian lungfish, *Neoceratodus forsteri* (Osteichthyes: Dipnoi). *Journal of Zoology* 257: 325-331.
- Kemp, A. (2005). New insights into ancient environments using dental characters in Australian Cenozoic lungfish. *Alcheringa* 29: 123-149.
- Kemp, A. and Molnar, R.E. (1981). *Neoceratodus forsteri* from the Lower Cretaceous of New South Wales, Australia. *Journal of Paleontology* 55: 211-217.
- Krupina, N.I. and Reisz, R.R. (1999). Reconstruction of dentition in hatchlings of *Andreyevichthys epitomus*, a Late Famennian dipnoan from Russia. *Modern Biology* 24: 99-108.
- Krupina, N.I., Reisz, R.R. and Scott, D. (2001). The skull and tooth system of *Orlovichthys limnatis*, a Late Devonian dipnoan from Russia. *Canadian Journal of Earth Sciences* 38: 1301-1311.
- Long, J.A. (1987). A redescription of the lungfish *Eoectenodus* Hills 1929, with reassessment of other Australian records of the genus *Dipterus* Sedgwick & Murchison 1828. *Records of the Western Australian Museum* 13: 297-314.
- Long, J.A. (1990). Heterochrony and the origin of tetrapods. *Lethaia* 23: 157-166.
- Long, J.A. (1992). *Gogodipterus paddyensis* (Miles) gen. nov., a new chirodipterid lungfish from the Late Devonian Gogo Formation, Western Australia. *The Beagle: Records of the Northern Territories Museum of Arts and Sciences* 9: 11-20.
- Long, J.A. (1993). Cranial ribs in Devonian lungfish and the origin of dipnoan air-breathing. *Memoirs of the Association of Australasian Palaeontologists* 15: 199-209.