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A MARINE STEM-TETRAPOD FROM THE DEVONIAN OF WESTERN NORTH AMERICA AND THE EVOLUTION OF TETRAPOD LOCOMOTOR (AD)APTATIONS AND ENVIRONMENTS

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BY

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ABSTRACT

A MARINE STEM-TETRAPOD FROM THE DEVONIAN OF WESTERN NORTH AMERICA AND THE EVOLUTION OF TETRAPOD LOCOMOTOR (AD)APTATIONS AND ENVIRONMENTS

BY
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Major evolutionary transitions transpire in an environmental context. Thus, to understand the advent of novelty or exaptation in evolution, aptations and nonaptations must be resolved with ecological insight. Previous work on the origin of terrestrial vertebrates has focused on reconstructions of paleoenvironments or isolated examples of axial and appendicular function, but little work has been done to synthesize the role of evolutionary morphology and evolutionary theory in the origin of terrestrial locomotion, or to integrate paleoecological reconstructions to address the environments within which these changes evolved.

To understand the origin of axial and appendicular systems in their ecological context, I have combined data from a description of a fully articulated stem-tetrapod taxon and comparative evolutionary and paleoenvironmental analyses of total-group tetrapods to answer four questions: (1) what are the traits that underpin the tetrapod condition?; (2) how well do current phylogenies explain the distribution of character-states among Devonian and Carboniferous stem-tetrapods?; (3) how do the environments of stem-tetrapods inform and contextualize these evolutionary changes?; and (4) given the distribution of synapomorphies, and what is known about how extant and extinct sarcopterygians (including tetrapods) negotiate their aquatic and terrestrial environments, how do insights from evolutionary morphology and evolutionary theory inform the origin of walking on land?

The discovery and description of the marine stem-tetrapod from the Devonian of Nevada helps to clarify the phylogenetic, environmental, and anatomical framework that underpins the tetrapod condition. This new taxon, *Tinirau clackae*, demonstrates that substantial parallelism pervaded the early history of stem-tetrapods, supports an earlier origin of the tetrapod lineage, and further documents that incipient stages of the terrestrial appendicular condition began when sarcopterygians still retained their median fins and occupied aquatic habitats. Moreover, the phylogeny helps structure the traits that diagnose crown-tetrapods, their paleoenvironmental history, and the origin of their locomotory strategies. Without this result, the early history of elpistostegalians would still begin with *Panderichthys* and Thomson's (1980) marine origins hypothesis (variant II) would remain uncorroborated.

The integration of these paleontological data with data from extant taxa suggests that (*i*) the trot evolved at least three times in gnathostome evolution; (*ii*) the tetrapod myaxial condition evolved in water ~35 million years before the origin of amphibious sarcopterygians; (*iii*) trackway data from modern and fossil records cannot verify whether the lateral sequence diagonal-couplet gait evolved by the end of the Devonian; (*iv*) the original function of the physical neck—i.e., a space between head and shoulder—was more likely related to the origin of terrestrial locomotion than to any requirement for neck mobility; and (*v*) distinguishing aptations and nonaptations in a continuum of historical, constructional, and functional influences is critical to elucidating evolutionary transformations.

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ACKNOWLEDGMENTS

Without exception, choosing a Ph.D. program was the most difficult decision of my life. Considering my interest in integrative and evolutionary biology, the decision distilled to the University of Chicago or the University of California, Berkeley. I still recall sitting in my small Cambridge bedroom on a gloomy British afternoon, thinking to myself, "this is like having to choose which one of my parents I would prefer to die. Either way, whatever the outcome, there will be something I'll miss, and there *is no* best choice." I made spreadsheets and consulted friends and colleagues in effort to measure the immeasurable, until finally, the great Samuel Spender Sweet hit home with these words: "These are the two best programs in the world, and they are simply … different."

Despite the insight, it took me some time to settle into Berkeley, but I now see that I was naïve. I was too obsessed with taxonomic approaches to intellectual inquiry. I accept that scientists are often specialists—but for me—maintaining an integrated, well-rounded, working knowledge of science, and biology in particular, is orders of magnitude more fulfilling than being master of my intellectual microcosm in a much larger universe. That is, thanks to this "difference" in my Berkeley mentors, I have found that the best scientists in the world are simultaneously generalists and specialists; they know their discipline, but also maintain firm command of the transcending questions, in both time and place, of related fields. Integrative science lies at the core of who they are and what they do, and they have helped make my graduate experience the memory of a lifetime. Opportunities to learn about the history and structure of evolutionary theory, evolutionary morphology, the nature of 'species', phylogenetic and paleobiological methods, big history, evolutionary medicine, and numerous other disciplines have been truly irreplaceable. I feel only privileged to have been given the chance to work with and learn from such a dynamic range of experts. I thank members of the UCMP, MVZ, and interdepartmental communities, including Kevin Padian, Marvalee Wake, Walter Alvarez, Brent Mishler, Dave Wake, Charles Marshall, Jim Valentine, Geerat Vermeij, Tony Barnosky, Dave Lindberg, and Lynn Ingram. I would like to extend a special thanks to Kevin Padian, who has helped more than anyone to frame my current knowledge of the history and structure of evolutionary theory, and to instill in me the importance of science education and scientific literacy. Many students (even professionals) appear to lack such a perspective. They ask and answer "chicken-" and "bullshit-type" questions, but never grasp the "elephant shit" that has haunted the field for centuries. Additionally, I would like to thank: Marvalee Wake for her inspiration as the most well-rounded integrative biologist I will likely ever know; Brent Mishler for his keen insights and perspectives on the nature of 'species' and their bearing on evolutionary theory; Dave Wake, whose pluralism has dramatically shaped my concepts of formalism and functionalism; and Walter Alvarez, whose lessons on contingency, the history of science, interdisciplinary investigations, and big history have forever expanded the scope of my intellectual interests.

I travelled considerably during my time at Berkeley, and my research would not have been possible with assistance from numerous others. I thank John Long, Gavin Young, Tim Senden, Ken Campbell, and Brian Choo (Melbourne Museum and the Australian National University); Ted Daeschler, Jason Downs, and Fred Mullison (Academy of Natural Sciences, Philadelphia); Jenny Clack

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I would also like to thank those who helped direct and foster my interest in science and evolutionary biology through the years, including: Gary Ogden, Sam Sweet, Armand Kuris, Susannah Porter, Bruce Tiffney, Todd Oaklay, and my parents, Larry Swartz and Martha-Lee Sanders. More than anyone else, Gary Ogden is likely to blame for my now decade long obsession with evolutionary biology. His sincerity and enthusiasm as an instructor, and willingness to raise challenging, counterintuitive, and 'controversial' questions are what originally turned me on to science. This thesis is a product of his inspiration, and his influence will truly be missed. However, the financial and emotional support of my parents permitted me to capitalize on this obsession. Their willingness to support me through all aspects of my intellectual endeavors has been invaluable to my ontogeny and achievements as "young adult Brian." I appreciate their help more than they know.

Lastly, I would like to thank my girlfriend and domestic partner, Jessie Atterholt, who has done a spectacular job of tolerating me during the waning days of my dissertation. Despite the busy evenings and restless nights, her support, care, and consideration has kept my spirits high and mind clear. I only hope that I have been able to provide her with a fraction of the help that she has given me. Jessie has sacrificed much of her time for the sake of mine. I can never adequately repay her kindness, but I treasure her more than I can express.

Brian Swartz
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Berkeley

CHAPTER ONE: INTRODUCTION

The origin of terrestrial vertebrates: an integrative perspective

The assembly of complex adaptations is critical to the evolution of major transformations in the history of life (Carroll et al. 2005, Raymond et al. 1968, Vermeij and Dudley 2000). The resolution of pattern and process in macroevolution has helped not only to reconcile how intricate adaptations evolve, but to build a framework for how they facilitate the expansion of lineages into new evolutionary and ecological space (Bambach et al. 2007, Butterfield 2007, Simpson 1952, Valentine 1980, Vermeij 1996). Key examples range from the origin of dinosaurian flight in the Jurassic (Gauthier and Padian 1986, Padian 2001), to when our fish-like vertebrate relatives took their first steps onto land over 300 million years ago (Clack 2002a). In recent years, this vertebrate water-to-land transition has gained increasing press in both scientific and popular literature (Clack 2002b, 2005, Coates et al. 2008, George and Blieck 2011, Niedźwiedzki et al. 2010, Zimmer 1998). However, until the later 20th century, relatively little was known about this pivotal episode in vertebrate history. Instead, *Ichthyostega* was seen as the poster child for stem-tetrapods, and *Eusthenopteron* as the sarcopterygian 'fish' whose "out of the ooze and born to cruise" depiction commonly led to its amphibious reconstruction in many artistic interpretations (Jarvik 1980, Matson and Troll 1995) (Figure 1.1).

Since the first discovery of fully articulated specimens of *Acanthostega* in 1987, and later publication of several influential papers throughout the 1990s (Clack 1994, 1998, Coates 1996, Coates and Clack 1990, 1991), new answers and questions began to arise among early vertebrate workers. Not only did *Acanthostega* have eight digits on its manus and pedes (Coates and Clack 1990) (unlike the hypothesized pentadactyl limb thought to diagnose crown-tetrapods primitively), but it also had well-developed gill arches and rudimentary wrist and anklebones (Coates 1996, Coates and Clack 1991). Thus, as a branchial respirator ill-adapted to terrestrial life, *Acanthostega* revealed that stem-tetrapods first evolved limbs with digits in the water. Other new questions concerned the developmental and evolutionary programs underlying the presence of eight digits. Are digits neomorphs or do they take their origin as exapted elements from sarcopterygian fins (Boisvert et al. 2008, Daeschler and Shubin 1998, Davis et al. 2004a, Johanson et al. 2007, Sordino and Duboule 1996)? How exactly does a lobed 'fin' evolve into a digit-bearing 'foot' (Coates 2003, Coates and Cohn 1998, Coates et al. 2002, Davis et al. 2004b, Shubin and Alberch 1986, Shubin et al. 2006)?

Over the next decade+, numerous journals and books published new stem-tetrapod taxa, localities, and environmental reconstructions of the Middle through Upper Devonian (~395-355 Ma) from around the world, including China, Australia, Europe, and North America (Ahlberg 1995, 1998, Blieck et al. 2010, Clément et al. 2004, Johanson and Ahlberg 2001, Long et al. 2006, Niedźwiedzki et al. 2010, Zhu et al. 2002). Whereas the general view remained that this transition occurred in freshwater (Clack 2002b, Long and Gordon 2004), few studies integrated sedimentological, assemblage, and isotopic data to address the marine versus freshwater ancestry of terrestrial vertebrates (Chidiac 1996, Cloutier and Lelievre 1998, Schmitz et al. 1991, Schultze and Cloutier 1996). Moreover, few authors have approached how exaptations and anatomical modifications of paired appendages underlie functional changes from fin to digit-bearing limb (Shubin et al. 2004, Shubin et al. 2006). In other words, if stem-

Figure 1.1. Classical depictions of popular stem-tetrapods. (A) *Ichthyostega* (Royal Scottish Museum, Edinburgh, photograph courtesy of Jenny Clack); (B) *Eusthenopteron* (Matson and Troll 1995).

tetrapods were still almost entirely aquatic, how did aptations in this medium foreshadow the first terrestrial steps of sarcopterygians on land? In addition, because much attention has focused on the so-called 'fin-to-limb' transition, an integrated view of the axial and appendicular systems in stem- and crown-tetrapods has been largely ignored. If the crown-tetrapod condition finds its origin in the tetrapod stem-lineage, then a step-wise sequence of changes that arose in water for other reasons should have bearing on the evolution of life on land. Thus, considering the intimate relationships of construction, function, and history (Gould 2002, Seilacher 1970), a comparative anatomical and phylogenetic investigation of stem- and crown-tetrapods should be key to the evolutionary signals that underpin terrestrial locomotion.

Major evolutionary transitions transpire in an environmental context, the evolutionary play in the ecological theatre (Hutchinson 1965). Thus, to understand the advent of novelty or exaptation in evolution, aptations and nonaptations must be resolved with ecological insight. Although past work has focused on reconstructions of stem-tetrapod paleoenvironments or isolated examples of axial and appendicular function, little work has been done to synthesize the role of evolutionary morphology and evolutionary theory in the origin of terrestrial locomotion, or to integrate paleoecological reconstructions to address the environments within which these changes evolved (Barrell 1916, Clack 2002b, 2006, Romer 1958, Thomson 1969, 1980, 1993). Therefore, to understand the origin of axial and appendicular systems in their ecological context, I have combined data from a description of a fully articulated stem-tetrapod taxon and comparative evolutionary and paleoenvironmental analyses of total-group tetrapods (Figure 1.2) to answer four questions: (1) what are the traits that underpin the tetrapod condition?; (2) how well do current phylogenies explain the distribution of character-states among Devonian and Carboniferous stem-tetrapods?; (3) how do the environments of stem-tetrapods inform and contextualize these evolutionary changes?; and (4) given the distribution of synapomorphies, and what is known about how modern and fossil sarcopterygians (including tetrapods) negotiate their aquatic and terrestrial environments, how do insights from evolutionary morphology and evolutionary theory underpin the origin of walking on land?

This research has bearing on several important macroevolutionary questions. Over the last 3.5 billion years of Earth history, there have been astonishingly few terrestrial invasions by marine clades with or without freshwater intermediates. Well-known fossil examples include embryophytes (Gray et al. 1982, Shear 1991), millipedes (Retallack and Feakes 1987), arachnids and apterygote insects

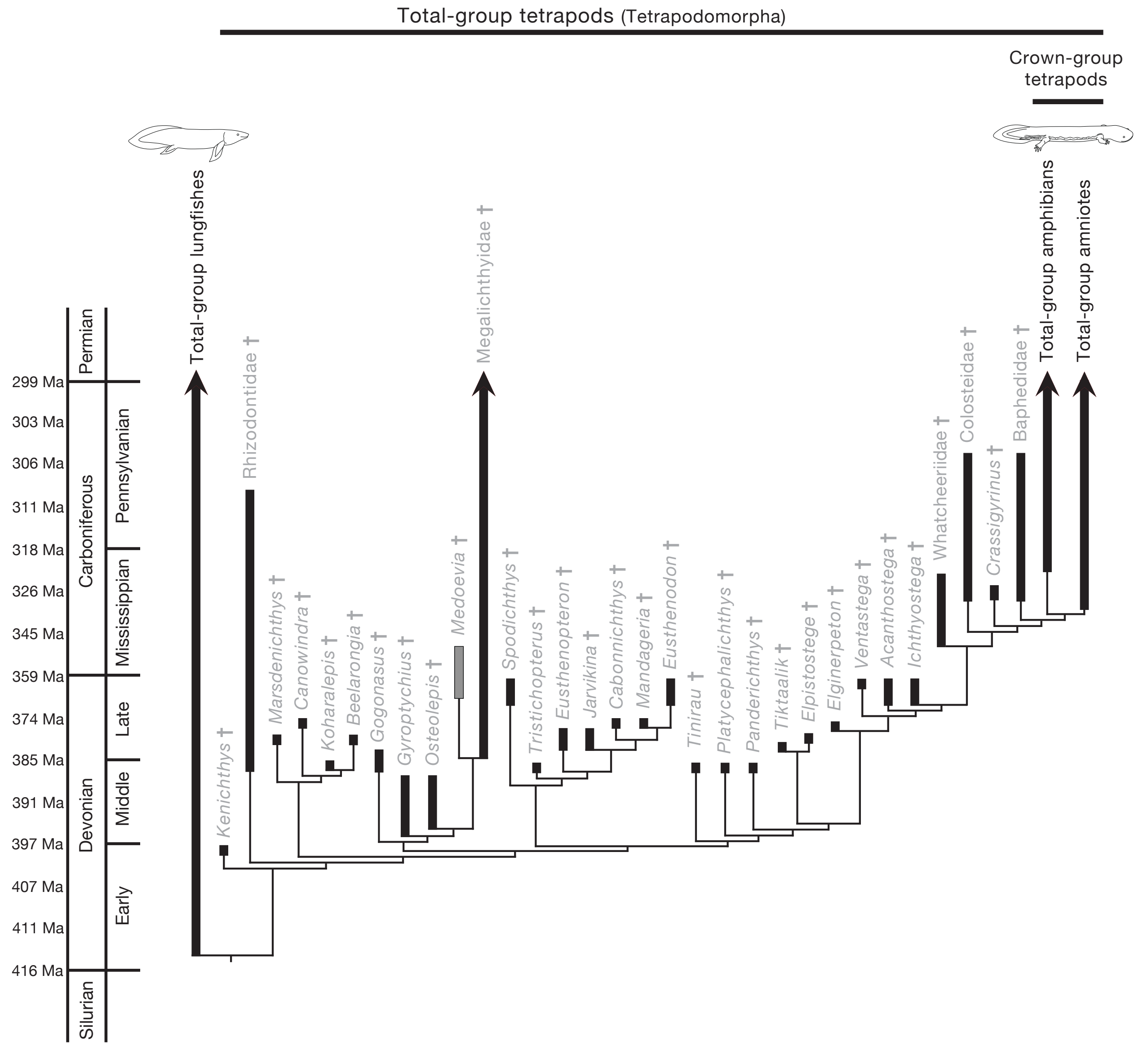

Figure 1.2. Definition of total-group tetrapods. Crown-group Tetrapoda is defined by all descendants of the last common ancestor of the two extant tetrapod lineages, total-group amphibians and total-group amniotes. Stem-tetrapods include all taxa more closely related to crown-group tetrapods than to total-group lungfishes. Total-group tetrapods (Tetrapodomorpha) simply includes all stem- and crown-group tetrapods. Extinct stem-tetrapod taxa are figured in gray and represented by a dagger. The stratigraphic range of *Medoevia* is shown in gray because it is uncertain.

(Rolfe 1980, Shear 1991, Shear et al. 1996), scorpions (Sissom 1990), and gastropods and bivalves (Dineley 1984, Kriz 1979). Past hypotheses about the ecological limitations of diversification include discussions about competition and evolutionary constraint (Gould 2002, Vermeij and Dudley 2000), whether considering physiology (Graham and Lee 2004), contingency in Earth history (Gould 1980, 1989b, Marshall 2006, Vermeij 2006), or historical and developmental constraint in biology (Gould 1984, 1989a, Wake 1991). The approaches and data in the following chapters help channel the aforementioned hypotheses within the context of various marine and freshwater environments. They help improve ideas about why there have been so few aquatic-to-terrestrial transitions, and how patterns from other clades compare with the evolutionary pre- (or rather, retro)dictions for tetrapods. Past studies indicate that the vertebrate water-to-land transition could have began at some point in a marine environment; however, the approaches and methods presented here will refine neontological questions about how we address evolutionary hypotheses in the fullness of time.

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CHAPTER TWO:
A MARINE STEM-TETRAPOD
FROM THE DEVONIAN OF WESTERN NORTH AMERICA

Abstract

The origin of terrestrial vertebrates represents one of the major evolutionary and ecological transformations in the history of life, and the established timing and environment of this transition has recently come under scrutiny. The discovery and description of a well-preserved fossil sarcopterygian (fleshy-limbed vertebrate) from the Middle Devonian of Nevada helps to clarify the temporal and anatomical framework that underpins the tetrapod condition. This new taxon, *Tinirau clackae*, demonstrates that substantial parallelism pervaded the early history of stem-tetrapods, supports an earlier origin of the tetrapod lineage, and further documents that incipient stages of the terrestrial appendicular condition began when sarcopterygians still retained their median fins and occupied aquatic habitats.

Introduction and background

The origin and early evolution of tetrapodomorphs (total-group tetrapods) has been firmly established by numerous studies over the last two decades (Ahlberg and Johanson 1997, Coates 1996, Daeschler et al. 2006, Johanson and Ahlberg 2001, Lebedev 1995, Long et al. 1997, Vorobyeva and Schultze 1991). However, knowledge of the interrelationships among fish-like 'osteolepiform'-grade taxa and the earliest elpistostegalians has remained elusive (Ahlberg and Johanson 1998, Chang and Yu 1997, Friedman et al. 2007, Long et al. 2006). Phylogenetic analyses have reinforced hypotheses of 'osteolepiform' paraphyly and parallelism among Devonian stem-tetrapods, but lack of robust statistical support for particular topologies has limited our knowledge of branching and divergence in these early lineages (Ahlberg and Johanson 1998, Snitting 2008). Few studies recover support for larger clades within the 'osteolepidids' (Coates and Friedman 2010), and several establish the close relationship of tristichopterids and elpistostegalians with a robust sister relationship between *Panderichthys* and early digited forms (Boisvert et al. 2008, Daeschler et al. 2006, Snitting 2008). However, no new taxa so far known document the assembly of traits leading from tristichopterids to elpistostegalians.

The discovery of a new stem-tetrapod from the Middle Devonian of western North America helps to fill this gap and provides a stronger phylogenetic backbone upon which future studies can build. The new material includes several specimens from marine sediments and represents an animal with numerous elpistostegalian apomorphies, yet also many symplesiomorphies, suggesting that early tetrapodomorph features have a more crownward distribution than previously considered. This mélange of characters extends ancestral tetrapodomorph traits across the early history of the first digited forms, and as part of a phylogenetic hypothesis, conforms to the predictions of the early Middle Devonian Zachełmie (Polish) trackways (Niedźwiedzki et al. 2010) in suggesting that the tetrapod lineage is at least 18 Ma older than previously hypothesized.

Geological Framework.—The material was discovered and excavated in the mid-late 1970s by University of California, Berkeley paleontologist Joseph T. Gregory and his graduate students at a field site in northeastern Nevada known as Red Hill I. The Red Hill I Beds are a series of silty limy mudstones alternating with thick-bedded limestones, bounded below and above by the Denay and Devils Gate Formations, respectively (Johnson et al. 1988). This University of California Museum of Paleontology field site (UCMP V74084) is located in the northern Simpson Park Mountains in Eureka County, Nevada. Conodont biostratigraphy places Red Hill I in the lower *Klapperina disparilis* zone (Johnson et al. 1988, Sandberg et al. 2003), the late Givetian stage of the Middle Devonian. The described sarcopterygian material was recovered from levels 8-12 of the roughly 1.5 m thick sequence of vertebrate-bearing beds immediately above the Denay Limestone (Figure 2.1).

The fauna and geology indicate that the sedimentary rocks comprising Red Hill I were deposited in a marine environment. Cnidarians such as conulariids, a clade known elsewhere only from marine strata (Simões et al. 2000), are preserved in levels 21-5 (Figure 2.1). Moreover, the widespread deposition of limestone and shale along the western margin of Laurentia suggests that the regional geology of the northern Simpson Park Range represents an open marine paleoenvironment (Johnson 1977), and in particular the outer continental shelf (Johnson et al. 1988, Schultze 2010). Trace fossils preserved between levels one and two suggest a short-term nearshore paleoenvironment (Schultze 2010).

Materials and methods

Phylogenetic Analysis.—203 morphological characters were used to assess the phylogenetic position of the new taxon described below (*Tinirau clackae*) relative to other early tetrapodomorphs. Primary character sources (Ahlberg et al. 2008, Ahlberg and Johanson 1998, Ahlberg et al. 2000, Coates and Friedman 2010, Daeschler et al. 2006, Zhu and Ahlberg 2004) are indicated parenthetically following each character description. Numbers following the citations refer to the character number in the original source. Characters modified from their original source are noted where applicable (see supplementary information). Very few characters are shared between this analysis and Coates and Friedman (2010); this was intentional with the goal of assessing how largely independent data sets converge on a similar result.

Characters were polarized by comparison to outgroup taxa such as *Porolepis*, *Glyptolepis*, *Powichthys*, *Youngolepis*, *Diabolepis*, and *Dipterus*. These taxa were selected because they represent a range of total-group lungfish that are known from reasonable material, are well studied, and generally accepted as sister to total-group tetrapods.

Characters were coded based on a combination of published descriptions, specimen illustrations, and firsthand examination of fossil material. Care was taken to avoid simply recycling codings in the published literature. Specimens from the following museums were examined, and are noted following each taxon in the supplementary information: Australian Museum, Sydney (AMF), Australian National University (ANU), Geologisk Museum, Copenhagen, Denmark (MGUH), Latvian Museum of Natural History (LDM), Muséum national d'Histoire naturelle, Paris (MNHN), Museum Victoria, Melbourne, Australia (NMV), The Natural History Museum, London (MNH), Palaeontological Institute of the Russian Academy of Sciences, Moscow (PIN), National Museums of Scotland (NMS),

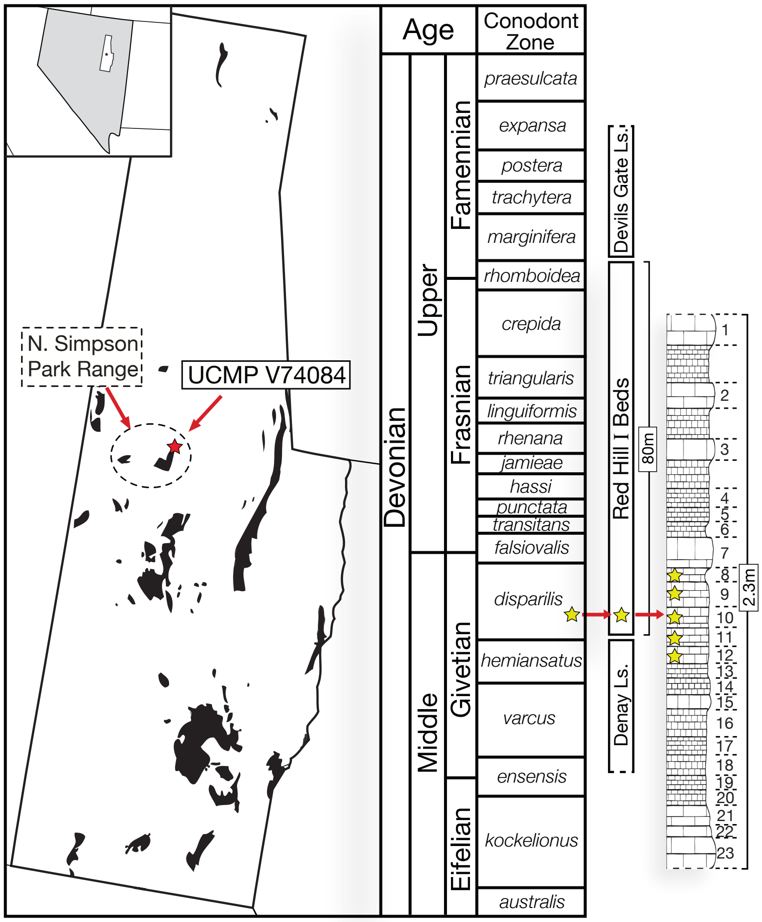

Figure 2.1. Geographic location and stratigraphic position of the Red Hill I field site (UCMP V74084) in Eureka Co., Nevada, USA. Black patterning within Eureka County represents exposed Devonian outcrops. Stars represent where the fossil material was collected. Red Hill I section courtesy of H.-P. Schultze.

Nunavut Fossil Vertebrate Collection (NUFV), Swedish Museum of Natural History, Stockholm (NR), University of California Museum of Paleontology (UCMP), University Museum of Zoology Cambridge (UMZC).

The data matrix was subjected to a maximum parsimony analysis in the software package PAUP (Swofford 2002) and a Bayesian analysis using the software package Mr. Bayes (Huelsenbeck 2001, Ronquist and Huelsenbeck 2003). All characters were assigned an equal weight, multistate characters were run unordered, and a heuristic search algorithm was used in PAUP to search for the shortest networks—rooted on *Porolepis*, *Glyptolepis*, *Powichthys*, *Youngolepis*, *Diabolepis*, and *Dipterus*. Bremer decay indices were calculated using PAUP (Swofford 2002) and TNT (Goloboff 1999, Nixon 1999), and Bayesian posterior probabilities were calculated with Mr. Bayes following an analysis that included 500,000 mcmc generations, sampling every 1,000 generations, and with 20 samples discarded as burnin. Character evolution was examined in MacClade (Maddison and Maddison 2000), which was also used to produce the character state distributions in the supplementary information.

Fossil Preparation.—The material was prepared by an acid immersion procedure including baths of 30% formic acid or 10-20% acetic acid for 10-48 hours, followed by washing in running water for one month, and air-drying for 12-24 hours. Exposed elements were strengthened with glyptal or Duco cement. The three UCMP specimens 117884, 118283, and 123125 were studied 30 years ago by former UC Berkeley graduate student John Reed, although never published (Reed 1980). Because so much has changed in the record, systematics, and nomenclature of stem-tetrapods, it was necessary to redo the study completely.

Anatomical Abbreviations.—**ba.a**, anal basal; **b.art**, basal articulation of the basipterygoid process; **Basb1**, basibranchial #1; **bas.f**, basicranial fenestra; **Ch**, ceratohyal; **Clth**, cleithrum; **Clv**, clavicle; **Co3**, posterior coronoid; **c.par**, crista parotica; **de.f**, dentary fang; **Dpt**, dermopalatine; **Enpt**, entopterygoid; **Ept**, ectopterygoid; **Exsc.l**, lateral extrascapular; **Exsc.m**, median extrascapular; **Fe**, femur; **fib**, fibula; **gle**, glenoid fossa; **Gu**, lateral gular; **Hh**, hypohyal; **Hu**, humerus; **Hyo**, hyomandibular; **hyo.art**, hyomandibular articulation; **Ic**, intercentrum; **Int**, intermedium; **It**, intertemporal; **Ju**, jugal; **La**, lacrimal; **Mk**, Meckelian bone; **mk.grv**, Meckelian groove; **Mx**, maxilla; **na.a**, anterior naris; **nc.c**, notochordal canal; **ns**, neural spine; **Op**, operculum; **pa.pl**, parietal pitline; **Part**, prearticular; **pin.f**, pineal foramen; **Plv**, pelvis; **Pmx**, premaxilla; **Po**, postorbital; **Pop**, preoperculum; **Pp**, postparietal; **Pq**, palatoquadrate; **Psph**, parasphenoid; **Qj**, quadratojugal; **Quad**, quadrate; **R**, radius; **ra**, radial; **ra.a**, anal radial; **ra.c**, caudal radial; **Ri**, rib; **Sang**, surangular; **Sbm**, submandibular; **Sca**, scale; **Sco**, scapulocoracoid; **Spl**, splenial; **St**, supratemporal; **st.f**, subtemporal fossa; **So.p**, posterior supraorbital; **Sq**, squamosal; **Tab**, tabular; **Te.a/Ro.l**, anterior tectal+lateral rostral; **tib**, tibia; **U**, ulna; **ul**, ulnare; **Uh**, urohyal; **Vo**, vomer. **(l)** or **(r)** refers to left or right when displaced from natural side.

Results

Systematic Paleontology.—Sarcopterygii(Romer 1955); Rhipidistia (Cloutier and Ahlberg 1996, Cope 1887); Tetrapodomorpha (Ahlberg 1991); Eotetrapodiformes (Coates and Friedman 2010); *Tinirau clackae* gen. et sp. nov.

Etymology.—Tinirau (tea-knee-/r/âu) is a character of legend in Polynesian culture and traces to islands located at approximately the same latitude as Nevada during the Middle Devonian. According to the Rarotonga and Mangaia Islanders, Tinirau was a half-man, half-fish lord of the ocean creatures (Pomare and Cowan 1987). The specific name *clackae* honors the Cambridge palaeontologist and former advisor Jenny Clack, for her contributions to our understanding of the earliest digited sarcopterygians.

Holotype.—UCMP 118605, skull and postcranium (Figure 2.2A; 2.2B for reconstruction).

Material.—This description is based on six specimens (UCMP 117884, 118283, 118605, 123135, 190998, 190999) from a single locality. All specimens preserve complete or partial skull remains. Two specimens (UCMP 118605, 190999) preserve postcrania and appendicular elements in some degree of articulation. Specimens UCMP 118283 and 123135 were preserved in association with one another. Not all specimens of *Tinirau* preserve every available character state. Consistent features among all specimens that indicate they represent a single taxon, include: elongate glenoid fossa (UCMP 118065, 190999), reduced posterior process on the maxilla (UCMP 118065, 190999), fused parietals (UCMP 117884, 118238, 118065, 190999), fused anterior tectal and lateral rostral (UCMP 11784, 118283), a row of non-fang teeth on an elongate posterior coronoid (UCMP 118605, 123135), and similar proportions and dentition of the dermopalatines and entopterygoids (UCMP 190998, 190999).

Locality.—USA, Eureka Co., Nevada, Simpson Park Mountains north of the Denay Valley, UCMP locality V74084.

Horizon.—Lower *disparilis* conodont zone of the Red Hill I beds, immediately above the Denay Formation.

Age.—Middle Devonian, upper Givetian stage.

Diagnosis.—An eotetrapodiform sarcopterygian distinguished from known tristichopterids by (*i*) an elongate posterior jugal process (Figure 2.2), (*ii*) a dermal cheek plate with fused squamosal, preopercular, and quadratojugal elements (Figure 2.2), (*iii*) highly reduced postaxial fibular processes (Figure 2.2), (*iv*) deep tongue-and-groove embayments along the posteromedial margins of the intertemporals (Figure 2.3A, S2.1), (*v*) fused anterior tectals with lateral rostrals (Figures 2.3A, S2.2), (*vi*) medially straight anterior parietal margins in the unfused skull-table (Figure S2.2), (*vii*) a fused ethmoid skull-table in larger specimens—i.e., later ontogenetic stages (Figures 2.2, 2.3A S2.3), (*viii*) ectopterygoids that contribute to the subtemporal fossae (Figure 2.3B), and (*ix*) splenials that remain unsutured to the prearticular (Figure 2.3C). Moreover, it is differentiated from elpistostegalians by (*I*) facially positioned anterior nostrils (Figure 2.3A), (*II*) a (inferred) lateral component to the ventral orbital margins (Figure 2.2), (*III*) the presence of a median postrostral (Figure S2.2), (*IV*) the absence of frontal bones (Figures 2.2-3, S2.2-3), (*V*) the presence of a (anteriorly positioned) postspiracular (Figure S2.3), (*VI*) long posterior vomerine processes (Figure S2.1), (*VII*) an absence of jugal-quadratojugal contact (Figure 2.2, S2.3), (*VIII*) a small scapulocoracoid (Figure 2.3C), and (*IX*) round body scales (Figure 2.3C).

Remarks.—Tetrapodomorpha here defines total-group tetrapods, and I restrict the use of the term tetrapod to the crown-group. I use the monophyletic definition of Elpistostegalia (Daeschler et al. 2006, Downs et al. 2008) to refer to the clade consisting of *Panderichthys* and crownward taxa. Moreover, following from the phylogenetic result presented below, I use Canowindridae as a stem-based name to refer to the clade constituting *Marsdenichthys*, *Canowindra*, *Koharalepis*, and *Beelarongia*, use the stem-based Megalichthyiformes (Coates and Friedman 2010) to reference the formerly paraphyletic (here recovered monophyletic, see supplementary information) 'osteolepidids', and apply the stem-based Tristichopteridae to define any taxon more closely related to *Tristichopterus* than to *Elpistostege*. In turn, I use 'osteolepiform' to encapsulate the grade of tetrapodomorph that includes canowindrids + megalichthyiforms + tristichopterids, and Eotetrapodiformes (Coates and Friedman 2010) as a node-based definition to refer to tristichopterids and elpistostegalians. Because of the curious morphology and phylogenetic position of the newly described taxon, I avoid calling this animal an elpistostegalian, and let future studies confirm or refute the phylogenetic hypothesis presented here. In addition, following from the revised phylogenetic placement of *Platycephalichthys bischoffi* (Coates and Friedman 2010), I refer to this taxon by its name only, as opposed to calling it a tristichopterid or an elpistostegalian.

Comparative Description.—The snout of *Tinirau* has one pair of facially positioned external nostrils as in all tetrapodomorphs except *Kenichthys* and elpistostegalians. However, in *Tinirau*, the nares penetrate a single, fused element consisting of the anterior tectal and lateral rostral (Figure 2.3A). Similar to 'osteolepiforms', *Platycephalichthys*, and elpistostegalians less crownward than *Ventastega*, the premaxilla forms a broad part of the choanal margin (Figure S2.1). Moreover, and differing from *Ventastega* and *Acanthostega*, a single median postrostral and several nasal bones create a solid snout lacking a dorsal fontanelle (Figures 2.2A, 2.3A, S2.2).

The anterior skull roof of *Tinirau* is plesiomorphic among tetrapodomorphs: about 25% of the skull extends anterior to the mid-orbital margins (Figures 2.2A, 2.3A). Such proportions are more similar to those of rhizodonts and canowindrids than to those of other eotetrapodiforms. The anterior-most paired roofing bones are the parietals, which are pierced by a pineal foramen that lies posterior to the orbits in larger specimens, or later ontogenetic stages (Figures 2.3A, S2.2). This condition is similar to early diverging 'osteolepiforms' such as *Koharalepis*, *Canowindra*, and *Gyroptychius*, and later-diverging tristichopterids more phylogenetically distal than *Eusthenopteron*. A functional dermal intracranial joint is unknown considering the tongue-and-groove articulations of the intertemporal and supratemporal bones that span this region. However, because the skull tends to be preserved in two parts, with the symplesiomorphic condition at least across the parietal/postparietal region, such a 'joint' is scored as present in *Tinirau* (Figures 2.2A, 2.3A, S2.3). The condition in *Tinirau* is thus either autapomorphic (considering that dermal suturing in *Panderichthys* involves only the parietals and postparietals) or 'intermediate' because of the simultaneous suturing and simple abutment found across its dermal intracranial division. Interestingly, *Platycephalihthys* also has posteriorly recessed intertemporals suggesting a similar intracranial configuration (Vorobyeva 1977).

The postparietal shield is not extremely wide posteriorly, as in canowindrids, nor do the parietals narrow to a point caudally, as in rhizodonts. Instead, the tabulars extend to the posterior margin of a postparietal shield that is approximately as wide as the ethmoid, a condition akin to that

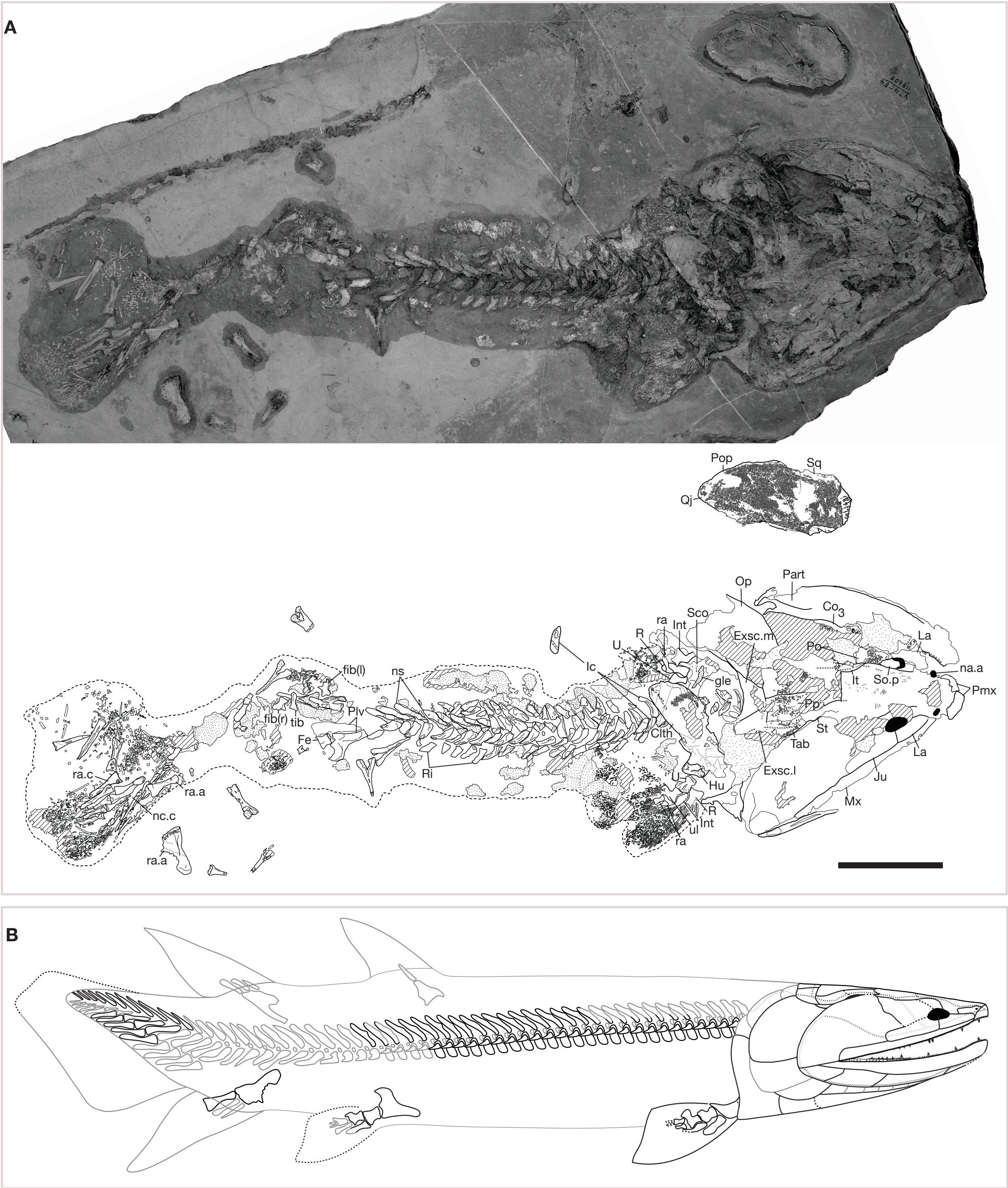

Figure 2.2. Holotype specimen UCMP 118605, interpretive drawing, and complete restoration of *Tinirau clackae*. (A) UCMP 118605, holotype, in dorsal, lateral and ventral view. See main text for details. Right is anterior. Scale bar equals 10 cm; (B) complete restoration; preserved elements outlined in black, inferred margins outlined in dashed black, hypothesized elements outlined in gray. See methods section for anatomical abbreviations. Note the reduced postaxial fibular processes on the fibulae (fib).

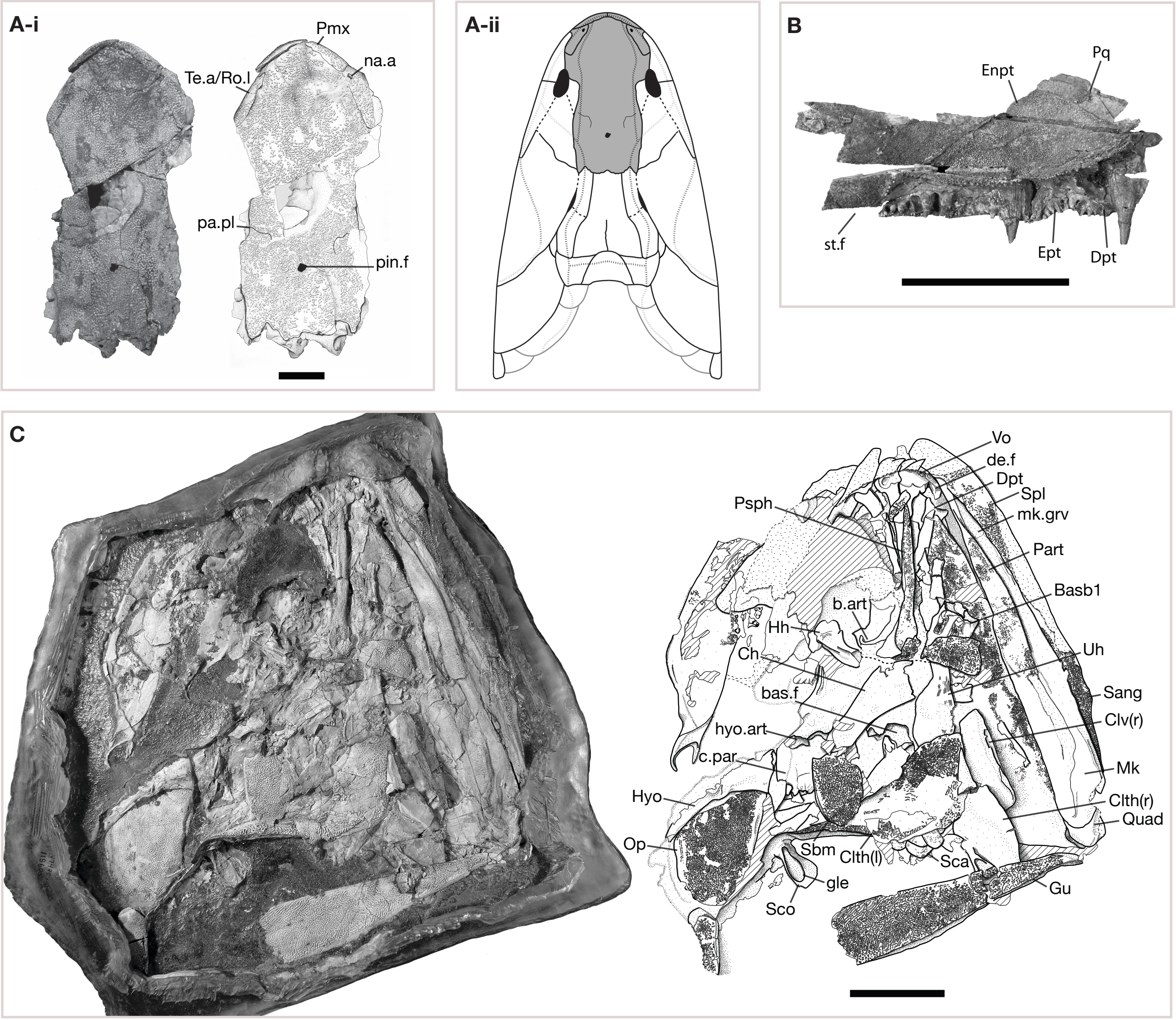

Figure 2.3. Ethmoid skull region and palate of *Tinirau clackae*. (A-i) UCMP 117884, ethmoid skull. Anterior is toward the top of the page. Scale bar equals 2 cm; (A-ii) dorsal skull reconstruction with infilled gray ethmoid region following from (A-i); (B) Left palatal fragment of UCMP 190998. Right is anterior. Scale bar equals 5 cm; (C) Skull, partial shoulder, and interpretive drawing of UCMP 190999. Uniform stipple covering distal jaw elements indicate unexposed portions of the specimen still covered by bioplastic; similarly, the dotted line posterior to the parasphenoid (Psph) notes the division between ethmoid and oticoccipital regions recovered from X-ray imaging. Anterior is toward the top of the page. Scale bar equals 5 cm. See methods section for anatomical abbreviations. Note the elongate glenoid fossa (gle) on the left scapulocoracoid (Sco).

seen in tristichopterids, *Panderichthys*, *Tiktaalik*, and *Ventastega* (Figure S2.3). Lateral to the tabular resides a postspiracular (=extratemporal) situated in the plesiomorphic anterior position, similar to the condition in Devonian tetrapodomorphs except tristichopterids phylogenetically distal of *Spodichthys* (Figure S2.3). The postspiracular is lost in known elpistostegalians.

Surrounding the orbit, the anterior and posterior supraorbitals (=prefrontals and postfrontals) are of similar size and contact one another anterior to the mid-orbital margin. The posterior supraortbitals do not extend anterior to the orbits, similar to the condition in other Devonian tetrapodomorphs except a few late-diverging tristichopterids (Figures 2.2A, S2.2). The lacrimal and jugal meet approximately at the mid-ventral orbital margin where, unlike in *Mandageria* and *Eusthenodon*, the postfrontal and lacrimal do not make contact (Figure 2.2A). Moreover, unlike in elpistostegalians, the squamosal (here, bound up in a fused cheek plate) precludes abutting of the jugal and quadratojugal (Figures 2.2, S2.3). It is not known *directly* if the postorbital contributes to the orbit of *Tinirau*, but based on the topology of this element and neighboring bones in UCMP 118605, it is inferred to make a minor contribution (Figure 2.2A).

The jaws of *Tinirau* are characteristically eotetrapodiform in form, although contain a unique combination of plesiomorphic and apomorphic traits. The premaxillary teeth are all of similar size as in early diverging tristichopterids and elpistostegalians (Figure S2.1). However, the maxilla lacks a posterodorsal process, a state shared with *Platycephalichthys* and elpistostegalians such as *Panderichthys* on crownward, but also with derived tristichopterids such as *Cabonnichthys* and *Mandageria* (Figures 2.2A, S2.3). Dentary fangs are present, similar to *Platycephalichthys* and elpistostegalians, though this character is also known in rhizodonts, megalichthyids, and derived tristichopterids (Figure 2.3C). The posterior coronoid is much longer than the anterior two coronoids, yet only carries one fang pair followed by a row or 5+ medium-sized teeth (Figure S2.4). This state combination is not present in any tristichopterid, and only shared with *Platycephalichthys* and early elpistostegalians such as *Panderichthys*. In other words, tristichopterids with long posterior coronoids also bear two posterior fang pairs, and those tristichopterids with one fang pair do not have very long posterior coronoids. A distinct Meckelian groove is visible in the lower jaw of UCMP 190999, and similar to the condition in non-elpistostegalian tetrapodomorphs, it bears an ossified posterior Meckelian region separating the prearticular/angular contact (Figure 2.3C). Splenials, postsplenials, surangulars, and angulars are similar to those of tristichopterid proportions (Figure S2.4).

The operculogular elements in UCMP 190999 are similar in shape and proportion to those of other Devonian 'osteolepiforms', and therefore are not diagnostic of a physical neck (i.e., a discrete, disconnecting region) between the shoulders and head (Figures 2.2A, S2.3). Similar to *Platycephalichthys*, a large preoperculum is sutured to the squamosal in a cheek plate and is also visible in visceral view in UCMP 118605 and 190999 (Figures 2.2A, S2.3). The spiracular notch is not well-preserved, but judging from the narrow space between the squamosal and postparietal shield, it is inferred to be small and thus more like the condition in most 'osteolepiforms' rather than to that of elpistostegalians (Figures 2.2A, 2.3A-ii). The presence and size of a median gular remain unknown.

The palate of *Tinirau* is broadly similar to the tristichopterid condition, although it differs in a few interesting ways. As in tristichopterids, the posterior vomerine processes are long and underlap the parasphenoid substantially, although the latter condition is also present in *Panderichthys* and *Tiktaalik* (Figures 2.3C, S2.1). However, unlike in tristichopterids, the ectopterygoids contribute to the subtemporal fossae (Figure 2.3B). Among Devonian tetrapodomorphs, only the megalichthyiforms *Gogonasus* and *Medoevia*, and taxa crownward of tristichopterids, are known to have ectopterygoids that make this contribution. Moreover, and unlike all tristichopterids except *Spodichthys*, *Tinirau* retains the ancestral tetrapodomorph condition of bearing one ectopterygoid fang pair (Figure 2.3B). Such a condition is also retained in *Panderichthys* and *Tiktaalik*. As in tristichopterids and Devonian elpistostegalians, the anterior end of a densely denticulated entopterygoid resides considerably anterior to the processus ascendens of the palatoquadrate. This process is not preserved directly in *Tinirau*, but judging from the relative proportions of the palatoquadrate complex and of the positions of its associated articulations, this inference can be drawn with comfortable precision (Figures 2.3B-C, S2.1).

The neurocranium is plesiomorphic in many ways, although it shares some similarities with those of tristichopterids. A fully ossified ethmoid extends below a narrow tectum orbitale and articulates with its posterior otic-occipital counterpart via an endoskeletal intracranial joint. In turn, a basicranial fanestra spans this division (Figures 2.3C, S2.1). These states are present in all Devonian tetrapodomorphs except for *Kenichthys* and taxa crownward of *Tiktaalik*. By contrast, *Tinirau* shares with tristichopterids a relatively anterior ventral hyomandibular facet (Figure 2.3C). In other words, this state is generally considered to diagnose tristichopterids, but is here reconstructed to be either convergent among these taxa, or to ancestrally diagnose eotetrapodiforms only primitively.

The cephalic branches of the sensory canal system are typical of most other Devonian tetrapdomorphs, although *Tinirau* retains a few traits—such as the postorbital junction of supra- and infraorbital canals, a line of continuous pores that comprise the mandibular canal, and a surangular pitline—that are otherwise lost in taxa crownward of *Tiktaalik* and *Acanthostega* (Figures 2.2A, S2.4). As in tristichopterids, *Platycephalichthys*, *Panderichthys*, and *Tiktaalik*, the sensory canals course through a tuberculate dermal skeleton that lacks the starburst ornamentation characteristic of the first digit-bearing elpistostegalians (Figures 2.2A-i, 2.3C, S2.2-4). Such elements also lack the thick 'shine' characteristic of cosmine-covered sarcopterygians such as megalichthyiforms.

The shoulder is typically tetrapodomorph in form, but it bears a few differences from those of key taxa. The anterior median extrascapular margin is "long" and therefore unlike those of canowindrids and *Mandageria* (Figures 2.2A, 2.3A-ii, S2.3). A postbranchial lamina is present on the cleithrum (Figure 2.2A), although posttemporals, supracleithra, anocleithra, and an interclavicle are not preserved. Unlike in elpistostegalians such as *Panderichthys* and *Tiktaalik*, a small scapulocorocoid is elevated from the ventral plane formed by the clavicles. However, the glenoid is relatively elongate and bears a medial 'accessory' region that is less reflexed than the condition seen in megalichthyiforms such as *Medoevia* and tristichopterids such as *Eusthenopteron* (Figures 2.2A, 2.3C). Although the humerus is crushed, judging from the shape of the glenoids, it appears that the convex caput humeri retains less of the oblate shape than is typical of 'osteolepiforms'. Such an elongate condition is more characteristic of elpistostegalians.

Paired appendages are only preserved in UCMP 118605 (Figure 2.2A). The left humerus is crushed and situated below the cleithrum, but it articulates with the rest of a well-preserved pectoral limb. The right humerus is missing, but the elongate glenoid and distal pectoral elements remain. The pectoral limb is symplesiomorphic, and generally similar to the 'osteolepiform' condition. As in 'osteolepiforms' and elpistostegalians such as *Panderichthys* and *Tiktaalik*, the ulna is about half as long as the radius and articulates with an ulnare and intermedium. As in 'osteolepiforms', the ulnare retains a postaxial process and only articulates with two additional distal radials. Proximal lepidotrichia are about three times longer than more distal ones (Figure 2.2A).

Caudally, the pelvis articulates with a femur that is preserved in association with the acetabulum, despite the disassociation of distal elements (Figure 2.2A). As in *Eusthenopteron*, the right and left disarticulated fibulae bear preaxial radial facets positioned about one half-step proximal to their postaxial counterparts. However, and unlike in *Gooloogongia* and *Eusthenopteron*, the postaxial fibular process is highly reduced and not simply the 'fibula-equivalent' of the condition seen in the ulnare. Interestingly, the pelvic limb of *Panderichthys* also displays a similar 'lip' overhanging the postaxial edge of the fibulare (Boisvert 2005)(figure 1, pg. 1146).

The vertebral elements are preserved in near complete articulation, and are known only from UCMP 118605 (Figure 2.2A). Paired intercentra are visible entirely in part/counterpart, and stout non-imbricate ribs radiate laterally, immediately posterior to the cleithrum. The axial skeleton proceeds through a left twist at ~90° around mid-body, and posterior to the pelvis folds over itself so that the distal tip of the heterocercal caudal fin skeleton comes to face the more anterior (dorsal) neural spines. Paired pleurocentra are not preserved and are presumed to have been cartilaginous. There is no evidence for dorsal fin radials, although dorsal fins are hypothesized to have been present. By contrast, a dissociated anal fin basal and radial are preserved immediately dorsal to the caudal fin. The notochordal canal is visible and arches dorsally through the neural and haemal arches of the caudal fin skeleton (Figure 2.2A).

Discussion

Phylogeny, Stratigraphy, and Evolutionary Patterns.—A phylogenetic analysis using PAUP (Swofford 2002) recovered a single most parsimonious tree. A Bayesian analysis (Huelsenbeck 2001, Ronquist and Huelsenbeck 2003) of the same data provided an additional metric. There are no major polytomies among the 'osteolepiform' grade taxa. Instead, the major clades, Rhizodontidae, Canowindridae, Megalichthyiformes, and Tristichopteridae form successive sister taxa to more crownward groups. *Tinirau* emerges as the sister to *Platycephalichthys* and elpistostegalians, one step crownward of tristichopterids (Figure 2.4).

The synapomorphies of *Tinirau* and crownward taxa include a pair of dentary fangs (Figure 2.3C), a posterior coronoid that is much longer than the anterior coronoids (Figures 2.2, S2.4), an organized tooth row on the posterior coronoid (Figures 2.2, S2.4), a weak posterodorsal maxillary process (Figures 2.2, S2.3), a pineal foramen that lies posterior to the orbits (Figures 2.2-3A), an elongate glenoid fossa (height:width ratio 40-50%) (Figures 2.2-3C), and a reduced postaxial fibular process (Figure 2.2). Unsurprisingly, considering the widespread homoplasy among rhipidistians, nearly all of these characters evolved independently in at least one other group of Devonian tetrapodomorph, especially derived tristichopterids. Interestingly, previous studies that included *Platycephalichthys* recovered a similar pattern: synapomorphies that link *Platycephalichthys* and elpistostegalians also evolved in derived tristichopterids (Coates and Friedman 2010). However, despite such convergences, the phylogenetic result (Figure 2.4) is supported because of *Tinirau*'s unique combination of aforementioned apomorphies with an interesting array of symplesiomorphies—e.g., a

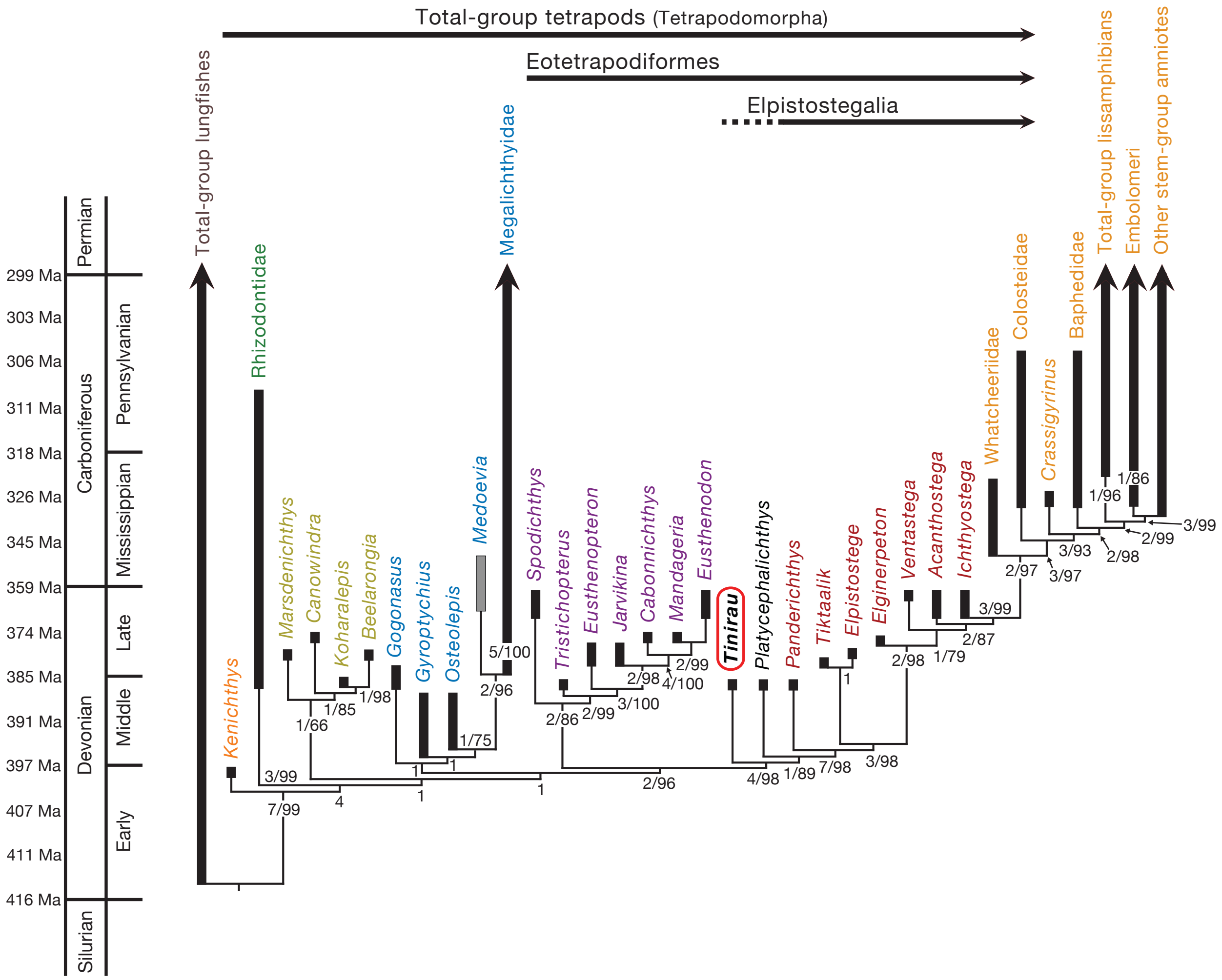

Figure 2.4. Interrelationships among Devonian and select Carboniferous tetrapodomorphs including new data from *Tinirau clackae*. Analysis includes 46 taxa and 203 characters. Tree length=459, consistency index=0.5468, retention index=0.8423; consistency index excluding the four autapomorphic (uninformative) characters=0.5428, retention index=0.8423. Numbers corresponding to respective nodes represent: Bremer decay value / Bayesian posterior probability. Ghost ranges are calibrated after the early Middle Devonian (Eifelian) Zachełmie footprints (Niedźwiedzki et al. 2010) and "scenario 1" from Friedman and Brazeau (2011). Tetrapodomorphs include all taxa that are not total-group lungfishes. Rhizodonts are in green, canowindrids are in yellow, megalichthyiforms are in blue, tristichopterids are in purple, Devonian elpistostegalians are in red, and Carboniferous elpistostegalians are in orange. The character list and data matrix are available as supplementary information.

single fang pair on the posterior coronoid (Figures 2.2, S2.4), an anteriorly positioned postspiracular (Figure S2.3), a single ectopterygoid fang pair (Figure 2.2B), about 25% of the dermatocranium anterior to the orbits (comparison of specimens in Figures 2.2-3), and a heterocercal caudal fin skeleton (Figure 2.2) (see character optimizations in the supporting information). Moreover, although the ectopterygoids of *Tinirau* contribute to the subtemporal fossae, the distribution of this trait in canowindrids and megalichthyiforms is too poorly known to be reconstructed as either symplesiomorphic among elpistostegalians, or as synapomorphic of *Tinirau* plus crownward taxa. Among Devonian tetrapodomorphs, only the megalichthyiforms *Gogonasus* and *Medoevia*, and eotetrapodiforms crownward of tristichopterids, have ectopterygoids that make this contribution.

This phylogenetic hypothesis implies that, (1) tristichopterid synapomorphies (see supporting information) have evolved in parallel during the early history of eotetrapodiforms; and (2) the 18+ elpistostegalian synapomorphies are cut in half (see supporting information) as taxa such as *Tinirau* and *Platycephalichthys* fill the graduated history of the tetrapod stem. This is predicted by current evidence, especially with the recent discovery of marine, digit-bearing trackways that predate the earliest elpistostegalian body fossils by 10 Ma (Niedźwiedzki et al. 2010). Though the trackway evidence has suggested a stratophylogenetic reassessment of early eotetrapodiforms, the discovery of *Tinirau* conforms with the timing of the body fossil record and fills an phylogenetic gap missing from previous discoveries. Yet, because 'genus'-level preservation rates for Devonian tetrapodomorphs are an order of magnitude lower than 'species'-level rates for groups considered to have dense records (Friedman and Brazeau 2011), the stratigraphic range of *Tinirau* is not surprising and conforms to expectations given the current state of body fossil data. Thus, when combined with the age of the trackways data, the late Middle Devonian (Givetian) age of *Tinirau*, its phylogenetic position as stem to the first digited forms, and its many symplesiomorphies speak to the length of this history and suggest a rich early tetrapodomorph record still to be discovered. This was unanticipated based upon morphology alone before the discovery of the Zachełmie trackways, and in this respect, *Tinirau*'s trait combinations and phylogenetic placement further credit the length of current ghost ranges. Questions about palaeoenvironment are more complicated, but *Tinirau*'s marine preservation is consistent with the marine influenced environments of the Zachełmie trackways and other closely related taxa (Schultze and Arsenault 1985, Upeniece 2001, Vorobyeva and Schultze 1991), although likely not with others (Bendix-Almgreen et al. 1990, Daeschler et al. 2006).

Evolutionary Morphology.—Overall, the skeleton of *Tinirau* retains many 'fish-like' traits, but they are combined with a suite of elpistostegalian apomorphies. Because the cooptability of many of these characters remains obscure, here I elaborate on two traits that emerge as relevant to current discussions in tetrapodomorph evolution: the origins of the shoulder and pelvic limbs in the first digit-bearing elpistostegalians.

As in tristichopterids such as *Eusthenopteron* and elpistostegalians such as *Panderichthys*, the shoulder of *Tinirau* retains the full osteichthyan complement of dermal and endochondral components. However, despite these general similarities, its glenoid is anteroposteriorly elongate and in this respect more similar to the condition found in *Panderichthys*, *Tiktaalik* and *Acanthostega* (Figure 2.5A). This pattern correlates with parallel changes observed in the flattening of the caput humeri, and has been

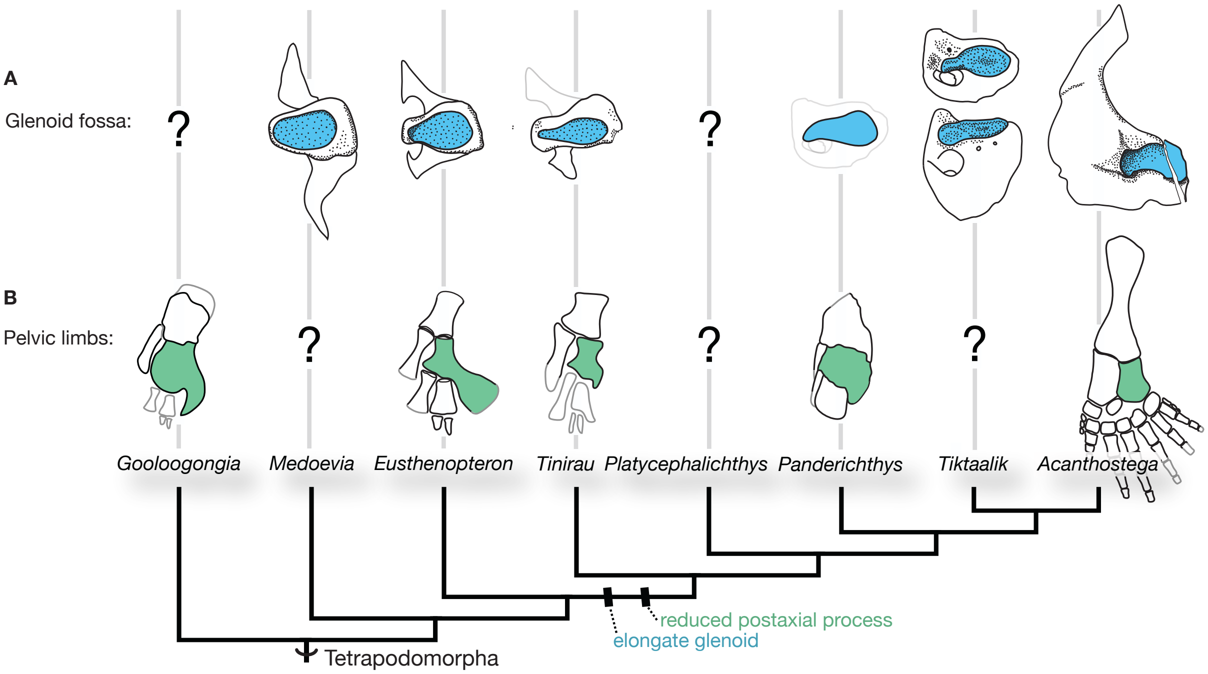

Figure 2.5. Glenoid fossae and pelvic limbs of select stem-tetrapods. Glenoids are illustrated in posterior view and highlighted in blue, fibulae are highlighted in green. The glenoid of *Tiktaalik* is depicted from two different perspectives, posterior view (above) and posteroventral view (below). The glenoid of *Panderichthys* was based on the shape of its caput humerus. See text for additional details. The in-plane glenoid measurement (height at maximum extent divided by maximum length) diagnoses an elongate glenoid fossa: *Medoevia* = 0.60; *Eusthenopteron* = 0.60; *Tinirau* = 0.42; *Panderichthys* = 0.48; *Tiktaalik* = 0.44; *Acanthostega* = 0.45.

noted as a feature that evolved early in the origin of digit-bearing limbs (Clack 2009, Shubin et al. 2004). Although the glenoids in *Medoevia*, *Eusthenopteron*, *Tinirau*, and *Panderichthys* have a strong posterior component, fossae in the former two taxa retain more of the oblate shape than the condition present in the latter forms. This reinforces the hypothesis that mosaic changes in the pectoral limb began proximally before the distal portions acquired a more characteristic tetrapod-like morphology (Clack 2009).

The femur, tibia, and fibula represent the only pelvic elements preserved in *Tinirau*, but they share an interesting similarity with *Panderichthys*, the only non-digit bearing elpistostegalian from which reasonable pelvic material is known (Boisvert 2005). One major difference between the fibulae of a rhizodont (e.g., *Gooloogongia*) or a tristichopterid (e.g., *Eusthenopteron*) and an elpistostegalian (e.g., *Panderichthys*) is that the postaxial process in *Panderichthys* is reduced to a mere lip or overhang bordering the posterior margin of the distal fibulare (Andrews and Westoll 1970, Boisvert 2005, Johanson and Ahlberg 2001) (Figure 2.4B). In this respect, the lack of a prominent postaxial process in the fibula of *Tinirau* is more similar to the condition observed in crownward taxa. This pattern underscores previous phylogenetic reconstructions of the appendicular skeleton in which conventional crown group limb characteristics first originate in the pelvic fins (Coates et al. 2002). In other words, *Tinirau* appears to answer questions about the origin of pelvic limbs that taxa like *Tiktaalik* unfortunately do not preserve.

The new phylogeny also helps to displace *Eusthenopteron* as our iconic surrogate piscine 'ancestor'. *Eusthenopteron* shares with other tristichopterids a sequence of traits that nest it well within tristichopterids, and not immediately along the tetrapod stem (Figure 2.6). Instead, this result builds upon the work of Coates and Friedman (2010), whereby *Tinirau* and *Platycephalichthys* fill this position and provide an anatomical record on the transition to land. These taxa spread primitive tetrapodomorph traits along the early history of elpistostegalians, suggest a deeper history of the tetrapod stem, and fill a gap between tristichopterids and the first digited sarcopterygians in interesting and unexpected ways.

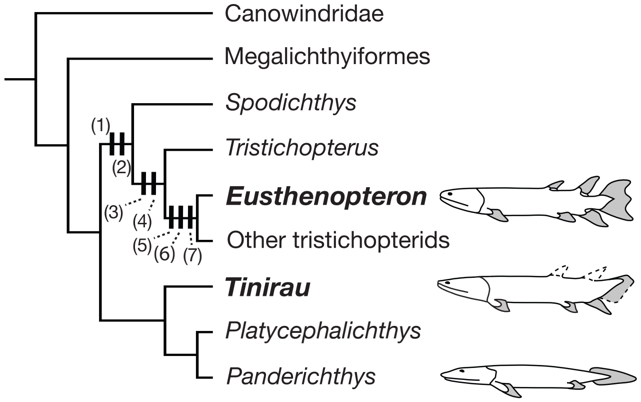

Figure 2.6. The nested phylogenetic position of *Eusthenopteron* within tristichopterids (*Spodichthys* + closest relatives) relative to *Tinirau*, *Platycephalichthys*, *Panderichthys*, and more crownward taxa. Character states supporting this topology: (1) a parasymphyseal plate not sutured to the anterior coronoid; (2) posterior coronoids longer than more anterior coronoids; (3) 33-40% of the dermatocranium anterior to the orbits; (4) a posteriorly displaced postspiracular; (5) posterior coronoids one third longer than the anterior coronoids; (6) two ectopterygoid fang pairs; and (7) a diphycercal caudal fin.

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SUPPLEMENTARY INFORMATION FOR:

A MARINE STEM-TETRAPOD FROM THE DEVONIAN OF WESTERN NORTH AMERICA

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Supplementary Information

Supporting Text

Figures S2.1, S2.2, S2.3, S2.4

References

Supporting Text

Part A.

Taxa and characters used in the phylogenetic analysis.—The following 203 morphological characters were used to assess the phylogenetic position of *Tinirau* relative to other early tetrapodomorphs. Not all specimens of *Tinirau* preserve every available character state. Consistent features among all specimens scored in this analysis that indicate they represent a single taxon, include: elongate glenoid fossa (UCMP 118065, 190999), reduced posterior process on the maxilla (UCMP 118065, 190999), fused parietals (UCMP 117884, 118238, 118065, 190999), fused anterior tectal and lateral rostral (UCMP 11784, 118283), a row of non-fang teeth on an elongate posterior coronoid (UCMP 118605, 123135), and similar proportions and dentition of the dermopalatines and entopterygoids (UCMP 190998, 190999).

Primary character sources (Ahlberg et al. 2008, Ahlberg and Johanson 1998, Ahlberg et al. 2000, Coates and Friedman 2010, Daeschler et al. 2006, Zhu and Ahlberg 2004) are indicated parenthetically following each character description. Numbers following the citations refer to the character number in the original source. Characters modified from their original source are noted where applicable. Very few characters are shared between this analysis and Coates and Friedman (2010); this was maintained intentionally to demonstrate how nearly independent data sets converge on a similar result. This analysis also recovered a monophyletic Megalichthyiformes, with 'osteolepidid'-grade tetrapodomorphs not simply emerging as lone lineages aligned as successive plesions to crownward forms. *Glyptopomus* was included in a separate analysis to test its influence on the phylogenetic result. Although its inclusion disrupted a monophyletic Canowindridae and pulled *Gyroptychius* and *Gogonasus* from Megalichthyiformes, it had no bearing on the phylogenetic position of any eotetrapodiform.

Characters were polarized by comparison to outgroup taxa such as *Porolepis*, *Glyptolepis*, *Powichthys*, *Youngolepis*, *Diabolepis*, and *Dipterus*. These taxa were selected because they represent a range of total-group lungfish that are known from reasonable material, are well studied, and generally accepted as sister to total-group tetrapods.

Characters were coded based on a combination of published descriptions, specimen illustrations, and firsthand examination of fossil material. Care was taken to avoid simply recycling codings in the published literature. Specimens from the following museums were examined, and are noted following each taxon below: Australian Museum, Sydney (AMF), Australian National University (ANU), Geologisk Museum, Copenhagen, Denmark (MGUH), Latvian Museum of Natural History (LDM), Muséum national d'Histoire naturelle, Paris (MNHN), Museum Victoria, Melbourne, Australia (NMV), The Natural History Museum, London (MNH), Palaeontological Institute of the Russian Academy of Sciences, Moscow (PIN), National Museums of Scotland (NMS), Nunavut Fossil Vertebrate Collection (NUFV), Swedish Museum of Natural History, Stockholm (NR), University of California Museum of Paleontology (UCMP), University Museum of Zoology Cambridge (UMZC).

Acanthostega (Ahlberg and Clack 1998, Clack 1988, 1989, 1994, 1998a, 2002a, Coates 1996) (MGUH f.n. 157, 255, 1227, 1258; UMZC T1291, T1300)
Balanerpeton (Milner and Sequeira 1993) (UMZC T1312, T1313)
Baphetes (Beaumont 1977, Milner and Lindsay 1998, Owen 1854, Watson 1929)
Barameda (Garvey 2005, Long 1989, Long and Ahlberg 1999) (NMV P10277, P160880, P160885, P212715)
Beelarongia (Long 1987) (NMV P160875, P160972)

Cabonnichthys (Ahlberg and Johanson 1997) (AMF96856, F96858a, F96863, F96902, F98037, F98038)
Canowindra (Long 1985a, Thomson 1973) (BMNH P.34420)
Cladarosymblema (Fox et al. 1995)
Crassigyrinus (Clack 1998b, Panchen and Smithson 1990) (BMNH R10000; UMZC T1250)
Dendrerpeton (Godfrey et al. 1987, Holmes et al. 1998, Owen 1853, Robinson et al. 2005) (UCMP 102367)
Diabolepis (Chang 1995, Chang and Yu 1984, Smith and Chang 1990)
Dipterus (Ahlberg and Trewin 1995, White 1965) (BMNH P.17410, P.33165, P.34544, P.53507; MNHN GBP71, P72; NR P.3108, P.4827; UCMP 43714, 43727, 43728, 43729, 43730, 93066, 93067, 93068, 93069, 93070, 93071, 93072, 115246; UMZC GN1043)
Ectosteorhachis (Thomson 1964)
Elginerpeton (Ahlberg 1991b, 1995, 1998)
Elpistostege (Schultze and Arsenault 1985) (BMNH P.60526 a,b)
Eoherepton (Andrews et al. 1977, Smithson 1985)
Eusthenodon (Jarvik 1952) (NR P.1475, P.1693)
Eusthenopteron (Andrews and Westoll 1970a, Jarvik 1980) (BMNH P.60386, P.60388, P.60397; NR P.222, P. 223, P249, P.287, P.290, P.330, P322 a,b, P.326b, P.382, P.2197, a,b, P2609, P.4611, P.6383; UMZC GN.790, GN.791, GN.797, GN.799)
Glyptolepis (Ahlberg 1989, Ahlberg 1991a, Jarvik 1972) (NR P.180, P.2503 a,b, P.8635)
Glyptopomus (Jarvik 1950a)
Gogonasus (Long et al. 1997, Long et al. 2006) (ANU 21885, 49259; NMV P221807)
Gooloogongia (Johanson and Ahlberg 2001)
Greererepton (Bolt and Lombard 2001, Godfrey 1989, Romer 1969, Smithson 1982) (UMZC T1220)
Gyroptychius (Jarvik 1950b, c, 1985) (MNHN GBP44, P63, P107, P138, P209, P264, P265, P307; NR P.1679, P. 1698, P.4116, P.4220; UMZC GN.240, GN.939)
Ichthyostega (Ahlberg et al. 2005, Jarvik 1996) (MGUH 6055, 6064, 6081, MGUH f.n. 200, 300, 301)
Jarvikina (Vorobyeva 1977)
Kenichthys (Chang and Zhu 1993, Zhu and Ahlberg 2004)
Koharalepis (Young et al. 1992)
Mandageria (Johanson and Ahlberg 1997, Johanson et al. 2003) (AMF96508, F96855a, F96857a,b,c, F98592c, F98593 a,b, F98594)
Marsdenichthys (Holland et al. 2010, Long 1985b) (NMV P179619, P186572)
Medoevia (Lebedev 1995)
Megalichthys (Andrews and Westoll 1970b, Jarvik 1948, 1967, Romer 1937, Thomson 1964, Watson 1926) (NR P.6157; UMCZ GN.638)
Osteolepis (Andrews and Westoll 1970b, Jarvik 1948, Jarvik 1980, Thomson 1965) (MNHN GBP67, P186, P188, P195, P269 a,b, P277, P280, P284; NR P.1675, P.4110, P.4139, P.11116; UCMP 43711, 43717, 43718, 43719, 43720, 43721, 43733, 58496, 58498, 58499)
Panderichthys (Ahlberg and Clack 1998, Ahlberg et al. 1996, Boisvert 2005, Boisvert et al. 2008, Brazeau and Ahlberg 2006, Vorobyeva 1995, Vorobyeva 2000, Vorobyeva and Schultze 1991) (NR P.6427; PIN 3547 [high resolution photograph]; LDM 60/123 [high resolution photograph])
Pederpes (Clack 2002b, Clack and Finney 2005)

Platycephalichthys (Coates and Friedman 2010, Vorobyeva 1962, 1977) (PIN 54/155, 54/156, 54/158, 54/159, 54/160, 54/160a, 54/161, 54/162, 54/163, 54/164, 54/165, 54/166, 54/183, 54/191, 54/192, 54/193, 54/194, 54/195 [high resolution photographs])
Porolepis (Clément 2004, Jarvik 1972) (MNHN SVD2001, 2034, 2158; NR A28633, A30483)
Powichthys (Clément and Janvier 2004, Jessen 1975, 1980)
Proterogyrinus (Holmes 1984, Romer 1970)
Silvanerpeton (Ruta and Clack 2006) (UMZC T1317, T1351)
Spodichthys (Jarvik 1985, Snitting 2008b) (MGUH VP 6705 (P.1659), VP 6708 (P.1662), VP 6714 (P.1668), VP 6715 (P.1669))
Tiktaalik (Daeschler et al. 2006, Downs et al. 2008, Shubin et al. 2006) (NUFV 108, 110)
Tristichopterus (Egerton 1861, Snitting 2008a) (BMNH 66653, 66660, 66661, 66664, 66666, 66670; NMS.G. 1875.29.220, G.1875.29.221, G.1875.29.224, G.1875.29.225, G.1995.4.28; NR P.4196)
Ventastega (Ahlberg et al. 1994, Ahlberg et al. 2008)
Whatcheeria (Lombard and Bolt 1995, Lombard and Bolt 2006)
Youngolepis (Chang 1982, 1991, 2004, Chang and Smith 1992)

Characters.

1. Ethmoid region
(Ahlberg et al. (2008): Character 25)

0 fully ossified
1 partly or wholly unossified

2. Rostral tubuli
(Coates and Friedman (2010): Character 1)

0 absent
1 present

3. Profundus foramen in postnasal wall
(Zhu and Ahlberg (2004): Character 81)

0 small
1 large

4. Fenestra ventrolateralis
(Coates and Friedman (2010): Character 5)

0 ventral to ethmoid articulation, in posterior view
1 extends dorsal to ethmoid articulation, in posterior view (post nasal wall unossified)

5. Pituitary vein exit

(Coates and Friedman (2010): Character 11)

0 anterior to basipterygoid process
1 dorsal to basipterygoid process

6. Extent of crista parotica

(Zhu and Ahlberg (2004): Character 33)

0 does not reach posterior margin of tabular
1 reaches posterior margin of tabular

7. Endoskeletal intracranial joint

(Coates and Friedman (2010): Character 14)

0 absent
1 present

8. Basicranial fenestra

(Zhu and Ahlberg (2004): Character 76)

0 absent
1 present

9. Processus descendens of sphenoid

(Zhu and Ahlberg (2004): Character 78)

0 absent
1 present

10. Posterior carotid opening in parasphenoid

(Zhu and Ahlberg (2004): Character 80)

0 large
1 small
2 absent

11. Tectum orbitale

(Zhu and Ahlberg (2004): Character 83)

0 narrow
1 extensive

12. Basipterygoid process

(Ahlberg et al. (2008): Character 24)

0 not strongly projecting with concave anterior face
1 strongly projecting with flat anterior face

13. Hypophysial region

(Ahlberg et al. (2008): Character 26)

0 solid side wall pierced by small foramina for pituitary vein and other vessels
1 single large foramen

14. Otic capsule lateral commissure bearing hyomandibular facets

(Ahlberg et al. (2008): Character 27)

0 present
1 absent

15. Relative positions of the hyomandibular facets

(Coates and Friedman (2010): Character 20)

0 dorsal directly above ventral
1 ventral anterior to dorsal
2 dorsal anterior to ventral

16. Parasymphysial plate

(Zhu and Ahlberg (2004): Character 1). *Platycephalichthys* scored after Snitting (2008b).

0 long, sutured to coronoid, denticulated or with tooth row
1 short, not sutured to coronid, denticulated
2 carrying tooth whorl

17. Parasymphysial plate dentition

(Modified from Ahlberg et al. (2008): Character 89)

0 Carrying a tooth whorl
1 shagreen or irregular tooth field
2 organised dentition aligned parallel to jaw margin

18. Parasymphsial fangs

(Modified from Ahlberg et al. (2008): Character 90)

0 absent
1 present

19. Parasymphysial plate: detachable whorl
(Zhu and Ahlberg (2004): Character 7)

0 detachable whorl
1 sutured plate with denticles or teeth

20. Lateral parasymphysial foramen
(Daeschler et al. (2006): Character 66)

0 absent
1 present

21. Mesial parasymphysial foramen
(Daeschler et al. (2006): Character 67)

0 absent
1 present

22. Length of dentary
(Zhu and Ahlberg (2004): Character 10)

0 long
1 short with lip fold

23. Dentary teeth
(Ahlberg et al. (2008): Character 85)

0 same size as maxillary teeth
1 larger than maxillary teeth
2 smaller than maxillary teeth

24. Accessory tooth rows on dentary
(Daeschler et al. (2006): Character 64)

0 present
1 absent

25. Dentary tooth row reaches symphysis
(Zhu and Ahlberg (2004): Character 11)

0 yes
1 no

26. Dentary fangs
(Modified from Zhu and Ahlberg (2004): Character 12)

0 absent
1 1 pair
2 1 unpaired (no replacement pit)

27. Dentary ventral edge
(Ahlberg et al. (2008): Character 55)

0 smooth continuous line
1 abruptly tapering or 'stepped' margin

28. Splenial
(Modified from Zhu and Ahlberg (2004): Character 2)

0 not sutured to prearticular
1 sutured to prearticular
2 postsplenial obstructing splenial-prearticular contact

29. Postsplenial suture with prearticular present
(Modified from Ahlberg et al. (2008): Character 69)

0 no
1 yes but interrupted by Meckelian foramina or fenestrae
2 uninterrupted suture

30. Postsplenial with mesial lamina
(Ahlberg et al. (2008): Character 67)

0 no
1 yes

31. Meckelian foramina/fenestrae, dorsal margins formed by
(Ahlberg et al. (2008): Character 63)

0 Meckelian bone
1 prearticular
2 infradentary

32. Meckelian foramina/fenestrae, height
(Ahlberg et al. (2008): Character 64)

0 much lower than adjacent prearticular
1 equal to or greater than depth of adjacent prearticular

33. Meckelian exposure in precoronoid fossa
(Daeschler et al. (2006): Character 65)

0 present
1 absent

34. Posterior coronoid longer than more anterior coronoids
0 no
1 yes

35. Posterior coronoid one-third longer than more anterior coronoids
(Modified from Zhu and Ahlberg (2004): Character 8)

0 no
1 yes

36. Coronoid fangs larger than marginal teeth
(Daeschler et al. (2006): Character 70)

0 yes
1 no

37. Coronoids: at least one carries shagreen
(Ahlberg et al. (2008): Character 80)

0 no
1 yes

38. Coronoids with a row of very small teeth or denticles lateral to tooth row
(Ahlberg et al. (2008): Character 81)

0 yes

1 no

39. Coronoids: size of teeth (excluding fangs) on anterior and middle coronoids relative to dentary tooth size

(Ahlberg et al. (2008): Character 82)

0 about the same
1 half height or less

40. Coronoid (anterior) contacts splenial

(Ahlberg et al. (2008): Character 49)

0 no
1 yes

41. Coronoid (middle) separated from splenial

(Ahlberg et al. (2008): Character 50)

0 yes, by prearticular
1 no
2 yes, by postsplenial

42. Coronoid (posterior) posterodorsal process

(Ahlberg et al. (2008): Character 52)

0 no
1 yes

43. Coronoid (posterior) posterodorsal process visible in lateral view

(Ahlberg et al. (2008): Character 53)

0 no
1 yes

44. Number of fang pairs on posteriormost coronoid

(Zhu and Ahlberg (2004): Character 13)

0 one
1 two
2 none

45. Non-fanged teeth on posterior coronoid

0 absent
1 organized tooth row
2 shagreen

46. Prearticular
(Zhu and Ahlberg (2004): Character 3)

0 not forked
1 forked

47. Prearticular sutures with mesial lamina of splenial
(Ahlberg et al. (2008): Character 71)

0 no, mesial lamina of splenial absent
1 yes
2 no, mesial lamina of splenial separated from prearticular by postsplenial

48. Prearticular-angular contact
(Ahlberg et al. (2008): Character 48)

0 separated by ventral exposure of Meckelian element
1 prearticular contacts angular edge to edge
2 mesial lamina of angular sutures with prearticular

49. Prearticular sutures with surangular
(Ahlberg et al. (2008): Character 70)

0 no
1 yes

50. Prearticular shagreen field, distribution
(Ahlberg et al. (2008): Character 92)

0 gradually decreasing from dorsal to ventral
1 well defined dorsal longitudinal band
2 scattered patches or absent

51. Prearticular with mesially projecting flange on dorsal edge along posterior border of adductor fossa
(Ahlberg et al. (2008): Character 73)

0 no
1 yes

52. Adductor crest

(Ahlberg et al. (2008): Character 47)

0 absent
1 peak anterior to adductor fossa, dorsal margin of fossa concave
2 peak above anterior part of adductor fossa, dorsal margin of fossa convex

53. Premaxillary tooth proportions

(Modified from Ahlberg et al. (2008): Character 38)

0 all approximately same size
1 enlarged anterior tooth
2 posteriormost teeth at least twice height of anteriormost teeth

54. Maxilla extends behind level of posterior margin of orbit

(Ahlberg et al. (2008): Character 12)

0 yes
1 no

55. Maxilla makes interdigitating suture with vomer

(Ahlberg et al. (2008): Character 10)

0 no
1 yes

56. Posterodorsal process of maxilla

(Zhu and Ahlberg (2004): Character 51)

0 present
1 very weak or absent

57. Vomer proportions

(Zhu and Ahlberg (2004): Character 22)

0 not much broader than long
1 much broader than long

58. Vomerine fangs

(Zhu and Ahlberg (2004): Character 24)

0 absent
1 present

59. Vomerine fang pairs noticeably smaller than other palatal fang pairs
(Ahlberg et al. (2008): Character 41)

0 no
1 yes

60. Vomerine row of small teeth
(Ahlberg et al. (2008): Character 43)

0 present
1 absent

61. Anterior wall of vomer (forming posterior margin of palatal fossa) bears tooth row meeting in midline
(Ahlberg et al. (2008): Character 42)

0 yes
1 no

62. Vomerine shagreen field
(Ahlberg et al. (2008): Character 44)

0 absent
1 present

63. Anteromedial process of vomer
(Zhu and Ahlberg (2004): Character 21)

0 absent, vomers separated
1 present
2 absent, vomers in close contact

64. Posterior process of vomers
(Zhu and Ahlberg (2004): Character 20)

0 absent
1 short
2 long

65. Relationship of vomer to parasphenoid
(Zhu and Ahlberg (2004): Character 23)

0 no contact (via small gap) or simple abutment
1 overlap
2 no contact via blockage by pterygoid elements

66. Parasphenoid, denticulated field
(Ahlberg et al. (2008): Character 29)

0 present
1 absent

67. Posterior end of parasphenoid
(Zhu and Ahlberg (2004): Character 26)

0 denticulated field extends into spiracular groove
1 denticulated field does not extend into spiracular groove

68. Parasphenoid
(Ahlberg et al. (2008): Character 28)

0 does not overlap basioccipital
1 overlaps basioccipital

69. Proportions of entopterygoid
(Zhu and Ahlberg (2004): Character 18)

0 anterior end level with processus ascendens
1 anterior end considerably anterior to processus ascendens

70. Entopterygoids meeting in midline
(Zhu and Ahlberg (2004): Character 19)

0 no
1 yes

71. Entopterygoid-quadrate ramus margin in the subtemporal fossa
(Ahlberg et al. (2008): Character 20)

0 concave
1 with some convex component

72. Dentition of palatoquadrate complex
(Zhu and Ahlberg (2004): Character 16)

0 marginal teeth
1 tooth plates

73. Entopterygoid shagreen
(Ahlberg et al. (2008): Character 37)

0 dense
1 a few discontinuous patches or absent

74. Anterior palatal fenestra
(Ahlberg et al. (2008): Character 93)

0 single
1 double
2 absent

75. Interentopterygoid vacuities
(Ahlberg et al. (2008): Character 95)

0 absent
1 at least 2 x longer than wide
2 < 2 x longer than wide

76. Dermopalatine exposure
(Modified from Ahlberg et al. (2008): Character 2)

0 more or less confined to margins of the tooth row
1 medial exposure in addition to the tooth row

77. Dermopalatine/ectopterygoid denticle row
(Ahlberg et al. (2008): Character 33)

0 present
1 absent

78. Dermopalatine/ectopterygoid shagreen field
(Ahlberg et al. (2008): Character 34)

0 absent
1 present

79. Ectopterygoid reaches subtemporal fossa
(Ahlberg et al. (2008): Character 4)

0 no
1 yes

80. Number of fangs on ectopterygoid
(Zhu and Ahlberg (2004): Character 17)

0 one pair
1 two pairs
2 none
3 one unpaired

81. Ectopterygoid row (3+) of smaller teeth
(Ahlberg et al. (2008): Character 32)

0 present
1 absent

82. Subterminal mouth
(Daeschler et al. (2006): Character 73)

0 absent
1 present

83. Number of nasals
(Zhu and Ahlberg (2004): Character 44)

0 many
1 one or two

84. Anterior tectal/septomaxilla
(Ahlberg et al. (2008): Character 1)

0 anterior tectal (external bone, dorsal to nostril)
1 septomaxilla (external or internal bone, posterior to nostril)
2 absent

85. Lateral rostral present
(Ahlberg et al. (2008): Character 9)

0 yes
1 no

86. Median postrostral
(Zhu and Ahlberg (2004): Character 43)

0 absent (postrostral mosaic)
1 present
2 absent (nasals meet in midline)

87. Dorsal fontanelle on snout
(Ahlberg et al. (2008): Character 94)

0 absent
1 present

88. Internasal pits
(Zhu and Ahlberg (2004): Character 25)

0 undifferentiated
1 strong midline ridge but shallow pits
2 deep pear-shaped pits

89. External nostrils
(Zhu and Ahlberg (2004): Character 29)

0 two pairs
1 one pair

90. Premaxilla forms part of choanal margin
(Ahlberg et al. (2008): Character 17)

0 broadly
1 point
2 not, excluded by vomer

91. Position of anterior external nostril
(Zhu and Ahlberg (2004): Character 30)

0 facial
1 edge of mouth

92. Lacrimal

(Ahlberg et al. (2008): Character 8)

0 contributes to orbital margin
1 excluded from margin

93. Contact between lacrimal and posterior supraorbital [postfrontal]

(Zhu and Ahlberg (2004): Character 56)

0 absent
1 present

94. Jugal

(Ahlberg et al. (2008): Character 7)

0 does not extend anterior to orbit
1 extends anterior to orbit

95. Jugal extends anterior to middle of orbit

(Daeschler et al. (2006): Character 78)

0 no
1 yes

96. Jugal-quadratojugal contact

(Zhu and Ahlberg (2004): Character 52)

0 absent
1 present

97. Position of orbits

(Zhu and Ahlberg (2004): Character 59)

0 lateral and widely separated
1 dorsal and close together

98. Postorbital bone

(Zhu and Ahlberg (2004): Character 54)

0 contributes to orbital margin
1 excluded from orbital margin

99. Contact between postorbital and lacrimal
(Daeschler et al. (2006): Character 84)

0 absent
1 present

100. Quadratojugal, squamosal and preopercular fused
(Zhu and Ahlberg (2004): Character 62)

0 no
1 yes

101. Subsquamosals
(Zhu and Ahlberg (2004): Character 61)

0 absent
1 present

102. Preoperculosubmandibular
(Zhu and Ahlberg (2004): Character 60)

0 absent
1 present

103. Width of ethmoid relative to its length, from snout tip to the posterior margin of the parietals
(Modified from Zhu and Ahlberg (2004): Character 32)
States based on clumped morphospace.

0 greater or = 80%
1 75%-45%
2 less than or = 35%

104. Proportion of skull roof (measured as length from tip of snout to posterior margin of postparietals) lying anterior to middle of orbits
(Modified from Daeschler et al. (2006): Character 75)
States based on clumped morphospace.

0 20-30%
1 33-40%

2 45-48%
3 >53%

105. B-bone
(Zhu and Ahlberg (2004): Character 46)

0 absent
1 present

106. Prefrontal (anterior supraorbital)
(Ahlberg et al. (2008): Character 15)

0 twice as long as broad, or less
1 three times as long as broad

107. Prefrontal (anterior supraorbital)
(Ahlberg et al. (2008): Character 16)

0 transverse anterior suture with tectal (or opens broadly into external nostril)
1 tapers to point anteriorly

108. Relative size of prefrontal [anterior supraorbital] and posterior supraorbital [postfrontal]
(Daeschler et al. (2006): Character 76)

0 similar
1 prefrontal much bigger

109. Postfrontals [posterior supraorbitals] extend anterior of orbits
(Daeschler et al. (2006): Character 86)

0 no
1 yes

110. Shape of postfrontals (posterior supraorbitals)
(Zhu and Ahlberg (2004): Character 58)

0 posterior process shorter than orbital margin
1 posterior process much longer than orbital margin

111. Contact between intertemporal and postfrontal (posterior supraorbital)
(Zhu and Ahlberg (2004): Character 55)

0 present
1 absent

112. Contact between parietal and postfrontal (posterior supraorbital)
(Zhu and Ahlberg (2004): Character 57)

0 present
1 absent

113. Frontals
(Zhu and Ahlberg (2004): Character 45)

0 absent
1 present

114. Parietals surround pineal foramen/eminence
(Zhu and Ahlberg (2004): Character 38)

0 yes
1 no

115. Pineal foramen
(Zhu and Ahlberg (2004): Character 36)

0 present
1 absent

116. Position of pineal foramen/eminence
(Zhu and Ahlberg (2004): Character 37)

0 level with posterior margin of orbits
1 well posterior to orbits

117. Shape of pineal series
(Zhu and Ahlberg (2004): Character 39)

0 round or oval
1 kite-shaped with distinct posterior corner. (non-applicable for *Kenichthys*)

118. Intemporal
(Ahlberg et al. (2008): Character 6)

0 present
1 absent

119. Dermal intracranial joint
(Zhu and Ahlberg (2004): Character 71)

0 present
1 absent

120. Postparietals narrow to a point posteriorly
(Zhu and Ahlberg (2004): Character 41)

0 no
1 yes

121. Proportions of postparietal shield
(Zhu and Ahlberg (2004): Character 40)

0 not extremely wide posteriorly
1 extremely wide posteriorly

122. Supratemporal
(Modified from Ahlberg and Johanson (1998): Character 49)

0 recognizable as a distinct bone
1 fused with postparietal

123. Posterior margin of tabulars
(Modified from Zhu and Ahlberg (2004): Character 42)

0 anterior to the posterior margin of postparietals
1 level with the posterior margin of postparietals
2 posterior to the posterior margin of the postparietals

124. Postspiracular (extratemporal)
(Zhu and Ahlberg (2004): Character 50)

0 present
1 absent

125. Position of the postspiracular (extratemporal)
0 anterior

1 posteriorly displaced

126. Contact between postspiracular [extratemporal] and supratemporal
(Zhu and Ahlberg (2004): Character 48)

0 absent
1 present

127. Premaxilla canal-bearing
(Zhu and Ahlberg (2004): Character 68)

0 yes
1 no

128. Infraorbital canal follows premaxillary suture
(Zhu and Ahlberg (2004): Character 69)

0 no
1 yes

129. Postotic sensory canal
(Zhu and Ahlberg (2004): Character 66)

0 runs through skull roof
1 follows edge of skull roof

130. Postorbital junction of supraorbital and infraorbital canals
(Zhu and Ahlberg (2004): Character 67)

0 absent
1 present

131. Mandibular sensory canal
(Ahlberg et al. (2008): Character 57)

0 prsesnt
1 absent

132. Mandibular canal exposure
(Ahlberg et al. (2008): Character 58)

0 entirely enclosed, opens through lines of pores

1 mostly enclosed, short sections of open grooves
2 mostly open, short sections with lines of pores
3 entirely open

133. Mandible: oral sulcus/surangular pit line
(Ahlberg et al. (2008): Character 59)

0 present
1 absent

134. Foramina (similar to infradentary foramina) on cheekplate
(Zhu and Ahlberg (2004): Character 63)

0 absent
1 present

135. Submandibulars and gulars
(Daeschler et al. (2006): Character 80)

0 present
1 absent

136. Large median gular
(Modified from Daeschler et al. (2006): Character 81)

0 absent
1 present

137. Preopercular
(Daeschler et al. (2006): Character 88)

0 large
1 small

138. Preopercular
(Ahlberg et al. (2008): Character 18)

0 present
1 absent

139. Opercular
(Ahlberg et al. (2008): Character 14)

0 present
1 absent

140. Spiracular notch
(Daeschler et al. (2006): Character 87)

0 absent
1 small opening
2 narrow groove
3 wide notch

141. Anterior margin of median extrascapular
(Zhu and Ahlberg (2004): Character 65)

0 long
1 very short

142. Extrascapular bones
(Zhu and Ahlberg (2004): Character 64)

0 median overlaps laterals
1 laterals overlap median

143. Extrascapular bones
(Daeschler et al. (2006): Character 77)

0 present
1 absent

144. Posttemporal
(Ahlberg et al. (2008): Character 109)

0 present
1 absent

145. Supracleithrum
0 present
1 absent

146. Anocleithrum
(Zhu and Ahlberg (2004): Character 85)

0 exposed
1 subdermal

147. Anocleithrum
(Ahlberg et al. (2008): Character 99)

0 oblong with distinct anterior overlap area
1 drop-shaped with no anterior overlap area
2 absent

148. Orientation of cleithrum
(Daeschler et al. (2006): Character 105)

0 vertically oriented: tilted less than 10 degrees caudally
1 angulated: tilted over 10 degrees caudally

149. Cleithrum, postbranchial lamina
(Ahlberg et al. (2008): Character 101)

0 present
1 absent

150. Contact margin for clavicle on cleithrum
(Zhu and Ahlberg (2004): Character 84)

0 straight or faintly convex
1 strongly concave

151. Scapulocoracoid
(Ahlberg et al. (2008): Character 115)

0 small and tripodal
1 large plate pierced by large coracoid foramen
2 very large plate without large coracoid foramen

152. Coracoid plate
(Daeschler et al. (2006): Character 103)

0 absent
1 present and extends ventromedially

153. Scapular blade

(Ahlberg et al. (2008): Character 114)

0 absent
1 small with narrow top
2 large with broad top

154. Shoulder joint polarity

(Zhu and Ahlberg (2004): Character 87)

0 caput humeri concave
1 caput humeri convex

155. Glenoid position

(Daeschler et al. (2006): Character 104)

0 elevated from plane formed by clavicles
1 offset ventrally to lie at same level as clavicular plane

156. Glenoid orientation

(Daeschler et al. (2006): Character 110)

0 posterior orientation
1 lateral component to glenoid orientation

157. Glenoid proportions

Measured in plane with glenoid orientation. Height at maximum extent divided by maximum length: *Medoevia* = 0.60; *Eusthenopteron* = 0.60; *Tinirau* = 0.42; *Panderichthys* = 0.48; *Tiktaalik* = 0.44; *Acanthostega* = 0.45; *Ichthyostega* = 0.44; *Greererpeton* = 0.44; *Proterogyrinus* = 0.40; *Eoherpeton* = 0.47.

0 height/width ratio 60% or greater
1 height/width ratio 40-50%

158. Interclavicle

(Ahlberg et al. (2008): Character 106)

0 small and concealed (unornamented) or absent
1 large and exposed (ornamented)

159. Interclavicle shape

(Ahlberg et al. (2008): Character 107)

0 ovoid
1 kite-shaped
2 with posterior stalk

160. Archipterygial pectoral fin
(Zhu and Ahlberg (2004): Character 86)

0 no
1 yes

161. Humerus
(Ahlberg et al. (2008): Character 103)

0 narrow tapering entepicondyle
1 square or parallelogram-shaped entepicondyle

162. Body of humerus
(Zhu and Ahlberg (2004): Character 89)

0 cylindrical
1 flattened rectangular

163. Deltoid and supinator process on humerus
(Zhu and Ahlberg (2004): Character 90)

0 absent
1 present

164. Anterior termination of ventral ridge
(Daeschler et al. (2006): Character 96)

0 adjacent to the caput humeri
1 offset distally toward the proximodistal mid-region of anterior margin of humerus

165. Ectepicondylar process
(Daeschler et al. (2006): Character 100)

0 terminates proximal to epipodial facets
1 extends distal to epipodial facets

166. Radius and ulna
(Ahlberg et al. (2008): Character 110)

0 radius much longer than ulna
1 approximately equal length

167. Radial facet
(Daeschler et al. (2006): Character 98)

0 faces distally
1 has some ventrally directed component

168. Area proximal to radial facet
(Daeschler et al. (2006): Character 102)

0 short, cylindrical leading edge, with no muscle scars
1 enlarged, sharp leading edge, with areas for muscle attachments

169. Shape of radius
(Daeschler et al. (2006): Character 94)

0 bladelike
1 subcylindrical

170. Radial length
(Daeschler et al. (2006): Character 101)

0 longer than humerus
1 shorter than humerus

171. Ulnar facet
(Daeschler et al. (2006): Character 99)

0 faces distally
1 has some ventrally directed component

172. Olecranon process on ulna
(Daeschler et al. (2006): Character 95)

0 absent
1 present

173. Transverse joint at the level of the ulnare, intermedium and radius
(Daeschler et al. (2006): Character 89)

0 absent
1 present

174. Articulations for more than two radials on ulnare
(Daeschler et al. (2006): Character 90)

0 absent
1 present

175. Postaxial process on ulnare
(Daeschler et al. (2006): Character 91)

0 absent
1 present

176. Branched radials distal to the ulnare
(Daeschler et al. (2006): Character 93)

0 absent
1 present

177. Radials
(Zhu and Ahlberg (2004): Character 91)

0 jointed
1 unjointed

178. Digits
(Ahlberg et al. (2008): Character 102)

0 absent
1 present

179. Lepidotrichia in paired appendages
(Ahlberg et al. (2008): Character 108)

0 present
1 absent

180. Basal segments of lepidotrichia elongated
(Zhu and Ahlberg (2004): Character 92)

0 no
1 yes

181. Expanded ribs
(Daeschler et al. (2006): Character 113)

0 absent
1 present

182. Imbricate ribs
(Daeschler et al. (2006): Character 114)

0 absent
1 present

183. Ribs, trunk
(Ahlberg et al. (2008): Character 111)

0 no longer than diameter of intercentrum
1 longer

184. Ribs, trunk
(Modified from Ahlberg et al. (2008): Character 112)

0 all straight
1 at least some ventral component

185. Ribs, trunk
(Ahlberg et al. (2008): Character 113)

0 all cylindrical
1 some or all bear flanges from posterior margin which narrow distally
2 some or all flare distally

186. Supraneural spines
(Zhu and Ahlberg (2004): Character 99)

0 present
1 absent

187. Ilium, iliac canal

(Ahlberg et al. (2008): Character 104)

0 absent
1 present

188. Ilium, posterior process
(Ahlberg et al. (2008): Character 105)

0 oriented posterodorsally
1 oriented approximately horizontally posteriorly

189. Postaxial process on fibula
0 present
1 absent

190. Postaxial process on fibula, size
0 large
1 small

191. Dorsal and anal fins
(Zhu and Ahlberg (2004): Character 93)

0 present
1 absent

192. Posterior radials in posterior dorsal fin
(Zhu and Ahlberg (2004): Character 94)

0 not branched
1 branched

193. Caudal fin
(Zhu and Ahlberg (2004): Character 95)

0 heterocercal
1 diphycercal

194. Epichordal radials in caudal fin
(Zhu and Ahlberg (2004): Character 96)

0 absent
1 present

195. Nature of dermal ornament

(Ahlberg et al. (2008): Character 97)

0 tuberculate
1 fairly regular pit and ridge
2 irregular
3 absent or almost absent

196. Nature of ornament: "starbursts" of radiating ornament on at least some bones

(Ahlberg et al. (2008): Character 98)

0 no
1 yes

197. Cleithral ornamentation

(Daeschler et al. (2006): Character 106)

0 present
1 absent

198. Basal scutes

(Zhu and Ahlberg (2004): Character 97)

0 absent
1 present

199. Body scale morphology

(Zhu and Ahlberg (2004): Character 98). *Platycephalichthys* scored after Snitting (2008b).

0 rhomboid with internal ridge
1 round

200. Squamation

(Ahlberg et al. (2008): Character 117)

0 complete body covering of scales
1 ventral armour of gastralia

201. Tooth folding

(Zhu and Ahlberg (2004): Character 14)

0 none
1 generalized polyplocodont
2 labyrinthodont
3 dendrodont

202. Cosmine
(Zhu and Ahlberg (2004): Character 34)

0 present
1 absent

203. Westoll lines
(Zhu and Ahlberg (2004): Character 35)

0 absent
1 present

Part B.

Taxon-by-character matrix and character optimizations.—The data matrix was subjected to a maximum parsimony analysis in the software package PAUP (Swofford 2002) and a Bayesian analysis using the software package Mr. Bayes(Huelsenbeck 2001, Ronquist and Huelsenbeck 2003). All characters were assigned an equal weight, multistate characters were run unordered, and a heuristic search algorithm was used in PAUP to search for the shortest networks—rooted on *Porolepis*, *Glyptolepis*, *Powichthys*, *Youngolepis*, *Diabolepis*, and *Dipterus*. Bremer decay indices were calculated using PAUP(Swofford 2002) and TNT(Goloboff 1999, Nixon 1999), and Bayesian posterior probabilities were calculated with Mr. Bayes following an analysis that included 500,000 mcmc generations, sampling every 1,000 generations, and with 20 samples discarded as burnin. Character evolution was examined in MacClade(Maddison and Maddison 2000), which was also used to produce the character state distributions below. *Eusthenopteron* is scored as *E. foordi* and *Platycephalichthys* scored as *P. bischoffi*.

A = 0 & 1; **B** = 0 & 2

	1		**1**		**2**		**3**		**4**	
			1		**1**		**1**		**1**	
Acanthostega	100-?	00002	0111?	02110	10010	10100	10100	10011	00-21	11001
Balanerpeton	10?-?	?0002	01???	-?1-0	00110	21221	20100	11-11	2??22	02202
Baphetes	10?-?	?0002	0111?	?111?	?0??0	0????	?????	1????	?????	?????
Barameda	00???	?1???	?????	?????	?0000	10???	?????	?????	?????	?????
Beelarongia	?0???	?????	?????	?????	?0???	?0???	?????	?????	?????	?????
Cabonnichthys	?0???	?1?02	0????	1????	?0000	101??	??0-1	00000	??-10	0???0
Canowindra	?0???	?????	?????	?????	?0???	?0???	?????	?????	?????	?????
Cladarosymblema	00000	01102	00000	01010	00000	10100	00000	00000	?0-00	00000
Crassigyrinus	?0???	?0002	0????	?2110	00110	?1100	10111	11-10	0???2	?1202
Dendrerpeton	10?-?	?0002	0111?	?????	?011?	?1?11	11???	?1-?1	?11??	??212
Diabolepis	01???	?0?0?	10?0?	?---?	?1?-?	0-?--	?????	-????	?????	?????
Dipterus	010??	?00?0	10???	?---?	?1?-?	0-0--	?????	-????	?????	??0??
Ectosteorhachis	00???	01102	?0??0	01010	00?00	10100	??000	00000	?0-00	00000
Elginerpeton	?????	?????	?????	?2111	10?00	10?00	001??	10000	0???1	11001
Elpistostege	?0???	?????	?????	?????	?????	?0???	?????	?????	?????	?????
Eoherepton	10?-?	?0002	01?1?	?????	??01?	?1111	10100	11011	0??22	01?12
Eusthenodon	?????	?????	0????	1??1?	?0?00	101??	???-1	0?00?	??10	0????
Eusthenopteron	00000	11102	00001	11010	00000	00100	000-1	00000	00-10	00000
Glyptolepis	00101	11101	00???	20-00	00001	00?00	??000	00000	??00	00000
Glyptopomus	?????	?1???	?????	?????	?00??	?????	?????	?????	?????	?????
Gogonasus	00000	01102	00000	01010	00000	00000	00000	000A0	??01	?0000
Gooloogongia	?0???	?1???	?????	01010	00000	1????	??0??	0???0	?????	?????
Greererepton	10?-?	?0002	0111?	?2110	00110	21100	111??	11111	01122	11202
Gyroptychius	?0???	01102	0??02	01010	00000	?0???	??00	00000	?0-00	?0?0?
Ichthyostega	10?-?	?0002	01?1?	02110	10210	10100	00100	10111	00-21	11102
Jarvikina	???0?	11102	00??1	1????	?0?00	001??	???-1	0????	?001?	0????
Kenichthys	000??	?1?02	10???	01010	00000	00000	??000	010A0	?0-00	000??
Koharalepis	?0???	?????	?????	?????	?000?	?0???	?????	?????	?????	?????
Mandageria	00???	11102	??02	?????	?0000	101??	?????	0?00?	?????	0????
Marsdenichthys	?????	?????	?????	?????	?0??0	00???	??00	0?0??	?????	?????
Medoevia	00000	01102	00000	01010	000?0	0?100	00000	00000	00-00	00000
Megalichthys	00???	?1102	00000	01010	00000	10100	??000	00000	?0-00	0000?
Osteolepis	00???	01102	00000	01010	00000	00?00	??0??	0????	?????	?????
Panderichthys	00010	01102	00000	01010	00000	10100	000-1	00000	00-01	00100
Pederpes	?0???	?0??2	01?1?	?????	?????	?????	?????	?????	?????	?????
Platycephalichthys	0??1?	?1???	?0???	01010	000?0	10???	000?1	00??0	00-01	000?0
Porolepis	?0101	11101	10?0?	20-00	00001	000??	??00	?0000	??00	00000
Powichthys	011?1	?1111	10?0?	20-0?	?0?01	0?0??	??00	??0??	??00	0?0??
Proterogyrinus	10?-?	?0002	01???	??110	00010	?1111	111??	11-11	??22	??212
Silvanerpeton	?0???	?0002	01???	?????	?0010	?1??1	101?0	11-1?	0??22	????2
Spodichthys	00???	11102	00001	1??1?	?0000	00100	00010	00??0	00-00	0000?
Tiktaalik	000-?	01102	00?00	0?010	00000	101?0	?00-1	00100	00-21	00100
Tinirau	0000?	?1102	00001	?????	?0000	10000	???-1	00000	00-01	00000
Tristichopterus	?0???	1110?	?0?01	1???0	00000	00?00	??010	00000	?0-00	?0???
Ventastega	10?-1	?0?02	?101?	?2011	100?0	10100	001-1	00111	00-21	11101
Whatcheeria	?????	?0002	01?1?	?2110	00210	20100	00100	10111	01021	11101
Youngolepis	01001	10010	10001	20-00	00?01	00000	??000	010A0	?0-00	00000

	51		61		71		81		91	
Acanthostega	00200	10100	00202	01011	00010	00012	00101	21011	11011	11000
Balanerpeton	01001	?0101	11200	0?110	10022	11110	1?121	20–12	00001	1100–
Baphetes	??000	?0101	11202	0?111	00020	11110	1?111	20–11	00001	1100–
Barameda	??10?	??1??	????0	????0	?0???	?????	?0100	00?1?	00000	?000?
Beelarongia	???0?	?????	?????	?????	?????	?????	?0???	10?1?	00?0?	001?0
Cabonnichthys	0?100	10100	00221	010?0	00000	00?01	00000	10010	00000	00100
Canowindra	???0?	?????	?????	?????	?????	?????	?00??	?0?1?	00000	00100
Cladarosymblema	00100	01100	00100	010?0	?0000	?????	?0010	10010	00000	00000
Crassigyrinus	?0001	?0100	10202	0?1?1	00010	11003	00111	21?12	00001	1100–
Dendrerpeton	0?00?	?0011	11200	??110	10022	1111?	10111	20–1?	00001	1100–
Diabolepis	?00?–	?00––	–1000	000?0	01?0?	–??–?	–?0??	?000–	1????	?0???
Dipterus	?0?––	?0?––	––20–	0?011	01?–?	–??–?	–00??	0000–	10?00	10000
Ectosteorhachis	00100	011?0	00100	010?0	?0?0?	?????	??010	10010	00000	0000?
Elginerpeton	??0??	?????	?????	?????	?????	?0???	?????	???1?	1????	?????
Elpistostege	??000	?????	?????	0????	?????	?????	?1000	00???	?0011	0101?
Eoherepton	1201?	?????	?????	1?11?	101?0	110?0	10121	21–1?	01011	1100–
Eusthenodon	?0100	10100	00221	???10	00?0?	000??	00000	10?10	00100	00100
Eusthenopteron	00000	00100	00221	01010	00000	00001	00000	10010	00000	00000
Glyptolepis	00000	10100	00000	00000	00000	10010	00000	0020–	00000	00000
Glyptopomus	??00?	00100	??2??	???10	0??00	???1?	??000	10?1?	00000	00000
Gogonasus	00000	001?0	00200	01000	00000	00010	00000	10010	00000	00000
Gooloogongia	???0?	0????	?????	?????	?0???	?????	?0100	00?1?	00001	00000
Greererepton	02200	???11	10??2	0?111	00011	1101?	00121	21?11	10001	1100–
Gyroptychius	00000	00100	00100	010?0	?0000	000?0	00000	10010	00000	00010
Ichthyostega	00201	10100	10202	01011	00100	1101B	0010?	20012	11011	11000
Jarvikina	?00?0	?010?	??221	?1??0	?0???	?????	??000	1001?	00000	000?0
Kenichthys	00000	0????	????0	010??	?0?0?	?00?0	00?00	?000–	00000	00001
Koharalepis	???0?	0?10?	?????	???10	?????	?????	?00??	?0?1?	00000	00100
Mandageria	??100	10100	00221	01010	00000	00001	00000	10010	00100	00110
Marsdenichthys	???0?	1010?	???0?	010?0	?00?0	0??0?	?0000	10?1?	00000	00?00
Medoevia	00100	00100	00100	01000	00000	00010	00???	?0?10	00000	00000
Megalichthys	00100	011?0	00100	01000	?0000	?00?0	00010	10010	00000	00000
Osteolepis	00000	0????	?????	010?0	00000	000?0	00000	10?10	00000	00000
Panderichthys	00000	10100	00211	01010	00000	00010	01000	00010	10000	110A0
Pederpes	???00	?????	????2	0???1	?00?0	11113	0???1	?????	?0001	11000
Platycephalichthys	0010?	101?0	002?1	?????	???00	?????	??000	10?10	00?00	0???1
Porolepis	00000	101??	??000	00000	00000	????0	?00??	0020–	00000	00000
Powichthys	?00?0	?0??0	00002	0000?	?0000	0????	??0??	0020–	0?0??	?0???
Proterogyrinus	12010	??0??	????2	1?111	100?0	11000	10121	20–1?	1?001	1100–
Silvanerpeton	02010	??001	11??2	0?111	10020	1??0?	?0121	20–1?	00001	1100–
Spodichthys	00?0?	00???	??22?	???10	000?0	0???0	?????	1??1?	0????	?0???
Tiktaalik	00000	1010?	0?211	01010	00000	00010	00?00	?001?	10011	11010
Tinirau	00000	10100	00221	01010	00000	00010	000––	10?10	00000	00??1
Tristichopterus	00000	0?100	00221	0?0?0	?0???	0????	?0???	10?10	00000	00000
Ventastega	00200	1?100	?0???	0?0?1	00000	010??	?01?1	21??1	?1011	11000
Whatcheeria	0020?	???01	10??2	??1?1	000?0	11000	00121	20?11	?1011	11000
Youngolepis	00000	001?–	–1000	000?0	?0?0?	001?0	0?0??	?010–	0?000	000?1

	101		**111**		**121**		**131**		**141**	
Acanthostega	00230	11100	-0100	1-110	0021-	-0000	01101	01013	--111	01101
Balanerpeton	00220	11000	00100	1-010	0021-	-????	1-101	0-113	--111	-2?1?
Baphetes	00230	11100	00100	1-010	0011-	-0000	03?01	0-113	--111	-2?1?
Barameda	??000	00000	00000	00001	00000	10001	?????	???0?	110??	????0
Beelarongia	00000	???00	00000	00000	11000	???0?	???0?	?0001	110??	??000
Cabonnichthys	00110	00001	00000	11000	00101	0000?	???00	00001	01000	00001
Canowindra	00100	???00	00000	10?00	11000	???0?	??00?	?000?	110??	000??
Cladarosymblema	00010	00000	00011	--000	00000	00001	00000	00001	01000	00000
Crassigyrinus	00230	11100	00100	1-010	0021-	-0000	03101	0-113	--111	-201?
Dendrerpeton	00230	11000	00100	1-010	0021-	-????	1-101	0-113	--111	-211?
Diabolepis	??001	????0	01011	0-?10	000??	?1110	?????	?????	?????	?????
Dipterus	0??11	0?000	01011	?-?10	0011-	-??01	00?0?	???00	00000	10001
Ectosteorhachis	0?010	????0	00011	--000	00???	?0001	00???	?????	010??	?????
Elginerpeton	????0	?????	?????	?????	?????	?????	000??	?????	?????	???1?
Elpistostege	??23?	10110	??1??	1-1?0	0?21-	-????	00??0	1????	?????	?????
Eoherepton	00230	01?00	00100	1-010	0021-	-????	1-101	0-11?	?????	?????
Eusthenodon	00110	00001	10000	11000	00101	0000?	???00	0000?	01000	0000?
Eusthenopteron	00110	00000	00000	00000	00101	00001	00000	00001	01000	00001
Glyptolepis	11000	???00	??011	0-000	1-000	00101	00000	00000	00000	10000
Glyptopomus	00100	00000	00000	00000	00000	0??0?	0???0	00001	0100?	????1
Gogonasus	00100	00000	00000	0-000	00000	00001	00000	00002	01000	000?0
Gooloogongia	00100	00000	00000	00001	00000	1000?	???00	00000	11000	100??
Greererepton	00220	10110	-0100	1-?10	0011-	-0000	01101	0-11?	-?111	-210?
Gyroptychius	00100	0??00	00000	10000	00000	00001	00000	00001	01000	00001
Ichthyostega	00230	11100	-0100	0-110	0021-	-0000	02101	01013	--111	-2101
Jarvikina	00110	????1	00000	10?00	001??	???0?	???0?	?????	010??	?????
Kenichthys	00000	???00	?0?10	0-?00	00000	01101	00?1?	?????	010??	????0
Koharalepis	00000	0?000	00000	10000	11000	???01	00000	00001	11000	??0??
Mandageria	00110	00001	10000	11000	01101	?000?	???00	0000?	11000	00001
Marsdenichthys	00110	????0	00000	00000	10000	0????	????0	?0002	11000	??0??
Medoevia	00010	0?110	00000	00000	01000	?????	????0	00001	01000	0?000
Megalichthys	00??0	???00	00011	--000	000??	?0001	???00	00001	010??	000?0
Osteolepis	00110	0?000	00000	00000	00000	00001	0000?	?0001	01000	00000
Panderichthys	00220	00010	00100	1-010	0011-	-0001	00000	1?002	01000	00101
Pederpes	00??0	01?0?	??1??	??0??	?011-	-????	???0?	?1013	--111	-211?
Platycephalichthys	??1?0	00???	??000	--0??	?????	?0?0?	0?0??	?00??	?????	?????
Porolepis	11000	????0	?1011	0-000	1-100	00101	00000	00001	00000	10000
Powichthys	?1000	????0	01010	10010	001??	?1101	?????	?????	00000	????0
Proterogyrinus	00230	11000	00100	0-010	0021-	-????	1-101	0-113	--111	-201?
Silvanerpeton	00230	01000	00100	0-010	0021-	-????	1-101	0-113	--111	-201?
Spodichthys	??100	???0?	00000	00000	00100	00?0?	0?000	???0?	??0??	??001
Tiktaalik	00230	1?1?0	-0100	0-?10	0011-	-??00	00000	10013	--110	00101
Tinirau	00100	0000?	?0000	1-000	00100	00001	00000	00001	0?0??	??001
Tristichopterus	00110	00000	00000	0-000	00101	???0?	?0?00	00001	010??	00001
Ventastega	00230	1??00	001??	1-010	0?11-	?0???	0000?	??013	-?111	01?11
Whatcheeria	00230	???00	00100	0-010	0011-	-????	01001	01013	--111	-2?0?
Youngolepis	00000	?????	?1?11	0-010	001??	?1110	???1?	?????	?????	????0

	151		**161**		**171**		**181**		**191**	
Acanthostega	21011	11110	11111	00111	00???	0011-	10102	1001-	1-111	11-01
Balanerpeton	21?11	1?110	111??	11111	110?0	0011-	10102	1001-	1-??1	11-?1
Baphetes	???11	1???0	11110	11111	11???	?????	?????	?001-	????1	11?01
Barameda	???1?	????0	0010?	00001	00010	?0001	?????	?????	????0	0??1?
Beelarongia	?????	?????	001??	?????	?????	???00	?????	?????	????0	00?0?
Cabonnichthys	???1?	????0	0010?	00000	00001	01000	?????	?????	0?100	00110
Canowindra	?????	?????	?????	?????	?????	?????	?????	?????	0?0?0	0?01?
Cladarosymblema	??010	0????	?????	?????	?????	???00	?????	?????	????3	00?00
Crassigyrinus	???1?	??110	11111	11111	11???	0011-	10110	1??1-	1-??2	11-?1
Dendrerpeton	21211	1?110	1111?	11111	11000	0011-	10110	1001-	1-??1	11-?1
Diabolepis	?????	?????	?????	?????	?????	?????	?????	?????	????3	0????
Dipterus	???0?	????1	?????	?????	?????	?0001	00100	0????	010?3	000?0
Ectosteorhachis	?????	?????	?????	?????	?????	???00	?????	?????	????3	0??0?
Elginerpeton	??01?	?????	111??	?????	?????	?????	?????	?11??	????1	11???
Elpistostege	?????	?????	?????	?????	?????	?????	?????	?????	????0	?????
Eoherepton	21211	11??0	111-0	1111?	1????	?????	10110	1001-	1-??1	0?-??
Eusthenodon	?????	?????	?????	?????	?????	?????	?????	?????	0???0	00?10
Eusthenopteron	00010	00000	00100	00000	00001	01000	00000	10-00	00100	00110
Glyptolepis	00000	0?0?1	000??	?????	?????	?0001	00000	0????	01003	00010
Glyptopomus	?????	?????	?????	?????	?????	???00	?????	?????	0?100	0?000
Gogonasus	???1?	????0	00100	00000	000?1	01000	?????	?????	????3	00?0?
Gooloogongia	?0???	??0?0	?????	00000	00010	???01	00???	???00	000?0	00010
Greererepton	21111	11110	11111	11111	11???	0011-	10111	1001-	1-??1	11-01
Gyroptychius	?????	?????	?????	?????	?????	???00	00000	1????	0?103	00100
Ichthyostega	21010	11120	11111	11111	11???	0011-	11111	1111-	1-111	11-??
Jarvikina	?????	?????	?????	?????	?????	?????	?????	?????	????0	0??1?
Kenichthys	?????	?????	?????	?????	?????	?????	?????	?????	????3	0?10?
Koharalepis	?????	?????	?????	?????	?????	???00	?????	?????	????0	00?0?
Mandageria	???1?	????0	001?0	00000	00001	01000	?????	?????	00100	00010
Marsdenichthys	?????	?????	?????	?????	?????	?????	?????	?????	0???0	00?10
Medoevia	00010	0000?	00100	?0???	?????	?????	?????	?????	0???3	00100
Megalichthys	00010	0?0?0	00100	00000	00001	01000	-----	1????	00003	00100
Osteolepis	?????	????0	?????	?????	?????	???00	-----	1????	00003	00100
Panderichthys	11011	110?0	01100	00100	00000	0?000	00101	1??01	1-1?0	00-00
Pederpes	21111	1?120	1111?	11111	11???	?011-	11111	1011-	1-??1	11-?1
Platycephalichthys	00???	0????	?????	?????	?????	?????	?????	?????	????0	0??0?
Porolepis	?????	?????	?????	?????	?????	?????	?????	?????	??0?3	00?00
Powichthys	?????	?????	?????	?????	?????	?????	?????	?????	????3	0??0?
Proterogyrinus	21211	11110	11110	11111	11???	0011-	10110	1001-	1-??1	11-01
Silvanerpeton	21211	1?120	111??	11111	11???	0011-	10110	1011-	1-??1	11-?1
Spodichthys	000??	?????	?????	?????	?????	?????	?????	?????	????0	00???
Tiktaalik	11011	110?0	01101	01101	00110	10001	11?01	?0-??	1-??0	00-00
Tinirau	00?10	01??0	?????	0??0?	??001	01000	00000	10-01	0?000	00?10
Tristichopterus	???1?	????0	00100	00000	00001	01000	?????	1????	00000	00110
Ventastega	210??	??110	?????	?????	?????	?????	?????	?00??	????1	11???
Whatcheeria	2121?	??120	111?1	?11??	1????	?????	11111	101??	1-??3	11-??
Youngolepis	000?0	0????	?????	?????	?????	?????	?????	?????	????3	0??0?

	201
Acanthostega	210
Balanerpeton	210
Baphetes	210
Barameda	?1?
Beelarongia	?00
Cabonnichthys	110
Canowindra	?1?
Cladarosymblema	100
Crassigyrinus	210
Dendrerpeton	?10
Diabolepis	?01
Dipterus	?01
Ectosteorhachis	?00
Elginerpeton	???
Elpistostege	???
Eoherepton	?10
Eusthenodon	110
Eusthenopteron	110
Glyptolepis	31?
Glyptopomus	?10
Gogonasus	100
Gooloogongia	?1?
Greererepton	210
Gyroptychius	100
Ichthyostega	210
Jarvikina	11?
Kenichthys	100
Koharalepis	100
Mandageria	110
Marsdenichthys	?1?
Medoevia	?00
Megalichthys	100
Osteolepis	100
Panderichthys	210
Pederpes	?10
Platycephalichthys	?1?
Porolepis	300
Powichthys	100
Proterogyrinus	210
Silvanerpeton	?10
Spodichthys	???
Tiktaalik	210
Tinirau	?10
Tristichopterus	?10
Ventastega	???
Whatcheeria	?10
Youngolepis	100

Character optimizations.

Rhizodonts + other tetrapodomorphs:

- 89, 0→1 = one pair of external nostrils
- 114, 1→0 = parietals surround a parietal foramen/eminance
- 127, 1→0 = premaxilla is canal bearing
- 128, 1→0 = infraorbital canal does not follow the premaxillary suture
- 195, 3→0 = tuberculate ornament
- 199, 0→1 = round body scales
- 202, 0→1 = loss of cosmine

Rhizodonts:

- 26, 0→1 = 1 pair of dentary fangs
- 83, 0→1 = 1 or 2 nasal bones
- 120, 0→1 = postparietals narrow to a point posteriorly
- 126, 0→1 = contact between postspiracular and supratemporal

'Osteolepiforms' + elpistostegalians:

- 86, 0→1 = median postrostral present
- 140, 0→1 = small opening to spiracular notch
- 146, 1→0 = exposed anocleithrum
- 180, 1→0 = basial lepidotrichial segments not elongate

Canowindrids:

- 121, 0→1 = PP shield extremely wide posteriorly

Canowindrids (minus *Marsdenichthys*):

- 122, 0→1 = supratemporal fused with postparietals

Canowindrids (*Koharalepis* + *Beelarongia* only):

- 103, 1→0 = width of ethmoid ≥80%
- 199, 1→0 = rhomboid body scales
- 202, 1→0 = cosmine present

Megalichthyiforms + eotetrapodiforms:

- 198, 0→1 = basal scutes present

Megalichthyiforms:

- 15, 1→0 = dorsal directly above ventral hyomandibular facet
- 69, 1→0 = anterior end of entopterygoid level with processus ascendens
- 195, 0→3 = ornament absent or almost absent
- 199, 1→0 = rhomboid body scales
- 202, 1→0 = cosmine present

Megalichthyiforms (minus *Gogonasus*):

- 63, 2→1 = anteromedial process of vomer present

Megalichthyiforms (minus *Gyroptychius*):

- 104, 0→1 = 33-40% of skull roof lies anterior to orbits

Osteolepidids (*Medoevia* + megalichthyids):

- 53, 0→1 = enlarged premaxillary tooth
- 103, 1→0 = width of ethmoid ≥80%

Megalichthyiforms (megalichthyids only)

- 26, 0→1 = 1 pair of dentary fangs
- 57, 0→1 = vomers much broader than long
- 114, 0→1 = parietals do not surround the pineal foramen
- 115, 0→1 = pineal foramen absent

Eotetrapodiforms:

- 64, 0→2 = long posterior processes on vomers
- 65, 0→1 = overlap of vomers and parasphenoid
- 123, 0→1 = posterior margin of tabular level with posterior margin of postparietals
- 150, 0→1 = contact margin for clavicle on cleithrum strongly concave

Tristichopterids:

- 16, 0→1 = parasymphyseal plate short not sutured to coronoid
- 34, 0→1 = Posterior coronoid longer than more anterior coronoids

Tristichopterids (minus *Spodichthys*):

- 104, 0→1 = 33-40% of skull roof anterior to orbits
- 125, 0→1 = posteriorly displaced PSP

Tristichopterids (*Eusthenopteron* + remaining tristichopterids):

- 35, 0→1 = posterior coronoid one-third longer than more anterior coronoids
- 44, 0→1 = 2 fang pairs on posteriormost coronoid
- 193, 0→1 = diphycercal caudal fin

Tristichopterids (*Jarvikina* + remaining tristichopterids):

- 110, 0→1 = posterior orbital process much longer than orbital margin
- 116, 0→1 = pineal foramen well posterior to orbital margin

Tristichopterids (*Cabonnichthys* + remaining tristichopterids):

- 26, 0→1 = 1 pair of dentary fangs
- 53, 0→1 = enlarged premaxillary tooth
- 98, 0→1 = postorbital excluded from orbital margin
- 117, 0→1 = pineal series kite-shaped

Tristichopterids (*Mandageria* + *Eusthenodon* only):

- 93, 0→1 = contact between lacrimal and posterior supraorbital
- 111, 0→1 = no contact between intertemporal and posterior supraorbital

Tinirau + [*Platycephalichthys* + Elpistostegalia]:

- 26, 0→1 = 1 pair of dentary fangs
- 35, 0→1 = posterior coronoid one-third longer than more anterior coronoids
- 45, 0→1 = organized tooth row on posterior coronoid
- 56, 0→1 = posterodorsal maxillary process weak/absent
- 116, 0→1 = pineal foramen posterior to orbits
- 157, 0→1 = height/width ratio of glenoid fossa, 40-50%
- 190, 0→1 = highly reduced postaxial process on fibula

Platycephalichthys + Elpistostegalia:

- 4, 0→1 = In posterior view, the fenestra ventrolateralis extends dorsal to the ethmoid articulation

- 199, 1→0 = rhomboid scales

Elpistostegalia:

- 48, 0→1 = prearticular contacts angular edge-to-edge
- 86, 1→0 = median postrostral absent
- 91, 0→1 = anterior nostril at edge of mouth
- 96, 0→1 = jugal/quadratojugal contact
- 103, 1→2 = ethmoid proportions ≤35%
- 113, 0→1 = frontals present
- 151, 0→1 = scapulocoracoid, large plate pierced by coracoid foramen
- 152, 0→1 = coracoid plate present
- 156, 0→1 = lateral component to glenoid orientation

Elpistostegalia minus *Panderichthys*:

- 44, 0→2 = no fang pairs on posterior-most coronoid
- 94, 0→1 = jugal extends anterior to front of orbit
- 95, 0→1 = jugal extends anterior to middle of orbit
- 106, 0→1 = anterior supraorbital 3x longer than broad
- 108, 0→1 = prefrontal much bigger than postfrontal
- 130, 1→0 = no fusion of supra and infraorbital canals
- 139, 0→1 = loss of opercular
- 143, 0→1 = loss of extrascapular bones
- 144, 0→1 = lost of posttemporals
- 165, 0→1 = ectepicondytlar processes extends distal to epipodial facets
- 170, 0→1 = radius is shorter than the humerus
- 181, 0→1 = expanded ribs present

Elpistostege + *Tiktaalik*:

- 99, 0→1 = contact between postorbital and lacrimal

Elginerpeton + remaining elpistostegalians:

- 21, 0→1 = mesial parasymphyseal foramen present
- 33, 0→1 = loss of Meckelian exposure in precoronoid fossa
- 46, 0→1 = forked prearticular
- 47, 0→1 = prearticular sutured to mesial lamina of splenial (i.e., mesial lamina of the splenial present)
- 50, 0→1 = well-defined dorsal longitudinal band of shagreen on prearticuular
- 161, 0→1 = square/parallelogram-shaped entepicondyle on humerus
- 195, 0→1 = fairly regular pit and ridge derma ornament
- 196, 0→1 = starbursts radiating on at least some bones
- 197, 0→1 = loss of cleithral ornamentation

Ventastega + remaining elpistostegalians:

- 39, 0→1 = anterior and middle coronoid teeth ≤½ the height of dentary teeth
- 40, 0→1 = anterior coronoid contacts splenial
- 53, 0→2 = posterior teeth ≥2x height of anterior teeth

Acanthostega + remaining elpistostegalians:

- 13, 0→1 = single large foramen in the hypophyseal region of braincase
- 35, 1→0 = posterior coronoid not substantially longer than anterior coronoids
- 132, 0→1 = mandibular line canal mostly enclosed but short sections with open grooves
- 133, 0→1 = no surangular pit line

Ichthyostega + remaining elpistostegalians:

- 23, 0→2 = dentary teeth smaller tan maxillary teeth
- 61, 0→1 = anterior wall of vomer lacks teeth along the ridge
- 76, 0→1 = medial exposure of dermopalatine, in addition to tooth roow
- 147, 1→2 = loss of anocleithrum
- 159, 1→2 = interclavicle with a posterior stalk
- 166, 0→1 = radius and ulna about equal in length
- 171, 0→1 = ulnar facet has some ventrally directed component
- 172, 0→1 = olecranon process present
- 184, 0→1 = at least some ventral component to ribs

Whatcheeria + remaining elpistostegalians:

- 21, 1→0 = no mesial parasymphyseal foramen
- 26, 1→2 = 1 unpaired dentary fang (i.e., no replacement pit)
- 42, 0→1 = posterodorsal process of posterior coronoid
- 60, 0→1 = no row of small teeth on the vomer
- 68, 0→1 = parasphenoid overlaps basioccipital
- 84, 0→2 = loss of anterior tectal

Pederpes + remaining elpistostegalians:

- 92, 1→0 = lacrimal contributes to orbital margin
- 94, 1→0 = jugal does not extend anterior to the anterior orbital margin

Greererpeton + remaining elpistostegalians:

- 138, 0→1 = loss of preoperculum
- 159, 2→1 = kite-shaped interclavicle (i.e., no posterior stalk)
- 182, 1→0 = loss of imbricate ribs
- 188, 1→0 = posterior process on ileum oriented posterodorsally

Crassigyrinus + remaining elpistostegalians:

- 53, 2→0 = all premaxillary teeth all the same size
- 91, 1→0 = facial position of anterior external nostril (not edge of mouth)
- 132, 1→3 = entirely open mandibular line canal
- 185, 1→0 = all ribs cylindrical

Baphetes + remaining elpistostegalians:

- 62, 0→1 = vomerine shagreen field present
- 74, 1→2 = anterior palatal fanestra absent
- 81, 0→1 = no row of 3+ smaller teeth on ectopterygoid
- 165, 1→0 = ectepicondylar process terminates proximal to epipodial facets

Stem-lissamphibians + stem-amniotes + embolomeres:

- 71, 0→1 = convex component to the ectopterygoid/quadratojugal in the subtemporal fossa
- 108, 1→0 = anterior and posterior surpraorbitals of similar size

- 131, 0→1 = loss of mandibular sensory line canal

Stem-lissamphibians (*Balanerpeton* + *Dendrerpeton*):

- 65, 2→0 = no contact (via gap – or simple abutment) between vomers and parasphenoid
- 70, 1→0 = entopterygoids do not meet at midline
- 75, 0→2 = interentopterygoid vacuities < 2x longer than wide

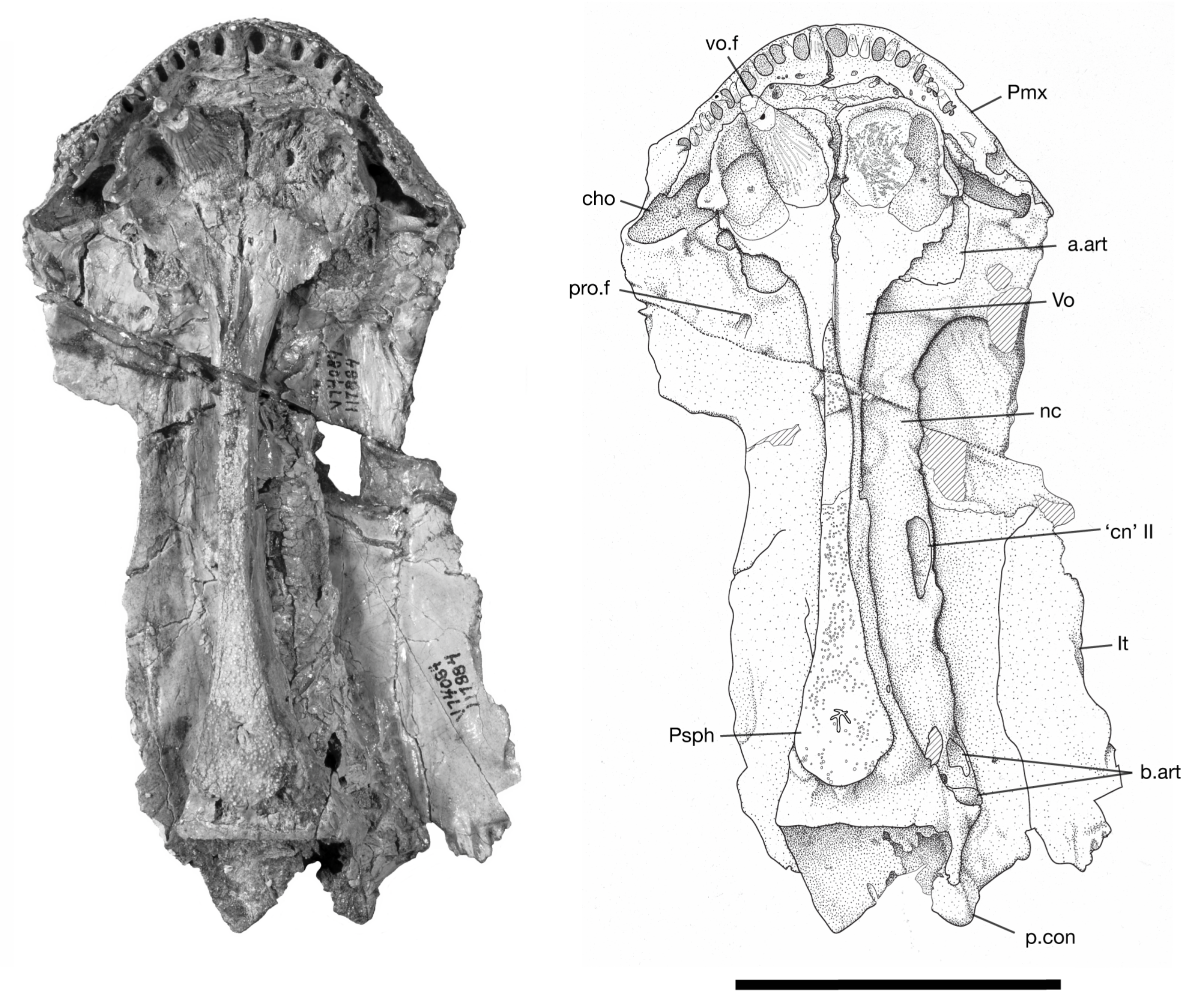
Stem-amniotes (*Sylvanerpeton* + embolomeres):

- 23, 1→0 = De teeth same size as Mx teeth
- 54, 0→1 = Mx does not extend behind posterior orbital margin
- 79, 1→0 = ectopterygoid does not reach subtemporal fossa

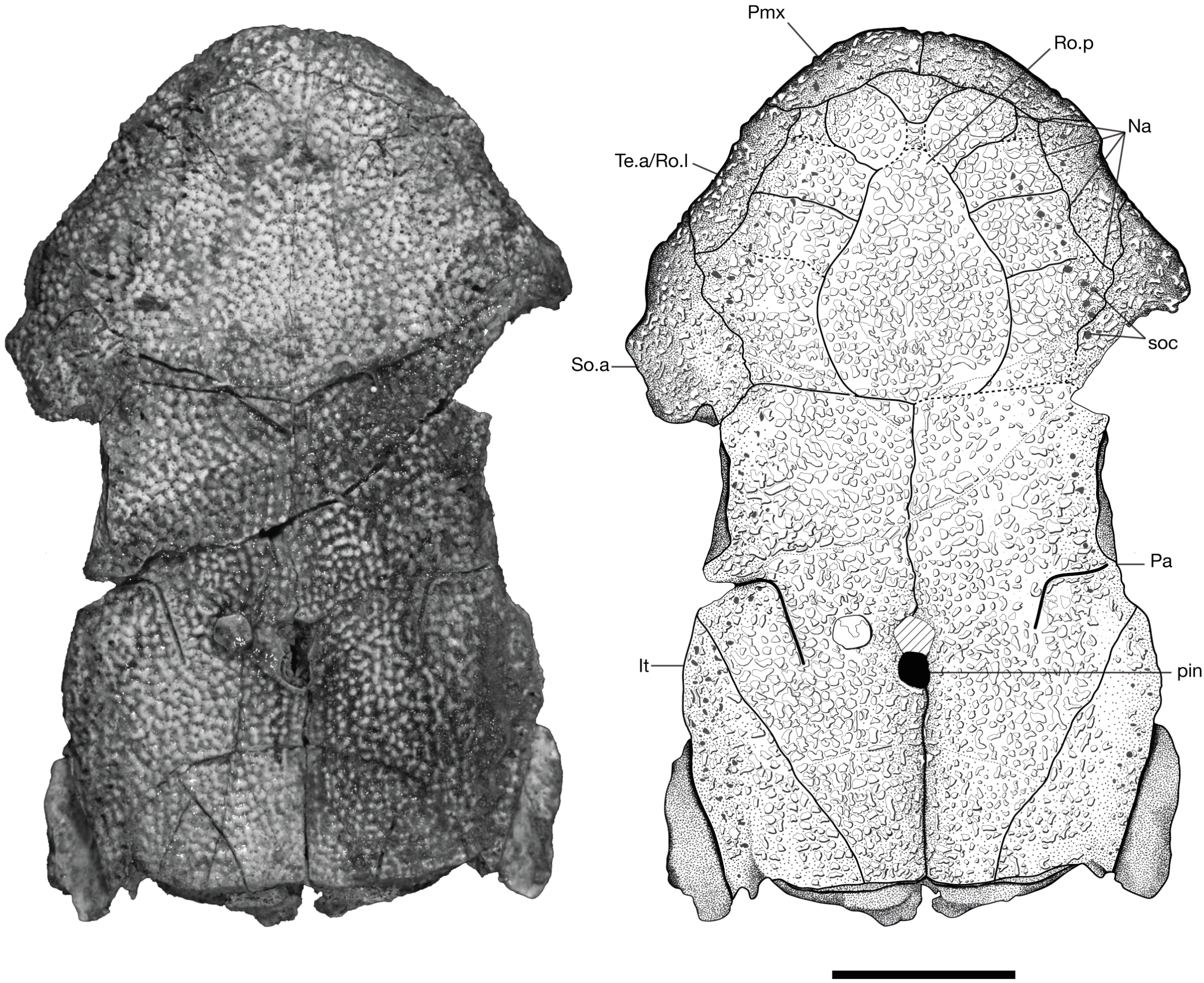
Embolomeres (*Proterogyrinus* + *Eoherpeton*):

- 51, 0→1 = Prearticular with mesially projecting flange on dorsal edge along posterior border of adductor fossa
- 66, 0→1 = denticulated field of parasphenoid absent

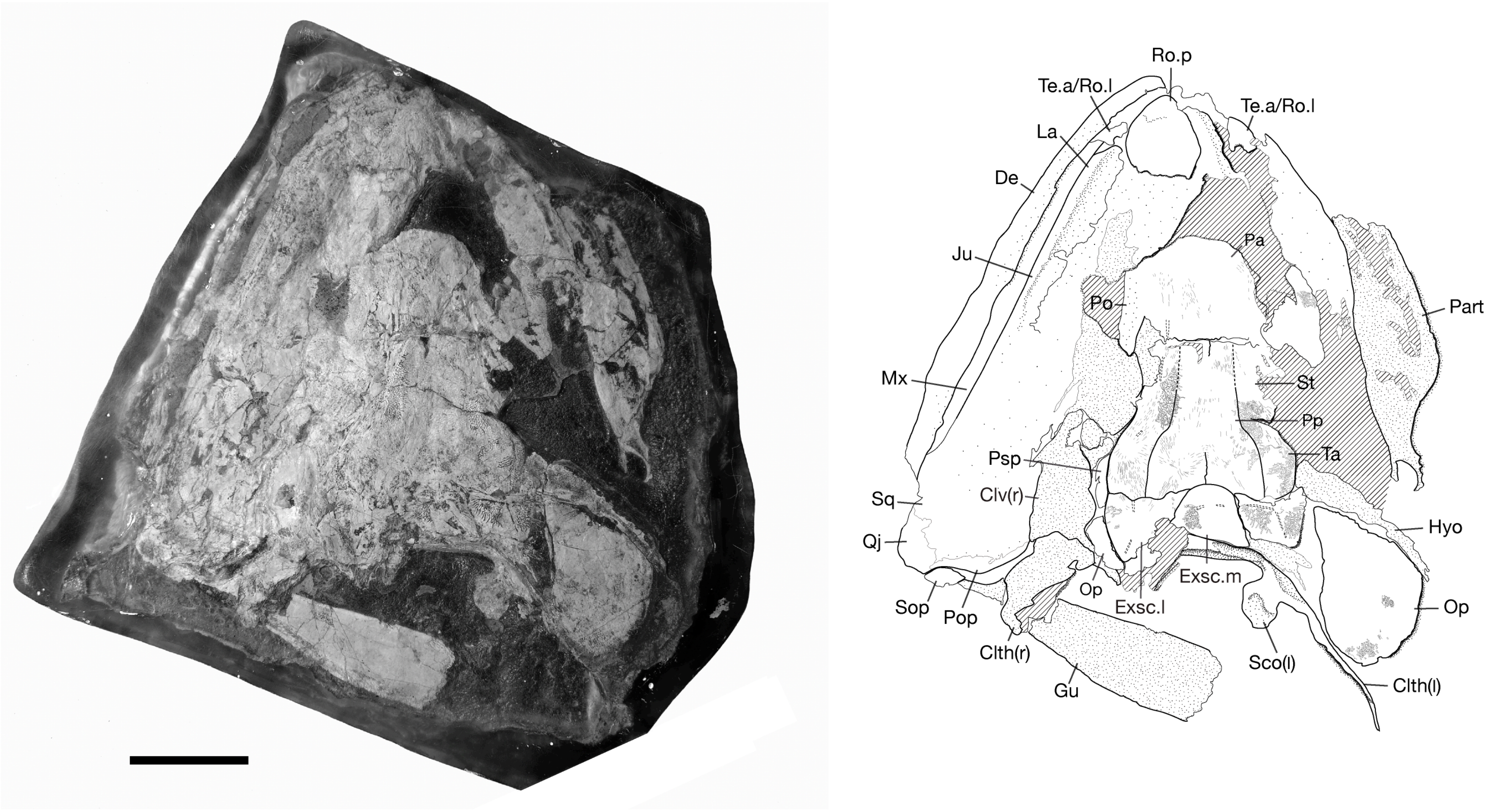
Figures



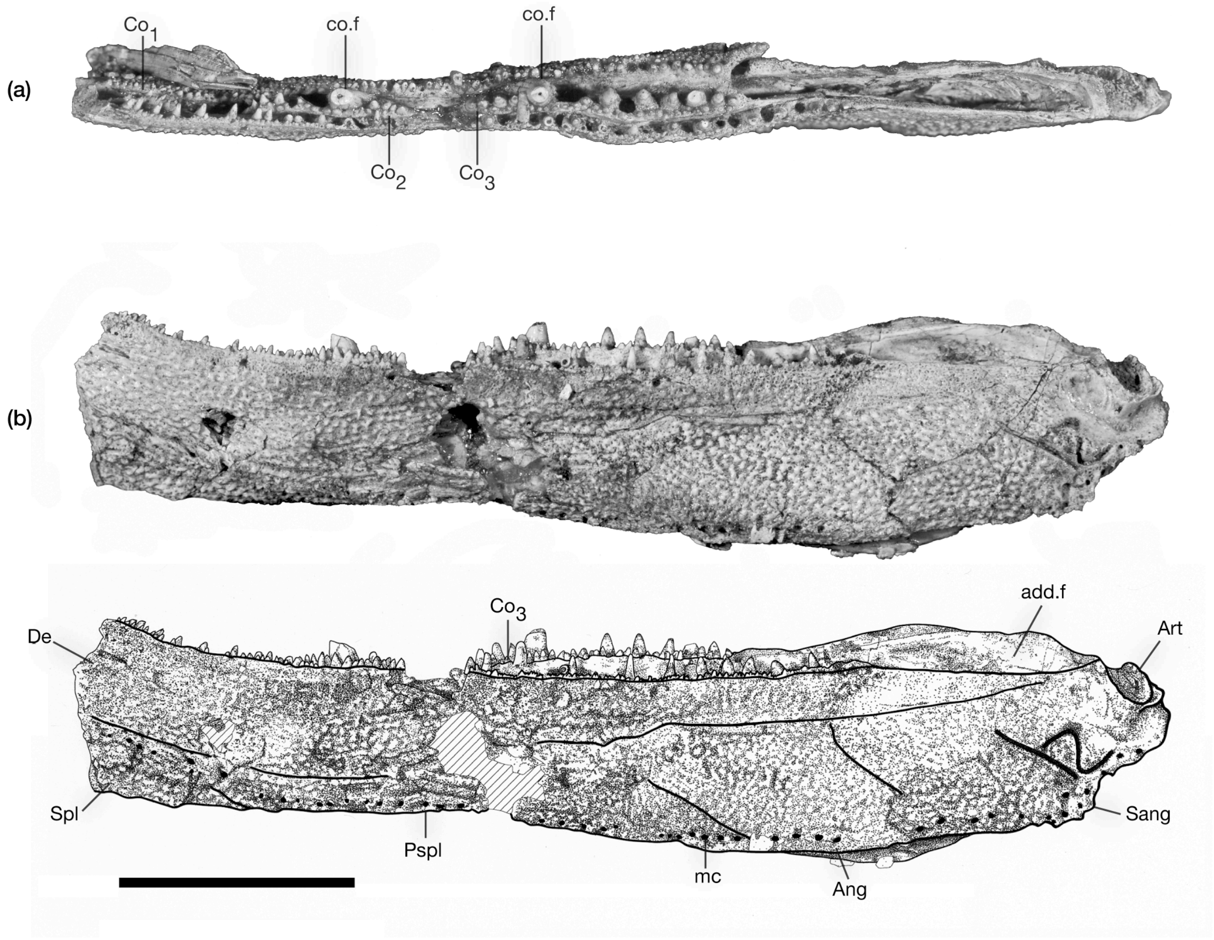
Supplementary Figure 2.1. Ethmoid palatal region and interpretive drawing of UCMP 117884. Anterior is toward the top of the page. Abbreviations: a.art, autopalatine articulation; b.art, basal articulation of basipterygoid process; cho, choana; 'cn' II, optic nerve; It, intertemporal, nc, neurocranium; p.con, processes connectens; Pmx, premaxilla; pro.f, profundus foramen; Psph, parasphenoid; Vo, vomer; vo.f, vomerine fang. 'CN' is in scare quotes because the optic nerve is not a real cranial nerve but a special-sensory extension of the diencephalon. Scale bar equals 5 cm.



Supplementary Figure 2.2. Ethmoid skull roof and interpretive drawing of juvenile specimen UCMP 118283. Aside from the fusion of the anterior tectal and lateral rostral (similar to the adult specimen, UCMP 117884), many of the remaining roofing bones are unfused. The snout of this specimen is also proportionally shorter than the adult (when pineal foramina are aligned), suggesting substantial allometric change during ontogeny. In addition, it lacks the recessed tongue-and-groove articulations spanning the dermal intracranial joint, suggesting acquisition later in life. Anterior is toward the top of the page. Abbreviations: It, intertemporal; Na, nasal; Pa, parietal; pin.f, pineal foramen; Pmx, premaxilla; Ro.p, median postrostral; So.a, anterior supraorbital; soc, supraorbital canal; Te.a/Ro.l, (fused) anterior tectal/lateral rostral. Scale bar equals 5 mm.



Supplementary Figure 2.3. Skull, partial shoulder, and interpretive drawing of UCMP 190999. Anterior is toward the top of the page. Abbreviations: Clth, cleithrum; Clv, clavicle; De, dentary; Exsc.l, lateral extrascapular; Exsc.m, median extrascapular; Gu, lateral gular; Hyo, hyomandibular; Ju, jugal; La, lacrimal; Mx, maxilla; Op, operculum; Pa, parietal; Part, prearticular; Pop, preoperculum; Pp, postparietal; Psp, postspiracular; Qj, quadratojugal; Ro.p, median postrostral; Sco, scapulocoracoid; Sop, suboperculum; Sq, squamosal; St, supratemporal; Ta, tabular; Te.a/Ro.l, (fused) anterior tectal/lateral rostral. (l) or (r) refers to left or right when displaced from natural side. Scale bar equals 5 cm.



Supplementary Figure 2.4. Lower Jaw of UCMP 123135. (a) Dorsal view; (b) lateral view and interpretive drawing. Left is anterior. Abbreviations: add.f, adductor fossa; Ang, angular; Art, articular; Co$_1$, anterior coronoid; Co$_2$, middle coronoid; Co$_3$, posterior coronoid; co.f, coronoid fang; De, dentary; mc, mandibular canal; Pspl, postsplenial; Sang, surangular; Spl, splenial. Scale bar equals 10 mm.

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CHAPTER THREE:
THE PALEOENVIRONMENTAL HISTORY OF STEM-TETRAPODS

Abstract

Interest in the environmental origin of the first digited sarcopterygians has been reinvigorated in recent years following the discovery of digit-bearing marine trackways from the early Middle Devonian (Eifelian) of Poland. The interpretation of stem-tetrapod paleoenvironments requires consideration of the evolution of physiological tolerances, osmoregulation, biogeography, and the near exclusive restriction of crown-group amphibians to freshwater environments. To test the paleoenvironmental origins question, I trace the environmental history of Devonian stem-tetrapods in a combined phylogenetic and paleoenvironmental analysis. Sedimentological, assemblage, and isotopic data are analyzed to elucidate how the Devonian rock record informs the evolution of tetrapodomorph habitats, and are used to reconstruct the ancestral environments of the first digit-bearing sarcopterygians. Data suggest that: (1) tetrapodomorphs (total-group tetrapods) evolved from either a freshwater or marginal marine origin; (2) both freshwater and marginal environments pervaded the early history of major groups, even though members of each clade were more often freshwater than not; (3) the first elpistostegalians moved into coastal environments; (4) later diverging elpistostegalians moved shoreward (most likely including the Polish trackmaker); and (5) the first digited sarcopterygian body fossils appear following at least four cladogenetic events in which extramontane freshwater habitats were the ancestral environment. Mollusks such as bivalves and gastropods also colonized freshwater at this time, which may suggest that the persistence of stem-tetrapods into the Carboniferous Earth-system may be linked to (1) their invasion into freshwater systems; and (2) the differential influence of Devonian events on continental and marine habitats.

Introduction and background

The paleoenvironmental origin of terrestrial vertebrates has been debated for nearly a century. Early analyses drew upon red beds from the Old Red Sandstone Continent (i.e., North America and Europe) to suggest that its landscape was subject to severe droughts that were linked to the origin of terrestriality and air breathing (Barrell 1916). Extending from this hypothesis, early vertebrates preserved in marine-influenced or nearshore marine environments were interpreted as allochthonous. Later work elaborated upon Barrell's (1916) red beds and drying ponds to argue that terrestrial vertebrates evolved from sarcopterygians driven onto land by freshwater droughts. In this respect, natural selection was argued to foster stem-tetrapods with locomotor adaptations (e.g., *Ichthyostega*, with its limbs, despite the fish-like tail) for moving among the drying ponds (Romer 1958). However, paleoenvironmental data were conflicting and the evidential basis of these drying ponds was coming under scrutiny. Red beds may not evidence consistently severe droughts after all (Krynine 1949), and the first digit-bearing taxa may have instead evolved in marginal aquatic environments (Cowles 1958, Gunter 1956, Inger 1957). Thus, many of Romer's (1958) pushing factors were modified into resource-driven pulling factors associated with living in humid, swampy, vegetative lake margins and wetlands

(Thomson 1969) or even estuarine environments (Thomson 1980). Other discoveries spanned this time (Vorobyeva 1962, 1977), but because of difficulties with phylogenetic methods and the limitations of evolutionary systematics, their importance in reconstructing the paleoenvironmental history of stem-tetrapods would not be recognized until later. Instead, when fully articulated polydactylous specimens of *Acanthostega gunnari* from the Upper Devonian (Famennian) of East Greenland were described and analyzed (Clack 1988, 1989, Coates and Clack 1990, 1991), freshwater environments became the locus for the first digited sarcopterygians. Debate continued with discoveries and reanalyses of several additional stem-tetrapods from freshwater and marine(-influenced) localities (Ahlberg et al. 1994, Ahlberg 1991, 1998, Ahlberg and Johanson 1997, Ahlberg et al. 2000, Clément et al. 2004, Daeschler et al. 2006, Daeschler et al. 1994, Johanson and Ahlberg 1997, Lebedev 2004, Lebedev and Clack 1993, Lebedev and Coates 1995, Long et al. 1997, Vorobyeva and Schultze 1991, Zhu et al. 2002), but the recent finding of early Middle Devonian (Eifelian) age, digit-bearing trackways in nearshore marine deposits of Poland (Niedźwiedzki et al. 2010) reinvigorated much interest in paleoenvironmental origins.

Digit-bearing taxa may have evolved from marine sarcopterygians (Cloutier and Lelievre 1998, George and Blieck 2011, Laurin and Soler-Gijon 2010, Schultze and Cloutier 1996), but it is important to distinguish among the shades of gray that diagnose aquatic habitats. Freshwater environments may be inter- or extramontane (i.e., landlocked with a pattern of internal drainage vs. coastal-plain deposits with large rivers, braided streams, and floodplains that often empty into the ocean), whereas marine environments range from marine-influenced (e.g., brackish or estuarine), to nearshore (e.g., intertidal or beach environments), or even coastal reef communities with shelf or basinal facies.

Here I explicitly test the paleoenvironmental origins question by assessing the relationship between the phylogenetic and paleoenvironmental histories of Devonian stem-tetrapods. I analyze sedimentological and assemblage data from 37 formations and localities that preserve stem-tetrapods, including more than 650 floral and faunal taxa, and map these data onto a phylogenetic tree of Devonian tetrapodomorphs. In contrast to Laurin and Solger-Gijón (2010), I avoid supertrees and construct my own phylogenetic hypothesis based on a broad sampling of Devonian taxa, and treat the sedimentological and assemblage data as potentially independent datasets. In addition, carbonate isotopes from over 45 samples of bone, matrix, and carbonate nodules from four localities were analyzed. However, aside from their general congruence with the other paleoenvironmental data, numerous bone and matrix samples did not contain carbonate. In this respect, even though isotopic results reinforce the emergent picture from other datasets, the larger pattern of paleoenvironmental evolution among Devonian stem-tetrapods is more greatly influenced by the sedimentological and assemblage analyses.

Following from this, also I integrate and test Thomson's (1980) five hypotheses about the environmental origin of digited sarcopterygians, and find that with respect to elpistostegalians, "marine hypothesis: variant II" is best supported by the data.

(1) *Freshwater hypothesis: variant I.*—The clade arose in freshwater and is restricted to freshwater. This predicts no marine fossils, and that taxa be restricted to inter- and extramontane environments of particular landmasses.

(2) *Freshwater hypothesis: variant II.*—Following a freshwater origin, certain taxa evolved tolerances to marine conditions. This predicts that fossils be largely freshwater but with a few marine

occurrences, that their distribution around a given landmass be large, and that their distribution among widely separated continents is unlikely.

(3) *Marine hypothesis: variant I.*—The clade of interest arose in marine conditions and radiated in shallow marine environments. This predicts that fossils only be found in marine rocks, and that they be distributed among shallow seas.

(4) *Marine hypothesis: variant II.*—The clade arose in wholly marine conditions, but part of its diversification includes taxa that invaded extramontane freshwater environments. This predicts that fossils be found in marine and extramontane environments, and should be widely distributed via shallow seas.

(5) *Marine hypothesis: variant III.*—The clade arose in a marine environment but proceeded through marine hypothesis II by the successful invasion of key members into intermontane environments. This predicts that range size should increase with the degree of marine tolerance, and that freshwater taxa should have narrow biogeographic ranges.

Materials and methods

Phylogenetic Analysis.—Numerous fossil taxa were examined to gain insight into the evolution of stem-tetrapod paleoenvironments. A phylogenetic analysis (Huelsenbeck 2001, Ronquist and Huelsenbeck 2003, Swofford 2002) of 43 taxa and 175 morphological characters was used to structure a topology upon which paleoenvironmental data were mapped; paleoenvironmental characters were not used to construct the cladogram. Characters were polarized by comparison to outgroup taxa such as *Porolepis*, *Glyptolepis*, *Powichthys*, *Youngolepis*, *Diabolepis*, and *Dipterus*. These taxa were selected because they represent a range of dipnomorphs (total-group lungfishes) that are known from reasonable material, are well studied, and generally accepted as sister to total-group tetrapods (Ahlberg and Johanson 1998, Snitting 2008a).

Tetrapodomorpha here defines total-group tetrapods, and I restrict the use of the term tetrapod to the crown-group (see Figure 3.1). I use the monophyletic definition of Elpistostegalia (Daeschler et al. 2006, Downs et al. 2008), although I apply it as a stem-based name to any tetrapodomorph more crownward than tristichopterids. In addition, following from the phylogenetic result presented below, I use Canowindridae as a stem-based definition to refer to the clade constituting *Marsdenichthys*, *Canowindra*, *Koharalepis*, and *Beelarongia*, I use the stem-based Megalichthyiformes (Coates and Friedman 2010) to reference the formerly paraphyletic (here recovered monophyletic, see supplementary information) 'osteolepidids', and I apply the stem-based Tristichopteridae to define any taxon more closely related to *Tristichopterus* than to *Elpistostege*. Specimen observations derive from the primary literature and first-hand observation of fossil material. See supplementary information for the taxon-by-character matrix and the list of examined taxa and specimens.

Paleoenvironmental Data and Analysis.—A survey of sedimentological data, isotopic composition, and floral/faunal assemblages was used to trace the history of stem-tetrapod paleoenvironments. Formations and/or localities for all dipnomorphs and tetrapodomorphs included in the phylogenetic analysis were analyzed for their paleoenvironmental signatures. All taxa are Devonian in age except the megalichthyid, *Cladarosymblema*, which is known from the Early Carboniferous (early-mid Viséan) of

Queensland, Australia (Fox 1995). The Russian megalichthyiform *Medoevia* was excluded from the paleoenvironmental analysis because its locality and formation are unknown (Lebedev 1995). All other taxa included in the phylogenetic analysis are present at a locality (or set of localities), that in turn lies within a geological formation (or formations, depending upon stratigraphic range). These data were organized as a function of: (1) stem-tetrapod or stem-lungfish locality; (2) fossil plant, invertebrate, and vertebrate taxa also present at the locality; (3) formation(s) containing the locality or localities of interest; (4) plant, invertebrate, and vertebrate taxa known elsewhere from the formation; (5) facies data for locality and formation if available for both; (6) paleoenvironmental interpretation based on sedimentology; and (7) age. However, there were several caveats to organizing these data. They include:

(1) In some cases, where local and regional geology are poorly resolved, the locality was treated as an entity independent of its formation. This isolated case includes the Scottish locality, Scat (=Scaat) Craig (for *Elginerpeton*) (Ahlberg 1991, 1995, 1998).

(2) In other cases, localities and formations were treated together. These include the Mount Howitt locality (Bindaree Formation (Long 1985, 1987, O'Halloran and Gaul 1997b)), the Canowindra fish fauna (Mandagery Sandstone Formation (Ahlberg and Johanson 1997, Young 1999)), the Lode Quarry (Gauja Formation (Ponten and Plink-Bjorklund 2007, 2009, Upeniece 2001)), the Pasta Muiza locality (Amata Formation (Ponten and Plink-Bjorklund 2009)), the Snezha beds (Snezha Formation (Zhuravlev et al. 2006)), the Jemalong Quarry (Cloghnan Shale Formation (Blieck et al. 2010, Campbell and Bell 1977, Young 1999)), and the *Sinostega* locality (Zhongning Formation (Zhu et al. 2002)). Stem-tetrapods sampled from these localities include *Beelarongia, Marsdenichthys, Gooloogongia, Canowindra*, *Cabonnichthys*, *Mandageria*, *Livoniana*, *Panderichthys*, *Platycephalichthys*, *Metaxygnathus*, and *Sinostega*. In all cases except Zhongning, floral and faunal data are well-known from the localities but poorly known from the remainder of their formations. By contrast, flora and fauna are well-known from the Zhongning Formation but not from the *Sinostega* site in particular. Because of this difference, these localities and formations were treated as individual units. Moreover, because few other taxa are described from the NV2K17 site of the Fram Formation (*Tiktaalik*) (Daeschler et al. 2006), this locality and formation were treated together as well.

(3) Similarly, other taxa with (a) unknown localities but known formations; or (b) broad stratigraphic ranges and thus from temporally diachronous localities, were also treated with their containing formations. Examples include *Porolepis* from the Wood Bay Formation (Harland 1997, Jarvik 1972), *Youngolepis* from the Xiaxishancun, Xitun, and Guijiatun Formations (Chang and Yu 1981, Chang and Zhu 1993, Zhao and Zhu 2010), *Diabolepis* from the Xitun Formation (Chang and Yu 1984, Zhao and Zhu 2010), *Kenichthys* from the Chuandong assemblage in the Chuandong Formation (Chinese localities: Qujing, Zhaotong, Pingle) (Chang and Zhu 1993, Zhao and Zhu 2010), *Koharalepis* and *Mahalalepis* from the Fish Hotel localities in the Aztec Siltstone Formation (Young and Long 2005, Young 1992), *Spodichthys* from an unknown locality in the Sofia Sund Formation (Blom et al. 2007, Jarvik 1985, Snitting 2008b), *Tristichopterus* from the south Ronaldsay locality in the Eday Flagstone Formation (Egerton 1861, Newman and Dean 2005), *Eusthenopteron* and *Elpistostege* from the Miguasha locality of the Escauminac Formation (Andrews and Westoll 1970, Cloutier et al. 1996, Schultze and Arsenault 1985), *Jarvikina* from the Porkhov (Stolbovo) and Svinord beds of the Rdeyskoe Formation (Vorobyeva 1962, 1977, 2004, Zhuravlev et al. 2006), *Obruchevichthys* from an

unknown locality (Velna Ala, western Russia) in the Ogre Formation (Esin et al. 2000, Lukševics 2001, Vorobyeva 1977), *Acanthostega* and *Ichthyostega* from Gauss Halvø of the Aina Dal Formation (Blom et al. 2007, Jarvik 1952), *Eusthenodon* and *Ichthyostega* from Ymer Ø of the Britta Dal Formation (Blom et al. 2007, Jarvik 1952, 1996), and LUPC 6106 (the '*Ichthyostega*-like' jaw) from the Strüd locality of the Evieux Formation (Clément et al. 2004, Janvier and Clément 2005).

(4) By contrast, some localities lack extensive stratigraphic ranges. They were analyzed independent of and in addition to the formations they fall within. Such cases include the Sigurdfjellet Division of the Wood Bay Formation (*Powichthys*) (Clément and Janvier 2004, Harland 1997), the Home Station Sandstone Member of the Snowy Plains Formation (*Barameda*) (Garvey and Hasiotis 2008, Long 1989), the Gogo fish fauna of the Gogo Formation (*Gogonasus*) (Long et al. 1997, Long and Trinajstic 2010, Wade 1936), the Achannaras Quarry of the Lybster Flagstone Formation (*Dipterus, Glyptolepis, Gyroptychius, Osteolepis*) (Jarvik 1948, 1950, 1972, Newman and den Blaauwen 2007, White 1965), the Police Mountain Track locality of the Raymond Formation (*Cladarosymblema*) (Fox 1995), the Red Hill I beds of the Denay Formation (*Tinirau*) (Johnson 1977, Pedder 2010, Reed 1980), the Red Hill locality of the Catskill Formation (*Hynerpeton*) (Brezinski et al. 2009, Daeschler et al. 1994), the Gornostayevka Quarry of the Zadonsk Formation (*Jakubsonia*) (Lebedev 2004, Moloshnikov 2008), the Pavari and Ketleri sites of the Ketleri Formation (*Ventastega*) (Ahlberg et al. 1994), and the Andreyevka-2 locality of the Khovanshchina Formation (*Tulerpeton*) (Lebedev 1992, Lebedev and Clack 1993).

In addition, the Red Hill I beds of Nevada, USA were originally a part of the underlying Denay Formation, but they were later excluded and informally given their current name (Johnson 1977). Following this history, and to place these beds in a larger stratigraphic context, I have treated the Denay Formation as the unit that contains the Red Hill I beds. Also, even though stem-tetrapod body fossils are absent from the Zachełmie Quarry (Wojciechowice Formation) in Poland, because of the age, paleoenvironment, and interest in these trackways data (Niedźwiedzki et al. 2010), this locality and formation were included together in the paleoenvironmental analysis.

Early Devonian localities/formations (e.g., the Wood Bay, Xiaxishancun, Xitun, Guijiatun, and Chuandong Formations) were excluded from the final assemblage analysis because their flora and fauna are too different from the remaining Middle and Late Devonian formations. In this respect, there appeared to be an overprint of biostratigraphy upon an analysis aimed at reconstructing paleoenvironments. Their inclusion clumped all later localities/formations together, and thus cluttered the pattern of marine-to-freshwater continuity otherwise obtained by a sole focus on the Middle-Late Devonian. Because the aim here was to resolve the paleoenvironmental history of stem-tetrapods, not stem-lungfishes, these formations/localities were dropped in the final assemblage analysis. It is important to note, however, that even though assemblage data from these formations were excluded from the comparative analysis, sedimentological data from these dipnomorph localities were mapped on to the phylogenetic result presented below.

Floral and faunal data from included formations were tallied and arranged (a) taxonomically; and (b) by locality and/or formation, in a data matrix using the Apple software, Numbers '09. Because localities and formations are nested data, a taxon present at a locality was also scored as present within the larger formation, but not vice versa, because taxa present elsewhere in the formation may not necessarily also exist at the locality of interest. The final list of localities and formations for the floral/faunal matrix (and analysis) are as follows, roughly ordered by the branching pattern of stem-tetrapods from the phylogenetic analysis presented below: (1) Home Station Sandstone Member of the Snowy Plains Formation; (2) Snowy Plains Formation; (3) Aztec Siltstone Formation (containing the "Fish Hotel" sites, horizons A-Z); (4) Bindaree Formation (including the Mt. Howitt locality); (5) Mandagery Formation (including the Canowindra fish fauna); (6) Gogo fish fauna (mostly of the *transitans* Conodont Zone) of the Gogo Formation; (7) Gogo Formation; (8) Achannaras Quarry of the Lybster Flagstone Formtaion; (9) Lybster Flagstone Formation; (10) Police Mountain Track Locality of the Raymond Formation; (11) Raymond Formation; (12) Sofia Sund Formation; (13) Eday Flagstone Formation (including the south Ronaldsay locality); (14) Rdeyskoe Formation (including the Porkhov and Svinord beds); (15) Red Hill I locality of the Denay Formation; (16) Denay Formation; (17) Snezha Beds (of the Snezah Fm); (18) Gauja Formation (including the Lode Quarry); (19) Amata Formation (including the Pasta Muiza locality); (20) Escuminac Formation (including the Miguasha locality); (21) Fram Formation (including the NV2K17 site); (22) Scat Craig locality; (23) Cloghnan Shale (including the Jemalong Quarry); (24) Red Hill, Pennsylvania locality of the Catskill Formation; (25) Catskill Formation; (26) Ogre Fm (including the Velna-Ala locality); (27) Gornostayevka locality of the Zadonsk Formation; (28) Zadonsk Formation; (29) Zhongning Formation (including the Ningxia Hui Site/*Sinostega* locality); (30) Pavari Site of the Ketleri Formation; (31) Ketleri Formation; (32) Aina Dal Formation (including Gauss Halvø); (33) Britta Dal Formation (including Ymer Ø); (34) Evieux Formation (including the Strüd locality); (35) Andreyevka-2 locality of the Khovanshchina Formation; (36) Khovanshchina Formation; (37) Wojciechowice Formation (including the Zachełmie Quarry).

Cells in the resulting matrix were coded as 1s and 0s for taxonomic presences and absences, respectively. Included taxa were based on their finest resolvable Linnaean rank. Most taxa comprise genus and species data, although some result from genus-only observations. Moreover, in some cases, examples such as "Conchostraca" (and equivalent higher clades) were the finest available unit. In these cases, a larger category (e.g., conchostracans) was created in the database, and sites were scored as present for this taxon when genus and species, genus-only, and non-descript clade-level presences were observed. For example, only "choncostracans" are noted from the Aztec Siltstone Formation in Antarctica (Woolfe 1990). However, the conchostracan *Asmusia membranacea* is known from the Escuminac Formation of Canada in particular (Martens 1996). Following from this higher-level order, both formations were scored as having conchostracans, though only the Escuminac formation received a "1" for that taxon specifically. Moreover, in other cases, I created higher-level groups like land plants, sponges, ostracodes, polychaetes, brachiopods, and conodonts, especially since different clade members were frequently present at different sites. Aside from the fact that many of these groups are paleoenvironmental indicators, establishing a level of taxonomic redundancy helped to find patterns that would have otherwise been missed. In addition, where possible, a similar level of redundancy was added at the genus level when more than one species of a genus were noted from different sites. This kind of hierarchy is common in database construction. For example, patterns related to latitudinal diversity gradients would have been missed if analyses had been restricted to the species level (Valentine and Jablonski 2010, Valentine et al. 2008). However, higher-level order was carefully kept to a minimum, especially since excessive tiers can impose artificial similarities among sites. In particular, groups like "spores," "vertebrates," or "gnathostomes"—grades and clades that would have effectively been present at nearly every site—were not built into the database.

A canonical correspondence analysis (CCA) of the assemblage data was conducted using the deconstructed standardization ("decostand") function (Anderson et al. 2006, Legendre and Gallagher 2001, Oksanen 1983) in the vegan package (Oksanen et al. 2011) of R. version 2.13.1 (R Development Core Team 2011). The decostand function was of particular interest because in a canonical correspondence analysis, it standardizes and log-transforms the presence/absence matrix to make sure that particular sites (i.e., those that preserve greater taxonomic diversity) do not cluster with other similar high diversity sites. This was important because sites range from a taxon diversity of n=4 (the Police Mountain Track locality of the Raymond Formation) to n=129 (the Gogo Formation). However, the mean and median numbers of taxa per site are 27.5 and 20, respectively.

Isotopic Analyses.—Carbonate isotopes were sampled from matrix, bone, and carbonate nodules from select localities. Access and availability of material, more than anything else, determined which localities were analyzed. Matrix was tested from the six facies of the Strüd locality in Belgium, bone and matrix from the Red Hill, PA and Aztec Fish Hotel localities in the USA and Antarctica, respectively, and matrix, bone, and carbonate nodules from the NV2K17 site in Ellesmere Island. See supplementary information for the list of specimens analyzed.

Material was ground into a fine powder with a mortar and pestle and cleaned with acetone and a Kim Wipe between samples. Samples containing about 10 to 100 micrograms of calcite/aragonite were used for both carbon and oxygen isotope analyses, which were determined using a GV IsoPrime mass spectrometer with Dual-Inlet and MultiCarb systems in the Laboratory for Environmental and Sedimentary Isotope Geochemistry (LESIG) at Department of Earth and Planetary Science, University of California, Berkeley. Several replicates of one international standard NBS19 and two lab standards were measured along with samples for each run. The overall external analytical precision is +0.04‰ for $\delta^{13}C$ and +0.07‰ for $\delta^{18}O$. The S-isotope composition is determined by SO_2 EA-combustion method with the Eurovector Elemental Analyser (EuroEA3028-HT) and the analytical precision is better than 0.2‰.

Results

Phylogenetic Analysis.—A parsimony analysis using PAUP (Swofford 2002) recovered nine equally most parsimonious trees. A Bayesian analysis (Huelsenbeck 2001, Ronquist and Huelsenbeck 2003) of the same data provided an additional metric. Two polytomies are present, and include trichotomies among (1) *Elginerpeton*, *Obruchevichthys*, and the *Ichthyostega*-like jaw taxon from Belgium; and (2) *Ichthyostega*, *Hynerpeton*, and *Tulerpeton*. There are no polytomies among non-elpistostegalians, and the major clades, Rhizodontidae, Canowindridae, Megalichthyiformes, and Tristichopteridae form successive sister taxa to more crownward groups (Figure 3.1).

This is the first phylogenetic analysis to include the Belgian *Ichthyostega*-like taxon, the Russian taxon, *Jakubsonia*, and the Chinese taxon, *Sinostega*, among other Devonian stem-tetrapods. Interestingly, and despite its common reference as an ichthyostegid (Blieck et al. 2007, Clément et al. 2004, Clément and Letenneur 2009), the Belgian taxon emerged not with *Ichthyostega* but with *Elginerpeton* and

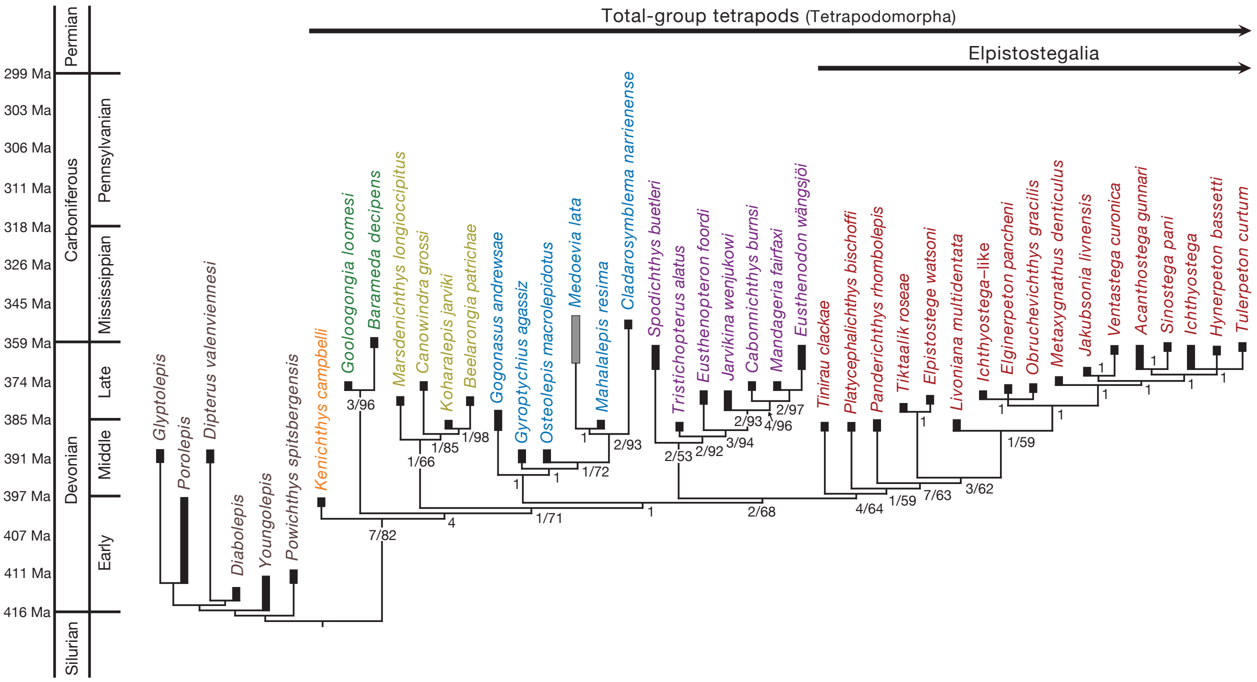

Figure 3.1. Interrelationships among Devonian and select Carboniferous stem-tetrapods. Analysis includes 43 taxa and 175 characters. Tree length=342, consistency index=0.61111, retention index=0.80584. Numbers corresponding to respective nodes represent: Bremer decay value / Bayesian posterior probability. Ghost ranges are calibrated after the early Middle Devonian (Eifelian) Zachełmie footprints (Niedźwiedzki et al. 2010) and "scenario 1" from Friedman and Brazeau (2011). Total-group lungfishes are in brown; tetrapodomorphs include all taxa that are not total-group lungfishes. Rhizodonts are in green, canowindrids are in yellow, megalichthyiforms are in blue, tristichopterids are in purple, and elpistostegalians are in red. The character list and data matrix are available as supplementary information.

Obruchevivhthys, united by a distinct furrow along the dentary-splenial suture. In addition, *Sinostega* emerged as sister to *Acanthostega* (similarly, united by lower jaw characters), and *Jakubsonia* as sister to *Ventastega* (united by features of the dermal skull roof and shoulder). See supplementary information for the taxon-by-character matrix and character optimizations for further details. Aside from these newly included taxa, *Tiktaalik* and *Elpistostege* form a newly supported clade united by postorbital-lacrimal contact. However, remaining topologies crownward of *Panderichthys*—e.g., the position of *Livoniana* and the relationship between *Elginerpeton* and *Obruchevichthys* (Ahlberg et al. 2000), the positions of *Metaxygnathus* and *Ventastega* relative each another and more crownward groups (Ahlberg et al. 2008, Ahlberg et al. 2000, Ruta et al. 2003), and the more crownward positions of *Ichthyostega* and *Hynerpeton* relative to *Acanthostega* (Ahlberg 1998, Coates 1996, Ruta et al. 2003)—are consistent with previous studies.

Paleoenvironmental Data.—An extensive survey of the 34 aforementioned formations and one locality for which formation data were lacking (Scat Craig) is presented below. Where available, data are organized by: (1) the locality of interest; (2) fossil plant, invertebrate, and vertebrate taxa also present at the locality; (3) the formation(s) containing the locality or localities; (4) plant, invertebrate, and vertebrate taxa known elsewhere from the formation; (5) facies data for locality and formation if available for both; (6) paleoenvironmental interpretation based on sedimentology; and (7) age.

Early Devonian Paleoenvironments

Xiaxishancun, Xitun, and Guijiatun (*Youngolepis & Diabolepis*):

Youngolepis is known from the Xiaxishancun, Xitun, and Guijiatun Formations of China. These three formations of the lower Cuifengshan Group are Lochkovian to early Pragian in age (Chang and Zhu 1993, Zhao and Zhu 2010). In contrast to *Youngolepis*, *Diabolepis* is restricted to the Xitun Formation. All three formations consist of marine-continental transitional facies. In particular, Xiaxishancun preserves marine tidal flat deposits, which become less common than estuarine sediments as one goes upsection into the Xitun and Guijiantun Formations (Kenrick and Li 1998). See Tables 3.1-3.3 for the flora and fauna of these formations.

Table 3.1. Taxa from the early-mid Lochkovian Xiaxishancun Formation, China.

TAXON			REFERENCE
PLANTS:	*Emphanisporites* sp.	ACRITARCHS	(Kenrick and Li 1998, Lianda 1981, Racheboeuf et al. 2005)
	Leiotriletes sp.		
SPORE TAXA	*Retusotriletes dittonensis*	DASYCLADALEAN ALGAE	
Apiculiretusispora picata	*R.* cf. *warringtonii*	*Chovanella* sp.	
Apiculiretusispora sp.	*R. minor*	*Discinella cuifengshanensis*	
Archaeozonotriletes chulus var. *nanus*	*R.* sp.	*Emplectophycus yunnanensis*	
	Streelispora newportensis	*Uncatoella verticillata*	
Brochotriletes sp.	*Synorisporites labutus*		
Chelinospora cassicula	*S.* cf. *verrucatus*	LAND PLANTS	
Clivosisporites verrucata	*S.* sp.	*Zosterophyllum* sp.	
Cymbosporites proteus			

INVERTEBRATES: OSTRACODES *Beyrichia* sp. *Cryptophyllus* sp.	*Leperditia* sp. *Sinoleperditia guangxiense* CHITINOZOANS	BRACHIOPODS *Lingula* sp. BIVALVES *Dysodonata*	(Kenrick and Li 1998, Racheboeuf et al. 2005)
VERTEBRATES: THELODONTS *Amaltheolepis winsneri* *Parathelodus scitulus* *P. trilobatus* *P. cornuformis* GALEASPIDS *Damaspis vartus* *Diandongaspis xishancunensis* *Dongfangaspis yunnanensis* *D. paradoxus* *D. qujingensis* *Laxaspis qujingensis* *L. rostrata* *Pentathyraspis pelta*	*Polybranchiaspis liaojiaoshanensis* *P. minor* *P. yulongssus* *P. zhanyiensis* *Nochelaspis maeandrine* *Stephaspis dipteriga* *Yunnanogaleaspis major* ANTIARCHS *Chuchinolepis gracilis* *Heteroyunnanolepis qujingensis* *Minicrania lirouyii* *Phymolepis cuifengshanensis* *Qujinollepis sp.* *Yunnanolepis chii* *Y. parvus*	*Yunnanolepis porifera* *Zhanjilepis aspratilis* PETALICHTHYIDS *Diandongpetalichthys liaojiaoshanensis* ARTHRODIRES *Szelepis* sp. STEM-SARCOPTERYGIANS *Psarolepis romeri* *Achoania jarviki* DIPNOMORPHS *Diablepis* *Youngolepis*	(Liu 1965, 1975, Zhao and Zhu 2010)

Table 3.2. Taxa from the mid-late Lochkovian Xitun Formation, China.

TAXON			REFERENCE
PLANTS: SPORE TAXA *Apiculiretusispora picata* *Apicuiatisporites microcanonus* *Breconisporites breconensis*	*Emphanisporites neglectus* *Stenozonotriletes pusillus* *Streelispora newportensis* DASYCLADALEAN ALGAE *Uncatoella verticillata*	LAND PLANTS *Zosterophyllum shengfengense* *Z. minorstachyum*	(Hao et al. 2010, Jinzhuang 2009)
INVERTEBRATES: OSTRACODES *Beyrichia xicunensis* *B. cuifengshanensis* *Beyrichia (Simplicibeyrichia) sinensis*	*Gannibeyrichia hudishanensis(=Hexophthalmoides yunnanensis)* *Leperditia* sp. *Sinoleperditia* cf. *Yulingensis* *S. liujingensis* *S. subbrevis*	BIVALVES *Dysodonta deprati* *Modiella* sp. *Modiolopsis yunnanensis* BRACHIOPODS *Lingula* sp.	(Ma et al. 2009, Racheboeuf et al. 2005)

VERTEBRATES: Galeaspids *Cyclodiscaspis ctenus* *Eugaleaspis changi* *Hyperaspis acclivi* *Laxaspis qujingensis* *Microholonaspis microthyris* *Nanpanaspis microculus* Antiarchs *Chuchinolepis gracilis* *C. qujingensis* *C. sulcata* *C. robusta* *Heteroyunnanolepis qujingensis*	*Phymolepis cuifengshanensis* *P. guoruii* *Yunnanolepis chii* *Y. parvus* *Y. porifera* *Zhanjilepis aspratilis* Arthrodires & Phyllolepids *Gavinaspis convergens* *Szelepis yunnanensis* (Stem-)chondrichthyans *Gualepis elegans* *Changolepis tricuspidus* *Ohiolepis? xitunensis* *Peilepis solida* Petalichthyids	Unsorted 'acanthodians' *Nostolepis* *Youngacanthus gracili* (Stem-)sarcopterygians *Psarolepis romeri* *Achoania jarviki* *Meemannia eos* *Styloichthys changae* Dipnomorphs *Diabolepis* *Youngolepis*	(Chang and Yu 1981, 1984, Dupret and Zhu 2008, Liu 1965, 1975, Pan 1992, Wang 1995, Zhu 1996, Zhu and Yu 2002, Zhu et al. 2001, Zhu et al. 1999, Zhu et al. 2006)

Table 3.3. Taxa from the early Pragian Guijiatun Formation, China.

TAXON			REFERENCE
PLANTS Spore taxa *Apiculiretusispora minuta* *A. polygonalis* *A. picata* *A.* cf. *spicula* *Archaeozonotriletes chulus* var. *chulus* *A. chulus* var. *nanus*	*Crissisporites guangxiensis* *Cymbosporites* cf. *minutus* *Retusotriletes dittonensis* *R.* cf. *dubius* *R.* cf. *warringtonii* *R. triangularis* *Streelispora newportensis* *Stenosonotriletes insessus* *Tholisporites* sp.	Acritarchs *Lophosphaeridium pilosum* *Micrhystridium* cf. *raspa* Land plants *Zosterophyllum australianum* *Z. myretonanum*	(Lianda 1981, Wang 1995)
INVERTEBRATES:			-
VERTEBRATES: Galeaspids *Yunnanogaleaspis* sp.	Antiarchs *Chuchinolepis* sp.	Dipnomorphs *Youngolepis*	(Wang 1995, Zhao and Zhu 2010)

Wood Bay (*Porolepis & Powichthys*):

Porolepis spans the entirety of the Wood Bay Formation of Spitsbergen (Harland 1997), although *Powichthys* is restricted to the lower Kronprinshøgda and Sigurdfjellet divisions (Clément and Janvier 2004). This formation is considered early Pragian through Emsian in age (Harland 1997), though some evidence suggests slightly different estimates that range from late Lochkovian (based on vertebrates (Goujet 1984)) to the middle Emsian (based on spore data (Allen 1967)) or early Eifelian (based on vertebrates (Ørvig 1969)). Sedimentological data suggest a few patterns that describe the depositional settings of the Wood Bay Formation: (1) continental molasse deposition under arid to semi-arid climatic conditions in three main depositional environments, (a) rivers; (b) alluvial plains; and (c) perennial lakes. This is evidenced by river channel deposits consisting of conglomerates and coarse to fine-grained sandstones arranged in fining-upward sequences, fine-grained sandstones to sandy siltstones and silty mudstones of overbank areas, and various lithofacies that reflect the formation of palaeosols, flood lakes, and boggy areas with high water tables (Blomeier et al. 2003); and (2) a similar depositional environment—but—located in a coastal setting with marine incursions. Many of the trace fossils (e.g., *Beaconites*, *Merostomichnites*, *Planolites*, *Siskemia*) are more typical for siliciclastic, fluvio-lacustrine environments. However, the arthropod traces (e.g., the phyllocarid crustacean *Svalbardichnus trilobus*, and the trilobite *Cruziana polaris*) are primarily marine (Friend and Moody-Stuart 1972, Wisshak et al. 2004). In addition, the inarticulate brachiopod *Lingula* appears in the uppermost Wood Bay Formation (Goujet 1984), where the freshwater charophyte *Trochiliscus* disappears (Racki 1982). Similar to the marginal marine Ben Nevis Formation (immediately below the Wood Bay Formation), this faunal/floral turnover may represent a transition to the marginal marine Grey Hoek Formation immediately above (Harland 1997). See Table 3.4 for the plants, invertebrates, and vertebrates known from the Wood Bay Formation.

Table 3.4. Taxa from the Early Devonian Wood Bay Formation, Spitsbergen.

TAXON			REFERENCE
PLANTS: Spore taxa *Ancyrospora trocha* *A. reuta* *Archaeozonotriletes meandricus* *Aulicosporites aulicus* *Bullatisporites ballatus* *Calamospora microrugosa* *C. nigrata* *C. witneyana* *Camptozonotriletes aliquantus* *Chelinospora perforata* *Craspodispora craspeda* *Cyclogranisporites plicatus* *Cyclogranulosporites plicatus* *Emphanisporites rotatus*	*E. neglectus* *E. minutus* *E. patagiatus* *Geminoapora svalbarine* *G. spinosa* *G. diamphida* *Granulatiaporites muninensis* *Leiotriletes pyramidalis* *L. parvus* *Perotrilites eximius* *P. ergatus* *P. pannosus* *Punctatisporites glaber* *P. laevigatus* *P. flavus* *Reticulatisporites emsiensis* *Rhabdoaporites cymatilus*	*Ryatricosporites mitratus* *Stenosonotriletes furtivus* *S. insessus* *Tholisporites ancylus* *Trileiten oxfordiansis* Charophytes Gyrogonites *Chara* sp. *Trochiliscus* sp. Land plants *Baringophyton* sp. *Bucheria longa* *Hostimella atrictissima* *Platyphyllum* sp. *Psilophyton* sp.	(Collins and Donovan 1977, Friend 1961, Racki 1982)
INVERTEBRATES: Ichnotaxa *Beaconites baretti* *Cruziana polaris* (a trilobite) *Diplichnites* sp. *Merostomichnites* sp.	*Planolites* sp. *Ruzophycus* sp. (a trilobite) *Siskemia* cf. *elegans* *Skolithos helicoidalis* *Svalbardichnus trilobus* (a phyllocarid) *Undichna septemsulcata*	Ostracodes *Isochilinina elliptica* *Holtedahlina teres* Polychaetes *Spirorbis* sp. Brachiopods	(Friend 1961, Ilyes 1995, Janvier et al. 1985, Volohonsky et al. 2008, Wisshak et al. 2004)

VERTEBRATES: HETEROSTRACANS *Amaltheolepis* sp. *Doryaspis arctica* *Doryaspis nathorsti* *Ennosveaspis minor* *Gigantaspis bocki* *Gigantaspis minima* *Hornalaspidella nitida* *Sigurdia* sp. *Xylaspis (=Spitsbergaspis) prima* *Turinia* sp. *Woodfjordaspis felixi* *Zascinaspis laticephala* OSTEOSTRACANS *Aceraspis robustus* *Atelaspis tessellata* *Axinaspis whitei* *Belonaspis minuta* *Benneviaspis batoides* *B. ceratops* *B. ginsburgi* *B. grandis* *B. holtedahli* *B. lövgreeni* *B. macrorhynchus* *B. maxima* *B. puella* *B. robusta* *B. rostrata* *Cephalaspis acuticornis* *C. caroli* *C. curta* *C. fracticomis* *C. isachseni* *C. laticornis* *C. producta* *C. watneliei* *Diademaspis poplinae* *D. jarviki* *Dicranaspis curtirostris* *D. circinus* *D. spinicornis* *Gustavaspis trinodis* *Hildenaspis digitalis* *Hoelaspis angulata* *Machairaspis isachseni* *M. battaili* *Meteoraspis oblonga* *M. lanternaria* *M. moythomasi* *M. semicircularis* *M. menoides* *M. caroli* *M. gigas* *M. lata* *M. oberon* *Nectaspis areolata* *Norselaspis glacialis* *Parameteoraspis gigas* *P. lanternaria* *P. hoegi* *Sigurdia lata* *Spatulaspis robusta* *S. costata* THELODONTS *Amaltheolepis winsneri* *Sigurdia* sp. *Turinia pagei* ARTHRODIRES & PHYLLOLEPIDS *Arctaspis maxima* *A. kiaeri* *A. holtedahli* *Arctolepis decipiens* *Arctonema crassum* *Dicksonosteus arcticus* *Elegantaspis reticornis* *Euleptaspididae* gen. et sp. indet. *Herasmius granulatus* *Heterogaspis gigantea* *Homosteus arcticus* *Lehmanosteus hyperboreus* *Paleocanthaspis* *Sigaspis lepidophora* *Svalbardaspis rotundus* *Wijdeaspis* sp. UNSORTED 'ACANTHODIANS' *Acanthodes* *Cheiracanthus* *Gomphonchus* *Nostolepis* *Onchus overathensis* *Ptychodichtyon* STEM-OSTEICHTHYANS ('ACANTHODIANS' *Xylacanthus grandis* *Xylacanthus minutus* ACTINOPTERYGIANS *Orvikuina* sp. DIPNOMORPHS *Heimenia ensis* *Porolepis brevis* *P. spitsbergensis* *P. elongata* *Powichthys spitsbergensis* ICHNOTAXA *Undichna septemsulcata*	(Clément and Janvier 2004, Friend 1961, Harland 1997, Pernègre 2006)

Chuandong (*Kenichthys*):

This taxon is known from the upper Emsian Chinese localities Quijing, Zhaotong, and Pingle of the Chuandong Formation. This formation is characterized by sandstones and siltstones intercalated with mudstones in facies typical of backshore-offshore shallow sea-shelf environments (Zhao and Zhu 2010). See Table 3.5 for the flora and fauna of the Chuandong Formation.

Table 3.5. Taxa from the upper Emsian Chuandong Formation, China.

TAXON			REFERENCE
PLANTS:	Spore taxa:	*Calyptosporites vetatus* *Rhabdosporites langii*	(Zhao and Zhu 2010)
INVERTEBRATES:	Ostracodes:	*Briatina* sp. *Hermmannina* sp.	(Zhao and Zhu 2010)
VERTEBRATES: Antiarchs *Bothriolepis chuandongensis* *B.* cf. *tungseni* *Hunanolepis* sp. *Microbrachius chuandongensis*	 *Wudinolepis* cf. *weni* *Xichonolepis qujingensis* Stem-chondrichthyans *Eurycaraspis incilis*	Dipnomorphs *Tarachomylax multicostatus* *Heimenia* sp. Tetrapodomorphs *Kenichthys campbelli*	(Ma et al. 2009, Zhao and Zhu 2010)

Middle and Late Devonian Paleoenvironments

Zachełmie, Wojciechowice (ichnofossil trackways):

The Middle Devonian (lower-middle Eifelian) Zachełmie Quarry of the Polish Wojciechowice Formation does not preserve any stem-tetrapod body fossils, but trackways data indicate the presence of digit-bearing taxa . The Wojciechowice Formation likely represents a tidal flat or lagoonal environment consisting of restricted, extremely shallow-water carbonate and siliclastic sedimentation. The trackways-containing part of the formation is almost completely devoid of fossils, but preserves abundant laminites with desiccation cracks and raindrop impressions. The facies characteristics of this interval indicate elevated salinity conducive to dolomite precipitation or $CaCO_3$ replacement, and therefore support for ephemeral infaunal communities, which appears to be reflected in the limited trace fossil record. However, these episodes also suggest a periodically open marine influence. Current paleogeographic interpretations for this area of the Polish Holy Cross Mountains reconstruct an extensive shallow, flat marine carbonate shelf located 100s of kilometres from the nearest continental areas (Niedźwiedzki et al. 2010). See Table 3.6 for taxa from the Wojciechowice Formation.

Table 3.6. Flora and fauna from the lower-middle Eifelian Wojciechowice Formation of Poland, and from the Zachełmie Quarry in particular*.

TAXON			REFERENCE
PLANTS:	Spore taxa?		(Niedźwiedzki et al. 2010)
INVERTEBRATES: Stromatoporids *Amphipora ramosa* Cnidarians *Calceola sandalina*	Ostracodes Ichnotaxa *Thalassinoides* sp.* *Skolithos* sp.* *Psilonichnus* sp.* *Cruziana* sp.*	Brachiopods *Bornhardtina skalensis* *Emanuella sanctacrucensis* *E. parva*	(Adamczak 1976, Malec and Turnau 1997, Niedźwiedzki et al. 2010)

VERTEBRATES:	CONODONTS:	_Bipennatus bipennatus montensis_*	(Niedźwiedzki et al. 2010)

Lybster Flagstone (*Dipterus valenciennesi*, *Glyptolepis* spp., *Gyroptychius agassizi*, *Osteolepis macrolepidotus*):

These dipnomorph and 'osteolepidid' taxa are preserved at the Achanaras Quarry of the Lybster Flagstone Formation in Caithness, Scotland. The Lybster Flagstone is Middle Devonian in age and corresponds to the *eiflius* and *ensensis* conodont zones, which places it in the late Eifelian to early Givetian (Marshall et al. 2007). The Achanarras beds are part of the Orcadian basin and are interpreted as hypersaline lacustrine deposits (Trewin 1985) that preserve numerous varves containing algal decay products and suspension deposits from overflow and aeolian sources (Andrews et al. 2010). Evidence of algal blooms is also consistent with deoxygenation models that explain the mass mortality of animals living in these intermontane Devonian lake waters. See Table 3.7 for the flora and fauna of the Lybster Flagstone Formation.

Table 3.7. Taxa from the late Eifelian-early Givetian Lybster Flagstone Formation, Scotland, and of the Achanarras Quarry in particular*. Note that (*) refers to taxa known from the quarry and the surrounding formation.

TAXON			REFERENCE
PLANTS: SPORE TAXA _Ancyrospora ancyrea_	_A. grandispinosa_* _A. longispinosa_ (*) _Calyptosporites microspinosus_ _Densosporites devonicus_	_Hystricosporites corystus_ _Perotriletes bifurcatus_	(Richardson 1962)
INVERTEBRATES:	CHELICERATES:	_Achanarraspis reedi_*	(Anderson et al. 2000)
VERTEBRATES: ANASPIDS _Achanarella_* _Cornovichthys blaauweni_* ANTIARCHS _Pterichthyodes milleri_* PTYCTODONTS _Rhamphodopsis threiplandi_* _Rhamphodopsis trispinatus_* ARTHRODIRES _Actinolepis magna_* _Coccosteus cuspidatus_	_Homosteus milleri_* STEM-CHONDRICHTHYANS _Diplacanthus crassisimus_* _D. longispinus_* _D. striatus_* _D. Tenuistriatus_* UNSORTED 'ACANTHODIANS' _Rhadinacanthus longispinus_* STEM-OSTEICHTHYANS _Cheiracanthus murchisoni_* _C. latus_* _Mesacanthus peachi_	ACTINOPTERYGIANS _Cheirolepis trailli_* DIPNOMORPHS _Dipterus valenciennesi_ (incl. _Palæospondylus gunni_)* _Glyptolepis leptopterus_* _G. paucidens_* _Pentalandia macroptera_* _Pinnalongus saxoni_ 'OSTEOLEPIDIDS' _Gyroptychius agassizi_* _Osteolepis macrolepidotus_* _Thursius macrolepidotus_ (=_moythomasi_)	(Cloutier and Lelievre 1998, Newman and Dean 2005, Newman and Trewin 2001, 2008)

Eday Flagstone (*Tristichopterus*):

This tristichopterid is from the Middle Devonian (middle or upper Givetian) south Ronaldsay locality of the Eday Flagstone Formation in Orkney, Scotland (Marshall 2000, Newman and Dean 2005, Piper et al. 2007, Plaster-Kirk et al. 1995). The Eday Flagstone is preceded stratigraphically by a long interval of Middle Devonian (Eifelian through earliest Givetian) lacustrine sedimentation. Immediately below the Eday Flagstone Formation, lacustrine sedimentation is interrupted by an episode of basin extension and uplift with fluvial deposition, but lacustrine sedimentation is reestablished to form the Eday Flagstone Formation. However, this is short lived, and succeeding Middle Devonian formations were intermittently flooded by the sea. Successions in areas surrounding Orkney at this time, such as in the Walls Group, Fair Island, and southeast Shetland, also contain lacustrine intervals that are equivalent to the Eday Flagstone Formation (Marshall 2000). See Table 3.8 for the fauna of the Eday Flagstone.

Table 3.8. Taxa from the mid-upper Givetian Eday Flagstone Formation, Scotland.

TAXON				REFERENCE
PLANTS:				-
INVERTEBRATES:				-
VERTEBRATES: ANTIARCHS *Microbrachius dicki* *Asterolepis* sp. cf. *A. thule,*	ARTHRODIRES *Watsonosteus fletti* *Coccosteus decipiens* STEM-OSTEICHTHYANS *Mesacanthus peachi*	DIPNOMORPHS *Pentalandia macroptera* TRISTICHOPTERIDS *Tristichopterus alatus*		(Cloutier and Lelievre 1998, Newman and Dean 2005)

Aztec Siltstone (*Koharalepis & Mahalalepis*):

These 'osteolepidids' are known from the Middle Devonian (Givetian) "Fish Hotel" sites of the Aztec Siltstone Formation in Victoria Land, Antarctica (Young and Long 2005, Young 1992). The Aztec Siltstone was part of a larger alluvial plain system deposited by highly sinuos meandering streams with temporary lakes (McPhearson 1978). The large size of some of the vertebrates, especially in the upper parts of the formation, indicates substantial bodies of permanent water. However, much of the sequence also includes paleosol horizons that indicate subaerial exposure (McPhearson 1979, Young 1989a). See Table 3.9 for the flora and fauna of the Aztec Siltstone Formation, and of its diachronous Fish Hotel sites.

Table 3.9. Taxa from the Givetian Aztec Siltstone Formation, Antarctica.

TAXON			REFERENCE
PLANTS:	SPORE TAXA *Geminospora lemurata*	LAND PLANTS *Haplostigma lineare* *Praeramunculus alternatiramus* Psilophytes	(Harmsen and Bradshaw 2007, McLoughlin and Long 1994, Retallack 1997)
INVERTEBRATES:	ICHNOTAXA *Beaconites baretti* *Metaichna*	*Scoyenia* CONCHOSTRACANS	(Harmsen and Bradshaw 2007)

VERTEBRATES: Thelodonts *Turinia antarctica* Antiarchs *Bothriolepis antarctica* *B. alexi* *B. askinae* *B. barretti* *B. karawaka* *B. kohni* *B. macphersoni* *B. mawsoni* *B. portalensis* *B. vuwae* *B.* sp. indet. 1-13 *Venezuelepis antarctica* Arthrodires & Phyllolepids *Antarctolepis gunni* *Austrophyllolepis quiltyi* *Boomeraspis goujeti* *Groenlandaspis antarcticus* Phlyctaeniids *Placolepis tingeyi* Stem-chondrichthyans *Anareodus statei* *Antarctilamna prisca* *Aztecodus harmsenae* *Mcmurdodus featherensis* *Portalodus bradshawae* Unsorted 'acanthodians' *Antarctonchus glacialis* *Byssacanthoides debenhami* *Culmacanthus antarctica* *Gyracanthides warreni* *Milesacanthus antarctica* *Nostalepis gaujensis* *Pechoralepis juozasi* Stem-osteichthyans Ischnacanthids Actinopterygians *Donnrosenia schaefferi* Dipnomorphs ?*Eoctenodus* sp. *Howidipterus* sp. ?Ctenodontids Rhizodonts *Aztecia mahalae* Canowindrids *Koharalepis jarviki* 'Osteolepidids' *Koharalepis jarviki* *Gyroptychius? antarcticus* *Mahalalepis resima* *Platyethmoidia antarctica* *Vorobjevaia dolonodon* Tristichopterids *Notorhizodon mackelveyi*	(Young and Long 2005)

Denay (*Tinirau*):

When originally described, the 95 m thick Red Hill I beds of the Simpson Park Mountain Range in Nevada, USA were included as the uppermost part of the Denay Formation. However, even though they were later excluded and informally termed 'Red Hill' (Johnson and Sandberg 1977), to place these beds within a larger stratigraphic context, I treat the Denay Formation as the unit containing the Red Hill I locality. The widespread deposition of limestone and shale along the western margin of Laurentia suggests that the regional geology of the northern Simpson Park Range is of an open marine paleoenvironment (Johnson 1977) and in particular the outer continental shelf (Johnson 1988, Schultze 2010). Thin-bedded dark mudstones of the lower Denay Formation intercalate occasionally with coarser-grained layers that consist of crinoid ossicles, brachiopod, and conodonts. Their lower surfaces are often irregular and characteristic of turbidity current deposits, which suggests a nearby slope to initiate flow into a lower slope environment (Johnson and Sandberg 1977). The Denay Formation, along with bounding formations, appears to be part of a transgressive sequence. Even the overlying Devil's Gate Formation represents a progradation of shallow water limestone and dolomite over mud dominated deeper water sediments (Murphy 1977). Considering that Red Hill I is at the boundary between the underlying Denay and overlying Devil's Gate Formations, it may represent more of a near shore paleoenvironment (Schultze 2010). See Table 3.10 for preserved members of the flora and fauna.

Table 3.10. Taxa from the upper Givetian Denay formation, Nevada, USA, and of the Red Hill I beds specifically*. $^{(*)}$ refers to taxa present at the locality and elsewhere in the formation.

TAXON			REFERENCE
PLANTS:	<u>CHAROPHYTES</u>?	?*Chara* ?*Nitella*	(Schultze 2010)
INVERTEBRATES: <u>SPONGES</u>* *Actinodictya nevadensis* *Actinodictya lamina* *Bulbospongia bullata* *Cyathophycella minuta* *C. grossa* *Cyathophycus simpsonenis* *Dictyospongia*(?) *robusta* *Dictyospongia*(?) *amplia* *Protospongia conica* *Rufuspongia* sp. *R. triporata* *Taleolaspongia modesta* *Teganiella ovata*	<u>CNIDARIANS</u> *Alveolitella* sp. A* *Cladopora** *Cystiphylloides* *Grabulites jacksoni* *Metrionaxon* *Microplasma* *Paraconularia recurvatus** *Prismatophyllum flexum* *Pseudomicroplasma* *Stratopora* *Thamnopora* sp. D* *Xystriphyllum trojani* *Zonophyllum* DACRYOCONARIDS* BRYOZOANS*	<u>BIVALVES</u> *Buchiola* sp.* *Modiella* sp.* *Praecardium* sp. A* *Praecardium* sp. B* *Solemya* (?*Janeia*) sp.* AMMONOIDS* <u>BRACHIOPODS</u> *Ladjia russelli** *Leiorhynchus hippocastanea*$^{(*)}$ *Leptathyris circula* *Pentamerella wintereri* *Rhyssochonetes** *Vallomyonia claudiae** CRINOIDS*	(Flory 1977, Gregory et al. 1977, Johnson and Sandberg 1977, Murphy 1977, Pedder 2010, Pedder and Murphy 2004, Schultze 2010)
VERTEBRATES: <u>CONODONTS</u> *Klapperina* (*Palmatolepis*) *disparilis** *Polygnathus angusticostatus* *P. beckmanni* *Polygnathus cristatus** *P. foliatus** *P. kennettensis* *P. kockelianus* *P. linguiformis linguiformis morphotype zeta* *P. linguiformis parawebbi* *P. ordinatus** *P. ovatinodosus*	*P. pseudofoliatus* *P. serotinus** *P. timorensis* *P. trigonicus* *Schmidtognathus* sp.* <u>ANTIARCHS</u> *Asterolepis* sp.* <u>ARTHRODIRES</u> *Coccosteus* sp.* cf. *Plourdosteus** <u>UNSORTED 'ACANTHODIANS'</u> *Machaeracanthus* sp.* *Persacanthus simpsonensis**	<u>ACTINOPTERYGIANS</u> *Cheirolepis schultzei** ONYCHODONTS* <u>DIPNOMORPHS</u> *Griphognathus* sp.* *Soederberghia* sp.* 'OSTEOLEPIDIDS'* TRISTICHOPTERIDS* <u>ELPISTOSTEGALIANS</u> *Tinirau clackae**	(Gregory et al. 1977, Murphy 1977, Schultze 2010)

Gauja (*Panderichthys & Livoniana*):

Late Givetian to earliest Frasnian in age, the Latvian Gauja Formation was deposited in a shallow, epicontinental basin by rivers transporting primarily sand (Blieck et al. 2002, Mark-Kurik et al. 1999, Pontén and Plink-Björklund 2009). It reached its maximum extent in the Givetian stage, but the active delta front began to contract during the transition to the overlying Amata Formation (Pontén and Plink-Björklund 2009). Depositional environments ranged from upper fluvial-dominated delta plains to lower tide-dominated delta fronts. This is evidenced by fluvial deposition restricted to the landward areas of the Gauja Formation, whereas tide-influenced channels are located in the lower stratigraphic seaward portions. Palaeocurrent directions show a net seaward transport of sediments, and reflect the dominance of river transport over tidal currents (Pontén and Plink-Björklund 2007). Overall, this system was very different from modern tropical tidal environments where streams frequently carry muds and terminate as estuaries (Pontén and Plink-Björklund 2009). See Table 3.11 for the flora and fauna of the Gauja Formation.

Table 3.11. Taxa from the late Givetian to early Frasnian Gauja Formation, Latvia. All taxa are known from the Lode Quarry specifically.

TAXON			REFERENCE
PLANTS: LAND PLANTS *Archaeopteris* sp.	*A. fissilis* ?*Charales* *Nematophyton* sp. *Platyphyllum* sp.	*Rhacophyton* sp *Svalbardia polymorpha* *Trochilliscus* sp.	(Upeniece 2001)
INVERTEBRATES:			-
VERTEBRATES: HETEROSTRACANS *Pasmmolepis abavica* *P. paradoxa* *P. alata* *P. heteraster* *P. venyukovi* *P. undulata* *P. praecursor* *Psammosteus sp.* (*ganensis*) ANTIARCHS *Bothriolepis* sp. *Asterolepis ornata* *Asterolepis cristata* *Asterolepis* sp. (*essica*)	ARTHRODIRES *Coccosteus panderi* *Livosteus grandis* *Plourdosteus livonicus* *Watsonosteus* sp. 'PLACODERMI' INCERTAE SEDIS *Hybosteus mirabilis* STEM-OSTEICHTHYANS *Lodeacanthus gaujicus* UNSORTED 'ACANTHODIANS' *Devononchus concinnus* *Haplacanthus ehrmanensis* *Nodacosta pauli* ACTINOPTERYGIANS *Chrieolepis* sp.	ONYCHODONTS *Strunius* sp. ACTINISTIANS *Miguashaia grossi* DIPNOMORPHS *Glyptolepis baltica* *Grossipterus crassus* *Laccognathus panderi* 'OSTEOLEPIDIDS' *Latvius* sp. *Osteolepis* sp. TRISTICHOPTERIDS *Eusthenopteron kurshi* ELPISTOSTEGALIANS *Panderichthys rhombolepis* *Livoniana multidentata*	(Ahlberg et al. 1994, Cloutier and Lelievre 1998, Upeniece 2001, Zupiņš 2008)

Gogo (*Gogonasus*):

The Gogo Formation undoubtedly represents a marine reef ecosystem (Long and Trinajstic 2010, Playford 1980, Wade 1936). It is Middle-Late Devonian in age (late Givetian to early Frasnian), although the Gogo fish fauna is primarily from the early Frasnian *transitans* conodont zone (Long and Trinajstic 2010, Nazarov et al. 1982, Nazarov and Ormiston 1983). Gogo is characterized by inter-reef basinal facies, and is located to the east of marginal slope and reefal platform facies of the Sadler and Pillara Limestones, respectively (Playford 1980). See Table 3.12 for the flora and fauna of the Gogo Formation.

Table 3.12. Taxa from the late Givetian-early Frasnian Gogo Formation, Western Australia, and of the Gogo fish fauna specifically*.

TAXON	REFERENCE
PLANTS: SPORE TAXA *Acinosporites* sp. *Ancyrospora* ap. A *Apiculatasporites* sp. *Apiculiretusispora* sp. ?*Archaeoperrisaccus* sp. *Auroraspora* sp. *Calamospora* sp. *Convolutispora* spp. *Cyclogranispora* sp. *Cyclogranisporites* sp. *Cymbosporites* sp. *Dibolisporites* sp. ?*Grandispora* sp. *Gemonospora* sp. *Hymenozonotriletes* sp. *Hystricosporites* sp. *Latosporites* sp. *Leiotriletes* sp. *Lophozonotriletes* sp. ?*Perotriletes* sp. *Punctatisporites* sp. *Reticulatisporites* sp. *Retusotriletes* sp. *Rhabdosporites* sp. *Samarisporites* spp. *Stenozonotriletes* sp. *Teichertospora torquata* *Verrucosisporites* sp.	(Grey 1973, McGregor 1990)
'INVERTEBRATES': RADIOLARIANS *Astroentactinia paronae* *A. stellata* *Ceratoikiscum planistellare* *C. vimenum* *Ceratoikiscum* sp. *Entactinia additiva* *E.* cf *dissora* *E.* cf *micula* *Entactinosphaera*? *echinata* *Entactinosphaera* cf *grandis* *Haplentactinia* cf *rhinophyusa* *Helenifore laticlavium* *Helioentactinia perjucunda* *Spongentactinia* sp. *Spongentactinella*? *veles* *S. corynacantha* *Stigmospherostylus additiva* SPONGES CORALS BIVALVES GASTROPODS TENTACULITIDS AMMONITES *Hoeninghausia pons* *Koenenites* *Manticoceras guppyi* *Ponticeras discoidale* *Probeloceras aveolatum* *Tamanites angustus* *Tornoceras contactum* *T. simplex* NAUTILOIDS BRYOZOANS BRACHIOPODS PHYLOCARID CRUSTRACEANS *Concavicaris* aff. *elytroides* *Eleutherocaris* sp. *Montecaris* sp. *M. lehmanni* *Schugurocaris* sp. CONCAVICARID CRUSTACEANS EURYPTERIDS *Rhenopterus waterstoni* CRINOIDS	(Choo et al. 2009, Glenister 1958, Nazarov and Ormiston 1983, Playford 1980, Rolfe 1966, Tetlie et al. 2004, Vishnevskaya et al. 2002)

VERTEBRATES: Conodonts *Acyrodella rotundiloba* *Gnamptognathus? lipperti* *Icriodus symmetricus* *Polygnathus varca* *P. asymmetrica* *P. normalis* *Platyfordia primitiva* *Roundia aurita* Antiarchs* *Bothriolepis* sp. Arthrodires* *Bullerichthys fascidens* *Bruntonichthys multidens* *Camuropiscis concinnus* *C. laidlawi* *Compagopiscis croucheri* *Eastmanosteus calliaspis* *Fallacosteus turnerae* *Gogopiscis gracilis* *Holonema westolli* *Harrytoombsia elegans* *Incisoscutum ritchiei* *I. (Gogosteus) sarahae* *Kendrickichthys cavernosus* *Kimberleyichthys cuspidatus* *K. whybrowi* *Mcnamaraspis kaprios* *Pinguosteus thulborni* *Rolfosteus canningensis* *Simosteus tuberculatus* *Torosteus tuberculatus* *T. pulchellus* *Tubonasus lennardensis* Ptyctodonts* *Austroptyctodus gardineri* *Campbellodus decipiens* *Materpiscis attenboroughi* (Stem-)Chondrichthyans* Gogo shark Unsorted 'acanthodians'* Acanthodiform sp. 1 Acanthodiform sp. 2 Actinopterygians* *Gogosardina coatesi* *Mimipiscis toombsi* *M. bartrami* *Moythomasis durgaringa* Stem-sarcopterygians* *Onychodus jandemarrai* Actinistians* "*Diplocercides*" sp. nov. Dipnomorphs* *Asthenorhynchus (Holodipterus) meemannae* *Adolopas moyasmithae* *Chirodipterus australis* *Gogodipterus paddyensis* *Griphognathus whitei* *Holodipterus gogoensis* *Holodipterus longi* *Holodipterus (Holodipteroides) elderae* *Pillararhynchus longi* *Rhinodipterus* sp. *Robinsondipterus longi* *Xeradipterus hatcheri* 'Osteolepidids'* *Gogonasus andrewsae*	(Long and Trinajstic 2010)

Amata (*Panderichthys*):

The earliest Frasnian Amata Formation succeeds the underlying Gauja Formation. The contracting active delta in the later stages of the Gauja Formation led to the tide-dominated estuarine complex that characterizes the Amata Formation. Five primary facies are present in this formation and include: (1) fluvial channels; (2) tide-influenced fluvial channels; (3) tidal channels; (4) marshes and tidal flats; and (5) tidal bars. Most facies are common throughout the estuarine succession of this formation, but their distribution varies somewhat with geography and stratigraphic position (Pontén and Plink-Björklund 2009). See Table 3.13 for taxa known from the Amata Formation.

Table 3.13. The vertebrate fauna from the early Frasnian Amata Formation, Latvia, and Pasta Muiza site in particular. (*) refers to taxa known from the locality and elsewhere in the formation.

TAXON	REFERENCE
PLANTS:	-
INVERTEBRATES:	-

VERTEBRATES: HETEROSTRACANS *Psammosteus asper* *P. cuneatus* *P. levis* *P. livonicus* *P. maeandrinus* *P. praecursor* *P. undulata* *P. venyukovi* ANTIARCHS *Asterolepis* sp. cf. *ornata*	*A. radiata* (*) *Bothriolepis obrutscewi* *B. prima* ARTHRODIRES *Coccosteus* sp. *indet.* *Plourdosteus livonicus* UNSORTED 'ACANTHODIANS' *Devononchus concinnus* ONYCHODONTS *Onychodus sp.*	DIPNOMORPHS *Glyptolepis baltica* *Holoptychius sp. cf. nobilissimus* *Laccognathus panderi* 'OSTEOLEPIDIDS' *Osteolepis sp.* TRISTICHOPTERIDS *Eusthenopteron obrutchevi* ELPISTOSTEGALIANS *Panderichthys rhombolepis*	(Cloutier and Lelievre 1998)

Sofia Sund (*Spodichthys*):

Spodichthys is from an unknown locality of the Late Devonian (lower Frasnian) Sofia Sund Formation in northeastern Greenland (Blom et al. 2007). The Sofia Sund Formation is composed almost entirely of sandy braidplain deposits (Nichols and Fisher 2007), although there are several local depositional systems that include eolian dune, ephemeral stream, meandering stream, and braided stream environments (Kelly and Olsen 1993, Larsen et al. 2008). The terminal fans are sand-dominated and terminate in eolian dunes. Overall, this sequence is interpreted as the distal part of a distributary system where ephemeral flow and eolian reworking were dominant and frequent parts of the environment(Kelly and Olsen 1993). See Table 3.14 for the Sofia Sund fauna.

Table 3.14. Taxa from the lower Frasnian Sofia Sund Formation, Greenland.

TAXON			REFERENCE
PLANTS:			-
INVERTEBRATES:			-
VERTEBRATES: ANTIARCHS *Asterolepis* cf. *A. saevesoederberghi* *Remigolepis? tuberculata*	ARTHRODIRES *Clarkeosteus* cf. *C. halmodeus* *Arthrodira* gen. et sp. indet. 1 DIPNOMORPHS *Holoptychius* spp.	'OSTEOLEPIDIDS' *Thursius? minor* TRISTICHOPTERIDS *Spodichthys buetleri* ELPISTOSTEGALIANS? ?*Panderichthys* sp.	(Blom et al. 2007)

Fram (*Tiktaalik*):

Tiktaalik is known from the NV2K17 site, located in the middle of the Late Devonian (early middle Frasnian) Fram Formation of Ellesmere Island, Canada (Daeschler et al. 2006, Embry and Klovan 1976). The Fram Formation is characterized by thick palaeosols cut by low-velocity, sinuous stream channels with cross-stratification, that suggests nearly continuous terrestrial deposition of low gradient meandering stream complexes in lowland foodplains (Algeo and Scheckler 1998, Embry and Klovan 1976). The NV2K17 site, specifically, is within a 30m-thick, siltstone-dominated sequence bounded by cross-bedded channel siltstones. The beds at this site where *Tiktaalik* was discovered consist of poorly sorted siltstones and dense concentrations of carbonate nodules and infraformational clasts, all of which are overlain by more massive siltstones and disarticulated vertebrate remains. The package at this site suggests a channel flooding event that carried sediment and fauna into an inter-channel area, that was followed by rapid deposition (Daeschler et al. 2006, Miller et al. 2007). See Table 3.15 for the flora and fauna of the Fram Formation.

Table 3.15. Taxa from the middle Frasnian Fram Formation, Ellesmere Island, and the NV2K17 site in particular*.

TAXON			REFERENCE
PLANTS: LAND PLANTS ?Aneurophytes	*Archaeopteris fissilis* *Archaeopteris obtusa* *Callixylon* sp. *Cephalopteris mirabilis*	*Leptophloeum rhombicum* *Lyginodendron sverdrupii* ?*Sphenopteridium keilhauiil*	(Algeo and Scheckler 1998, Hill et al. 1997)
INVERTEBRATES:			-
VERTEBRATES:* ANTIARCHS *Asterolepis* sp.	DIPNOMORPHS Lungfish Holoptychiids (incl. *Laccognathus* sp.)	‘OSTEOLEPIDIDS’ TRISTICHOPTERIDS ELPISTOSTEGALIANS *Tiktaalik roseae*	(Daeschler et al. 2006)

Escuminac (*Eusthenopteron & Elpistostege*):

The Late Devonian (middle Frasnian) Escuminac Formation in Quebéc, Canada is well-known for the flora and fauna from its Miguasha locality. There are numerous fossiliferous zones at Miguasha, with many of the same taxa found in each. For example, *Eusthenopteron foordi* is known from eight (diachronous) zones, although *Elpistostege* comes from the middle of this range (Cloutier et al. 1996). The Escuminac Formation is primarily siliclastic with alternating siltstones and shales, and the main lithologies include (in decreasing order of abundance): shale, sandstone, siltstone, laminite, and conglomerate. More than most other stem-tetrapod localities, Miguasha has been the focus of extensive paleoenvironmental analyses. It has been interpreted as lacustrine (Brideaux and Radforth 1970, Dineley and Williams 1968, Gray 1988, Greiner 1978), estuarine (Hesse and Sawh 1992), transitional (Schultze and Cloutier 1996), coastal marine (Schultze and Arsenault 1985, Vezina 1991), and fully marine (Schultze 1972); although in combination with recent isotopic evidence (Schmitz et al. 1991), as well as faunal data (Schultze and Cloutier 1996), the emerging picture is that it represents more of a transitional depositional environment (Schultze 2009). See Table 3.16 for the list of flora and fauna from the Escuminac Formation

Table 3.16. Taxa known from the middle Frasnian Escuminac Formation, Québec, Canada.

TAXON			REFERENCE
PLANTS:	Land plants: *Archaeopteris*	*Flabellifolium* *Protobarynophyton*	(Cloutier et al. 1996)
INVERTEBRATES: Scorpionids: Gigantoscorpionidae gen. et sp. indet. *Petaloscorpio bureaui*	Eurypterids Parastylonuridae gen. et sp. indet. *Pterygotus* sp. Conchostracans *Asmusia membranacea*	Annelids Polychaeta gen. et sp. indet. Ichnofossils *Gyrophyllites* ichnosp. *Planolites montanus*	(Cloutier et al. 1996, Maples 1996, Martens 1996, Schultze and Cloutier 1996)
VERTEBRATES: Naked 'anaspids' *Endeiolepis aneri* *Euphanerops longaevus* *Legendrelepis parenti* Osteostracans *Escuminaspis laticeps* *Levesquaspis patteni* Antiarchs *Bothriolepis canadansis* Arthrodires *Plourdosteus canadensis*	Stem-osteichthyans *Homalacanthus concinnus* *Triazeugacanthus affinis* Unsorted 'acanthodians' *Diplacanthus ellsi* *D. horridus* Actinopterygians *Cheirolepis canadensis* Actinistians *Miguashaia bureaui* Dipnomorphs *Fleurantia denticulata*	*Holoptychius jarviki* Holoptychiidae gen. et sp. indet. *Quebecius quebecensis* *Scaumenacia curta* 'Osteolepidids' *Callistiopterus clappi* Tristichopterids *Eusthenopteron foordi* Elpistostegalians *Elpistostege watsoni*	(Cloutier and Lelievre 1998)

Rdeyskoe (*Jarvikina*):

This tristichopterid is preserved in the Late Devonian (middle Frasnian) Porkhov and Svinord beds of the Rdeyskoe Formation in western Russia (Krupina 1995, Vorobyeva 2004, Zhuravlev et al. 2006). Both beds contain shallow water carbonate and terriginous sediments, and document a general marine transgression leading up to the overlying late middle Frasnian Snezha Formation. Facies changes document a strongly marine influenced, nearshore, epreiric sea, that track the increased diversity (or preservation) of brachiopod, ostracode, and conodont groups during this transgressive phase (Zhuravlev et al. 2006). See Table 3.17 for the fauna of the Rdeyskoe Formation.

Table 3.17. Taxa from the middle Frasnian Rdeyskoe Formation, western Russia.

TAXON	REFERENCE
PLANTS:	-

INVERTEBRATES: Ostracodes *Acantonodella lutkevichi* *A. terciocornuta* *Acratia* sp. *Acratia gassanovae* *A. galinae* *Acratia mayselae* *Bairdia* sp. *Bairdiocypris* sp. *Buregia* sp. *Buregia bispinosa* *Cavellina* sp. *Cryptophyllus* sp. *Gravia* sp. *Heladianella* cf. *svinordensis* *Kloedenellitina* sp. *Kloedenellitina sygmaeformis*	*Kozlowskiella* sp. *Knoxiella* sp. *Knoxina* cf. *alexandrovae* *Knoxina* sp., aff. *costata* *Knoxites* sp. *Mennerites* sp., aff. *svinordenis* *M. svinordensis* *M. porezkyae* *Mennerella* sp. *Mennerella schelonica* *Milanovskya bicristata* *Mossolovella sp.* *Mossolovella philippovae* *Neodrepanella* sp. *Neodrepanella parva* *Neodrepanella tricornis* *Nodella* sp. *Nodella conotuberculata*	*Paraparchites* sp. *Paraparchites calculus* *Pseudonodella plana* *Tetracornella schelonica* *T. tetraspinosa* *T.* cf. *glebovskaja* *T.* sp. n., aff. *schelonica* *T. formosa* *Timanella* sp. B *Uchtovia* sp. Brachiopods *Anathyris svinordensis* *Cyrtospirifer* sp. A *Cyrtospirifer schelonicus* Rhynchonellids Gastropods Stromatoporids	(Evdokimova 2006, Rzhonsnitskaya and Modzalevskaya 1996, Sokiran 2006, Zhuravlev et al. 2006)
VERTEBRATES: Conodonts *Ancyrognathus ancyrognathoideus* *Icriodus symmetricus* *Pelekysgnathus* *Polygnathus efimovae* *P. imenensis* *P. lanei* *P. mosquensis* *P. pollocki* *P. reimersi* *P. strictus* *P. ukhtensis* *P. xylus*	*P. zinaidae* Heterostracans *Psammosteus megalopteryx* Antiarchs *Bothriolepis traudscholdi* *B. panderi* Arthrodires *Coccosteus* spp. *Plourdosteus* spp. Unsorted 'acanthodians' *Atopacanthus* sp.	Dipnomorphs *Holoptychius* sp. *Rhinodipterus stolbovi* *Glypeolepis* sp. 'Osteolepidids' Tristichopterids *Jarvikina* Elpistostegalians *Parapanderichthys*	(Evdokimova 2006, Krupina 1995, Moloshnikov 2008, Vorobyeva 1977, 2004)

Bindaree (*Beelarongia & Marsdenichthys*):

These 'osteolepidid' taxa are known from the Late Devonian (middle Frasnian) Mount Howitt locality of the Bindaree Formation in Victoria, Australia. The three primary units of the Bindaree Formation, oldest-to-youngest, include: (1) the Boulder Conglomerate Unit, which is interpreted as a stream-dominated alluvial deposit, with cobble and boulder conglomerates deposited during flood events; (2) the Green Mudstone Unit, containing fine-scale laminations in mudstones that indicate deposition following suspension in a standing body of water; and (3) the Black Shale Unit, containing finely varved black anaerobic shales deposited in a low energy, quiet water environment. This third unit preserves the Mt. Howitt fish fauna in black shale lacustrine phases, with intermittent influx of fine sand into the basin. Bioturbation structures and invertebrate fossils are very rare, although root casts are present and appear to indicate swamp deposits. (Marsden 1976). Alluvial fan, braided stream, and meandering stream deposits and overbank floodplain environments have been recognized in the

Mount Howitt Province specifically. However, more broadly, the Bindaree sequence illustrates the transformation of these facies, which includes an intervening lacustrine phase, and culminates in extensive flood-plain red-bed facies (Marsden 1976). See Table 3.18 for the flora and fauna of the Bindaree Formation.

Table 3.18. Taxa from the middle Frasnian Bindaree Formation, Victoria, Australia, including the Mount Howitt Locality.

TAXON			REFERENCE
PLANTS:	"Plant matter"		(O'Halloran and Gaul 1997a)
INVERTEBRATES:	-		(Cloutier and Lelievre 1998, Marsden 1976)
VERTEBRATES: ANTIARCHS *Bothriolepis cullodenensis* *B. fergusoni* *B. gippslandiensis* *B. bindareei* ARTHRODIRES & PHYLLOLEPIDS *Austeophyllolepis ritchiei* *A. youngi* *Groenlandaspis*	STEM-CHONDRICHTHYANS *Culmacanthus stewarti* UNSORTED 'ACANTHODIANS' *Howittacanthus* ACTINOPTERYGIANS *Howqualepis rostridens* ACTINISTIANS Actinistia gen. et sp. indet.	DIPNOMORPHS *Barwickia downunda* *Glyptolepis* sp. *Howidipterus donnae* CANOWINDRIDS *Beelarongia patrichae* *Marsdenichthys longioccipitus* ?ELPISTOSTEGALIANS *Howittichthys warrenae*	(Cloutier and Lelievre 1998)

Snezha (*Platycephalichthys bischoffi*):

The Snezha Beds of Russia and Latvia are Late Devonian (late middle Frasnian) in age and therefore only slightly younger than the Rdeyskoe Formation. Following a general transgressive phase in the early middle Frasnian eastern European Platform, regional uplift produced a substantial drop in sea level that led to the late middle Frasnian Snezha regression. Similar to the underlying Rdeyskoe Formation, the Snezha beds represent a nearshore epeiric sea, but because of this regressive phase, may represent primarily shallow water deposition. Ostracode, brachiopod, and conodont faunas are studied less extensively in these beds, so despite their waxing (whether biological or taphonomic) in the Rdeyskoe transgression, their waning remains unconfirmed in the succeeding regression (Zhuravlev et al. 2006). See Table 3.19 for the Snezha fauna.

Table 3.19. Invertebrate and vertebrate taxa from the middle Frasnian Snezha Formation, Latvia and western Russia.

TAXON	REFERENCE
PLANTS:	-

INVERTEBRATES:	OSTRACODES *Acantonodella terciocornuta* *Bairdia* *Buregia bispinosa*	*Milanovskya bicristata* BRACHIOPODS	(Evdokimova 2006, Zhuravlev et al. 1997, Zhuravlev et al. 2006)
VERTEBRATES: CONODONTS *Ancryognathus ancryognathoideus*	*Polygnathus alatus* *P. aspelundi* *P. efimovae* *P. pollocki* *P. subincompletus*	*P. xylus* ELPISTOSTEGALIANS *Platycephalichthys bischoffi*	(Vorobyeva 1977, 2004, Zhuravlev et al. 2006)

Scat Craig (*Elginerpeton*):

The Late Devonian (lower-upper Frasnian) Scat Craig beds are located just south of Elgin, Scotland (Ahlberg 1998). Their relationship to the regional geology is poorly understood, but the site itself consists of reddish to pale yellow channel sands with bands of small pebbles, clay clasts and silt lenses (Clack 1997). The vertebrate fauna is usually associated with these pebbles and clasts, but the fossils are often highly abraded and possibly reworked. In this respect, Scat Craig may represent a fluvial deposit, but the contemporary and similar Old Red Sandstone deposits in the Baltic region are considered deltaic to coastal marine (Ahlberg 1998, Kuršs 1992). See Table 3.20 for the Scat Craig fauna.

Table 3.20. Taxa from the upper Frasnian Scat Craig locality, Scotland.

TAXON			REFERENCE
PLANTS:	-		(Ahlberg 1998)
INVERTEBRATES:			-
VERTEBRATES: HETEROSTRACANS Psammosteids ANTIARCHS *Asterolepis major*	*Bothriolepis* sp. DIPNOMORPHS *Holoptychius princeps* *Duffyichthys mirabilis*	UNSORTED 'ACANTHODIANS' *Cosmacanthus* sp. ELPISTOSTEGALIANS *Elginerpeton pancheni*	(Ahlberg 1998, Clack 2006, Woodward and Sherborn 1890)

Mandagery (*Gooloogongia*, *Canowindra*, *Cabonnichthys*, *& Mandageria*):

These rhizodont, 'osteolepidid', and tristichopterid taxa are part of the Late Devonian (late Frasnian) Canowindra fish fauna, known from the Mandagery Sandstone Formation of Victoria, Australia (Ahlberg and Johanson 1997, Johanson and Ahlberg 1997, 2001, Thomson 1973, Young 1999). The Mandagery Sandstone contains more than ten cyclothems in the upper portion of the formation, where the Canowindra fauna is located. The thickness of the cyclothems varies from 20 to 200 ft, and begins with a sandstone unit that rests on siltstones. Sandstone beds are the dominant lithology in the base, but siltstone interbeds become more common towards the top, culminating in what are often thick sequences of red siltstone. The siltstones in the upper half of the cyclothems are frequently cross-stratified with current ripple-marks, mudcracks, and burrows (Conolly 1965). Lingulid facies and the

Canowindra fauna occur within these beds below the overlying, finer-grained Mount Cole Formation. This lingulid-vertebrate association may indicate a marine influence in the upper Mandagery Sandstone and represent a late Frasnian sea-level high suggested by equivalently aged conodont fossils to the east (Blieck et al. 2007). See Table 3.21 for the fauna from the Mandagery Sandstone.

Table 3.21. Taxa from the late Frasnian Mandagery Sandstone Formation, Victoria, Australia.

TAXON			REFERENCE
PLANTS:			-
INVERTEBRATES:	BRACHIOPODS:	Lingulids	(Blieck et al. 2007)
VERTEBRATES: ANTIARCHS *Bothriolepis yeungae* *Remigolepis walkeri*	ARTHRODIRES *Groenlandaspis* sp. DIPNOMORPHS *Soederberghi simpsoni* RHIZODONTS *Gooloogongia loomsei*	CANOWINDRIDS *Canowindra grossi* TRISTICHOPTERIDS *Cabonnichthys burnsi* *Mandageria farfaxi*	(Cloutier and Lelievre 1998)

Ogre (*Obruchevichthys*):

The holotype of this elpistostegalian comes from Velna Ala of the Late Devonian (upper Frasnian) Ogre Formation in Latvia (Avkhimovitch et al. 1993, Vorobyeva 1977). *Obruchevichthys* is also known from western Russia, but because the locality there is not known precisely, the focus here will be on Velna Ala (Esin et al. 2000, Vorobyeva 1977). This type-locality is within the lower Lielvarde Member of the Ogre Formation. This member primarily consists of fine-grained calcareous sandstones, with a gypsum cement in lower stratigraphic sections and clay silt and dolomitic marl toward the top. These facies are interpreted to represent shallow water deposits in a Baltic paleobasin under conditions of fluctuating salinity (Sorokin 1978). See Table 3.22 for taxa of the Ogre Formation.

Table 3.22. Fauna from the late Frasnian Ogre Formation, Latvia.

TAXON			REFERENCE
PLANTS:			-
INVERTEBRATES:			-
VERTEBRATES: HETEROSTRACANS *Psammosteus* spp.	ANTIARCHS *Bothriolepis* sp. *Bothriolepis maxima* *Grossilepis spinosa* UNSORTED 'ACANTHODIANS' *Devononchus* sp.	DIPNOMORPHS *Holopytchius* sp. gen. et. sp. indet. ELPISTOSTEGALIANS *Obruchevichthys gracilis*	(Clack 1997, Lukševičs 2001, Vorobyeva 1977)

Cloghnan Shale (*Metaxygnathus*):

This elpistostegalian is from the Jemalong Quarry, part of the Late Devonian Cloghnan Shale of New South Wales, Australia. The Cloghnan Shale was originally considered late Frasnian or early Famennian in age (Campbell and Bell 1977), but after extensive remapping of its containing Hervey Group (Young et al. 2000) and analysis of its fossil vertebrate assemblages (Young 1999), is more likely Frasnian in age. The Cloghnan Shale overlies the Troffs Formation, where despite marine fossils in its lower beds, contains fossil plant fragments and abundant red siltstones and shales toward the top. This suggests a transition from shallow-water marine to terrestrial deposition between the bottom and the top of the formation. The stabilization of this terrestrial environment is indicated by similar siltstones and shales still present in the overlying Clognnan Shale (Conolly 1965). See Table 3.23 for the vertebrate fauna.

Table 3.23. Taxa from the Upper Devonian Jemalong Quarry of the Cloghnan Shale, NSW, Australia.

TAXON			REFERENCE
PLANTS:			-
INVERTEBRATES:			-
VERTEBRATES: ANTIARCHS *Bothriolepis* sp. *Remigolepis* sp.	ARTHRODIRES & PHYLLOLEPIDS *Groenlandaspis* sp. *Phyllolepis* sp. DIPNOMORPHS *Holoptychius* sp. *Soederberghi groenlandica*	Tristichopterid scales ELPISTOSTEGALIANS *Metaxygnathus denticulus*	(Blieck et al. 2010, Campbell and Bell 1977, Young et al. 2010)

Zadonsk (*Jakubsonia*):

This elpistostegalian is known from Gornostayevka of the early Famennian Zadonsk Formation in Livny, Russia (Lebedev 2004, Moloshnikov 2008). The lower Zadonsk Formation consists of nodular algal floatstones and reefal deposits that likely accumulated on the shallow sea bottom, but transitions to mudstones and wackestones in later stages (Deliya and Danshina 2010). Overall, it is interpreted as a deltaic, near-shore paleoenvironment (Lebedev 2004). See Table 3.24 for members of the Zadonskian fauna.

Table 3.24. Taxa from the lower Famennian Zadonsk Formation, Russia, and Gornostayevka in particular*.

TAXON			REFERENCE
PLANTS:			-
INVERTEBRATES: BIVALVES	NAUTILOIDS	BRACHIOPODS	(Moloshnikov 2004)

VERTEBRATES: CONODONTS ANTIARCHS *Bothriolepis zadonica** *Bothriolepis sosnensis** *B.* cf. *leptocheira** *Livnolepis* sp. *Remigolepis* ? sp.* *Rossolepis* sp. PTCYTODONTS *Chelyophorus* sp.*	ARTHRODIES Pachyosteomorphs* (STEM-)CHONDRICHTHYANS *Protacrodus* sp.* UNSORTED ‘ACANTHODIANS’ *Devononchus cf. laevis** STEM-SARCOPTERYGIANS *Strunius** DIPNOMORPHS *Conchodus* sp.*	*Dipterus* sp.* *Holodipterus* sp.* *Chirodipterus* sp. *Holoptychius* sp. OSTEOLEPIDIDS’ *Glyptopomus* sp.* *Megapomus markovskyi** ELPISTOSTEGALIANS *Jakubsonia livnensis**	(Lebedev 2004, Lebedev et al. 2010, Moloshnikov 2004, 2008)

Zhongning (*Sinostega*):

The Zhongning Formation is located in the Ningxia Hui region of northwestern China. It was originally considered uppermost Famennian (Pan et al. 1987), although based on miospore data is likely closer to (if not entirely) Frasnian in age (Blieck et al. 2007). It consists of thick, terrestrial-lacustrine sections of red arkosic sandstones, sandy shales, conglomerates, and a few limestones and marls, with the shaly parts (on the basis of their color) interpreted to have formed under drier climatic conditions (Huang et al. 2000, Xingxue and Xiuyuan 1996). See Table 3.25 for the flora and fauna of the Zhongning Formation.

Table 3.25. Taxa from the Upper Devonian Zhongning Formation, northwestern China.

TAXON			REFERENCE
PLANTS: SPORE TAXA *Aneurospora greggsii* *Apiculiretusispora granulata* *A. plicata* *A. septalata var. minor*	*Archaeozonotriletes variabilis* *Calamospora atava* *C. nigrata* *Geminospora lemurata* *G. parvibasilaris* *Stenozonotriletes conformis* *Verrucosisporites omalus*	LAND PLANTS *Leptopholeum rhombicum* *Sublepidodendron mirabile* *Eolepidodendron wusihense* *Hamatophyllum verticalIatum* *Sphenopteridium taihuenensis*	(Blieck et al. 2007, Jia et al. 2010, Pan et al. 1987)
INVERTEBRATES:			-
VERTEBRATES: POLYBRANCHIASPIDS ANTIARCHS *Bothriolepis* sp. *Jiangxilepis* sp.	*Ningxialepis spinosa* *Remigolepis microcephala* *R. major* *R. xiangshanensis* *R. xixiaensis* *R. zhongmingensis* *R. zhongningensis*	*R. zhongweiensis* *Sinolepis* szei TRISTICHOPTERIDS ELPISTOSTEGALIANS *Sinostega pani*	(Blieck et al. 2010, Burrett et al. 1990, Jia et al. 2010, Pan et al. 1987, Zhu et al. 2002)

Evieux (LUPC 6106: *Ichthyostega*-like taxon):

This lower jaw taxon comes from the Strüd locality in the Late Devonian (upper-middle Famennian) Evieux Formation of Belgium. Two depositional environments are present in the Evieux Formation, and it is generally considered to represent a coastal alluvial plain. Lower beds record a lagoonal environment, whereas the sedimentation becomes more fluviatile toward the top (Prestianni et al. 2010). The stratigraphic position of the Strüd Quarry within the Evieux Formation is unclear. However, the microconglomerate-sandstone surrounding the lower jaw (consisting of shale and paleosol clasts) was generated by riverbank flood erosion upstream of a deltaic flood plain (Clément et al. 2004). This suggests that the fossiliferous beds of Strüd were non-marine, and possibly stratigraphically higher in section. See Table 3.26 for the flora and fauna of the Evieux Formation.

Table 3.26. Taxa from the middle Famennian Exieux Formation, Belgium.

TAXON			REFERENCE
PLANTS:	Land plants *Dorinnotheca*- and *Condrusia*-types	*Callixylon brownii* *C. trifilievi* *C. zalesskyi*	(Cressler et al. 2010b, Prestianni et al. 2010)
INVERTEBRATES:			-
VERTEBRATES: Antiarchs *Bothriolepis* sp. Arthrodires & Phyllolepids *Geonlandaspis thorezi* *Phyllolepis undulata* Unsorted 'acanthodians' *Gyracanthus* sp.	Actinopterygians undescribed Dipnomorphs *Holoptychius* sp. '*Dipterus*' sp. *Jarvikia* sp. *Soederberghia* cf. *groenlandica* Rhizodonts undescribed	'Osteolepidids' *Glyptopomus* sp. *Megalichthys* sp. Tristichopterids *Langleria socqueti* *Eusthenodon wängsjöi* Elpistostegalians LUPC 6106	(Clack 2006, Clément 2002, Clément et al. 2004, Clément et al. 2009, Janvier and Clément 2005)

Ketleri (*Ventastega*):

This elpistostegalian is known from the Pavari and Ketleri sites of the Late Devonian (upper Famennian) Ketleri Formation of Latvia (Ahlberg et al. 1994). The rhythmic interbedding of sands with siltstones, and clay and dolomitic marl deposits suggests that the Ketleri Formation preserves a low-tidal, marginal marine near-shore paleoenvironment (Lukševičs 1992, Lukševičs and Zupiņš 2004). See Table 3.27 for the Ketleri fauna.

Table 3.27. Taxa from the upper Famennian Ketleri Formation, Latvia.

TAXON	REFERENCE
PLANTS:	-
INVERTEBRATES:	-

VERTEBRATES: Antiarchs *Bothriolepis ciecere* Unsorted 'acanthodians' *Devononchus ketleriensis* *D. tenuispinus* Stem-sarcopterygians *Onychodus* sp.	Dipnomorphs *Orlovichthys* sp. cf. *limnatis* *Holoptychius* sp. cf. *nobilissimus* *Ventalepis ketleriensis* 'Osteolepidids' *Cryptolepis grossi* *Glyptopomus* sp.	Tristichopterids gen. et. sp. indet. Elpistostegalians *Panderichthys bystrovi* *Ventastega curonica*	(Ahlberg et al. 1994, Clack 2006, Cloutier and Lelievre 1998)

Britta and Aina Dal (*Acanthostega*, *Eusthenodon*, & *Ichthyostega*):

The Late Devonian (upper Famennian) Britta and Aina Dal Formations of East Greenland represent extensive yet ephemeral fluvial depositional environments. Britta Dal contains large terminal alluvial fans with extensive mud rich flood plains and poorly channelized streams that were part of a major distributary system that flooded periodically. *In situ* specimens of *Acanthostega* preserved in sheet sandstones were almost certainly carried downstream by at least two of these flooding events. A braided stream system was only partially active during these major floods (Astin et al. 2010). By contrast, the overlying Aina Dal Formation marks the transition to meandering rivers, with more extensive overbank deposits, channel sandstones, and point bar sequences (Olsen and Larsen 1993). Here, braids became more widely separated in a system dominated by silt-rich floodplains and extensive vertisols (Astin et al. 2010). See Table 3.28 for the flora and fauna of these formations.

Table 3.28. Taxa from the upper Famennian Britta and Aina* Dal Formations of East Greenland, including the Gauss Halvø and Ymer Ø localities, respectively. (*) indicates taxa known from both formations.

TAXON			REFERENCE
PLANTS:	Land Plants	Lycopods Fern-like taxa	(Astin et al. 2010)
INVERTEBRATES:			-

VERTEBRATES: ANTIARCHS _Bothriolepis nielseni_* _Remigolepis acuta_ _R. incisa_ _R. kullingi_* _R. kochi_* ARTHRODIRES & PHYLLOLEPIDS _Phyllolepis nielseni_* Unidentified taxon	(STEM-)CHONDRICHTHYANS gen. et sp. indet. UNSORTED 'ACANTHODIANS' Unidentified scales DIPNOMORPHS _Holoptychius_ sp.(*) _Jarvikia arctica_* _Oervigia nordica_ _Soederberghia groenlandica_(*) 'OSTEOLEPIDIDS' _Gyroptychius groenlandicus_*	_Thursius? minor_* TRISTICHOPTERIDS Unidentified taxon _Eusthenodon waengsjoei_ ELPISTOSTEGALIANS _Acanthostega gunnari_(*) Ichthyostega stensioei(*) _I. watsoni_ _I. eigili_	(Blom et al. 2007)

Catskill (*Hynerpeton*):

Hynerpeton bassetti is known from the Red Hill field site of the Late Devonian (upper Famennian) Catskill Formation in northcentral Pennsylvania (Daeschler et al. 1994). The Catskill Formation represents a sequence of clastic sediments that were shed into a foreland basin during the Acadian Orogeny (Faill 1985). Three members compose the Catskill Formation, and the vertical succession of lithologic units records a progression from marginal marine to deltaic estuarine, and then to alluvial plain facies (Brezinski et al. 2009, Cotter and Driese 1998). The lower two members are more marine-influenced (Cotter and Driese 1998), but the upper Duncannon Member at Red Hill is indisputably fluvial in character (Cressler et al. 2010a). It exhibits several fining upward sequences that grade from large-scale crossbedded channel sands to alternating sands and silts capped by massive mudstones. These cycles were deposited by meandering stream systems on a low-gradient alluvial plane (Sevon 1985), however, vertisol horizons suggest seasonally flooded, vegetated floodplains as well (Woodrow et al. 1995). Elpistostegalians such as *Hynerpeton* appear to be known from the wetter parts of this cycle (Retallack et al. 2009). See Table 3.29 for the flora and fauna of the Catskill Formation.

Table 3.29. Taxa from the upper Famennian Catskill Formation, Pennsylvania, USA, and the Red Hill locality* specifically.

TAXON			REFERENCE
PLANTS: SPORE TAXA _Geminospora lemurata_* _Grandispora cornuta_* _Retusotriletes communis_* _Rugospora flexuosa_* _Verrucosisporites tumulentus_*	LAND PLANTS _Aglosperma quadripartita_* _Archaeopteris obtusa_* _A. halliana_* _A. hibernica_* _A. macilenta_* _Barinophyton obscurum_* _B. sibericum_*	_Duodimidia pfefferkornii_* _Eospermatopteris_ _Gillespiea randolphensis_* _Lepidodendropsis_* _Lepidosigillaria_ _Otzinachsonia beerboweri_* _Protobarynophyton sp._* _Rhacophyton ceratangium_*	(Cressler et al. 2010a, Cressler et al. 2010b, Rimmer et al. 2004)

INVERTEBRATES:	Diplopods Orsadesmus rubecollus*	Arachnids Gigantocharinus szatmaryi*	(Shear 2000, Wilson et al. 2005)
VERTEBRATES: Antiarchs *Bothriolepis* sp. *Remigolepis* sp. Arthrodires & Phyllolepids *Groenlandaspis* sp.* *Phyllolepis* sp. *Phyllolepis rossimontina** Dinichthyids (Stem-)Chondrichthyans *Ageleodus* (cf) sp.* *Ctenacanthus* sp.*	Unsorted 'acanthodians' *Gyracanthus* sp.* *Gyracanthus* sp. gen. et. sp. indet. Actinopterygians *Limnomis delanyi** Dipnomorphs *Apatorhynchus opistheretmus* *Holoptychius* sp.* *Soederberghia* sp.* Rhizodonts gen. et. sp. indet.*	*Strepsodus** 'Osteolepidids' gen. et. sp. indet.* *Sterropterygion* Tristichopterids cf. *Eusthenodon* sp.* *Hyneria lindae** Elpistostegalians *Hynerpeton bassetti** *Densignathus rowei** ANSP 21350*	(Clack 2006, Cressler et al. 2010a, Daeschler et al. 1994, Friedman and Daeschler 2006, Sullivan et al. 1999)

Khovanshchina (*Tulerpeton*):

This elpistostegalian is known from the Late Devonian (uppermost Famennian) Andreyevka-2 locality of the Khovanshchina Formation in Tula, Russia (Lebedev and Clack 1993, Lebedev and Coates 1995). Andreyevka-2 is situated in the Zavolzhsky Horizon, in the lower part of the Khovanshchina Formation. This sequence consists of limestones and clays and has been interpreted to represent an epicontinental basin located at least 200 km offshore (Alekseev et al. 1994). See Table 3.30 for flora and fauna from the Khovanshchina Formation.

Table 3.30. Taxa from the uppermost Famennian Khovanshchina Formation, Russia, and Andreyevka-2* specifically.

TAXON			REFERENCE
FLORA:	Stromatolites*	Charophyte algae*	(Alekseev et al. 1994)
INVERTEBRATES: Annelids* *Serpula vipera*	Ostracodes* *Aparchitellina* sp. *Aparchites globulus* *Bykovites nativus*	*Carbonita* sp. *Evlanella sokolovi* *Glyptolichwinella* ct. *spiralis* *Healdianella punctata*	(Alekseev et al. 1994)

VERTEBRATES: Conodonts *Bispathodus stabilis* *B. aculeatus aculeatus* *B. aculeatus plumulus* *Icriodus costatus* *Pandorinellina nota* *Polygnathus collinsoni* *P. lobatus* *P. paprothae* *Pseudopolygnathus dentilineatus* *P. conili*	Antiarchs* *Bothriolepis* sp. *Remigolepis armata* Unsorted 'acanthodians'* *Devononchus* sp. Actinopterygians* cf. *Moythomasia* Stem-Sarcopterygians* *Strunius* sp.	Dipnomorphs* *Andreyevichthys epitomus* *Holoptychius* sp. 'Osteolepidids'* *Chrysolepis* Tristichopterids* cf. *Eusthenodon* Elpistostegalians* *Tulerpeton curtum*	(Alekseev et al. 1994, Clack 2006)

Snowy Plains (*Barameda decipiens*):

This rhizotont is known from the Home Station Sandstone Member of the Snowy Plains Formation in Victoria, Australia. This formation extends from the Late Devonian (Famennian) to the Early Carboniferous (Garvey and Hasiotis 2008, Roberts et al. 1972, Young 1989b). The main facies of the Snowy Plains Formation include broad channelized sandstones that lie within cross-stratified red and purple mudstones. These sandstones record the migration of sandy, in-channel bar and dune forms, under moderate flow regimes. The enveloping red mudstones are typical of overbank floodplain units, with the stratified sandstone bodies recording overbank deposition. Plaeosols and rootlet structures are commonly preserved within the mudstone facies. Overall, sedimentology is consistent with a meandering fluvial depositional environment (O'Halloran and Gaul 1997b). See Table 3.31 for the flora and fauna of the Snowy Plains Formation.

Table 3.31. Taxa from the Late Devonian-Early Carboniferous Snowy Plains Formation, Victoria, Australia, and of its Home Station Sandstone Member*.

TAXON			REFERENCE
PLANTS:	Land plants *Archaeopteris howitti* *Cordaites australis*	*Leptophloeum australe* *Sphenopteris* sp.	(Roberts et al. 1972)
INVERTEBRATES: Ichnotaxa* *Cruziana*	*Fuersichnus* sp. *Margaritichnus* sp. *Palaeophycus*	*Platicytes lioparadus* *Rusophycus* (a trilobite) *Sagittichnus*	(Garvey and Hasiotis 2008)
VERTEBRATES: Unsorted 'acanthodians' *Acanthodes*	*Eupleurogmus* *Gyracanthides* Dipnomorphs *Ctenodus*	Rhizodonts *Strepsodus* *Barameda decipiens** Actinopterygians *Elonichthys*	(Roberts et al. 1972)

Early Carboniferous Paleoenvironments

Raymond (*Cladarosymblema*):

The Police Mountain Track locality of the Raymond Formation is part of the Early Carboniferous (early to mid Viséan) Drummond Basin of Queensland, Australia. Local and regional sedimentological data appear to suggest slightly different paleoenvironmental patterns. In the Raymond Formation, and near the Police Mountain Track locality in particular, sandstones and siltstones show evidence of shallow water deposition. Surface ripples, sand-filled mud cracks, and channels filled with cross-stratified sands are common within and adjacent to the fossil beds. These structures are interpreted to derive from fluviatile and lacustrine environments (Fox 1995). However, even though many sediments in the Drummond Basin were deposited from rivers flowing from the north to northwest, there were periodic marine incursions into the northern region of the basin (Olgers 1972). In addition, the marine polychaete, *Spirorbis*, and the 'acanthodian', *Gyracanthus* cf *hawkinsi* are known from the Raymond Formation (Turner 1993, Turner et al. 2005). Interestingly, *G.* cf *hawkinsi* is also known elsewhere from the non-marine to marginal marine Ducabrook Formation, which is also part of the Drummond Basin (Turner et al. 2005). See Table 3.32 for the flora and fauna of the Raymond Formation.

Table 3.32. Taxa from the early-mid Viséan Raymond Formation, Queensland, Australia, and the Police Mountain Track locality specifically*.

TAXON			REFERENCE
PLANTS:	LAND PLANTS:	*Lepidodendron velthrimanianum** *Microcodium**	(Fox 1995)
INVERTEBRATES:	POLYCHAETES:	*Spirorbis**	(Turner 1993)
VERTEBRATES: UNSORTED 'ACANTHODIANS' Unidentified taxon* Acanthodian-type scales *Gyracanthus* cf *hawkinsi*	(STEM-)CHONDRICHTHYANS *Ageleodus* cf Xenacanths ACTINOPTERYGIANS unidentified taxa (x3 indet.)*	SARCOPTERYGIANS Unidentified taxon* *Cladarosymblema narrienense**	(Fox 1995, Turner et al. 2005)

Floral and Faunal Analysis.—The results of the assemblage analysis are almost entirely consistent with the sedimentological reconstructions and interpretations of these formations. Figure 3.2 depicts the spread of the 37 localities and formations, along correspondence axis 1 (CA1) of marine to freshwater paleoenvironments. At the far left are the most heavily influenced marine environments, and to the far right are those with the strongest freshwater signal. Overall, the pattern includes (from left to right—i.e., negative-to-positive Eigenvalues): coastal marine (Gogo, Denay, Rdeyskoe), nearshore marine (Snezha, Zadonsk, Khovanshchina, Wojciechowice), marginal marine (Gauga, Amata, ?Escuminac, Ketleri, ?Scat Craig), and then freshwater of some type, whether extra- or intermontane, fluvial or lacustrine (all other formations and localities).

Most formations cluster toward the middle of this spread, but a pattern still emerges from their

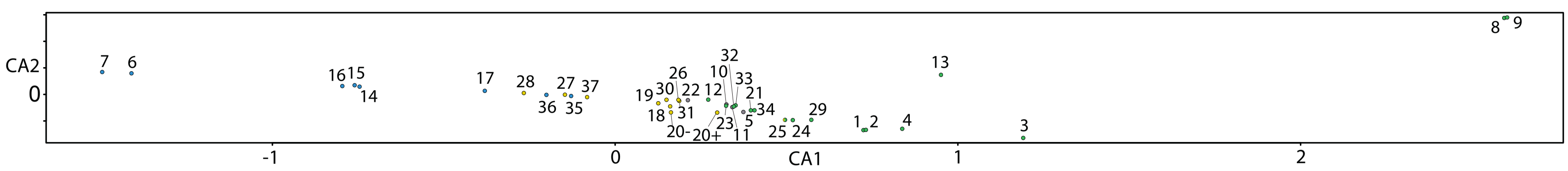

Figure 3.2. Faunal comparison using CCA of Middle and Late Devonian stem-tetrapod formations and localities. Correspondence axis 1 (CA1) tracks salinity. CA2 is uninformative. Increasingly negative CA1 Eigenvalues represent coastal and nearshore marine environments and more positive Eigenvalues represent marine-influenced, extramontane, and intermontane freshwater habitats. The analysis was run scoring the Escuminac Formation as both preserving (20+) or lacking (20–) plants. (1) Home Station Sandstone Member of the Snowy Plains Formation; (2) Snowy Plains Formation; (3) Aztec Siltstone Formation (containing the "Fish Hotel" site, horizons A-Z); (4) Bindaree Formation (including the Mt. Howitt locality); (5) Mandagery Formation (including the Canowindra fish fauna); (6) Gogo fish fauna (mostly of the *transitans* Conodont Zone) of the Gogo Formation; (7) Gogo Formation; (8) Achannaras Quarry of the Lybster Flagstone Formtaion; (9) Lybster Flagstone Formation; (10) Police Mountain Track Locality of the Raymond Formation; (11) Raymond Formation; (12) Sofia Sund Formation; (13) Eday Flagstone Formation (including the south Ronaldsay locality); (14) Rdeyskoe Formation (including the Porkhov and Svinord beds); (15) Red Hill I locality of the Denay Formation; (16) Denay Formation; (17) Snezha Beds (of the Snezah Fm); (18) Gauja Formation (including the Lode Quarry); (19) Amata Formation (including the Pasta Muiza locality); (20) Escuminac Formation (including the Miguasha locality); (21) Fram Formation (including the NV2K17 site); (22) Scat Craig locality; (23) Cloghnan Shale (including the Jemalong Quarry); (24) Red Hill, Pennsylvania locality of the Catskill Formation; (25) Catskill Formation; (26) Ogre Fm (including the Velna-Ala locality); (27) Gornostayevka locality of the Zadonsk Formation; (28) Zadonsk Formation; (29) Zhongning Formation (including the Ningxia Hui Site/*Sinostega* locality); (30) Pavari Site of the Ketleri Formation; (31) Ketleri Formation; (32) Aina Dal Formation (including Gauss Halvø); (33) Britta Dal Formation (including Ymer Ø); (34) Evieux Formation (including the Strüd locality); (35) Andreyevka-2 locality of the Khovanshchina Formation; (36) Khovanshchina Formation; (37) Wojciechowice Formation (including the Zachełmie Quarry). For clarity, CA1 has been stretched out of proportion with CA2. To illustrate the general congruence between sedimentological and assemblage data, the core color for each data point corresponds to the paleoenvironmental reconstruction provided by the assessment of sedimentological data. Blue (coastal or nearshore marine), yellow (marine-influenced), green (freshwater), grey (unclear). See text for additional details.

distribution. Similar to the general result, marine-influenced and freshwater sites skew to the left and right, respectively. Interestingly, the Escuminac Formation falls out with known extramontane freshwater localities such as the Aina and Britta Dal Formations. However, because the Miguasha locality preserves copious plant matter—a known terrestrial indicator—if plant taxa are removed from the Escuminac assemblage and the data re-analyzed, then it plots with marine-influenced paleoenvironments such as the Gauja and Amata Formations. In this respect, an Escuminac Formation 'lacking plants' produces a fauna that converges on current isotopic and sedimentological interpretations of its paleoenvironment. However, because Miguasha really does preserve plant matter, its position in the canonical correspondence analysis raises legitimate questions about whether important components of the flora and fauna have been washed in.

There are a few cases where sedimentological data are unclear—like with the Scat Craig locality, the Raymond Formation, and the Mandagery Sandstone Formation—and that require comment following the assemblage result. As mentioned, even though local sedimentological data suggest that Scat Craig was a fluvial environment, equivalent deposits in the Baltic region appear to be deltaic or nearshore. Interestingly, the assemblage analysis plots Scat Craig reasonably close to the marginal marine Ketleri and Ogre Formations, but its position may be a bit too 'in between' marginal and extramontane freshwater sites to make for a compelling argument either way. Similarly, the local and regional geology of the Raymond Formation present conflicting pictures. Site data at the Police Mountain Track locality seem to suggest a freshwater depositional environment; however, marine incursions were periodic at the regional scale. In addition, even though polychaetes at Police Mountain Track are also known from the more heavily marine-influenced Khovanshchina Formation, their presence in the Raymond fauna did not seem to affect the marine character of its signal. In this case, local geological and assemblage data have converged on the more freshwater result. Finally, regarding the Mandagery Sandstone, there appears to be a moderate marine influence up-section, including a lingulid-vertebrate association in the Canodwindra fish fauna. However, and although sedimentological and assemblage data from all other brachiopod-containing formations (e.g., Rdeyskoe, Denay, Snezha, Zadonsk, and Wojciechowice) suggest that they are marine-influenced, the overprint of the vertebrate signal from the Mandagery Sandstone appears to trump and skew its reconstruction as a (?extramontane) freshwater paleoenvironment.

Within a phylogenetic context, mapping these data onto the tree in Figure 3.1 produces similar though slightly different results. The assemblage data are continuous, and each taxon in the phylogenetic analysis traces to a locality and/or formation (i.e., a 'point') in the canonical correspondence result that has a specific Eigenvalue. Treating these values as character states and mapping them onto this cladogram produces the pattern in Figure 3.3A. Branches are color-coded by Eigenvalue in ~0.4 increments, and colors are coordinated with the pattern employed in Figure 3.2; shades of green signify freshwater environments, and yellow on through darker blue represent degrees of marine influence. Similarly, in a set of discrete character states, sedimentological data were also mapped onto the same cladogram, illustrated in Figure 3.3B. The color scheme here follows the same rationale, albeit sans the spectrum of freshwater states, since in the cases of the Eday Flagstone, Sofia Sund, Cloghnan Shale, Zhongning, Snowy Plains, and Raymond Formations, it is unclear as to whether these formations represent inter- and/or extramontane environments.

It is important to note that in Figure 3.3A, because Eigenvalue ranges are uniformly distributed

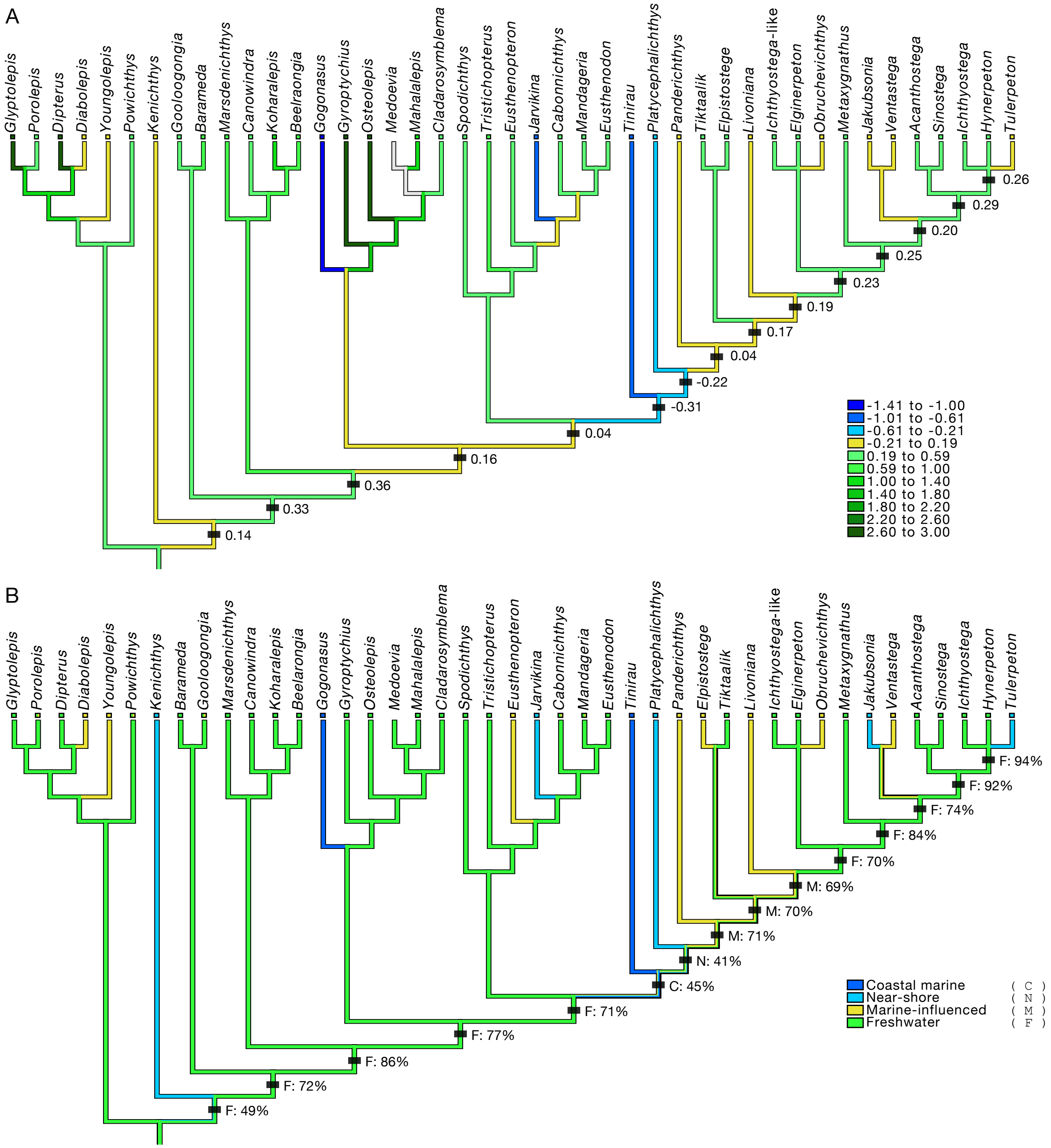

Figure 3.3. Combined phylogenetic and paleoenvironmental data tracing the environmental history of stem-tetrapods. (A) Results from the assemblage analysis (Figure 3.2) mapped onto the phylogeny from Figure 3.1. Early Devonian sites excluded from the assemblage analysis were assigned Eigenvalues that correspond to what the sedimentological reconstructions suggest about their paleoenvironment. (B) Sedimentological data mapped onto the phylogeny from Figure 3.1. Considering the sedimentology of their formations, *Porolepis*, *Powichthys*, *Gooloogongia*, *Cabonnichthys*, and *Mandageria* were scored as polymorphic, freshwater/marine-influenced. *Elginerpeton* was scored as 'freshwater' following the local sedimentological signal from Scat Craig. See text for additional details.

in ~0.4 increments, localities/formations that cluster in the canonical correspondence analysis (Figure 3.2) will not necessarily all receive the same color in Figure 3.3A. This applies only in a few cases that are necessary to clarify. The Gauja Formation (including Lode), the Amata Formation (including Pasta Muiza), the Escuminac Formation (including Miguasha, though scored without plants), the Scat Craig locality (possibly), the Ogre Formation (including Velna-Ala), the Pavari site of the Ketleri Formation, and the Ketleri Formation itself all emerge as marginal marine paleoenvironments in the CCA. This is expected, because the geological data also suggest such an interpretation. However, some members of the data-cluster immediately to the left of these marginal marine environments (i.e., with slightly negative Eigenvalues)— e.g., the Snezha Formation, Gornostayevka and the Zadonsk Formation, Andreyevka-2 and the Khovanshchina Formation, and the Wojciechowice Formation (including the Zachełmie Quarry)—are not colored the same "light blue" (near-shore reconstruction) simply because the less negative CA1 localities/formations from this cluster are captured by the previous ~0.4 'yellow' (marginal marine) bin. In this respect, it is important that even though taxa like *Tulerpeton* (from Andreyevka-2 of the Khovanshchina Formation, Eigenvalues = -0.1286628 and -0.2007378, respectively), and *Jakubsonia* (from Gornostayevka Quarry of the Zadonsk Formation, Eigenvalues = -0.1463004 and -0.2664945, respectively) terminate yellow branches, their localities fall near the lower limit (i.e., more negative) of the 'marginal marine' ~0.4 group. In addition, because the localities and formations for each of these taxa were included separately in the CCA, the average of the aforementioned Eigenvalues in each case was used to score each taxon. If by contrast, I used only the Eigenvalue from the Zadonsk Formation to score *Jakubsonia* (Eigenvalue = -0.2664945), it would have emerged as 'light blue' (near shore), and not 'yellow' (marginal marine) as it does when scored from the average of its quarry and formation Eigenvalues. This does not apply to *Tulerpeton*, because its locality and formation are both captured by the marginal marine bracket. Ultimately, considering the continuous nature of these states, it is likely best to consider the 'yellow' is these cases to represent a "*strong* marine influence." Moreover, considering the Miguasha taxa *Eusthenopteron* and *Elpiststege*, whether scored with (Eigenvalue = 0.2974831) or without (Eigenvalue = 0.1984463) plants, both taxa are reconstructed with a 'light green' freshwater paleoenvironment. However, because the lower limit for this category is 0.19419118, a Miguasha lacking plants just barely falls outside the yellow, marine-influenced bin. In this respect, similar to *Tulerpeton* and *Jakubsonia* (albeit at the other end of the spectrum), *Eusthenopteron* and *Elpistostege* should be considered in Figure 3.3A to exist at a locality with a "*slight* marine influence."

Nonetheless, independent of color, several patterns emerge when focusing on the range of Eigenvalues and their influence on ancestral state reconstructions: (1) a marginal marine environment ancestrally characterized tetrapodomorphs; (2) both freshwater and marginal environments pervaded the early history of major clades, even though members of each clade were more often freshwater than not; (3) the phylogenetic placement and strong negative Eigenvalue for *Gogonasus* are what influence the ancestral (marginal marine) reconstruction leading to megalichthyiforms and tristichopterids; (4) the first elpistostegalians moved into coastal environments; (5) later diverging elpistostegalians moved shoreward; and (6) the first digited body fossils appear following at least four cladogenetic events where a freshwater habitat was the ancestral environment. Similar though slightly different patterns emerge from mapping the sedimentological data onto the same cladogram, represented in Figure 3B. They include: (1) a freshwater (as opposed to marine-influenced) environment ancestrally characterized tetrapodomorphs; (2) freshwater environments pervaded the early history of tetrapodomorphs, despite the phylogenetic position of *Gogonasus*; (3) the first elpistostegalians moved into coastal environments; (4) later-diverging elpistostegalians move shoreward; and (5) the first digited body fossils appear following at least four cladogenetic events in which a freshwater habitat was the ancestral environment.

Both of these reconstructions fit nicely with Thomson's (1980) "marine hypothesis: variant II." Elpistostegalians as a clade arose in wholly marine conditions, but a substantial part of their later diversification included numerous taxa that invaded extramontane freshwater environments. Elpistostegalian fossils are certainly found in marine and extramontane habitats, and are present pan-globally in near all major Devonian continental provinces.

Isotopic Results.—Samples from Red Hill, PA (of the Catskill Formation), the NV2K17 site (of the Fram Formation), the Strüd locality (of the Evieux Formation), and the Aztec Sandstone Formation were analyzed for $\delta^{13}C$ and $\delta^{18}O$ isotopes. See Table 3.33 for the results of this analysis. Because of the many aberrant $\delta^{18}O$ values, the comparison here will focus on $\delta^{13}C$. Nevertheless, the consistently negative $\delta^{13}C$ values from all localities fit with the freshwater picture reconstructed from assemblage and sedimentological data. This contrasts with more positive $\delta^{13}C$ values typically obtained from taxa in marine environments (Bruckschen and Veizer 1997, Korte et al. 2005). In this respect, the isotopic data do not add much to the emergent picture from other data sets, but they do reinforce the current freshwater interpretations of analyzed sites.

Table 3.33. $\delta^{13}C$ and $\delta^{18}O$ values from sampled stem-tetrapod localities. * refers to $\delta^{18}O$ values that are no good because of interference caused by an absence of CO_2 gases generated from the samples. All values are reported in ‰ relative to PDB standard.

LOCALITY	SAMPLE	$\delta^{13}C$	$\delta^{18}O$
Red Hill, PA, Catskill Fm:	*Limnonis*, reduced zone	No carbonate	
	Hyneria fang, reduced zone	-9.41	*203.83
	'Osteolepidid' scale, reduced zone	-7.70	*121.82
	Hyneria matrix, lag layer	No carbonate	
	Hyneria bone, lag layer	-9.68	0.46
	Gyracanthus matrix, lag layer	-11.06	*17.34
	Gyracanthus spine, lag layer	-8.98	*31.05
	Hyneria scale and matrix, lag layer	-9.57	*11.53
	Turrisaspis bone, lag layer	-9.63	-6.63
	Gyracanthus spine, Hyner outcrop	-10.24	-5.21
	Matrix and bone bits, Hyner outcrop	No carbonate	

NV2K17, Fram Fm:	Carbonate nodule-1	-3.70	-6.70
	Carbonate nodule-2	-4.21	-6.27
	Carbonate nodule-3	-4.46	-6.49
	Carbonate nodule-4	-4.47	-6.38
	Carbonate nodule-5	-4.25	-6.43
	Carbonate nodule-6	-3.20	-6.24
	Bone fragment-1	-3.13	-6.75
	Bone fragment-2	-2.88	-6.85
	Bone fragment-3	-1.63	-5.10
	Bone fragment-4	-2.66	-6.24
	Bone fragment-5	-3.50	-7.81
	Bone fragment-6	-3.03	-6.77
	Matrix-1	-3.32	*5.01
	Matrix-2	-3.50	-5.37
	Matrix-3	-1.47	-6.49
Strüd locality, Evieux Fm: facies 1-6, x 18 samples	Matrix	No carbonate	
Aztec Siltstone Fm:	Matrix-1	-5.11	*28.64
	Matrix-2	-5.13	*26.03

Discussion

Drying ponds and inflated lungs.—Despite older ideas related to drying ponds (Romer 1958) and their adaptive link to the origin of lungs (Mayr 1960), current phylogenetic reconstructions unambiguously show that lungs are apomorphic for crown-osteichthyans, and in this respect, predate the origin of amphibion-grade sarcopterygians by at least 25 million years (Hurley et al. 2007, Niedźwiedzki et al. 2010). In addition, given the sedimentological and assemblage data, even though the first digited body fossils hail from a freshwater ancestry, ancestral states for earlier elpistostegalians place them in marginal marine environments where drying pond scenarios are ecologically improbable.

Patterns in the Devonian and Carboniferous Records.—Similar to recent work on the evolution of stem-tetrapod paleoenvironments (Laurin and Soler-Gijon 2010), the analyses here also reconstruct early (though not the earliest) elpistostegalians to have ancestrally inhabited marginal-marine settings. By contrast, and unlike the analyses of Laurin and Soler Gijon (2010), these analyses do not reconstruct this ancestral environment to also characterize the first known digited forms. Figure 3.3 focuses on Devonian taxa, and in this respect, differs from the analyses of Laurin and Soler Gijon (2010), who included a suite of post-Devonian taxa. It is possible that the exclusion of these taxa may affect the ancestral state reconstructions of earlier elpistostegalians, but a combined supertree shows that this is not the case (Figure 3.4). Moreover, exclusion by Laurin and Soler Gijon (2010) of the numerous Devonian taxa included in this analysis led them to inaccurately reconstruct a marine habitat for the earliest tetrapodomorphs. Groups such as rhizodonts, canowindrids, megalichthyiforms, and tristichopterids are distilled to three terminal taxa that happen to have been preserved in marine or marine-influenced environments. Alternatively, representative sampling of Middle and Late Devonian sarcopterygians yields the picture presented in Figure 3.3 above. Freshwater environments (ancestrally) characterized most of the early diversification of tetrapodomorphs—despite the strongly negative Eigenvalue for *Gogonasus*, though this 'marine-influenced' ancestral state may suggest that 'osteolepiforms' increased their biogeographic range by invading marine environments, only to again colonize extramontane freshwater habitats. Nevertheless, it appears that the earliest elpistostegalians moved into coastal and nearshore environments and then proceeded shoreward on the road to the first known digited taxa.

More on Tiktaalik *and the Zachełmie trackways*.—These patterns also raise questions about the pectoral propping mechanisms and freshwater habitat of *Tiktaalik*. If at this point in elpistostegalian history a freshwater environment was more autapomorphic than synapomorphic (see Figure 3.3), then it is possible that *Tiktaalik*'s mode of body support was specific to its environment. Thus, despite the appeal to emphasize seamless transitions over morphological disparity, certain aspects of *Tiktaalik*'s anatomy may tell us less about the about the origin of life on land than other taxa at this time that inhabited marine-influenced environments. In this light, unpredicted observations such as uniquely shared pectoral similarities between *Panderichthys* and digited taxa (e.g., a transverse fan shape arrangement of distal radials/digits, or an ulna that is much longer than the ulnare) are more understandable.

There is about an 18 million year gap between the first evidence of digit-bearing taxa as read from the trace fossil record (e.g., the Zachełmie tracks from lower Middle Devonian (Eifelian) of Poland) versus the body fossil record (e.g., *Acanthostega gunnari* from the Upper Devonian (Famennian) of East Greenland) (Niedźwiedzki et al. 2010). However, genus-level preservation rates for Devonian tetrapodomorphs are an order of magnitude lower than species-level rates for groups considered to have dense records (e.g., mammals). Thus, as long as the Zachełmie trackmaker diverged immediately prior to *Livoniaia*, this gap does not overturn the stratophylogenetic fit known from the early elpistostegalian body fossil record (Friedman and Brazeau 2011). In other words, assuming this phylogenetic placement, the Zachełmie trackways do not tell us anything not already resolved by the faunal and assemblage analyses in Figure 3.3: the first digited members of the body fossil record descended from elpistostegalians that ancestrally inhabited marine-influenced environments (see Figure 3.5).

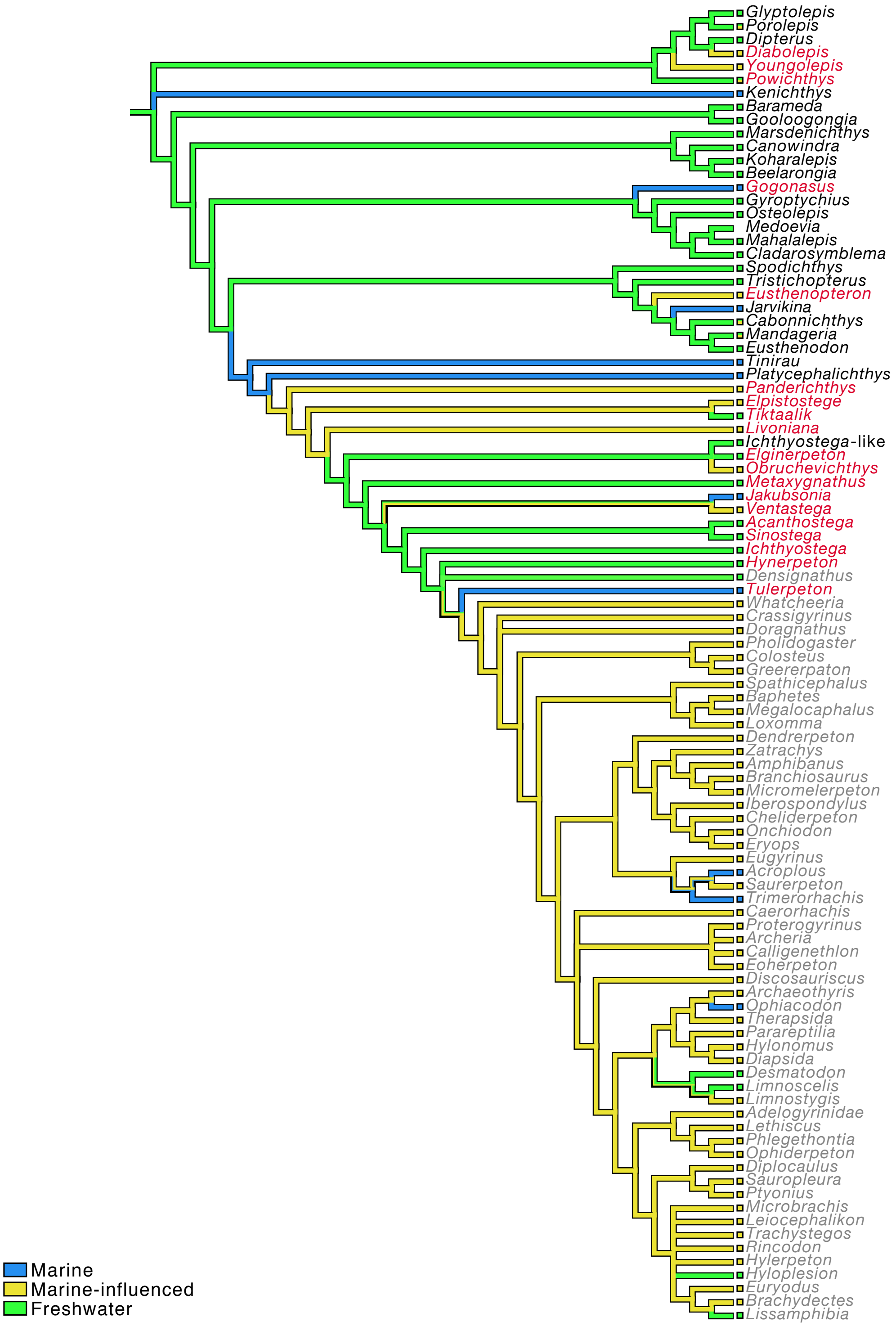

Figure 3.4. Supertree complied from the phylogenetic analysis presented in Figure 3.1, and the suite of post-Devonian taxa analyzed by Laurin and Soler Gijon (2010). The result from Figure 3.3 is still supported, despite the inclusion of additional Carboniferous taxa. The trichotomous scoring (freshwater, marine-influenced, marine) follows from Laurin and Soler Gijon (2010). Taxa common to both analyses are in red, taxa excluded from Laurin and Soler Gijon (2010) are in black, taxa excluded from this analysis are in gray. See text for additional details.

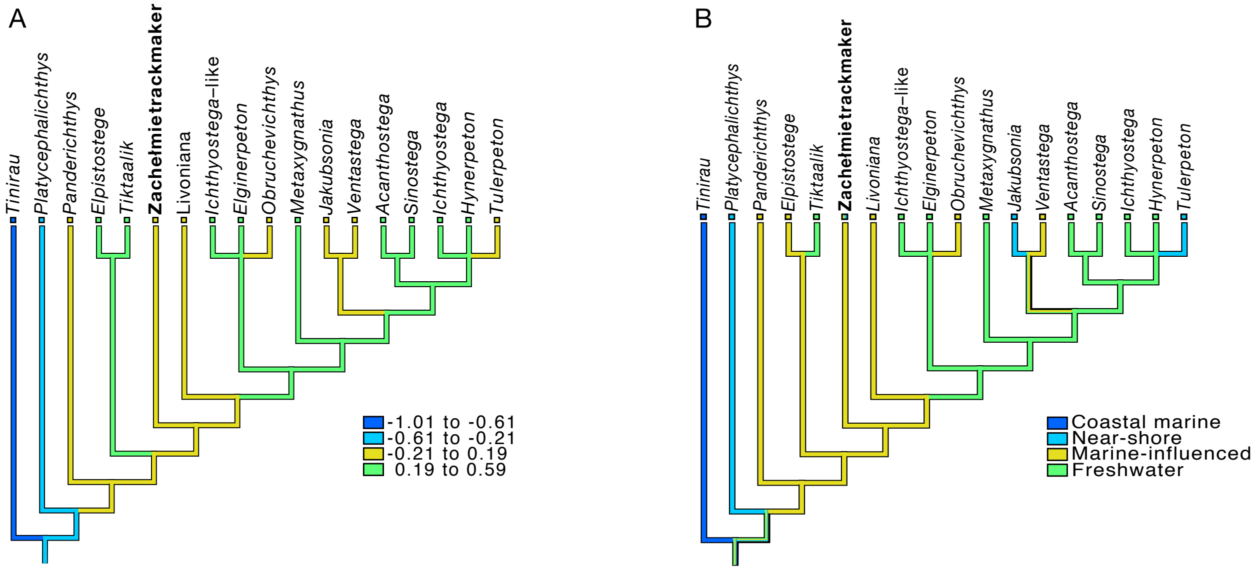

Figure 3.5. The likely phylogenetic position of the Polish, Zachełmie trackmaker following the 95% credibility estimate from "scenario 1" after Friedman and Brazeau (2011). (A) The pattern following the results of the assemblage analysis in Figures 3.2 and 3.3; (B) The pattern following the analysis of sedimentological data. The Zachełmie trackmaker was scored as polymorphic, marine-influenced/nearshore. *Elginerpeton* was scored as 'freshwater' following the local sedimentological signal from Scat Craig. See text for additional details.

Thomson's (1980) marine hypothesis: variant II.—Following the phylogenetic result presented in Figure 3.1, this variant of Thomson's paleoenvironmental origins hypotheses best fits the clade Elpistostegalia. They arose in coastal marine conditions and eventually moved shoreward, but several descendants, including the first digited body fossil taxa, invaded extramontane freshwater environments. Elpistostegalians are found in environments predicted by this hypothesis, and maintain a wide biogeographic range that appears to have been connected via shallow seas from the Middle through Upper Devonian. By contrast, the geographic positions of *Metaxygnathus* (Australia) and *Sinostega* (China) may speak to the recently hypothesized Lower Devonian origin of elpistostegalians (George and Blieck 2011, Niedźwiedzki et al. 2010), thereby providing ample time to achieve a more widespread distribution. See Figure 3.6.

Extinction and the Devonian Earth System.—We may never know the proximate causes for why elpistostegalians eventually invaded fresh water. However, once they inhabited more continental environments, the macroecological patterns from other groups may resolve why living in such habitats was ecologically fortuitous. A succession of five extinction events from the Middle through Late Devonian pummeled marine and continental environments, killing an estimated 75% of species. Global cooling (followed by global warming) possibly tied to the diversification of land plants (associated with weathering, paedogenesis, and the drawdown of global CO_2), widespread deep-water anoxia, the spread of anoxic waters by marine transgressions, and possible bolide impacts all appear to be linked to these extinctions (Algeo and Scheckler 1998, Algeo et al. 2000, McGhee 1996, Murphy et al. 2000, Sandberg et al. 2002). In particular, four signals seem to arise from these patterns: (1) diversity loss is more severe near the equator than at higher latitudes; (2) life in shallow water marine systems is decimated relative to deeper water habitats; (3) clades that extended their latitudinal ranges leading into these events lost those geographic extensions; and (4) for clades inhabiting both marine and freshwater systems, continental members were affected less severely than their marine counterparts (McGhee 1996). By contrast, recent work on Devonian vertebrates suggests that marine and freshwater taxa were equally affected by these Devonian events, although no attempt was made to separate marine-influenced from freshwater (whether inter- or extramontane) assemblages in this comparison (Sallan and Coates 2010).

Near-equatorial environments, such as those where *Tinirau*, *Platycephalichthys*, *Panderichthys*, *Elpistostege*, *Livoniana*, *Obruchevichthys*, *Ventastega*, and *Tulerpeton* may have lived, seem to have been especially affected during these events and lost a tremendous amount of diversity. The upper water column was severely impacted; an estimated 90% of preservable phytoplankton became extinct (McGhee 1996) and reef tracts that once covered 5,000,000 km^2 of marine coastlines were reduced to 1,000 km^2 (Copper 1994). Tabulate corals lost 80% of their generic diversity (Hill 1981). Rugose corals lost 60% of their genera, which included a 96% decline in species that inhabited shallow water environments (Oliver and Pedder 1994). Additionally, the number of stromatoporid genera was cut in half (Stearn 1987); brachiopods lost over 75% of their genera (McGhee 1996); 33% of bryozoan genera went extinct (Taylor and Larwood 1988); benthic ostracodes lost about 20% of their families (Gooday and Becker 1979); and phyllocarid crustaceans lost 60-70% of species from the Givetian through Frasnian, and another 88% at the Famennian–Carboniferous boundary despite re-radiations (Rolfe and Edwards 1979).

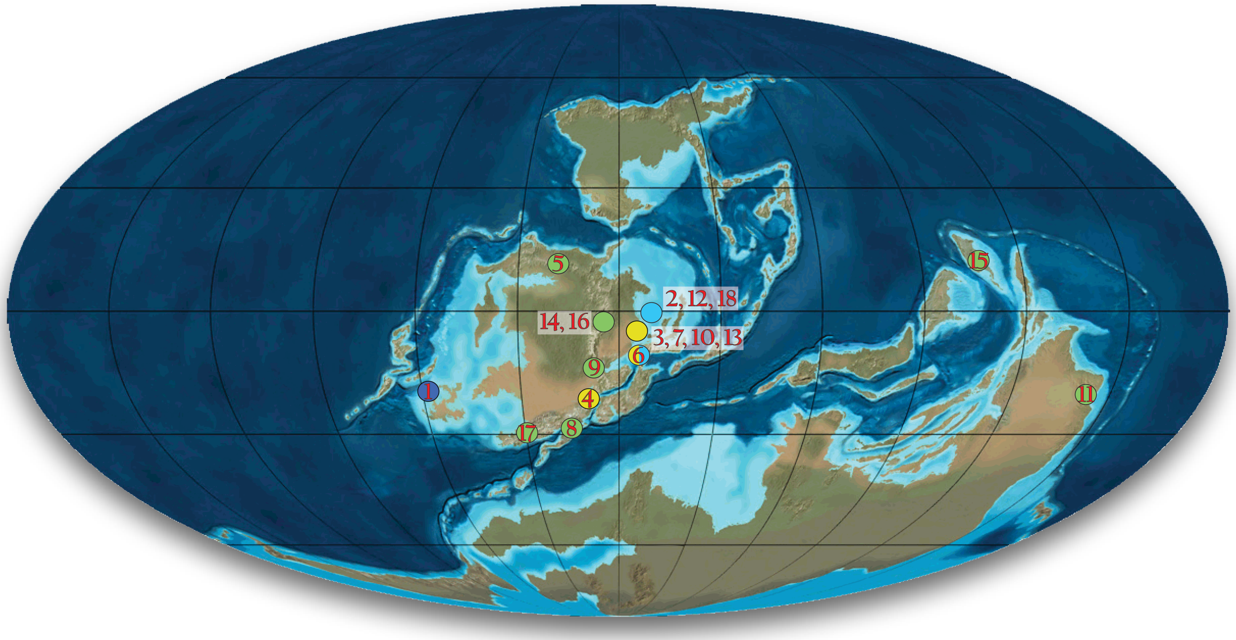

Figure 3.6. Middle–Upper Devonian (387-359 Ma) paleogeographic map reconstructing the biogeographic range of elpistostegalians in Figure 3.5. Colors follow reconstructions from the paleoenvironmental analyses: dark blue (coastal marine), light blue (nearshore), yellow (marine-influenced), green (freshwater). Scat Craig reconstructed in green following the local freshwater sedimentological signal. Middle and Upper Devonian sites include: 1, Red Hill I Beds of the Denay Formation, Nevada, USA (upper Givetian; *Tinirau*); 2, Snezha Beds, Russia and Latvia (late middle Frasnian; *Platycephalichthys*); 3, Gauja Formation, Latvia and Estonia (upper Givetian; *Panderichthys*); 4, Escuminac Formation, Miguasha, Quebéc, Canada (lower Frasnian; *Elpistostege*); 5, Fram Formation, Ellesmere Island, Nunavut, Canada (lower Frasnian; *Tiktaalik*); 6, Wojciechowice Formation, Poland (lower-middle Eifelian; Zachełmie trackmaker); 7, Gauja Formation, Latvia and Estonia (upper Givetian; *Livoniana*); 8, Evieux Formation, Belgium (upper Famennian; *Ichthyostega*-like taxon); 9, Scat Crag, Scotland (upper Frasnian, *Elginerpeton*); 10, Ogre Formation, Velna-Ala, Latvia (upper Frasnian; *Obruchevichthys*); 11, Jemalong Quarry of the Cloghnan Shale, New South Wales, Australia (upper Frasnian-lower Famennian; *Metaxygnathus*); 12, Zadonsk Formation , Russia (lower Famennian; *Jakubsonia*); 13, Ketleri Formation, Latvia (upper Famennian; *Ventastega*); 14, Aina Dal Formation, East Greenland (upper Famennian; *Acanthostega*); 15, Zhongning Formation, Ningxia, China (upper Famennian; *Sinostega*); 16, Britta Dal Formation, East Greenland (upper Famennian; *Ichthyostega*); 17, Catskill Formation, Pennsylvania, USA (upper Famennian; *Hynerpeton*); 18, Khovanshchina Formation, Andreyevka-2, Russia (uppermost Famennian; *Tulerpeton*). Redrawn from original paleomap by Ron Blakey, Northern Arizona University.

It can be difficult to compare diversity changes in marine and continental habitats during mass extinctions, since clades inhabiting these two environments differed in their physiologies, ecologies, and evolutionary histories. However, if freshwater systems reflect continental events, then studying taxa that inhabited both freshwater and marine systems might provide the basis for useful comparison (McGhee 1996). There are several 'placoderm' and 'acanthodian' groups (grades as opposed to clades by most recent data (Brazeau 2009)) that inhabited both environments. There is little doubt that continental systems were impacted by Devonian extinction events (Niklas et al. 1983), but the severity of these changes relative to those in marine systems is of key importance.

All works to date have treated freshwater and marine-influenced environments together to compare diversity changes in marine vertebrate assemblages (Long 1993, McGhee 1982, Sallan and Coates 2010). Whereas Sallan and Coates (2010) found no evidence for freshwater-influenced (i.e., any environment, including marine-influenced habitats, that receive freshwater input) or fully marine refugia, McGhee's (1982) analysis suggests that 70% of freshwater-influenced 'acanthodian' species (and 77% of 'placoderm' species) persist into the Famennian, whereas this is limited to 12% of fully marine species (35% for fully marine 'placoderms'). Furthermore, for one-third of 'placoderm' families (such as asterolepidids, bothriolepidids, and groenlandaspids) that inhabited both freshwater-influenced and fully marine Frasnian habitats, only the freshwater-influenced member survived into the Famennian (Long 1993). It will be key to tease apart the relative changes in vertebrate diversity between marine-influenced and fully freshwater environments, but clues as to why elpistostegalians invaded freshwater may lie with certain mollusk groups. Similar to the paleoenvironmental patterns in Figures 3.3 and 3.5, bivalves (Kriz 1979) and gastropods (Dineley 1984) colonized Mid-Late Devonian freshwater environments as well. Thus, independent of the classic pushing (Romer 1958) or pulling factors (Thomson 1969, 1980) that initiated a habitat change, the differential survival of freshwater over marine taxa may hold important clues to why elpistostegalians swam upstream, and how continental systems may have functioned as safe havens on their road to the Carboniferous Earth system.

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SUPPLEMENTARY INFORMATION FOR:

THE PALEOENVIRONMENTAL HISTORY OF STEM-TETRAPODS

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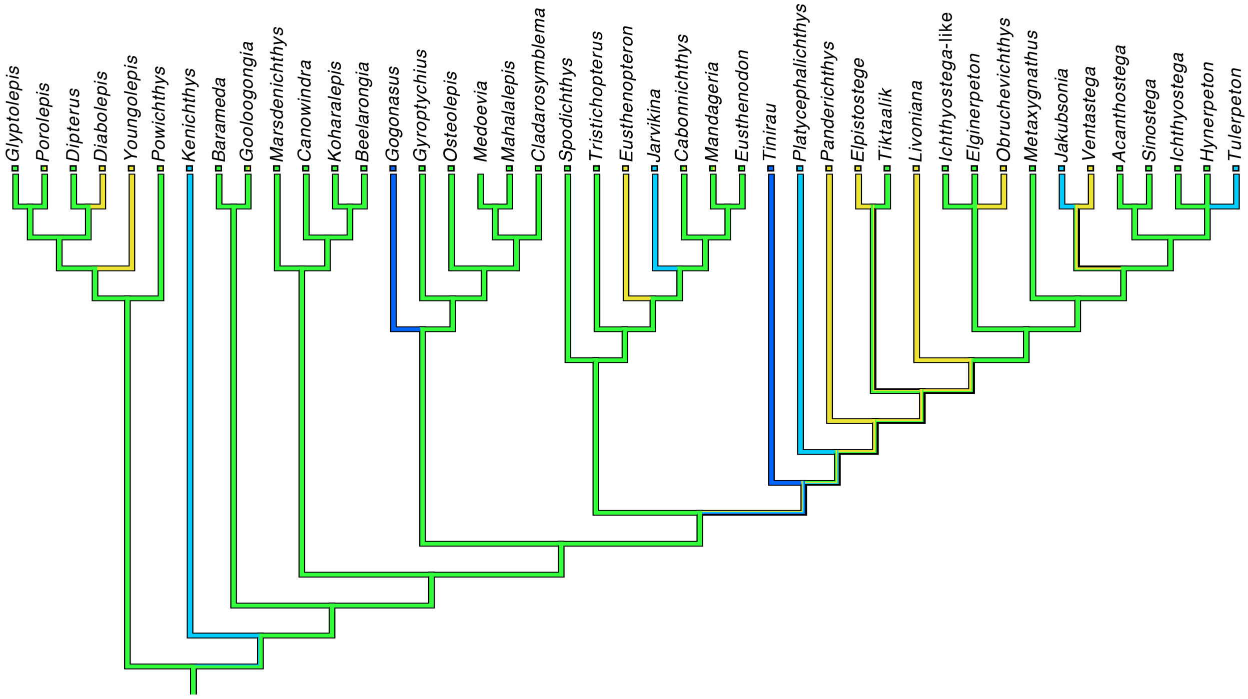

Supplementary Information

Supporting Text

References

Supporting Text

Part A.

Taxa and characters used in the phylogenetic analysis.—The following 175 morphological characters were used to construct a cladogram including 43 stem-tetrapod taxa, upon which their paleoenvironmental data were mapped. Primary character sources (Ahlberg et al. 2008, Ahlberg and Johanson 1998, Ahlberg et al. 2000, Coates and Friedman 2010, Daeschler et al. 2006, Zhu and Ahlberg 2004) are indicated parenthetically following each character description. Numbers following the citations refer to the character number in the original source. Characters modified from their original source are noted where applicable.

Characters were polarized by comparison to outgroup taxa such as *Porolepis*, *Glyptolepis*, *Powichthys*, *Youngolepis*, *Diabolepis*, and *Dipterus*. These taxa were selected because they represent a range of total-group lungfish that are known from reasonable material, are well studied, and generally accepted as sister to total-group tetrapods.

Characters were coded based on a combination of published descriptions, specimen illustrations, and firsthand examination of fossil material. Care was taken to avoid simply recycling codings in the published literature. Specimens from the following museums were examined, and are noted following each taxon below: Australian Museum, Sydney (AMF), Australian National University (ANU), Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra (CPC), Geologisk Museum, Copenhagen, Denmark (MGUH), Latvian Museum of Natural History (LDM), Muséum national d'Histoire naturelle, Paris (MNHN), Museum Victoria, Melbourne, Australia (NMV), The Natural History Museum, London (MNH), Palaeontological Institute of the Russian Academy of Sciences, Moscow (PIN), National Museums of Scotland (NMS), Nunavut Fossil Vertebrate Collection (NUFV), Swedish Museum of Natural History, Stockholm (NR), University of California Museum of Paleontology (UCMP), University Museum of Zoology Cambridge (UMZC).

Acanthostega (Ahlberg and Clack 1998, Clack 1988, 1989, 1994, 1998, 2002, Coates 1996) (MGUH f.n. 157, 255, 1227, 1258; UMZC T1291, T1300)
Barameda (Garvey 2005, Long 1989, Long and Ahlberg 1999) (NMV P10277, P160880, P160885, P212715)
Beelarongia (Long 1987) (NMV P160875, P160972)
Cabonnichthys (Ahlberg and Johanson 1997) (AMF96856, F96858a, F96863, F96902, F98037, F98038)
Canowindra (Long 1985a, Thomson 1973) (BMNH P.34420)
Cladarosymblema (Fox et al. 1995)
Diabolepis (Chang 1995, Chang and Yu 1984, Smith and Chang 1990)
Dipterus (Ahlberg and Trewin 1995, White 1965) (BMNH P.17410, P.33165, P.34544, P.53507; MNHN GBP71, P72; NR P.3108, P.4827; UCMP 43714, 43727, 43728, 43729, 43730, 93066, 93067, 93068, 93069, 93070, 93071, 93072, 115246; UMZC GN1043)
Elginerpeton (Ahlberg 1991b, 1995, 1998)
Elpistostege (Schultze and Arsenault 1985) (BMNH P.60526 a,b)
Eusthenodon (Jarvik 1952) (NR P.1475, P.1693)
Eusthenopteron (Andrews and Westoll 1970a, Jarvik 1980) (BMNH P.60386, P.60388, P.60397; NR P.222, P. 223, P249, P.287, P.290, P.330, P322 a,b, P.326b, P.382, P.2197, a,b, P2609, P.4611, P.6383; UMZC GN.790, GN.791, GN.797, GN.799)

Glyptolepis (Ahlberg 1989, Ahlberg 1991a, Jarvik 1972) (NR P.180, P.2503 a,b, P.8635)
Gogonasus (Long et al. 1997, Long et al. 2006) (ANU 21885, 49259; NMV P221807)
Gooloogongia (Johanson and Ahlberg 2001)
Gyroptychius (Jarvik 1950a, b, 1985) (MNHN GBP44, P63, P107, P138, P209, P264, P265, P307; NR P.1679, P. 1698, P.4116, P.4220; UMZC GN.240, GN.939)
Hynerpeton (Daeschler 2000, Daeschler et al. 1994)
Ichthyostega (Ahlberg et al. 2005, Jarvik 1996) (MGUH 6055, 6064, 6081, MGUH f.n. 200, 300, 301)
Jakubsonia (Lebedev 2004)
Jarvikina (Vorobyeva 1977)
Kenichthys (Chang and Zhu 1993, Zhu and Ahlberg 2004)
Koharalepis (Young et al. 1992)
Livoniana (Ahlberg et al. 2000)
LUPC 6106 (*Ichthyostega*–like taxon) (Clément et al. 2004)
Mahalalepis (Young et al. 1992) (CPC27839)
Mandageria (Johanson and Ahlberg 1997, Johanson et al. 2003) (AMF96508, F96855a, F96857a,b,c, F98592c, F98593 a,b, F98594)
Marsdenichthys (Holland et al. 2010, Long 1985b) (NMV P179619, P186572)
Medoevia (Lebedev 1995)
Metaxygnathus (Ahlberg et al. 2000, Campbell and Bell 1977) (ANU28780A)
Obruchevichthys (Ahlberg 1991b, 1995, Ahlberg and Clack 1998, Vorobyeva 1977)
Osteolepis (Andrews and Westoll 1970b, Jarvik 1948, Jarvik 1980, Thomson 1965) (MNHN GBP67, P186, P188, P195, P269 a,b, P277, P280, P284; NR P.1675, P.4110, P.4139, P.11116; UCMP 43711, 43717, 43718, 43719, 43720, 43721, 43733, 58496, 58498, 58499)
Panderichthys (Ahlberg and Clack 1998, Ahlberg et al. 1996, Boisvert 2005, Boisvert et al. 2008, Brazeau and Ahlberg 2006, Vorobyeva 1995, Vorobyeva 2000, Vorobyeva and Schultze 1991) (NR P.6427; PIN 3547 [high resolution photograph]; LDM 60/123 [high resolution photograph])
Platycephalichthys (Coates and Friedman 2010, Vorobyeva 1962, 1977) (PIN 54/155, 54/156, 54/158, 54/159, 54/160, 54/160a, 54/161, 54/162, 54/163, 54/164, 54/165, 54/166, 54/183, 54/191, 54/192, 54/193, 54/194, 54/195 [high resolution photographs])
Porolepis (Clément 2004, Jarvik 1972) (MNHN SVD2001, 2034, 2158; NR A28633, A30483)
Powichthys (Clément and Janvier 2004, Jessen 1975, 1980)
Sinostega (Zhu et al. 2002)
Spodichthys (Jarvik 1985, Snitting 2008b) (MGUH VP 6705 (P.1659), VP 6708 (P.1662), VP 6714 (P.1668), VP 6715 (P.1669))
Tiktaalik (Daeschler et al. 2006, Downs et al. 2008, Shubin et al. 2006) (NUFV 108, 110)
Tristichopterus (Egerton 1861, Snitting 2008a) (BMNH 66653, 66660, 66661, 66664, 66666, 66670; NMS.G. 1875.29.220, G.1875.29.221, G.1875.29.224, G.1875.29.225, G.1995.4.28; NR P.4196)
Tulerpeton (Lebedev and Clack 1993, Lebedev and Coates 1995)
Ventastega (Ahlberg et al. 1994, Ahlberg et al. 2008)
Youngolepis (Chang 1982, 1991, 2004, Chang and Smith 1992)

Characters.

1. Ethmoid

(Ahlberg et al. (2008): Character 25)

0 fully ossified
1 partly or wholly unossified

2. Rostral tubuli

(Coates & Friedman (2010): Character 1)

0 absent
1 present

3. Profundus foramen in postnasal wall

(Zhu & Ahlberg (2004): Character 81)

0 small
1 large

4. Fenestra ventrolateralis

The posterior wall of the nasal capsule appears to be unossified in *Panderichthys* (Vorobyeva & Schultze 1991) and *Platycephalichthys* (Vorobyeva 1962: figs. 22, 23). Thus, the fenestra ventrolateralis in these taxa extends well above the dorsal margin of the ethmoid facets. This character is coded as not applicable for digit-bearing taxa because they lack an anteriorly ossified ethmoid region (character 1). (Coates & Friedman (2010): Character 5)

0 ventral to ethmoid articulation, in posterior view
1 extends dorsal to ethmoid articulation, in posterior view (post nasal wall unossified)

5. Pituitary vein exit

(Coates & Friedman (2010): Character 11)

0 anterior to basipterygoid process
1 dorsal to basipterygoid process

6. Extent of crista parotica

(Zhu & Ahlberg (2004): Character 33)

0 does not reach posterior margin of tabular
1 reaches posterior margin of tabular

7. Endoskeletal intracranial joint
(Coates & Friedman (2010): Character 14)

0 absent
1 present

8. Basicranial fenestra
(Zhu & Ahlberg (2004): Character 76)

0 absent
1 present

9. Processus descendens of sphenoid
(Zhu & Ahlberg (2004): Character 78)

0 absent
1 present

10. Posterior carotid opening in parasphenoid
(Zhu & Ahlberg (2004): Character 80)

0 large
1 small
2 absent

11. Tectum orbitale
(Zhu & Ahlberg (2004): Character 83)

0 narrow
1 extensive

12. Basipterygoid process
(Ahlberg et al. (2008): Character 24)

0 not strongly projecting with concave anterior face
1 strongly projecting with flat anterior face

13. Otic capsule lateral commissure bearing hyomandibular facets
(Ahlberg et al. (2008): Character 27)

0 present
1 absent

14. Relative positions of the hyomandibular facets

(Coates & Friedman (2010): Character 20)

0 dorsal directly above ventral
1 ventral anterior to dorsal
2 dorsal anterior to ventral

15. Parasymphysial plate

Too mother F'ing difficult to score objectively. (Zhu & Ahlberg (2004): Character 1)

0 long, sutured to coronoid, denticulated or with tooth row
1 short, not sutured to coronid, denticulated
2 carrying tooth whorl

16. Parasymphysial plate dentition

Should change the states here: (0) = carrying a tooth whorl (state #2 of character 15 for basal taxa); (1) shagreen or irregular tooth field; (2) dentition aligned parallel to jaw margin. --> Thus, modified from Ahlberg et al. (2008) Ch. 89 and Ch. 1. (Ahlberg et al. (2008): Character 89)

0 Carrying a tooth whorl
1 shagreen or irregular tooth field
2 organised dentition aligned parallel to jaw margin

17. Parasymphsial fangs

(Modified from Ahlberg et al. (2008): Character 90)

0 absent
1 present

18. Parasymphysial plate: detachable whorl

(Zhu & Ahlberg (2004): Character 7)

0 detachable whorl
1 sutured plate with denticles or teeth

19. Lateral parasymphysial foramen

(Daeschler et al. (2006): Character 66)

0 absent
1 present

20. Mesial parasymphysial foramen
(Daeschler et al. (2006): Character 67)

0 absent
1 present

21. Length of dentary
(Zhu & Ahlberg (2004): Character 10)

0 long
1 short with lip fold

22. Dentary tooth row reaches symphysis
(Zhu & Ahlberg (2004): Character 11)

0 yes
1 no

23. Dentary fangs
(Modified from Zhu & Ahlberg (2004): Character 12)

0 absent
1 1 pair
2 1 unpaired (no replacement pit)

24. Furrow along the dentary-splaenial suture
(Ahlberg et al. (2000): Charecter 13)

0 absent
1 present

25. Splenial
(Modified from Zhu & Ahlberg (2004): Character 2)

0 not sutured to prearticular
1 sutured to prearticular
2 postsplenial obstructing splenial-prearticular contact

26. Thickened splenial
(Ahlberg et al. (2000): Charecter 12)

0 absent

1 present

27. Meckelian foramina/fenestrae, dorsal margins formed by
(Ahlberg et al. (2008): Character 63)

0 Meckelian bone
1 prearticular
2 infradentary

28. Meckelian exposure in precoronoid fossa
(Daeschler et al. (2006): Character 65)

0 present
1 absent

29. Posterior coronoid longer than more anterior coronoids
0 no
1 yes

30. Posterior coronoid one third longer than more anterior coronoids
(Modified from Zhu & Ahlberg (2004): Character 8)

0 no
1 yes

31. Coronoid fangs larger than marginal teeth
(Daeschler et al. (2006): Character 70)

0 yes
1 no

32. Coronoid fangs mesial to marginal tooth row
0 yes
1 no

33. Coronoids: at least one carries shagreen
(Ahlberg et al. (2008): Character 80)

0 no
1 yes

34. Coronoids with a row of very small teeth or denticles lateral to tooth row

(Ahlberg et al. (2008): Character 81)

0 yes
1 no

35. Coronoids: size of teeth (excluding fangs) on anterior and middle coronoids relative to dentary tooth size
(Ahlberg et al. (2008): Character 82)

0 about the same
1 half height or less

36. Anterior end of anterior coronoid
(Ahlberg et al. (2000): Charecter 10)

0 toothless
1 toothed

37. Coronoid (anterior) contacts splenial
(Ahlberg et al. (2008): Character 49)

0 no
1 yes

38. Number of fang pairs on posteriormost coronoid
(Zhu & Ahlberg (2004): Character 13)

0 one
1 two
2 none

39. Non-fanged teeth on posterior coronoid
0 absent
1 organized tooth row
2 shagreen

40. Prearticular
(Zhu & Ahlberg (2004): Character 3)

0 not forked
1 forked

41. Prearticular sutures with mesial lamina of splenial
(Ahlberg et al. (2008): Character 71)

0 no, mesial lamina of splenial absent
1 yes
2 no, mesial lamina of splenial separated from prearticular by postsplenial

42. Prearticular-angular contact
(Ahlberg et al. (2008): Character 48)

0 separated by ventral exposure of Meckelian element
1 prearticular contacts angular edge to edge
2 mesial lamina of angular sutures with prearticular

43. Prearticular shagreen field, distribution
(Ahlberg et al. (2008): Character 92)

0 gradually decreasing from dorsal to ventral
1 well defined dorsal longitudinal band
2 scattered patches or absent

44. Premaxillary tooth proportions
(Modified from Ahlberg et al. (2008): Character 38)

0 all approximately same size
1 enlarged anterior tooth
2 posteriormost teeth at least twice height of anteriormost teeth

45. Posterodorsal process of maxilla
(Zhu & Ahlberg (2004): Character 51)

0 present
1 very weak or absent

46. Vomer proportions
(Zhu & Ahlberg (2004): Character 22)

0 not much broader than long
1 much broader than long

47. Vomerine shagreen field
(Ahlberg et al. (2008): Character 44)

0 absent
1 present

48. Anteromedial process of vomer
(Zhu & Ahlberg (2004): Character 21)

0 absent, vomers separated
1 present
2 absent, vomers in close contact

49. Posterior process of vomers
(Zhu & Ahlberg (2004): Character 20)

0 absent
1 short
2 long

50. Relationship of vomer to parasphenoid
(Zhu & Ahlberg (2004): Character 23)

0 no contact (via small gap) or simple abutment
1 overlap
2 no contact via blockage by pterygoid elements

51. Posterior end of parasphenoid
(Zhu & Ahlberg (2004): Character 26)

0 denticulated field extends into spiracular groove
1 denticulated field does not extend into spiracular groove

52. Proportions of entopterygoid
(Zhu & Ahlberg (2004): Character 18)

0 anterior end level with processus ascendens
1 anterior end considerably anterior to processus ascendens

53. Entopterygoids meeting in midline
(Zhu & Ahlberg (2004): Character 19)

0 no
1 yes

54. Dentition of palatoquadrate complex
(Zhu & Ahlberg (2004): Character 16)

0 marginal teeth
1 tooth plates

55. Dermopalatine/ectopterygoid denticle row
(Ahlberg et al. (2008): Character 33)

0 present
1 absent

56. Ectopterygoid reaches subtemporal fossa
(Ahlberg et al. (2008): Character 4)

0 no
1 yes

57. Number of fangs on ectopterygoid
(Zhu & Ahlberg (2004): Character 17)

0 one pair
1 two pairs
2 none
3 one unpaired

58. Subterminal mouth
(Daeschler et al. (2006): Character 73)

0 absent
1 present

59. Number of nasals
(Zhu & Ahlberg (2004): Character 44)

0 many
1 one or two

60. Anterior tectal/septomaxilla
(Ahlberg et al. (2008): Character 1)

0 anterior tectal (external bone, dorsal to nostril)
1 septomaxilla (external or internal bone, posterior to nostril)
2 absent

61. Lateral rostral present
(Ahlberg et al. (2008): Character 9)

0 yes
1 no

62. Median postrostral
(Zhu & Ahlberg (2004): Character 43)

0 absent (postrostral mosaic)
1 present
2 absent (nasals meet in midline)

63. Dorsal fontanelle on snout
(Ahlberg et al. (2008): Character 94)

0 absent
1 present

64. Internasal pits
(Zhu & Ahlberg (2004): Character 25)

0 undifferentiated
1 strong midline ridge but shallow pits
2 deep pear-shaped pits

65. External nostrils
(Zhu & Ahlberg (2004): Character 29)

0 two pairs
1 one pair

66. Premaxilla forms part of choanal margin
(Ahlberg et al. (2008): Character 17)

0 broadly
1 point
2 not, excluded by vomer

67. Position of anterior external nostril
(Zhu & Ahlberg (2004): Character 30)

0 facial
1 edge of mouth

68. Lacrimal
(Ahlberg et al. (2008): Character 8)

0 contributes to orbital margin
1 excluded from margin

69. Contact between lacrimal and posterior supraorbital [postfrontal]
(Zhu & Ahlberg (2004): Character 56)

0 absent
1 present

70. Jugal
(Ahlberg et al. (2008): Character 7)

0 does not extend anterior to orbit
1 extends anterior to orbit

71. Jugal extends anterior to middle of orbit
(Daeschler et al. (2006): Character 78)

0 no
1 yes

72. Jugal-quadratojugal contact
(Zhu & Ahlberg (2004): Character 52)

0 absent
1 present

73. Position of orbits
(Zhu & Ahlberg (2004): Character 59)

0 lateral and widely separated
1 dorsal and close together

74. Postorbital bone
(Zhu & Ahlberg (2004): Character 54)

0 contributes to orbital margin
1 excluded from orbital margin

75. Contact between postorbital and lacrimal
(Daeschler et al. (2006): Character 84)

0 absent
1 present

76. Quadratojugal, squamosal and preopercular fused
(Zhu & Ahlberg (2004): Character 62)

0 no
1 yes

77. Subsquamosals
(Zhu & Ahlberg (2004): Character 61)

0 absent
1 present

78. Preoperculosubmandibular
(Zhu & Ahlberg (2004): Character 60)

0 absent
1 present

79. Width of ethmoid relative to its length, from snout tip to the posterior margin of the parietals
Modified states based on clumped morphospace. (Modified from Zhu & Ahlberg (2004): Character 32)

0 greater or = 80% (greater or equal togrea)
1 75%-45%
2 less than or = 35%

80. Proportion of skull roof (measured as length from tip of snout to posterior margin of postparietals) lying anterior to middle of orbits

Modified states to account for clumped morphospace (Modified from Daeschler et al. (2006): Character 75)

0 20-30%
1 33-40%
2 45-48%
3 >53%

81. B-bone
(Zhu & Ahlberg (2004): Character 46)

0 absent
1 present

82. Prefrontal (anterior supraorbital)
(Ahlberg et al. (2008): Character 15)

0 twice as long as broad, or less
1 three times as long as broad

83. Prefrontal (anterior supraorbital)
(Ahlberg et al. (2008): Character 16)

0 transverse anterior suture with tectal (or opens broadly into external nostril)
1 tapers to point anteriorly

84. Relative size of prefrontal [anterior supraorbital] and posterior supraorbital [postfrontal]
(Daeschler et al. (2006): Character 76)

0 similar
1 prefrontal much bigger

85. Lateral side of prefrontal [anterior supraorbital] adjoins lateral side of frontals and postfrontals [posterior supraorbital] together, and lateral process of postorbital abuts posterolateral part of frontal
(Lebedev (2004), description in text)

0 absent
1 present

86. Postfrontals [posterior supraorbitals] extend anterior of orbits
(Daeschler et al. (2006): Character 86)

0 no
1 yes

87. Shape of postfrontals (posterior supraorbitals)
(Zhu & Ahlberg (2004): Character 58)

0 posterior process shorter than orbital margin
1 posterior process much longer than orbital margin

88. Contact between intertemporal and postfrontal (posterior supraorbital)
(Zhu & Ahlberg (2004): Character 55)

0 present
1 absent

89. Contact between parietal and postfrontal (posterior supraorbital)
(Zhu & Ahlberg (2004): Character 57)

0 present
1 absent

90. Frontals
(Zhu & Ahlberg (2004): Character 45)

0 absent
1 present

91. Parietals surround pineal foramen/eminence
(Zhu & Ahlberg (2004): Character 38)

0 yes
1 no

92. Pineal foramen
(Zhu & Ahlberg (2004): Character 36)

0 present
1 absent

93. Position of pineal foramen/eminence
(Zhu & Ahlberg (2004): Character 37)

0 level with posterior margin of orbits
1 well posterior to orbits

94. Shape of pineal series
(Zhu & Ahlberg (2004): Character 39)

0 round or oval
1 kite-shaped with distinct posterior corner. (non-applicable for *Kenichthys*)

95. Intemporal
(Ahlberg et al. (2008): Character 6)

0 present
1 absent

96. Dermal intracranial joint
(Zhu & Ahlberg (2004): Character 71)

0 present
1 absent

97. Postparietals narrow to a point posteriorly
(Zhu & Ahlberg (2004): Character 41)

0 no
1 yes

98. Proportions of postparietal shield
(Zhu & Ahlberg (2004): Character 40)

0 not extremely wide posteriorly
1 extremely wide posteriorly

99. Supratemporal
(Modified from Ahlberg & Johanson (1998): Character 49)

0 recognizable as a distinct bone
1 fused with postparietal

100. Posterior margin of tabulars
(Modified from Zhu & Ahlberg (2004): Character 42)

0 anterior to the posterior margin of postparietals
1 level with the posterior margin of postparietals
2 posterior to the posterior margin of the postparietals

101. Postspiracular (extratemporal)
(Zhu & Ahlberg (2004): Character 50)

0 present
1 absent

102. Position of the postspiracular (extratemporal)
0 anterior
1 posteriorly displaced

103. Contact between postspiracular [extratemporal] and supratemporal
(Zhu & Ahlberg (2004): Character 48)

0 absent
1 present

104. Premaxilla canal-bearing
(Zhu & Ahlberg (2004): Character 68)

0 yes
1 no

105. Infraorbital canal follows premaxillary suture
(Zhu & Ahlberg (2004): Character 69)

0 no
1 yes

106. Postotic sensory canal
(Zhu & Ahlberg (2004): Character 66)

0 runs through skull roof
1 follows edge of skull roof

107. Postorbital junction of supraorbital and infraorbital canals
(Zhu & Ahlberg (2004): Character 67)

0 absent

1 present

108. Mandibular canal exposure
(Ahlberg et al. (2008): Character 58)

0 entirely enclosed, opens through lines of pores
1 mostly enclosed, short sections of open grooves
2 mostly open, short sections with lines of pores
3 entirely open

109. Mandible: oral sulcus/surangular pit line
(Ahlberg et al. (2008): Character 59)

0 present
1 absent

110. Foramina (similar to infradentary foramina) on cheekplate
(Zhu & Ahlberg (2004): Character 63)

0 absent
1 present

111. Submandibulars and gulars
(Daeschler et al. (2006): Character 80)

0 present
1 absent

112. Large median gular
(Modified from Daeschler et al. (2006): Character 81)

0 absent
1 present

113. Preopercular
(Daeschler et al. (2006): Character 88)

0 large
1 small

114. Opercular
(Ahlberg et al. (2008): Character 14)

0 present
1 absent

115. Spiracular notch
(Daeschler et al. (2006): Character 87)

0 absent
1 small opening
2 narrow groove
3 wide notch

116. Anterior margin of median extrascapular
(Zhu & Ahlberg (2004): Character 65)

0 long
1 very short

117. Extrascapular bones
(Zhu & Ahlberg (2004): Character 64)

0 median overlaps laterals
1 laterals overlap median

118. Extrascapular bones
(Daeschler et al. (2006): Character 77)

0 present
1 absent

119. Posttemporal
(Ahlberg et al. (2008): Character 109)

0 present
1 absent

120. Supracleithrum
0 present
1 absent

121. Anocleithrum
(Zhu & Ahlberg (2004): Character 85)

0 exposed
1 subdermal

122. Anocleithrum
(Ahlberg et al. (2008): Character 99)

0 oblong with distinct anterior overlap area
1 drop-shaped with no anterior overlap area
2 absent

123. Orientation of cleithrum
(Daeschler et al. (2006): Character 105)

0 vertically oriented: tilted less than 10 degrees caudally
1 angulated: tilted over 10 degrees caudally

124. Cleithrum: expanded dorsal blade occupies more than 1/2 of bone length
(Lebedev 2004, description in text.)

0 no
1 yes

125. Cleithrum, postbranchial lamina
(Ahlberg et al. (2008): Character 101)

0 present
1 absent

126. Contact margin for clavicle on cleithrum
(Zhu & Ahlberg (2004): Character 84)

0 straight or faintly convex
1 strongly concave

127. Co-ossification of cleithrum and scapulocoracoid
0 absent
1 present

128. Scapulocoracoid
(Ahlberg et al. (2008): Character 115)

0 small and tripodal
1 large plate pierced by large coracoid foramen
2 very large plate without large coracoid foramen

129. Coracoid plate
(Daeschler et al. (2006): Character 103)

0 absent
1 present and extends ventromedially

130. Shoulder joint polarity
(Zhu & Ahlberg (2004): Character 87)

0 caput humeri concave
1 caput humeri convex

131. Glenoid position
(Daeschler et al. (2006): Character 104)

0 elevated from plane formed by clavicles
1 offset ventrally to lie at same level as clavicular plane

132. Glenoid orientation
(Daeschler et al. (2006): Character 110)

0 posterior orientation
1 lateral component to glenoid orientation

133. Glenoid proportions

In plane with glenoid orientation?height at maximum extent divided by maximum length: *Medoevia* = 0.60; *Eusthenopteron* = 0.60; *Tinirau* = 0.42; *Panderichthys* = 0.48; *Tiktaalik* = 0.44; *Acanthostega* = 0.45; *Ichthyostega* = 0.44; *Tulerpeton* = 0.46

0 height/width ratio 60% or greater
1 height/width ratio 40-50%

134. Infraglanoid buttress
(Coates (1996) in text)

0 absent
1 present

135. Interclavicle
(Ahlberg et al. (2008): Character 106)

0 small and concealed (unornamented) or absent
1 large and exposed (ornamented)

136. Interclavicle shape
(Ahlberg et al. (2008): Character 107)

0 ovoid
1 kite-shaped
2 with posterior stalk

137. Archipterygial pectoral fin
(Zhu & Ahlberg (2004): Character 86)

0 no
1 yes

138. Humerus
(Ahlberg et al. (2008): Character 103)

0 narrow tapering entepicondyle
1 square or parallelogram-shaped entepicondyle

139. Body of humerus
(Zhu & Ahlberg (2004): Character 89)

0 cylindrical
1 flattened rectangular

140. Anterior termination of ventral ridge
(Daeschler et al. (2006): Character 96)

0 adjacent to the caput humeri
1 offset distally toward the proximodistal mid-region of anterior margin of humerus

141. Ectepicondylar process
(Daeschler et al. (2006): Character 100)

0 terminates proximal to epipodial facets
1 extends distal to epipodial facets

142. Radius and ulna
(Ahlberg et al. (2008): Character 110)

0 radius much longer than ulna
1 approximately equal length

143. Radial facet
(Daeschler et al. (2006): Character 98)

0 faces distally
1 has some ventrally directed component

144. Area proximal to radial facet
(Daeschler et al. (2006): Character 102)

0 short, cylindrical leading edge, with no muscle scars
1 enlarged, sharp leading edge, with areas for muscle attachments

145. Shape of radius
(Daeschler et al. (2006): Character 94)

0 bladelike
1 subcylindrical

146. Radial length
(Daeschler et al. (2006): Character 101)

0 longer than humerus
1 shorter than humerus

147. Olecranon process on ulna
(Daeschler et al. (2006): Character 95)

0 absent
1 present

148. Articulations for more than two radials on ulnare
(Daeschler et al. (2006): Character 90)

0 absent
1 present

149. Postaxial process on ulnare

(Daeschler et al. (2006): Character 91)

0 absent
1 present

150. Radials

(Zhu & Ahlberg (2004): Character 91)

0 jointed
1 unjointed

151. Digits

(Ahlberg et al. (2008): Character 102)

0 absent
1 present

152. Lepidotrichia in paired appendages

(Ahlberg et al. (2008): Character 108)

0 present
1 absent

153. Basal segments of lepidotrichia elongated

(Zhu & Ahlberg (2004): Character 92)

0 no
1 yes

154. Expanded ribs

(Daeschler et al. (2006): Character 113)

0 absent
1 present

155. Imbricate ribs

(Daeschler et al. (2006): Character 114)

0 absent
1 present

156. Ribs, trunk

(Ahlberg et al. (2008): Character 111)

0 no longer than diameter of intercentrum
1 longer

157. Ribs, trunk

(Ahlberg et al. (2008): Character 113)

0 all cylindrical
1 some or all bear flanges from posterior margin which narrow distally
2 some or all flare distally

158. Supraneural spines

(Zhu & Ahlberg (2004): Character 99)

0 present
1 absent

159. Ilium, iliac canal

(Ahlberg et al. (2008): Character 104)

0 absent
1 present

160. Ilium, posterior process

(Ahlberg et al. (2008): Character 105)

0 oriented posterodorsally
1 oriented approximately horizontally posteriorly

161. Postaxial process on fibula
0 present
1 absent

162. Postaxial process on fibula, size
0 large
1 small

163. Dorsal and anal fins

(Zhu & Ahlberg (2004): Character 93)

0 present
1 absent

164. Posterior radials in posterior dorsal fin
(Zhu & Ahlberg (2004): Character 94)

0 not branched
1 branched

165. Caudal fin
(Zhu & Ahlberg (2004): Character 95)

0 heterocercal
1 diphycercal

166. Epichordal radials in caudal fin
(Zhu & Ahlberg (2004): Character 96)

0 absent
1 present

167. Nature of dermal ornament
(Ahlberg et al. (2008): Character 97)

0 tuberculate
1 fairly regular pit and ridge
2 irregular
3 absent or almost absent

168. Nature of ornament: "starbursts" of radiating ornament on at least some bones
(Ahlberg et al. (2008): Character 98)

0 no
1 yes

169. Cleithral ornamentation
(Daeschler et al. (2006): Character 106)

0 present
1 absent

170. Basal scutes

(Zhu & Ahlberg (2004): Character 97)

0 absent
1 present

171. Body scale morphology

(Zhu & Ahlberg (2004): Character 98)

0 rhomboid with internal ridge
1 round
2 ovoid

172. Squamation

(Ahlberg et al. (2008): Character 117)

0 complete body covering of scales
1 ventral armour of gastralia

173. Tooth folding

(Zhu & Ahlberg (2004): Character 14)

0 none
1 generalized polyplocodont
2 labyrinthodont
3 dendrodont

174. Cosmine

(Zhu & Ahlberg (2004): Character 34)

0 present
1 absent

175. Westoll lines

(Zhu & Ahlberg (2004): Character 35)

0 absent
1 present

Part B.

Taxon-by-character matrix and character optimizations.—The data matrix was subjected to a maximum parsimony analysis in the software package PAUP (Swofford 2002) and a Bayesian analysis using the software package Mr. Bayes(Huelsenbeck 2001, Ronquist and Huelsenbeck 2003). All characters were assigned an equal weight, multistate characters were run unordered, and a heuristic search algorithm was used in PAUP to search for the shortest networks—rooted on *Porolepis*, *Glyptolepis*, *Powichthys*, *Youngolepis*, *Diabolepis*, and *Dipterus*. Bremer decay indices were calculated using PAUP(Swofford 2002) and TNT(Goloboff 1999, Nixon 1999), and Bayesian posterior probabilities were calculated with Mr. Bayes following an analysis that included 500,000 mcmc generations, sampling every 1,000 generations, and with 20 samples discarded as burnin. Character evolution was examined in MacClade(Maddison and Maddison 2000), which was also used to produce the character state distributions below. *Eusthenopteron* is scored as *E. foordi* and *Platycephalichthys* scored as *P. bischoffi*.

A = 0 & 1; **B** = 0 & 2

	1		**1**		**2**		**3**		**4**	
			1		**1**		**1**		**1**	
Acanthostega	100-?	00002	011?0	21101	00101	01100	11001	11211	10121	00202
Barameda	00???	?1???	?????	?????	0010?	?????	?????	?????	???1?	????0
Beelarongia	?0???	?????	?????	?????	0??0?	?????	?????	?????	?????	?????
Cabonnichthys	?0???	?1?02	0???1	?????	00101	0?0-1	0?000	00100	??011	00221
Canowindra	?0???	?????	?????	?????	0??0?	?????	?????	?????	?????	?????
Cladarosymblema	00000	01102	00000	10100	00101	00000	0?000	00000	00010	10100
Diabolepis	01???	?0?0?	100??	---??	1?0??	?????	-????	?????	???0?	01000
Dipterus	010??	?00?0	10???	---??	1?0?0	0????	-????	?????	?0???	0-20-
Elginerpeton	?????	?????	?????	21111	0011?	101??	10000	10?11	1010?	?????
Elpistostege	?0???	?????	?????	?????	???0?	?????	?????	?????	???0?	?????
Eusthenodon	?????	?????	0???1	??1??	00101	0??-1	0??00	??100	???11	00221
Eusthenopteron	00000	11102	00011	10100	00001	000-1	00000	00100	00000	00221
Glyptolepis	00101	11101	00??2	0-000	0100?	??000	0?000	00000	00001	00000
Gogonasus	00000	01102	00000	10100	00000	00000	0?00A	0001?	00000	00200
Gooloogongia	?0???	?1???	????0	10100	001??	??0??	0????	00???	????0	?????
Gyroptychius	?0???	01102	0?020	10100	00?0?	???00	0?000	0000?	0??00	00100
Hynerpeton	?????	?????	?????	?????	?????	?????	?????	?????	??1??	?????
Ichthyostega	10?-?	?0002	011?0	21101	00101	00100	11011	01211	11221	00202
Jakubsonia	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Jarvikina	???0?	11102	00?11	?????	00001	0??-1	0????	??1?0	???0?	0?221
Kenichthys	000??	?1?02	10??0	10100	00000	0?000	0?10A	00000	00?00	????0
Koharalepis	?0???	?????	?????	?????	0??0?	?????	?????	?????	????0	?????
Livoniana	?????	?????	?????	???11	?01?1	1?1??	?????	00??1	?????	?????
LUPC 6106	?????	?????	?????	?????	???1?	?????	?????	?????	?????	?????
Mahalalepis	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Mandageria	00???	11102	??02?	?????	00101	0????	0??00	????0	???11	00221
Marsdenichthys	?????	?????	?????	?????	0000?	???00	0??0?	?????	????1	0??0?
Medoevia	00000	01102	00000	10100	000?1	00000	0?000	00000	00010	00100
Metaxygnathus	?????	?????	????0	211?1	00?01	0?1??	01??1	10010	11???	?????
Obruchevichthys	?????	?????	?????	21?11	??111	1????	?0?1?	1????	1????	?????
Osteolepis	00???	01102	00000	10100	0000?	??0??	0????	?????	???00	?????
Panderichthys	00010	01102	00000	10100	00101	000-1	0?000	00010	01001	00211
Platycephalichthys	0??1?	?1???	?0???	10100	0010?	?00?1	000??	00010	00011	002?1
Porolepis	?0101	11101	100?2	0-000	01000	0??00	??000	00000	00001	0?000
Powichthys	011?1	?1111	100?2	0-0??	010?0	0??00	???0?	??000	?0?0?	00002
Sinostega	?????	?????	?????	?????	?????	?1???	?????	?????	?01??	?????
Spodichthys	00???	11102	00011	??1??	00001	00010	0?0??	00000	00??0	0?22?
Tiktaalik	000-?	01102	00000	?0100	00101	??0-1	0?010	00210	01001	0?211
Tinirau	0000?	?1102	0001?	?????	0010?	???-1	0?000	00010	00001	00221
Tristichopterus	?0???	1110?	?0011	???00	0000?	??010	0?000	0000?	0??00	?0221
Tulerpeton	?????	?????	?????	?????	?????	?????	?????	?????	???2?	?????
Ventastega	10?-1	?0?02	?11??	20111	00101	001-1	01011	11211	11121	?0???
Youngolepis	01001	10010	10012	0-000	01000	0?000	0?10A	00000	00000	01000

	5		6		7		8		9	
	1		1		1		1		1	
Acanthostega	11100	12010	12101	11101	11100	00023	01110	00-01	001-1	10002
Barameda	??00?	??010	000?1	?0000	0?000	???00	0000-	00000	00000	01000
Beelarongia	?????	??0??	?10?1	?00?0	?001?	00000	0????	00000	00000	00110
Cabonnichthys	1?000	01000	01001	00000	00010	00011	0000-	01000	00110	00001
Canowindra	?????	??00?	??0?1	?0000	00010	00010	0????	00000	0010?	00110
Cladarosymblema	1?00?	??001	01001	00000	00000	00001	0000-	00000	11--0	00000
Diabolepis	0?01?	-??0?	??000	-1???	??0??	???00	1????	?0010	110-?	10000
Dipterus	?111?	-?00?	?0000	-10?0	01000	00??1	10?0-	00010	11?-?	10001
Elginerpeton	????0	?????	????1	?1???	?????	?????	0????	?????	?????	?????
Elpistostege	?????	??100	000??	??001	10101	???23	?1010	10??1	??1-1	?00?2
Eusthenodon	?1000	??000	010?1	00010	00010	00011	0000-	01100	00110	00001
Eusthenopteron	11000	01000	01001	00000	00000	00011	0000-	00000	00000	00001
Glyptolepis	00000	10000	00020	-0000	00000	01100	0????	00??0	110-0	001-0
Gogonasus	10000	10000	01001	00000	00000	00010	0000-	00000	000-0	00000
Gooloogongia	???0?	??010	000?1	?0000	10000	00010	0000-	00000	00000	01000
Gyroptychius	1?000	?0000	01001	00000	00001	00010	00???	00000	00100	00000
Hynerpeton	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Ichthyostega	11101	1B010	?2001	21101	11100	00023	01110	00-01	000-1	10002
Jakubsonia	?????	?????	??1??	?????	?????	?????	????1	10?01	?????	???0?
Jarvikina	1?00?	???00	01001	?0000	0000?	00011	0????	?1000	0010?	00001
Kenichthys	1??00	?00?0	0?000	-0000	00000	10000	0????	00?0?	100-?	00000
Koharalepis	?10??	??00?	??0?1	?0000	00010	00000	00?0-	00000	00100	00110
Livoniana	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
LUPC 6106	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Mahalalepis	?????	????1	0?0?1	?0???	??0??	???0?	?000-	10?00	????0	?????
Mandageria	11000	01000	01001	00010	00011	00011	0000-	01100	00110	00011
Marsdenichthys	1?00?	0?000	010?1	?0000	000?0	00011	0????	?0000	00000	00100
Medoevia	10000	100??	??0?1	00000	00000	00001	00?1-	10000	00000	00010
Metaxygnathus	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Obruchevichthys	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Osteolepis	1?000	?0000	010?1	00000	00000	00011	00?0-	00000	00000	00000
Panderichthys	11000	10100	00001	01000	0110A	00022	00000	10001	001-0	10001
Platycephalichthys	?????	???00	010?1	000?0	00???	1??1?	000??	????0	00--0	?????
Porolepis	0000?	?000?	?0020	-0000	00000	01100	0????	?0?10	110-0	001-1
Powichthys	00?0?	???0?	?0020	-0?0?	??0??	??100	0????	?0010	10100	10001
Sinostega	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Spodichthys	?100?	?0???	?1??1	?0???	??0??	???10	0????	0?000	00000	00001
Tiktaalik	11000	100?0	0?001	?1001	11101	00023	01?10	?0-01	000-?	10001
Tinirau	11000	1000-	-10?1	00000	000??	10010	0000-	0??00	001-0	00001
Tristichopterus	??00?	??0??	?10?1	00000	00000	00011	0000-	00000	000-0	00001
Tulerpeton	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Ventastega	??101	??01?	121??	1?101	11100	00023	01??1	00001	??1-0	100?1
Youngolepis	0?000	?0?0?	??010	-0?00	0000?	10000	0????	???1?	110-0	10001

	101		111		121		131		141	
Acanthostega	1--00	00110	10113	--111	01100	11211	11101	10111	10011	10??0
Barameda	00100	01???	???0?	110??	?????	0???1	?????	?0000	?0000	10100
Beelarongia	00???	0???0	??001	110??	??0-0	0????	?????	??00?	?????	?????
Cabonnichthys	01000	0???0	00001	01000	000-0	1???1	?????	?0000	?0000	00011
Canowindra	00???	0??00	??00?	110??	000-?	?????	?????	?????	?????	?????
Cladarosymblema	00000	01000	00001	01000	000-0	0???1	00???	?????	?????	?????
Diabolepis	???11	10???	?????	?????	?????	?????	?????	?????	?????	?????
Dipterus	1--??	010?0	???00	00000	100-0	1???0	?????	?1???	?????	????0
Elginerpeton	?????	??00?	?????	?????	????1	????1	?????	??11?	?????	?????
Elpistostege	1--??	??0??	01???	?????	?????	?????	?????	?????	?????	?????
Eusthenodon	01000	0???0	0000?	01000	000-0	?????	?????	?????	?????	?????
Eusthenopteron	01000	01000	00001	01000	000-0	10001	00000	00000	00000	00011
Glyptolepis	00001	01000	00000	00000	100-0	00000	00??0	?100?	?????	????0
Gogonasus	00000	01000	00002	01000	000-?	0???1	?????	?0000	00000	00?11
Gooloogongia	00100	0???0	00000	11000	100-?	???0?	????0	?0???	?0000	0010?
Gyroptychius	00000	01000	00001	01000	000-0	1????	?????	?????	?????	?????
Hynerpeton	?????	?????	?????	?????	??101	?1211	0??1?	?????	?????	?????
Ichthyostega	1--00	00210	10113	--111	-2100	11211	01111	20111	11111	11??0
Jakubsonia	?????	??1??	?????	?????	???11	?????	?????	?????	?????	?????
Jarvikina	?????	0???0	?????	010??	?????	?????	?????	?????	?????	?????
Kenichthys	00011	010?1	?????	010??	?????	0????	?????	?????	?????	?????
Koharalepis	00???	01000	00001	11000	??0-?	?????	?????	?????	?????	?????
Livoniana	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
LUPC 6106	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Mahalalepis	???0?	0????	?????	?????	?????	?????	?????	?????	?????	?????
Mandageria	01?00	0???0	0000?	11000	000-0	1???1	?????	?000?	00000	00011
Marsdenichthys	000??	?????	0?002	11000	??0-?	?????	?????	?????	?????	?????
Medoevia	00???	?????	00001	01000	0?0-0	00001	00000	0?000	0?0??	?????
Metaxygnathus	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Obruchevichthys	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Osteolepis	00000	01000	??001	01000	000-0	0????	?????	?0???	?????	?????
Panderichthys	1--00	01000	01?02	01000	00100	10111	11100	?0010	00010	0000?
Platycephalichthys	???0?	0??0?	??0??	?????	?????	?000?	?0???	?????	?????	?????
Porolepis	00001	01000	00001	00000	100-0	0????	?????	?????	?????	?????
Powichthys	???11	01???	?????	00000	?????	0????	?????	?????	?????	?????
Sinostega	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Spodichthys	0000?	0??00	0??0?	??0??	??0-0	1000?	?????	?????	?????	?????
Tiktaalik	1--??	00000	01013	--110	00100	10111	11100	?0010	10110	10100
Tinirau	00000	01000	00001	0?0??	??0-0	10001	0010?	?0???	?0??0	??011
Tristichopterus	01???	0?0?0	00001	010??	000-0	1???1	?????	?0000	00000	00011
Tulerpeton	?????	??3??	?????	?????	01101	10??1	01111	10111	111?1	11000
Ventastega	1-?0?	??000	???13	-?111	01?11	1021?	????1	10???	?????	?????
Youngolepis	???11	10??1	?????	?????	?????	0000?	00???	?????	?????	?????

	151		161		171
Acanthostega	11-10	12100	1-1-1	1111-	01210
Barameda	001??	?????	?????	?00??	1??1?
Beelarongia	?00??	?????	?????	?000?	0??00
Cabonnichthys	000??	?????	??0?1	00001	10110
Canowindra	?????	?????	??0?0	?00?0	1??1?
Cladarosymblema	?00??	?????	?????	?300?	00100
Diabolepis	?????	?????	?????	?30??	???01
Dipterus	00100	100??	??010	?3000	?0?01
Elginerpeton	?????	???11	?????	?111?	?????
Elpistostege	?????	?????	?????	?0???	?????
Eusthenodon	?????	?????	??0??	?000?	10110
Eusthenopteron	00000	0010-	00001	00001	10110
Glyptolepis	00100	000??	??010	03000	1031?
Gogonasus	000??	?????	?????	?300?	0?100
Gooloogongia	?0100	?????	00000	?0000	10?1?
Gyroptychius	?0000	001??	??0?1	03001	00100
Hynerpeton	?????	?????	?????	??11?	?????
Ichthyostega	11-11	11111	1-1-1	1111-	??210
Jakubsonia	?????	?????	?????	?1?1?	?????
Jarvikina	?????	?????	?????	?00??	1?11?
Kenichthys	?????	?????	?????	?30?1	0?100
Koharalepis	?00??	?????	?????	?000?	0?100
Livoniana	?????	?????	?????	??0??	?????
LUPC 6106	?????	?????	?????	?????	?????
Mahalalepis	?????	?????	?????	?30??	???0?
Mandageria	000??	?????	??001	00000	10110
Marsdenichthys	?????	?????	??0??	?000?	10?1?
Medoevia	?????	?????	??0??	?3001	00?00
Metaxygnathus	?????	?????	?????	?????	?????
Obruchevichthys	?????	?????	?????	?????	?????
Osteolepis	?00--	--1??	??000	03001	00100
Panderichthys	00000	111??	011-1	?000-	00210
Platycephalichthys	?????	?????	?????	?00??	0??1?
Porolepis	?????	?????	????0	?300?	00300
Powichthys	?????	?????	?????	?30??	0?100
Sinostega	?????	?????	?????	?????	?????
Spodichthys	?????	?????	?????	?000?	?????
Tiktaalik	00111	?1?0-	??1-?	?000-	00210
Tinirau	00000	0010-	010?0	0000?	10?10
Tristichopterus	000??	??1??	??000	00001	10?10
Tulerpeton	11-??	?????	1-???	???1?	21?1?
Ventastega	?????	???00	?????	?111?	?????
Youngolepis	?????	?????	?????	?30??	0?100

Character optimizations.

Rhizodonts + other tetrapodomorphs:

- 65, 0→1 = one pair of external nostrils
- 91, 1→0 = parietals surround a parietal foramen/eminance
- 104, 1→0 = premaxilla is canal bearing
- 105, 1→0 = infraorbital canal does not follow the premaxillary suture
- 167, 3→0 = tuberculate ornament
- 171, 0→1 = round body scales
- 174, 0→1 = loss of cosmine

Rhizodonts:

- 23, 0→1 = 1 pair of dentary fangs
- 59, 0→1 = 1 or 2 nasal bones
- 97, 0→1 = postparietals narrow to a point posteriorly
- 103, 0→1 = contact between postspiracular and supratemporal

'Osteolepiforms' + elpistostegalians:

- 62, 0→1 = median postrostral present
- 115, 0→1 = small opening to spiracular notch
- 121, 1→0 = exposed anocleithrum
- 153, 1→0 = basal lepidotrichial segments not elongate

Canowindrids:

- 98, 0→1 = PP shield extremely wide posteriorly

Canowindrids (minus *Marsdenichthys*):

- 99, 0→1 = supratemporal fused with postparietals

Canowindrids (*Koharalepis* + *Beelarongia* only):

- 79, 1→0 = width of ethmoid ≥80%
- 171, 1→0 = rhomboid body scales
- 174, 1→0 = cosmine present

Megalichthyiforms + eotetrapodiforms:

- 170, 0→1 = basal scutes present

Megalichthyiforms:

- 14, 1→0 = dorsal directly above ventral hyomandibular facet
- 167, 0→3 = ornament absent or almost absent
- 171, 1→0 = rhomboid body scales
- 174, 1→0 = cosmine present

Megalichthyiforms (minus *Gogonasus*):

- 48, 2→1 = anteromedial process of vomer present

Megalichthyiforms (minus *Gyroptychius*):

- 80, 0→1 = 33-40% of skull roof lies anterior to orbits

Osteolepidids (*Medoevia* + *Mahalalepis* + megalichthyids):

- 44, 0→1 = enlarged premaxillary tooth
- 60, 0→1 = septomaxilla (external or internal bone) posterior to nostril
- 79, 1→0 = width of ethmoid relative to its length ≥80%

Medoevia + *Mahalalepis*:

- 86, 0→1 = postfrontals (posterior supraorbitals) extend anterior to orbits

Megalichthyiforms (megalichthyids only):

- 23, 0→1 = 1 pair of dentary fangs

- 46, 0→1 = vomers much broader than long
- 91, 0→1 = parietals do not surround the pineal foramen
- 92, 0→1 = pineal foramen absent

Eotetrapodiforms:

- 49, 0→2 = long posterior processes on vomers
- 50, 0→1 = overlap of vomers and parasphenoid
- 100, 0→1 = posterior margin of tabular level with posterior margin of postparietals
- 126, 0→1 = contact margin for clavicle on cleithrum strongly concave

Tristichopterids:

- 15, 0→1 = parasymphyseal plate short not sutured to coronoid
- 29, 0→1 = Posterior coronoid longer than more anterior coronoids

Tristichopterids (minus *Spodichthys*):

- 80, 0→1 = 33-40% of skull roof anterior to orbits
- 102, 0→1 = posteriorly displaced PSP

Tristichopterids (*Eusthenopteron* + remaining tristichopterids):

- 30, 0→1 = posterior coronoid one-third longer than more anterior coronoids
- 38, 0→1 = 2 fang pairs on posteriormost coronoid
- 165, 0→1 = diphycercal caudal fin

Tristichopterids (*Jarvikina* + remaining tristichopterids):

- 87, 0→1 = posterior orbital process much longer than orbital margin
- 93, 0→1 = pineal foramen well posterior to orbital margin

Tristichopterids (*Cabonnichthys* + remaining tristichopterids):

- 23, 0→1 = 1 pair of dentary fangs
- 44, 0→1 = enlarged premaxillary tooth
- 74, 0→1 = postorbital excluded from orbital margin
- 94, 0→1 = pineal series kite-shaped

Tristichopterids (*Mandageria* + *Eusthenodon* only):

- 69, 0→1 = contact between lacrimal and posterior supraorbital
- 88, 0→1 = no contact between intertemporal and posterior supraorbital

Elpistostegalia:

- 23, 0→1 = 1 pair of dentary fangs
- 30, 0→1 = posterior coronoid one-third longer than more anterior coronoids
- 39, 0→1 = organized tooth row on posterior coronoid
- 45, 0→1 = posterodorsal maxillary process weak/absent
- 93, 0→1 = pineal foramen posterior to orbits
- 133, 0→1 = height/width ratio of glenoid fossa, 40-50%
- 162, 0→1 = highly reduced postaxial process on fibula

Elpistostegalia (minus *Tinirau*):

- 4, 0→1 = In posterior view, the fenestra ventrolateralis extends dorsal to the ethmoid articulation
- 171, 1→0 = rhomboid scales

Elpistostegalia (minus *Platycephalichthys*):

- 42, 0→1 = prearticular contacts angular edge-to-edge
- 62, 1→0 = median postrostral absent
- 67, 0→1 = anterior nostril at edge of mouth
- 72, 0→1 = jugal/quadratojugal contact

- 79, 1→2 = ethmoid proportions ≤35%
- 90, 0→1 = frontals present
- 128, 0→1 = scapulocoracoid, large plate pierced by coracoid foramen
- 129, 0→1 = coracoid plate present
- 132, 0→1 = lateral component to glenoid orientation

Elpistostegalia (minus *Panderichthys*):

- 34, 0→1 = coronoids with a row of very small teeth or denticles lateral to tooth row
- 70, 0→1 = jugal extends anterior to front of orbit
- 71, 0→1 = jugal extends anterior to middle of orbit
- 82, 0→1 = anterior supraorbital 3x longer than broad
- 84, 0→1 = prefrontal much bigger than postfrontal
- 107, 1→0 = no fusion of supra and infraorbital canals
- 114, 0→1 = loss of opercular
- 118, 0→1 = loss of extrascapular bones
- 119, 0→1 = lost of posttemporals
- 141, 0→1 = ectepicondytlar processes extends distal to epipodial facets
- 146, 0→1 = radius is shorter than the humerus
- 154, 0→1 = expanded ribs present

Elpistostege + *Tiktaalik*:

- 75, 0→1 = contact between postorbital and lacrimal

Livoniana + remaining elpistostegalians:

- 19, 0→1 = lateral parasymphysial foramen
- 20, 0→1 = mesial parasymphysial foramen
- 28, 0→1 = no Meckelian exposure in precoronoid fossa
- 40, 0→1 = forked prearticular

[*Elginerpeton* + *Obruchevichthys* + *Ichthyostega*-like jaw] + remaining elpistostegalians:

- 36, 0→1 = tooth-bearing anterior end of anterior coronoid
- 168, 0→1 = "starburst" ornament radiating on at least some bones

Elginerpeton + *Obruchevichthys* + *Ichthyostega*-like jaw

- 24, 0→1 = furrow along the dentary-splaenial suture

Metaxygnathus + remaining elpistostegalians:

- 32, 0→1 = no coronoid fangs mesial to marginal tooth row
- 35, 1→0 = size of teeth (excluding fangs) on anterior and middle coronoids relative to dentary tooth size, half the height or less

[*Jakubsonia* + *Ventastega*] + remaining elpistostegalians:

- 37, 0→1 = anterior coronoid contacts splenial

Jakubsonia + *Ventastega:*

- 85, 0→1 = lateral side of the prefrontal (anterior supraorbital) adjoins lateral side of the postfrontals (posterior supraorbital) and frontals together, while the lateral process of the postorbital abuts the posterolateral part of frontal
- 124, 0→1 = expanded dorsal blade of cleithrum occupies more than ½ of bone length

[*Sinostega* + *Acanthostega*] + remaining elpistostegalians:

- 19, 1→0 = lateral parasymphysial foramen absent
- 30, 1→0 = posterior coronoid is not one third longer than more anterior coronoids
- 31, 0→1 = coronoid fangs larger than marginal teeth
- 100, 1→2 = posterior tabular margin is posterior to the posterior margin of the postparietals

- 109, 0→1 = oral sulcus/surangular pit line absent

Sinostega + Acanthostega:

- 27, 0→1 = dorsal margins of Meckelian foramina/fenestrae formed by the prearticular
- 42, 1→0 = prearticular-angular contact separated by ventral exposure of the Meckelian element

Ichthyostega + Hynerpeton + Tulerpeton:

- 131, 1→0 = prearticular-angular contact separated by ventral exposure of the Meckelian element
- 134, 0→1 = buttressed infraglenoid

Part C.

Assemblage analysis.—Floral/faunal assemblages were used, in part, to trace the history of stem-tetrapod paleoenvironments. Formations and/or sites for all dipnomorphs and tetrapodomorphs included in the phylogenetic analysis were analyzed for their paleoenvironmental signatures. All taxa are Devonian in age except the megalichthyid, *Cladarosymblema*, which is known from the Early Carboniferous (early-mid Viséan) (Fox et al. 1995). Moreover, the Russian megalichthyiform *Medoevia* was excluded from this analysis because its locality and formation are unknown (Lebedev 1995). Floral and faunal data from included sites were tallied and arranged (a) taxonomically; and (b) by locality and/or formation, in a data matrix using the Apple software, Numbers '09. Because of the nested nature of localities and formations, a taxon present at a locality was also scored as present within the larger formation, but not vice versa, because taxa present elsewhere in the formation may not necessarily also exist at the locality of interest. Sampled formations and localities include:

(1) Home Station Sandstone Member of the Snowy Plains Formation
(2)Snowy Plains Formation
(3)Aztec Siltstone Formation (containing the "Fish Hotel" sites, horizons A-Z)
(4)Bindaree Formation (including the Mt. Howitt locality)
(5)Mandagery Formation (including the Canowindra fish fauna)
(6)Gogo fish fauna (mostly of the *transitans* Conodont Zone) of the Gogo Formation
(7)Gogo Formation
(8)Achannaras Quarry of the Lybster Flagstone Formation
(9)Lybster Flagstone Formation
(10)Police Mountain Track Locality of the Raymond Formation
(11)Raymond Formation
(12)Sofia Sund Formation
(13)Eday Flagstone Formation (including the south Ronaldsay locality)
(14)Rdeyskoe Formation (including the Porkhov and Svinord beds)
(15)Red Hill I locality of the Denay Formation
(16)Denay Formation
(17)Snezha Beds (of the Snezah Formation)
(18)Gauja Formation (including the Lode Quarry)
(19)Amata Formation (including the Pasta Muiza locality)
(20)Escuminac Formation (including the Miguasha locality)
(21)Fram Formation (including the NV2K17 site)

(22)Scat Craig locality
(23)Cloghnan Shale (including the Jemalong Quarry)
(24)Red Hill, Pennsylvania locality of the Catskill Formation
(25)Catskill Formation
(26)Ogre Fm (including the Velna-Ala locality)
(27)Gornostayevka locality of the Zadonsk Formation
(28)Zadonsk Formation
(29)Zhongning Formation (including the Ningxia Hui Site/*Sinostega* locality)
(30)Pavari Site or the Ketleri Formation
(31)Ketleri Formation
(32)Aina Dal Formation (including Gauss Halvø)
(33)Britta Dal Formation (including Ymer Ø)
(34)Evieux Formation (including the Strüd locality)
(35)Andreyevka-2 locality of the Khovanshchina Fm
(36)Khovanshchina Formation
(37)Wojciechowice Formation (including the Zachełmie Quarry)

	1	**6**	**11**	**16**	**21**	**26**	**31**	**36**
STROMATOLITES	00000	00000	00000	00000	00000	00000	00001	10
Acinosporites sp.	00000	01000	00000	00000	00000	00000	00000	00
Aneurospora greggsii	00000	00000	00000	00000	00000	00010	00000	00
Ancyrospora sp.	00000	01000	00000	00000	00000	00000	00000	00
Ancyrospora ancyrea	00000	00110	00000	00000	00000	00000	00000	00
Ancyrospora grandispinosa	00000	00110	00000	00000	00000	00000	00000	00
Apiculiretusispora sp.	00000	01000	00000	00000	00000	00000	00000	00
Apiculiretusispora granulata	00000	00000	00000	00000	00000	00010	00000	00
Apiculiretusispora picata	00000	00000	00000	00000	00000	00010	00000	00
Apiculiretusispora septalata	00000	00000	00000	00000	00000	00010	00000	00
Archaeozonotriletes variabilis	00000	00000	00000	00000	00000	00010	00000	00
Auroraspora sp.	00000	01000	00000	00000	00000	00000	00000	00
Calamospora sp.	00000	01000	00000	00000	00000	00000	00000	00
Calamospora atava	00000	00000	00000	00000	00000	00010	00000	00
Calamospora nigrata	00000	00000	00000	00000	00000	00010	00000	00
Calyptosporites microspinosus	00000	00110	00000	00000	00000	00000	00000	00
Convolutispora sp.	00000	01000	00000	00000	00000	00000	00000	00
Cyclogranispora sp.	00000	01000	00000	00000	00000	00000	00000	00
Cyclogranisporites	00000	01000	00000	00000	00000	00000	00000	00
Cymbosporites	00000	01000	00000	00000	00000	00000	00000	00
Dibolisporites sp.	00000	01000	00000	00000	00000	00000	00000	00
Densosporites devonicus	00000	00110	00000	00000	00000	00000	00000	00
Geminospora	00100	01000	00000	00000	00011	00010	00000	00
Geminospora parvibasilaris	00000	00000	00000	00000	00000	00010	00000	00
Geminospora lemurata	00100	00000	00000	00000	00011	00010	00000	00
Grandispora sp.	00000	01000	00000	00000	00000	00000	00000	00
Grandispora cornuta	00000	00000	00000	00000	00011	00000	00000	00
Hymenozonotriletes sp.	00000	01000	00000	00000	00000	00000	00000	00
Hystricosporites sp.	00000	01000	00000	00000	00000	00000	00000	00
Hystricosporites corystus	00000	00110	00000	00000	00000	00000	00000	00
Latosporites sp.	00000	01000	00000	00000	00000	00000	00000	00
Leiotriletes	00000	01000	00000	00000	00000	00000	00000	00
Lophozonotriletes sp.	00000	01000	00000	00000	00000	00000	00000	00
Perotriletes sp.	00000	01000	00000	00000	00000	00000	00000	00
Perotriletes bifurcatus	00000	00110	00000	00000	00000	00000	00000	00
Punctatisporites sp.	00000	01000	00000	00000	00000	00000	00000	00
Reticulatisporites sp.	00000	01000	00000	00000	00000	00000	00000	00
Retusotriletes sp.	00000	01000	00000	00000	00000	00000	00000	00
Retusotriletes communis	00000	00000	00000	00000	00011	00000	00000	00
Rhabdosporites	00000	01000	00000	00000	00000	00000	00000	00
Rugospora flexuosa	00000	00000	00000	00000	00011	00000	00000	00
Samarisporites sp.	00000	01000	00000	00000	00000	00000	00000	00
Stenozonotriletes sp.	00000	01000	00000	00000	00000	00000	00000	00
Stenozonotriletes conformis	00000	00000	00000	00000	00000	00010	00000	00
Teichertospora torquata	00000	01000	00000	00000	00000	00000	00000	00
Verrucosisporites	00000	00000	00000	00000	00011	00010	00000	00

	1	6	1	1	2	2	3	3
			1	6	1	6	1	6
Verrucosisporites omalus	00000	00000	00000	00000	00000	00010	00000	00
Verrucosisporites tumulentus	00000	00000	00000	00000	00011	00000	00000	00
CHAROPHYTES	00000	00000	00001	10100	00000	00000	00001	10
Charales	00000	00000	00000	00100	00000	00000	00000	00
Trochiliscus	00000	00000	00000	00100	00000	00000	00000	00
LAND PLANTS	01110	00001	10000	00101	10011	00010	01110	00
Aglosperma quadripartita	00000	00000	00000	00000	00011	00000	00000	00
Archaeopteris	01000	00000	00000	00101	10011	00000	00010	00
Archaeopteris obtusa	00000	00000	00000	00000	10011	00000	00000	00
Archaeopteris halliana	00000	00000	00000	00000	00011	00000	00000	00
Archaeopteris hibernica	00000	00000	00000	00000	00011	00000	00000	00
Archaeopteris howitti	01000	00000	00000	00000	00000	00000	00000	00
Archaeopteris fissilis	00000	00000	00000	00100	10000	00000	00000	00
Archaeopteris macilenta	00000	00000	00000	00000	00011	00000	00000	00
Baringophyton	00000	00000	00000	00000	00011	00000	00000	00
Barinophyton obscurum	00000	00000	00000	00000	00011	00000	00000	00
Barinophyton sibericum	00000	00000	00000	00000	00011	00000	00000	00
Callixylon trifilievi	00000	00000	00000	00000	00000	00000	00010	00
Callixylon zalesskyi	00000	00000	00000	00000	00000	00000	00010	00
Callixylon brownii	00000	00000	00000	00000	00000	00000	00010	00
Cephalopteris mirabilis	00000	00000	00000	00000	10000	00000	00000	00
Cordaites australis	01000	00000	00000	00000	00000	00000	00000	00
Duodimidia pfefferkornii	00000	00000	00000	00000	00011	00000	00000	00
Eolepidodendron wusihense	00000	00000	00000	00000	00000	00010	00000	00
Eospermatopteris	00000	00000	00000	00000	00001	00000	00000	00
Flabellifolium sp.	00000	00000	00000	00001	00000	00000	00000	00
Gillespiea randolphensis	00000	00000	00000	00000	00011	00000	00000	00
Hamatophyllum verticalIatum	00000	00000	00000	00000	00000	00010	00000	00
Haplostigma lineare	00100	00000	00000	00000	00000	00000	00000	00
Lepidodendron velthrimanianum	00000	00001	10000	00000	00000	00000	00000	00
Lepidodendropsis	00000	00000	00000	00000	00011	00000	00000	00
Lepidosigillaria	00000	00000	00000	00000	00001	00000	00000	00
Leptophloeum	01000	00000	00000	00000	10000	00010	00000	00
Leptophloeum rhombicum	00000	00000	00000	00000	10000	00010	00000	00
Leptophloeum australe	01000	00000	00000	00000	00000	00000	00000	00
Lyginodendron sverdrupii	00000	00000	00000	00000	10000	00000	00000	00
Microcodium	00000	00001	10000	00000	00000	00000	00000	00
Platyphyllum sp.	00000	00000	00000	00100	00000	00000	00000	00
Nematophyton sp.	00000	00000	00000	00100	00000	00000	00000	00
Otzinachsonia beerboweri	00000	00000	00000	00000	00011	00000	00000	00
Praeramunculus alternatiramus	00100	00000	00000	00000	00000	00000	00000	00
Protobarynophyton sp.	00000	00000	00000	00001	00011	00000	00000	00
Rhacophyton	00000	00000	00000	00100	00011	00000	00000	00
Rhacophyton ceratangium	00000	00000	00000	00000	00011	00000	00000	00
Sphenopteridium taihuenensis	00000	00000	00000	00000	00000	00010	00000	00
Sphenopteris sp.	01000	00000	00000	00000	00000	00000	00000	00
Sublepidodendron mirabile	00000	00000	00000	00000	00000	00010	00000	00

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Svalbardia polymorpha	00000	00000	00000	00100	00000	00000	00000	00
Astroentactinia stellata	00000	01000	00000	00000	00000	00000	00000	00
Astroentactinia paronae	00000	01000	00000	00000	00000	00000	00000	00
Calceola sandalina	00000	00000	00000	00000	00000	00000	00000	01
Ceratoikiscum planistellare	00000	01000	00000	00000	00000	00000	00000	00
Ceratoikiscum vimenum	00000	01000	00000	00000	00000	00000	00000	00
Ceratoikiscum sp.	00000	01000	00000	00000	00000	00000	00000	00
Entactinia additiva	00000	01000	00000	00000	00000	00000	00000	00
Entactinia cf *dissora*	00000	01000	00000	00000	00000	00000	00000	00
Entactinia cf *micula*	00000	01000	00000	00000	00000	00000	00000	00
Entactinosphaera? *echinata*	00000	01000	00000	00000	00000	00000	00000	00
Entactinosphaera cf *grandis*	00000	01000	00000	00000	00000	00000	00000	00
Haplentactinia cf *rhinophyusa*	00000	01000	00000	00000	00000	00000	00000	00
Helenifore laticlavium	00000	01000	00000	00000	00000	00000	00000	00
Helioentactinia perjucunda	00000	01000	00000	00000	00000	00000	00000	00
Spongentactinia sp.	00000	01000	00000	00000	00000	00000	00000	00
Spongentactinella? *veles*	00000	01000	00000	00000	00000	00000	00000	00
Spongentactinella corynacantha	00000	01000	00000	00000	00000	00000	00000	00
Stigmospherostylus additiva	00000	01000	00000	00000	00000	00000	00000	00
SPONGES	00000	01000	00001	10000	00000	00000	00000	01
Actinodictya nevadensis	00000	00000	00001	10000	00000	00000	00000	00
Actinodictya lamina	00000	00000	00001	10000	00000	00000	00000	00
Amphipora	00000	00000	00000	10000	00000	00000	00000	01
Amphipora ramosa	00000	00000	00000	00000	00000	00000	00000	01
Bulbospongia bullata	00000	00000	00001	10000	00000	00000	00000	00
Cyathophycella minuta	00000	00000	00001	10000	00000	00000	00000	00
Cyathophycella grossa	00000	00000	00001	10000	00000	00000	00000	00
Cyathophycus simpsonenis	00000	00000	00001	10000	00000	00000	00000	00
Desquamatia	00000	00000	00000	10000	00000	00000	00000	00
Dictyospongia? *robusta*	00000	00000	00001	10000	00000	00000	00000	00
Dictyospongia? *amplia*	00000	00000	00001	10000	00000	00000	00000	00
Hexagonaria	00000	00000	00000	10000	00000	00000	00000	00
Protospongia conica	00000	00000	00001	10000	00000	00000	00000	00
Rufuspongia triporata	00000	00000	00001	10000	00000	00000	00000	00
Rufuspongia sp.	00000	00000	00001	10000	00000	00000	00000	00
Taleolaspongia modesta	00000	00000	00001	10000	00000	00000	00000	00
Teganiella ovata	00000	00000	00001	10000	00000	00000	00000	00
Alveolitella sp. A	00000	00000	00001	10000	00000	00000	00000	00
Cladopora	00000	00000	00001	10000	00000	00000	00000	00
Cystiphylloides	00000	00000	00000	10000	00000	00000	00000	00
Grabulites jacksoni	00000	00000	00000	10000	00000	00000	00000	00
Microplasma	00000	00000	00000	10000	00000	00000	00000	00
Paraconularia recurvatus	00000	00000	00001	10000	00000	00000	00000	00
Prismatophyllum flexum	00000	00000	00000	10000	00000	00000	00000	00
Thamnopora sp. D	00000	00000	00001	10000	00000	00000	00000	00
Metrionaxon	00000	00000	00000	10000	00000	00000	00000	00
Pseudomicroplasma	00000	00000	00000	10000	00000	00000	00000	00

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Stratopora	00000	00000	00000	10000	00000	00000	00000	00
Xystriphyllum trojani	00000	00000	00000	10000	00000	00000	00000	00
Zonophyllum	00000	00000	00000	10000	00000	00000	00000	00
Cruziana	11000	00000	00000	00000	00000	00000	00000	01
Fuersichnus	11000	00000	00000	00000	00000	00000	00000	00
Gyrophyllites	00000	00000	00000	00001	00000	00000	00000	00
Margaritichnus	11000	00000	00000	00000	00000	00000	00000	00
Metaichna	00100	00000	00000	00000	00000	00000	00000	00
Palaeophycus	11000	00000	00000	00000	00000	00000	00000	00
Planolites montanus	00000	00000	00000	00001	00000	00000	00000	00
Platicytes lioparadus	11000	00000	00000	00000	00000	00000	00000	00
Psilonichnus	00000	00000	00000	00000	00000	00000	00000	01
Ruzophycus	11000	00000	00000	00000	00000	00000	00000	00
Sagittichnus	11000	00000	00000	00000	00000	00000	00000	00
Scoyenia	00100	00000	00000	00000	00000	00000	00000	00
Skolithos	00000	00000	00000	00000	00000	00000	00000	01
Thalassinoides	00000	00000	00000	00000	00000	00000	00000	01
Concavicaris aff. *elytroides*	00000	01000	00000	00000	00000	00000	00000	00
Eleutherocaris sp.	00000	01000	00000	00000	00000	00000	00000	00
Montecaris lehmanni	00000	01000	00000	00000	00000	00000	00000	00
Schugurocaris sp.	00000	01000	00000	00000	00000	00000	00000	00
CONCAVICARIDS	00000	01000	00000	00000	00000	00000	00000	00
CONCHOSTRACANS	00100	00000	00000	00001	00000	00000	00000	00
Asmusia membranacea	00000	00000	00000	00001	00000	00000	00000	00
OSTRACODES	00000	00000	00010	01000	00000	00000	00001	11
Acantonodella lutkevichi	00000	00000	00010	00000	00000	00000	00000	00
A. terciocornuta	00000	00000	00010	01000	00000	00000	00000	00
Acratia galinae	00000	00000	00010	00000	00000	00000	00000	00
A. gassanovae	00000	00000	00010	00000	00000	00000	00000	00
Acratia mayselae	00000	00000	00010	00000	00000	00000	00000	00
Aparchites globulus	00000	00000	00000	00000	00000	00000	00001	10
Aparchitellina	00000	00000	00000	00000	00000	00000	00001	10
Bairdia	00000	00000	00010	01000	00000	00000	00000	00
Bairdiocypris	00000	00000	00010	00000	00000	00000	00000	00
Buregia bispinosa	00000	00000	00010	01000	00000	00000	00000	00
Bykovites nativus	00000	00000	00000	00000	00000	00000	00001	10
Carbonita sp.	00000	00000	00000	00000	00000	00000	00001	10
Cavellina sp.	00000	00000	00010	00000	00000	00000	00000	00
Cryptophyllus sp.	00000	00000	00010	00000	00000	00000	00000	00
Evlanella sokolovi	00000	00000	00000	00000	00000	00000	00001	10
Glyptolichwinella ct. *spiralis*	00000	00000	00000	00000	00000	00000	00001	10
Gravia sp.	00000	00000	00010	00000	00000	00000	00000	00
Healdianella punctata	00000	00000	00000	00000	00000	00000	00001	10
Heladianella cf. *svinordensis*	00000	00000	00010	00000	00000	00000	00000	00
Indivisia semilukiana	00000	00000	00010	00000	00000	00000	00000	00
Kloedenellitina sygmaeformis	00000	00000	00010	00000	00000	00000	00000	00
Knoxiella	00000	00000	00010	00000	00000	00000	00000	00

	1	6	11	16	21	26	31	36
Knoxina cf. *alexandrovae*	00000	00000	00010	00000	00000	00000	00000	00
K. sp. aff. *costata*	00000	00000	00010	00000	00000	00000	00000	00
Knoxites	00000	00000	00010	00000	00000	00000	00000	00
Kozlowskiella	00000	00000	00010	00000	00000	00000	00000	00
Mennerella schelonica	00000	00000	00010	00000	00000	00000	00000	00
Mennerites svinordensis	00000	00000	00010	00000	00000	00000	00000	00
M. porezkyae	00000	00000	00010	00000	00000	00000	00000	00
Milanovskya bicristata	00000	00000	00010	01000	00000	00000	00000	00
Mossolovella philippovae	00000	00000	00010	00000	00000	00000	00000	00
Neodrepanella tricornis	00000	00000	00010	00000	00000	00000	00000	00
N. parva	00000	00000	00010	00000	00000	00000	00000	00
Nodella conotuberculata	00000	00000	00010	00000	00000	00000	00000	00
Paraparchites calculus	00000	00000	00010	00000	00000	00000	00000	00
Pseudonodella plana	00000	00000	00010	00000	00000	00000	00000	00
Tetracornella schelonica	00000	00000	00010	00000	00000	00000	00000	00
T. tetraspinosa	00000	00000	00010	00000	00000	00000	00000	00
T. cf. *glebovskaja*	00000	00000	00010	00000	00000	00000	00000	00
T. sp. n., aff. *schelonica*	00000	00000	00010	00000	00000	00000	00000	00
T. formosa	00000	00000	00010	00000	00000	00000	00000	00
Timanella sp. B	00000	00000	00010	00000	00000	00000	00000	00
Uchtovia sp.	00000	00000	00010	00000	00000	00000	00000	00
Achanarraspis reedi	00000	00110	00000	00000	00000	00000	00000	00
Orsadesmus rubecollus	00000	00000	00000	00000	00011	00000	00000	00
Gigantocharinus szatmaryi	00000	00000	00000	00000	00011	00000	00000	00
Petaloscorpio bureaui	00000	00000	00000	00001	00000	00000	00000	00
Gigantoscorpionidae	00000	00000	00000	00001	00000	00000	00000	00
EURYPTERIDS	00000	01000	00000	00001	00000	00000	00000	00
Rhenopterus waterstoni	00000	01000	00000	00000	00000	00000	00000	00
Parastylonuridae	00000	00000	00000	00001	00000	00000	00000	00
Pterygotus sp.	00000	00000	00000	00001	00000	00000	00000	00
GASTROPODS	00000	01000	00011	10000	00000	00000	00000	00
BIVALVES	00000	01000	00001	10000	00000	00100	00000	00
Buchiola sp.	00000	00000	00001	10000	00000	00000	00000	00
Modiella sp.	00000	00000	00001	10000	00000	00000	00000	00
Praecardium sp. A	00000	00000	00001	10000	00000	00000	00000	00
Praecardium sp. B	00000	00000	00001	10000	00000	00000	00000	00
Solemya (?*Janeia*) sp.	00000	00000	00001	10000	00000	00000	00000	00
TENTACULITIDS	00000	01000	00001	10000	00000	00000	00000	00
Dacryoconarids	00000	00000	00001	10000	00000	00000	00000	00
AMMONITES	00000	01000	00001	10000	00000	00000	00000	00
Hoeninghausia pons	00000	01000	00000	00000	00000	00000	00000	00
Koenenites	00000	01000	00000	00000	00000	00000	00000	00
Manticoceras guppyi	00000	01000	00000	00000	00000	00000	00000	00
Ponticeras discoidale	00000	01000	00000	00000	00000	00000	00000	00
Probeloceras aveolatum	00000	01000	00000	00000	00000	00000	00000	00
Tamanites angustus	00000	01000	00000	00000	00000	00000	00000	00
Tornoceras simplex	00000	01000	00000	00000	00000	00000	00000	00

	1	**6**	**1**	**1**	**2**	**2**	**3**	**3**
			1	**6**	**1**	**6**	**1**	**6**
Tornoceras contactum	00000	01000	00000	00000	00000	00000	00000	00
NAUTILOIDS	00000	01000	00000	00000	00000	00100	00000	00
GASTROPODS	00000	01000	00000	00000	00000	00000	00000	00
POLYCHETES	00000	00000	10000	00001	00000	00000	00001	10
Spirorbis	00000	00000	10000	00000	00000	00000	00000	00
Serpula vipera	00000	00000	00000	00000	00000	00000	00001	10
BRACHIOPODS	00001	00000	00011	11000	00000	00100	00000	01
Anathyris svinordensis	00000	00000	00010	00000	00000	00000	00000	00
Bornhardtina skalensis	00000	00000	00000	00000	00000	00000	00000	01
Cyrtospirifer schelonicus	00000	00000	00010	00000	00000	00000	00000	00
Cyrtospirifer sp. A	00000	00000	00010	00000	00000	00000	00000	00
Emanuella sanctacrucensis	00000	00000	00000	00000	00000	00000	00000	01
E. parva	00000	00000	00000	00000	00000	00000	00000	01
Ladjia russelli	00000	00000	00001	10000	00000	00000	00000	00
Leiorhynchus hippocastanea	00000	00000	00001	10000	00000	00000	00000	00
Pentamerella wintereri	00000	00000	00000	10000	00000	00000	00000	00
Leptathyris circula	00000	00000	00000	10000	00000	00000	00000	00
Rhyssochonetes	00000	00000	00000	10000	00000	00000	00000	00
Vallomyonia claudiae	00000	00000	00001	10000	00000	00000	00000	00
BRYOZOANS	00000	01000	00000	10000	00000	00000	00000	00
CRINOIDS	00000	01000	00001	10000	00000	00000	00000	00
CONODONTS	00000	11000	00001	11000	00000	01100	00000	11
Acyrodella rotundiloba	00000	01000	00000	00000	00000	00000	00000	00
Ancyrognathus ancyrognathoideus	00000	00000	00010	01000	00000	00000	00000	00
Bipennatus bipennatus montensis	00000	00000	00000	00000	00000	00000	00000	01
Bispathodus stabilis	00000	00000	00000	00000	00000	00000	00000	10
Bispathodus aculeatus aculeatus	00000	00000	00000	00000	00000	00000	00000	10
Bispathodus aculeatus plumulus	00000	00000	00000	00000	00000	00000	00000	10
Gnamptognathus? lipperti	00000	01000	00000	00000	00000	00000	00000	00
Icriodus	00000	01000	00010	00000	00000	00000	00000	10
Icriodus costatus	00000	00000	00000	00000	00000	00000	00000	10
Icriodus symmetricus	00000	01000	00010	00000	00000	00000	00000	00
Klapperina disparilis	00000	00000	00001	10000	00000	00000	00000	00
Pandorinellina nota	00000	00000	00000	00000	00000	00000	00000	10
Pelekysgnathus sp.	00000	00000	00010	00000	00000	00000	00000	00
Polygnathus	00000	01000	00011	11000	00000	00000	00000	10
Polygnathus alatus	00000	00000	00000	01000	00000	00000	00000	00
Polygnathus angusticostatus	00000	00000	00000	10000	00000	00000	00000	00
Polygnathus aspelundi	00000	00000	00000	01000	00000	00000	00000	00
Polygnathus asymmetrica	00000	01000	00000	00000	00000	00000	00000	00
Polygnathus beckmanni	00000	00000	00000	10000	00000	00000	00000	00
Polygnathus collinsoni	00000	00000	00000	00000	00000	00000	00000	10
Polygnathus cristatus	00000	00000	00001	10000	00000	00000	00000	00
Polygnathus efimovae	00000	00000	00010	01000	00000	00000	00000	00
Polygnathus foliatus	00000	00000	00001	10000	00000	00000	00000	00
Polygnathus imenensis	00000	00000	00010	00000	00000	00000	00000	00
Polygnathus kennettensis	00000	00000	00000	10000	00000	00000	00000	00

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Polygnathus kockelianus	00000	00000	00000	10000	00000	00000	00000	00
Polygnathus lanei	00000	00000	00010	00000	00000	00000	00000	00
P. linguiformis linguiformis	00000	00000	00000	10000	00000	00000	00000	00
P. linguiformis parawebbi	00000	00000	00000	10000	00000	00000	00000	00
Polygnathus lobatus	00000	00000	00000	00000	00000	00000	00000	10
Polygnathus mosquensis	00000	00000	00010	00000	00000	00000	00000	00
Polygnathus normalis	00000	01000	00000	00000	00000	00000	00000	00
Polygnathus ordinatus	00000	00000	00001	10000	00000	00000	00000	00
Polygnathus ovatinodosus	00000	00000	00000	10000	00000	00000	00000	00
Polygnathus paprothae	00000	00000	00000	00000	00000	00000	00000	10
Polygnathus pollocki	00000	00000	00010	01000	00000	00000	00000	00
Polygnathus pseudofoliatus	00000	00000	00000	10000	00000	00000	00000	00
Polygnathus reimersi	00000	00000	00010	00000	00000	00000	00000	00
Polygnathus serotinus	00000	00000	00000	10000	00000	00000	00000	00
Polygnathus strictus	00000	00000	00010	00000	00000	00000	00000	00
Polygnathus subincompletus	00000	00000	00000	01000	00000	00000	00000	00
Polygnathus timorensis	00000	00000	00000	10000	00000	00000	00000	00
Polygnathus trigonicus	00000	00000	00000	10000	00000	00000	00000	00
Polygnathus ukhtensis	00000	00000	00010	00000	00000	00000	00000	00
Polygnathus varca	00000	01000	00000	00000	00000	00000	00000	00
Polygnathus xylus	00000	00000	00010	01000	00000	00000	00000	00
Polygnathus zinaidae	00000	00000	00010	00000	00000	00000	00000	00
Platyfordia primitiva	00000	01000	00000	00000	00000	00000	00000	00
Pseudopolygnathus conili	00000	00000	00000	00000	00000	00000	00000	10
Pseudopolygnathus dentilineatus	00000	00000	00000	00000	00000	00000	00000	10
Roundia aurita	00000	01000	00000	00000	00000	00000	00000	00
Schmidtognathus sp.	00000	00000	00001	10000	00000	00000	00000	00
HETEROSTRACANS	00000	00000	00010	00110	01000	10000	00000	00
Psammosteus	00000	00000	00000	00110	01000	10000	00000	00
Psammosteus asper	00000	00000	00000	00010	00000	00000	00000	00
Psammosteus cuneatus	00000	00000	00000	00010	00000	00000	00000	00
Psammosteus ganensis	00000	00000	00000	00100	00000	00000	00000	00
Psammosteus levis	00000	00000	00000	00010	00000	00000	00000	00
Psammosteus livonicus	00000	00000	00000	00010	00000	00000	00000	00
Psammosteus maeandrinus	00000	00000	00000	00010	00000	00000	00000	00
Psammosteus megalopteryx	00000	00000	00010	00000	00000	00000	00000	00
Psammosteus praecursor	00000	00000	00000	00010	00000	00000	00000	00
Psammolepis	00000	00000	00000	00110	00000	00000	00000	00
Pasmmolepis abavica	00000	00000	00000	00100	00000	00000	00000	00
Psammolepis paradoxa	00000	00000	00000	00100	00000	00000	00000	00
Psammolepis alata	00000	00000	00000	00100	00000	00000	00000	00
Psammolepis heteraster	00000	00000	00000	00100	00000	00000	00000	00
Psammolepis venyukovi	00000	00000	00000	00110	00000	00000	00000	00
Psammolepis undulata	00000	00000	00000	00110	00000	00000	00000	00
Psammolepis praecursor	00000	00000	00000	00100	00000	00000	00000	00
Achanarella	00000	00110	00000	00000	00000	00000	00000	00
Cornovichthys blaauweni	00000	00110	00000	00000	00000	00000	00000	00

	1	**6**	**1**	**1**	**2**	**2**	**3**	**3**
			1	**6**	**1**	**6**	**1**	**6**
Endeiolepis aneri	00000	00000	00000	00001	00000	00000	00000	00
Euphanerops longaevus	00000	00000	00000	00001	00000	00000	00000	00
Legendrelepis parenti	00000	00000	00000	00001	00000	00000	00000	00
Levesquaspis patteni	00000	00000	00000	00001	00000	00000	00000	00
Turinia antarctica	00100	00000	00000	00000	00000	00000	00000	00
Galeaspids	00000	00000	00000	00000	00000	00010	00000	00
Asterolepis sp.	00000	00000	00000	00000	10000	00000	00000	00
Asterolepis sp.	00000	00000	00001	10000	00000	00000	00000	00
Asterolepis sp. cf. *thule*	00000	00000	00100	00000	00000	00000	00000	00
Asterolepis ornata	00000	00000	00000	00110	00000	00000	00000	00
Asterolepis cristata	00000	00000	00000	00100	00000	00000	00000	00
Asterolepis essica	00000	00000	00000	00100	00000	00000	00000	00
Asterolepis major	00000	00000	00000	00000	01000	00000	00000	00
Asterolepis radiata	00000	00000	00000	00010	00000	00000	00000	00
Bothriolepis antarctica	00100	00000	00000	00000	00000	00000	00000	00
Bothriolepis alexi	00100	00000	00000	00000	00000	00000	00000	00
Bothriolepis askinae	00100	00000	00000	00000	00000	00000	00000	00
Bothriolepis canadansis	00000	00000	00000	00001	00000	00000	00000	00
Bothriolepis ciecere	00000	00000	00000	00000	00000	00001	10000	00
Bothriolepis cullodenensis	00010	00000	00000	00000	00000	00000	00000	00
Bothriolepis fergusoni	00010	00000	00000	00000	00000	00000	00000	00
Bothriolepis gippslandiensis	00010	00000	00000	00000	00000	00000	00000	00
Bothriolepis bindareei	00010	00000	00000	00000	00000	00000	00000	00
Bothriolepis barretti	00100	00000	00000	00000	00000	00000	00000	00
Bothriolepis karawaka	00100	00000	00000	00000	00000	00000	00000	00
Bothriolepis kohni	00100	00000	00000	00000	00000	00000	00000	00
Bothriolepis cf. *leptocheira*	00000	00000	00000	00000	00000	01100	00000	00
Bothriolepis macphersoni	00100	00000	00000	00000	00000	00000	00000	00
Bothriolepis maxima	00000	00000	00000	00000	00000	10000	00000	00
Bothriolepis mawsoni	00100	00000	00000	00000	00000	00000	00000	00
Bothriolepis nielseni	00000	00000	00000	00000	00000	00000	01000	00
Bothriolepis obrutscewi	00000	00000	00000	00010	00000	00000	00000	00
Bothriolepis prima	00000	00000	00000	00010	00000	00000	00000	00
Bothriolepis panderi	00000	00000	00010	00000	00000	00000	00000	00
Bothriolepis portalensis	00100	00000	00000	00000	00000	00000	00000	00
Bothriolepis sosnensis	00000	00000	00000	00000	00000	01100	00000	00
Bothriolepis traudscholdi	00000	00000	00010	00000	00000	00000	00000	00
Bothriolepis vuwae	00100	00000	00000	00000	00000	00000	00000	00
Bothriolepis yeungae	00001	00000	00000	00000	00000	00000	00000	00
Bothriolepis zadonica	00000	00000	00000	00000	00000	01100	00000	00
Grossilepis spinosa	00000	00000	00000	00000	00000	10000	00000	00
Jiangxilepis sp.	00000	00000	00000	00000	00000	00010	00000	00
Livnolepis	00000	00000	00000	00000	00000	00100	00000	00
Microbrachius dicki	00000	00000	00100	00000	00000	00000	00000	00
Ningxialepis spinosa	00000	00000	00000	00000	00000	00010	00000	00
Pterichthyodes milleri	00000	00110	00000	00000	00000	00000	00000	00
Remigolepis sp.	00000	00000	00000	00000	00000	00100	00000	00

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			1	6	1	6	1	6
Remigolepis sp.	00000	00000	00000	00000	00001	00000	00000	00
Remigolepis sp.	00000	00000	00000	00000	00100	00000	00000	00
Remigolepis acuta	00000	00000	00000	00000	00000	00000	00100	00
Remigolepis armata	00000	00000	00000	00000	00000	00000	00001	10
Remigolepis incisa	00000	00000	00000	00000	00000	00000	00100	00
Remigolepis kullingi	00000	00000	00000	00000	00000	00000	01000	00
Remigolepis kochi	00000	00000	00000	00000	00000	00000	01000	00
Remigolepis major	00000	00000	00000	00000	00000	00010	00000	00
Remigolepis microcephala	00000	00000	00000	00000	00000	00010	00000	00
Remigolepis xiangshanensis	00000	00000	00000	00000	00000	00010	00000	00
Remigolepis xixiaensis	00000	00000	00000	00000	00000	00010	00000	00
Remigolepis zhongmingensis	00000	00000	00000	00000	00000	00010	00000	00
Remigolepis zhongweiensis	00000	00000	00000	00000	00000	00010	00000	00
Remigolepis walkeri	00001	00000	00000	00000	00000	00000	00000	00
Remigolepis zhongningensis	00000	00000	00000	00000	00000	00010	00000	00
Rossolepis	00000	00000	00000	00000	00000	00100	00000	00
Sinolepis szei	00000	00000	00000	00000	00000	00010	00000	00
Venezuelepis antarctica	00100	00000	00000	00000	00000	00000	00000	00
Campbellodus decipiens	00000	11000	00000	00000	00000	00000	00000	00
Chelyophorus	00000	00000	00000	00000	00000	01100	00000	00
Austroptyctodus gardineri	00000	11000	00000	00000	00000	00000	00000	00
Materpiscis attenboroughi	00000	11000	00000	00000	00000	00000	00000	00
Rhamphodopsis threiplandi	00000	00110	00000	00000	00000	00000	00000	00
Rhamphodopsis trispinatus	00000	00110	00000	00000	00000	00000	00000	00
Antarctolepis gunni	00100	00000	00000	00000	00000	00000	00000	00
Actinolepis magna	00000	00110	00000	00000	00000	00000	00000	00
Austrophyllolepis	00110	00000	00000	00000	00000	00000	00000	00
Austeophyllolepis ritchiei	00010	00000	00000	00000	00000	00000	00000	00
Austrophyllolepis youngi	00010	00000	00000	00000	00000	00000	00000	00
Austrophyllolepis quiltyi	00100	00000	00000	00000	00000	00000	00000	00
Boomeraspis goujeti	00100	00000	00000	00000	00000	00000	00000	00
Camuropiscis concinnus	00000	11000	00000	00000	00000	00000	00000	00
Camuropiscis laidlawi	00000	11000	00000	00000	00000	00000	00000	00
Coccosteus sp.	00000	00000	00010	00000	00000	00000	00000	00
Coccosteus sp.	00000	00000	00000	00010	00000	00000	00000	00
Coccosteus cuspidatus	00000	00110	00000	00000	00000	00000	00000	00
Coccosteus decipiens	00000	00000	00100	00000	00000	00000	00000	00
Coccosteus panderi	00000	00000	00000	00100	00000	00000	00000	00
Compagopiscis croucheri	00000	11000	00000	00000	00000	00000	00000	00
Clarkeosteus cf. *halmodeus*	00000	00000	01000	00000	00000	00000	00000	00
Fallacosteus turnerae	00000	11000	00000	00000	00000	00000	00000	00
Gogopiscis gracilis	00000	11000	00000	00000	00000	00000	00000	00
Groenlandaspis	00111	00000	00000	00000	00111	00000	00010	00
Groenlandaspis antarcticus	00100	00000	00000	00000	00000	00000	00000	00
Geonlandaspis thorezi	00000	00000	00000	00000	00000	00000	00010	00
Harrytoombsia elegans	00000	11000	00000	00000	00000	00000	00000	00
Holonematids	00000	11000	00010	00000	00000	00000	00000	00

	1	6	11	16	21	26	31	36
Holonema westolli	00000	11000	00000	00000	00000	00000	00000	00
Homosteus milleri	00000	00110	00000	00000	00000	00000	00000	00
Incisoscutum ritchiei	00000	11000	00000	00000	00000	00000	00000	00
Incisoscutum (*Gogosteus*) *sarahae*	00000	11000	00000	00000	00000	00000	00000	00
Kendrickichthys cavernosus	00000	11000	00000	00000	00000	00000	00000	00
Kimberleyichthys cuspidatus	00000	11000	00000	00000	00000	00000	00000	00
Kimberleyichthys whybrowi	00000	11000	00000	00000	00000	00000	00000	00
Livosteus grandis	00000	00000	00000	00100	00000	00000	00000	00
Mcnamaraspis kaprios	00000	11000	00000	00000	00000	00000	00000	00
Phyllolepis	00000	00000	00000	00000	00111	00000	01010	00
Phyllolepis nielseni	00000	00000	00000	00000	00000	00000	01000	00
Phyllolepis rossimontina	00000	00000	00000	00000	00011	00000	00000	00
Phyllolepis undulata	00000	00000	00000	00000	00000	00000	00010	00
Plourdosteus	00000	00000	00011	10111	00000	00000	00000	00
Plourdosteus canadensis	00000	00000	00000	00001	00000	00000	00000	00
Plourdosteus livonicus	00000	00000	00000	00110	00000	00000	00000	00
Phlyctaeniids	00100	00000	00000	00000	00000	00000	00000	00
Pinguosteus thulborni	00000	11000	00000	00000	00000	00000	00000	00
Placolepis tingeyi	00100	00000	00000	00000	00000	00000	00000	00
Rolfosteus canningensis	00000	11000	00000	00000	00000	00000	00000	00
Simosteus tuberculatus	00000	11000	00000	00000	00000	00000	00000	00
Torosteus tuberculatus	00000	11000	00000	00000	00000	00000	00000	00
Torosteus pulchellus	00000	11000	00000	00000	00000	00000	00000	00
Tubonasus lennardensis	00000	11000	00000	00000	00000	00000	00000	00
Watsonosteus sp.	00000	00000	00000	00100	00000	00000	00000	00
Watsonosteus fletti	00000	00000	00100	00000	00000	00000	00000	00
Dinichthyids	00000	11000	00000	00000	00001	00000	00000	00
Bullerichthys fascidens	00000	11000	00000	00000	00000	00000	00000	00
Bruntonichthys multidens	00000	11000	00000	00000	00000	00000	00000	00
Eastmanosteus calliaspis	00000	11000	00000	00000	00000	00000	00000	00
Ageleodus (cf) sp.	00000	00000	10000	00000	00011	00000	00000	00
Anareodus statei	00100	00000	00000	00000	00000	00000	00000	00
Antarctilamna prisca	00100	00000	00000	00000	00000	00000	00000	00
Aztecodus harmsenae	00100	00000	00000	00000	00000	00000	00000	00
Ctenacanthus sp.	00000	00000	00000	00000	00011	00000	00000	00
Culmacanthus stewarti	00010	00000	00000	00000	00000	00000	00000	00
Diplacanthus striatus	00000	00110	00000	00000	00000	00000	00000	00
Diplacanthus crassisimus	00000	00110	00000	00000	00000	00000	00000	00
Diplacanthus longispinus	00000	00110	00000	00000	00000	00000	00000	00
Diplacanthus tenuistriatus	00000	00110	00000	00000	00000	00000	00000	00
Diplacanthus ellsi	00000	00000	00000	00001	00000	00000	00000	00
Diplacanthus horridus	00000	00000	00000	00001	00000	00000	00000	00
Mcmurdodus featherensis	00100	00000	00000	00000	00000	00000	00000	00
Portalodus bradshawae	00100	00000	00000	00000	00000	00000	00000	00
Protacrodus	00000	00000	00000	00000	00000	01100	00000	00
Antarctonchus glacialis	00100	00000	00000	00000	00000	00000	00000	00
Atopacanthus sp.	00000	00000	00010	00000	00000	00000	00000	00

	1	**6**	**1**	**1**	**2**	**2**	**3**	**3**
			1	**6**	**1**	**6**	**1**	**6**
Byssacanthoides debenhami	00100	00000	00000	00000	00000	00000	00000	00
Cosmacanthus	00000	00000	00000	00000	01000	00000	00000	00
Culmacanthus antarctica	00100	00000	00000	00000	00000	00000	00000	00
Devononchus	00000	00000	00000	00110	00000	11101	10001	10
Devononchus concinnus	00000	00000	00000	00110	00000	00000	00000	00
Devononchus cf. *laevis*	00000	00000	00000	00000	00000	01100	00000	00
Devononchus ketleriensis	00000	00000	00000	00000	00000	00001	10000	00
Devononchus tenuispinus	00000	00000	00000	00000	00000	00001	10000	00
Eupleurogmus	01000	00000	00000	00000	00000	00000	00000	00
Gyracanthus	00000	00000	10000	00000	00011	00000	00010	00
Gyracanthus cf. *hawkinsi*	00000	00000	10000	00000	00000	00000	00000	00
Gyracanthides	01100	00000	00000	00000	00000	00000	00000	00
Gyracanthides warreni	00100	00000	00000	00000	00000	00000	00000	00
Haplacanthus ehrmanensis	00000	00000	00000	00100	00000	00000	00000	00
Howittacanthus	00010	00000	00000	00000	00000	00000	00000	00
Machaeracanthus sp.	00000	00000	00001	10000	00000	00000	00000	00
Milesacanthus antarctica	00100	00000	00000	00000	00000	00000	00000	00
Nodacosta pauli	00000	00000	00000	00100	00000	00000	00000	00
Nostalepis gaujensis	00100	00000	00000	00000	00000	00000	00000	00
Pechoralepis juozasi	00100	00000	00000	00000	00000	00000	00000	00
Persacanthus simpsonensis	00000	00000	00001	10000	00000	00000	00000	00
Rhadinacanthus longispinus	00000	00110	00000	00000	00000	00000	00000	00
Acanthodes	01000	00000	00000	00000	00000	00000	00000	00
Cheiracanthus	00000	00110	00000	00000	00000	00000	00000	00
Cheiracanthus murchisoni	00000	00110	00000	00000	00000	00000	00000	00
Cheiracanthus latus	00000	00110	00000	00000	00000	00000	00000	00
Homalacanthus concinnus	00000	00000	00000	00001	00000	00000	00000	00
Lodeacanthus gaujicus	00000	00000	00000	00100	00000	00000	00000	00
Mesacanthus peachi	00000	00110	00100	00000	00000	00000	00000	00
Ischnacanthids	00100	00000	00000	00000	00000	00000	00000	00
Triazeugacanthus affinis	00000	00000	00000	00001	00000	00000	00000	00
Cheirolepis	00000	00000	00000	00100	00000	00000	00000	00
Cheirolepis canadensis	00000	00000	00000	00001	00000	00000	00000	00
Cheirolepis schultzei	00000	00000	00001	10000	00000	00000	00000	00
Cheirolepis trailli	00000	00110	00000	00000	00000	00000	00000	00
Limnomis delanyi	00000	00000	00000	00000	00011	00000	00000	00
Mimipiscis toombsi	00000	11000	00000	00000	00000	00000	00000	00
Mimipiscis bartrami	00000	11000	00000	00000	00000	00000	00000	00
Gogosardina coatesi	00000	11000	00000	00000	00000	00000	00000	00
Moythomasia	00000	11000	00000	00000	00000	00000	00001	10
Moythomasis durgaringa	00000	11000	00000	00000	00000	00000	00000	00
cf. *Moythomasia*	00000	00000	00000	00000	00000	00000	00001	10
Donnrosenia schaefferi	00100	11000	00000	00000	00000	00000	00000	00
Elonichthys	01000	00000	00000	00000	00000	00000	00000	00
Howqualepis rostridens	00010	00000	00000	00000	00000	00000	00000	00
Onychodonts	00000	11000	00001	10110	00000	01101	00001	10
Onychodus jandemarrai	00000	11000	00000	00000	00000	00000	00000	00

	1	**6**	**1**	**1**	**2**	**2**	**3**	**3**
			1	**6**	**1**	**6**	**1**	**6**
Strunius sp.	00000	00000	00000	00100	00000	01100	00001	10
"*Diplocercides*" sp.	00000	11000	00000	00000	00000	00000	00000	00
Miguasha	00000	00000	00000	00101	00000	00000	00000	00
Miguashaia grossi	00000	00000	00000	00100	00000	00000	00000	00
Miguashaia bureaui	00000	00000	00000	00001	00000	00000	00000	00
Adolopas moyasmithae	00000	11000	00000	00000	00000	00000	00000	00
Andreyevichthys epitomus	00000	00000	00000	00000	00000	00000	00001	10
Apatorhynchus opistheretmus	00000	00000	00000	00000	00001	00000	00000	00
Asthenorhynchus meemannae	00000	11000	00000	00000	00000	00000	00000	00
Barwickia downunda	00010	00000	00000	00000	00000	00000	00000	00
Chirodipterus	00000	11000	00000	00000	00000	00100	00000	00
Chirodipterus australis	00000	11000	00000	00000	00000	00000	00000	00
Conchodus	00000	00000	00000	00000	00000	01100	00000	00
Ctenodus	01000	00000	00000	00000	00000	00000	00000	00
Dipterus sp.	00000	00000	00000	00000	00000	01100	00000	00
Dipterus valenciennesi	00000	00110	00000	00000	00000	00000	00000	00
Duffyichthys mirabilis	00000	00000	00000	00000	01000	00000	00000	00
?*Eoctenodus* sp.	00100	00000	00000	00000	00000	00000	00000	00
Fleurantia denticulata	00000	00000	00000	00001	00000	00000	00000	00
Glyptolepis baltica	00000	00000	00000	00110	00000	00000	00000	00
Glyptolepis paucidens	00000	00110	00000	00000	00000	00000	00000	00
Glyptolepis leptopterus	00000	00110	00000	00000	00000	00000	00000	00
Gogodipterus paddyensis	00000	11000	00000	00000	00000	00000	00000	00
Griphognathus	00000	11000	00001	10000	00000	00000	00000	00
Griphognathus whitei	00000	11000	00000	00000	00000	00000	00000	00
Grossipterus crassus	00000	00000	00000	00100	00000	00000	00000	00
Holodipterus	00000	11000	00000	00000	00000	01100	00000	00
Holodipterus gogoensis	00000	11000	00000	00000	00000	00000	00000	00
Holodipterus longi	00000	11000	00000	00000	00000	00000	00000	00
Holodipterus elderae	00000	11000	00000	00000	00000	00000	00000	00
Holoptychius sp.	00000	00000	01000	00000	00000	00000	00000	00
Holoptychius sp.	00000	00000	00010	00000	00000	00000	00000	00
Holoptychius sp.	00000	00000	00000	00000	00100	00000	00000	00
Holoptychius sp.	00000	00000	00000	00000	00011	00000	00000	00
Holoptychius sp.	00000	00000	00000	00000	00000	10000	00000	00
Holoptychius sp.	00000	00000	00000	00000	00000	00100	00000	00
Holoptychius sp.	00000	00000	00000	00000	00000	00000	01100	00
Holoptychius sp.	00000	00000	00000	00000	00000	00000	00010	00
Holoptychius sp.	00000	00000	00000	00000	00000	00000	00001	10
Holoptychius jarviki	00000	00000	00000	00001	00000	00000	00000	00
Holoptychius sp. cf. *nobilissimus*	00000	00000	00000	00010	00000	00001	10000	00
Holoptychius princeps	00000	00000	00000	00000	01000	00000	00000	00
Howidipterus	00110	00000	00000	00000	00000	00000	00000	00
Howidipterus donnae	00010	00000	00000	00000	00000	00000	00000	00
Jarvikia	00000	00000	00000	00000	00000	00000	01010	00
Jarvikia arctica	00000	00000	00000	00000	00000	00000	01000	00
Laccognathus sp.	00000	00000	00000	00000	10000	00000	00000	00

	1	**6**	**1**	**1**	**2**	**2**	**3**	**3**
			1	**6**	**1**	**6**	**1**	**6**
Laccognathus panderi	00000	00000	00000	00110	00000	00000	00000	00
Oervigia nordica	00000	00000	00000	00000	00000	00000	00100	00
Orlovichthys sp. cf. *limnatis*	00000	00000	00000	00000	00000	00001	10000	00
Pentalandia macroptera	00000	00110	00100	00000	00000	00000	00000	00
Pillararhynchus longi	00000	11000	00000	00000	00000	00000	00000	00
Pinnalongus saxoni	00000	00010	00000	00000	00000	00000	00000	00
Quebecius quebecensis	00000	00000	00000	00001	00000	00000	00000	00
Robinsondipterus longi	00000	11000	00000	00000	00000	00000	00000	00
Rhinodipterus	00000	11000	00010	00000	00000	00000	00000	00
Rhinodipterus stolbovi	00000	00000	00010	00000	00000	00000	00000	00
Scaumenacia curta	00000	00000	00000	00001	00000	00000	00000	00
Soederberghia	00001	00000	00001	10000	00111	00000	01010	00
Soederberghia groenlandica	00000	00000	00000	00000	00100	00000	01010	00
Soederberghi simpsoni	00001	00000	00000	00000	00000	00000	00000	00
Ventalepis ketleriensis	00000	00000	00000	00000	00000	00001	10000	00
Xeradipterus hatcheri	00000	11000	00000	00000	00000	00000	00000	00
RHIZODONTS	11101	00000	00000	00000	00011	00000	00010	00
Aztecia mahalae	00100	00000	00000	00000	00000	00000	00000	00
Barameda	11000	00000	00000	00000	00000	00000	00000	00
Gooloogongia loomsei	00001	00000	00000	00000	00000	00000	00000	00
Strepsodus	01000	00000	00000	00000	00011	00000	00000	00
CANOWINDRIDS	00111	00000	00000	00000	00000	00000	00000	00
Beelarongia patrichae	00010	00000	00000	00000	00000	00000	00000	00
Canowindra grossi	00001	00000	00000	00000	00000	00000	00000	00
Koharalepis jarviki	00100	00000	00000	00000	00000	00000	00000	00
Marsdenichthys longioccipitus	00010	00000	00000	00000	00000	00000	00000	00
Callistiopterus clappi	00000	00000	00000	00001	00000	00000	00000	00
Cladarosymblema	00000	00001	10000	00000	00000	00000	00000	00
Crysolepis sp.	00000	00000	00000	00000	00000	00000	00001	10
Cryptolepis gross	00000	00000	00000	00000	00000	00001	10000	00
Glyptopomus	00000	00000	00000	00000	00000	01101	10010	00
Gogonasus andrewsae	00000	11000	00000	00000	00000	00000	00000	00
Gyroptychius	00100	00110	00000	00000	00000	00000	00000	00
Gyroptychius? *antarcticus*	00100	00000	00000	00000	00000	00000	00000	00
Gyroptychius agassizi	00000	00110	00000	00000	00000	00000	00000	00
Latvius sp.	00000	00000	00000	00100	00000	00000	00000	00
Megapomus markovskyi	00000	00000	00000	00000	00000	01100	00000	00
Megalichthys sp.	00000	00000	00000	00000	00000	00000	00010	00
Mahalalepis resima	00100	00000	00000	00000	00000	00000	00000	00
Osteolepis macrolepidotus	00000	00110	00000	00000	00000	00000	00000	00
Platyethmoidia antarctica	00100	00000	00000	00000	00000	00000	00000	00
Sterropterygion	00000	00000	00000	00000	00001	00000	00000	00
Thursius macrolepidotus	00000	00010	00000	00000	00000	00000	00000	00
Thursius? *minor*	00000	00000	01000	00000	00000	00000	00000	00
Vorobjevaia dolonodon	00100	00000	00000	00000	00000	00000	00000	00
Spodichthys buetleri	00000	00000	01000	00000	00000	00000	00000	00
Tristichopterus	00000	00000	00100	00000	00000	00000	00000	00

	1	6	1	1	2	2	3	3
			1	6	1	6	1	6
Eusthenopteron	00000	00000	00000	00111	00000	00000	00000	00
Eusthenopteron foordi	00000	00000	00000	00001	00000	00000	00000	00
Eusthenopteron kurshi	00000	00000	00000	00100	00000	00000	00000	00
Eusthenopteron obrutchevi	00000	00000	00000	00010	00000	00000	00000	00
Notorhizodon mackelveyi	00100	00000	00000	00000	00000	00000	00000	00
Langleria socqueti	00000	00000	00000	00000	00000	00000	00010	00
Cabonnichthys burnsi	00001	00000	00000	00000	00000	00000	00000	00
Mandageria farfaxi	00001	00000	00000	00000	00000	00000	00000	00
Eusthenodon	00000	00000	00000	00000	00000	00000	00110	00
cf. *Eusthenodon* sp.	00000	00000	00000	00000	00011	00000	00000	00
cf. *Eusthenodon* sp.	00000	00000	00000	00000	00000	00000	00001	10
Eusthenodon waengsjoei	00000	00000	00000	00000	00000	00000	00110	00
Hyneria lindae	00000	00000	00000	00000	00011	00000	00000	00
Howittichthys warrenae	00010	00000	00000	00000	00000	00000	00000	00
Jarvikina	00000	00000	00010	00000	00000	00000	00000	00
Tinirau clackae	00000	00000	00001	10000	00000	00000	00000	00
Platycephalichthys bischoffi	00000	00000	00000	01000	00000	00000	00000	00
Parapanderichthys	00000	00000	00000	00000	00000	00000	00000	00
Panderichthys	00000	00000	00000	00110	00000	00001	10000	00
Panderichthys rhombolepis	00000	00000	00000	00110	00000	00000	00000	00
Panderichthys bystrovi	00000	00000	00000	00000	00000	00001	10000	00
Panderichthys sp.?	00000	00000	01000	00000	00000	00000	00000	00
Elpistostege	00000	00000	00000	00001	00000	00000	00000	00
Livoniana (Gauja specimen only)	00000	00000	00000	00100	00000	00000	00000	00
Tiktaalik roseae	00000	00000	00000	00000	10000	00000	00000	00
Elginerpeton	00000	00000	00000	00000	01000	00000	00000	00
Metaxygnathus	00000	00000	00000	00000	00100	00000	00000	00
Hynerpeton	00000	00000	00000	00000	00011	00000	00000	00
Densignathus	00000	00000	00000	00000	00011	00000	00000	00
ANSP Humerus	00000	00000	00000	00000	00011	00000	00000	00
Obruchevichthys	00000	00000	00000	00000	00000	10000	00000	00
Jakubsonia	00000	00000	00000	00000	00000	01100	00000	00
Sinostega	00000	00000	00000	00000	00000	00010	00000	00
Ventastega	00000	00000	00000	00000	00000	00001	10000	00
Acanthostega gunnari	00000	00000	00000	00000	00000	00000	01100	00
Ichthyostega	00000	00000	00000	00000	00000	00000	01100	00
Ichthyostega stensioei	00000	00000	00000	00000	00000	00000	01000	00
Ichthyostega watsoni	00000	00000	00000	00000	00000	00000	00100	00
Ichthyostega eigili	00000	00000	00000	00000	00000	00000	00100	00
Ichthyostega-like jaw	00000	00000	00000	00000	00000	00000	00010	00
Tulerpeton	00000	00000	00000	00000	00000	00000	00001	10

Part D.

Isotopic data.—Samples analyzed for carbonate isotopes.

Red Hill, Pennsylvania: RH-#

RH-1a: *Limnomis* reduced zone
RH-1b: *Limnomis* reduced zone
RH-2: *Hyneria* tooth, reduced zone (below 93-08; tetrapod site)
RH-3: Megalichthyid scale, reduced zone (below 93-08; tetrapod site)
RH-4: *Hyneria* matrix, lag layer, 95-04 Pond Site, drawer RT-120
RH-5: *Hyneria*, lag layer, Drawer RT-120 (15-04 Pond Site)
RH-6: *Gyracanthus* matrix, lag layer
RH-7: *Gyracanthus* spine, lag layer
RH-8: *Hyneria* scale + matrix, lag layer
RH-9: *Turrisaspis*, lag layer
RH-10: *Gyracanthus* spine, Hyner outcrop, 93-08, tetrapod site
RH-11: Matrix + bone bits, Hyner outcrop, 93-08, tetrapod site

Nunavut, Canadian Arctic: NUV-

NUV-C-1–6: carbonate nodules
NUV-B-1–6: bone fragments
NUV-M-1–3: matrix

Evieux Formation, Belgium: EV-

EV1-1–3: sample from facies 1
EV2-1–3: sample from facies 2
EV3-1–3: sample from facies 3
EV4-1–3: sample from facies 4
EV5-1–3: sample from facies 5
EVO-1–3: sample from "other" facies, to the right of facies 5 at the field site

Aztec Siltstone, Antarctica: AZ-#

AZ-1: placoderm bone and matrix
AZ-2: placoderm bone and matrix

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CHAPTER FOUR:
THE ORIGIN AND EARLY EVOLUTION OF TERRESTRIAL LOCOMOTION

Abstract

The origin of terrestrial vertebrates involved an integrated series of changes to the ancestral sarcopterygian bauplan. However, many traits often considered apomorphic for tetrapods have a much deeper origin in vertebrate history. Terrestrial locomotion integrates many such plesiomorphies that facilitated the diversification of vertebrate life on land. In a phylogenetic assessment of over 150 modern and fossil taxa, I incorporate data from osteological, myological, and locomotor records to test how gaits have evolved over gnathostome evolution, and how variation in the historical, constructional, and functional components of the axial and appendicular systems underpins these changes. I show that (a) the trot evolved at least three times in gnathostome evolution; (b) similarities in the trunk muscles of extant lungfishes and tetrapods suggest that the tetrapod myaxial condition evolved in water ~35 million years before the origin of amphibious sarcopterygians; (c) trackway data from modern and fossil records cannot verify whether the lateral sequence diagonal-couplet gait evolved by the end of the Devonian; and (d) the original function of the physical neck—i.e., a space between head and shoulder—was more likely related to the origin of terrestrial locomotion than to any requirement for neck mobility. A pluralistic approach to thinking about macroevolutionary changes—those that distinguish aptations and nonaptations in a continuum of historical, constructional, and functional influences—better elucidates evolutionary transformations than a functionalism that focuses on the cycling of adaptations and exaptations.

Introduction and background

Naturalists have long noted the clear distinction between vertebrates that swim and those that move on land (Peck and Forster 1937). The evolution of vertebrate locomotion has been a longtime focus in particular (Peck and Forster 1937), and more recent functional studies continue relating aquatic and terrestrial locomotory systems (Brainerd and Simons 2000, Carrier 1993, Edwards 1977, 1989, Gemballa and Ebmeyer 2003, Pridmore 1995). Terrestrial vertebrates use a variety of gaits to move on land (Ashley-Ross 1994, Ashley-Ross and Bechtel 2004, Hildebrand 1980, 1985), though not all of them include the lateral undulations (however slight) typical of most fishes (Hildebrand 1977, 1985). Similarly, not all fishes incorporate a traveling axial wave into all aspects of their locomotory repertoire (Altringham and Ellerby 1999, Drucker and Lauder 2000). Despite existing variation, aquatic and terrestrial vertebrates use both axial and appendicular components to aid movement in their respective media, whether or not they contact the substrate (Ashley-Ross and Bechtel 2004, Carrier 1993, Edwards 1977, Fricke 1987, McKenzie et al. 2007, Pridmore 1995, Wilga and Lauder 2001).

Locomotion in modern chondrichthyans (chimeras and sharks), actinopterygians (ray-finned fishes), and non-terrestrial sarcopterygians (lungfishes and coelacanths) frequently incorporates both musculoskeletal systems. Propelled by the caudal fin and aided by axial contractions, locomotion ancestrally involved a traveling wave that migrated rostrocaudally, while pectoral, pelvic, dorsal, and anal fins stabilized and refined adjustments in yaw, pitch, and roll (McKenzie et al. 2007) (Figure 4.1). Apart from buoyancy control mechanisms, it is through such actions that gnathostomes swam through their environments and controlled their positions in the water column. There is much variation in living members of each clade, but

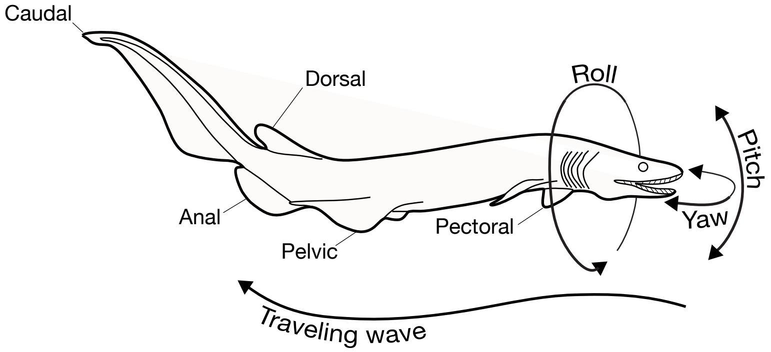


Figure 4.1. The ancestral crown-gnathostome condition, and the biomechanical challenges of locomoting in water. Pectoral fins are low on the body, pelvic fins are positioned posteriorly, and the caudal fin is heterocercal. Yaw, pitch, and roll include side-to-side, up-down, and laterally rotating movements, respectively. Pectoral and pelvic fins work with the caudal fin to provide lift, including adjustments to yaw, pitch, and roll; dorsal and anal fins work with the paired fins to stabilize the tendency to roll; and the caudal fin, in association with the paired fins and a traveling axial wave, provides forward propulsion and lift.

nonetheless, this appears to be the plesiomorphic condition.

Tetrapodomorphs (total-group tetrapods) inherited this ancestral aquatic locomotor mode, but have altered many aspects of their biological support mechanisms to contend with a more gravity-centered adaptive zone. They evolved zygapohyses (Coates 1996), joined their hips with ribs and vertebrae (Coates 1996, Jarvik 1996), lost their median fins (Vorobyeva and Schultze 1991), decoupled their shoulders and head (Daeschler et al. 2006), evolved digits and weight-bearing limbs (Boisvert 2008, Coates and Clack 1990, Shubin et al. 2006), and transformed the traveling wave into a standing wave (Ashley-Ross and Bechtel 2004, Deban and Schilling 2009, Lauder and Tytell 2005). Among amniotes, mammals and archosaurs have taken this to extremes, associated with energy conservation during flight (Norberg 1985) and dorsoventral undulation while galloping (Hildebrand 1977, Zug 1974). However, besides anurans and turtles (Baudinette et al. 2000), most limbed amphibians and non-avian reptiles still retain the ancestral aquatic sinusoidal mode in at least some aspects of their terrestrial gaits (Bennett et al. 2001, Carrier 1990, Reilly and Delancey 1997, Renous et al. 2002, Renous et al. 2008, Zaaf et al. 2001). Moreover, even though most extant frogs specialize in hopping, few invariably hop, and many retain the ability to walk (Ahn et al. 2004, Anderson et al. 1991, Walton et al. 1994).

Discerning the origin of terrestrial locomotion from fossils is challenging, but the trace fossil record demonstrates clearly that stem-tetrapods were walking with a (likely submerged) terrestrial gait by at least the Middle Devonian (395 Ma) (Niedźwiedzki et al. 2010). However, there is more to terrestrial locomotion than the patterned molds of a few pedes in the rock record. The Devonian record of stem-tetrapods is rich with material, and many taxa help document the assembly of the tetrapod condition long before sarcopterygians colonized land (Coates 1996, Daeschler et al. 2006, Jarvik 1996, Johanson and Ahlberg 2001, Lebedev 1995, Snitting 2008, Vorobyeva and Schultze 1991). In other words, in combination with data from extant vertebrates, the fossil record complements a picture that appears to be emerging from both datasets.

I present data from an analysis of both records in order to assess and to understand the origin and early evolution of terrestrial locomotion. In the context of a phylogenetic hypothesis, I (a) incorporate comparative myological and gait analyses of extant groups; and (b) integrate fossil data to clarity how the stem-tetrapod record informs the results obtained from extant taxa. I test within a phylogenetic framework how locomotion evolved among gnathostomes, what the ancestral terrestrial gait may have been, and how traits already present in aquatic vertebrates underpin the tetrapod condition. I then use these data to trace the relationships between formalist and functionalist propositions, and discuss their relationship to evolutionary morphology, evolutionary theory, and the origin of terrestrial mobility.

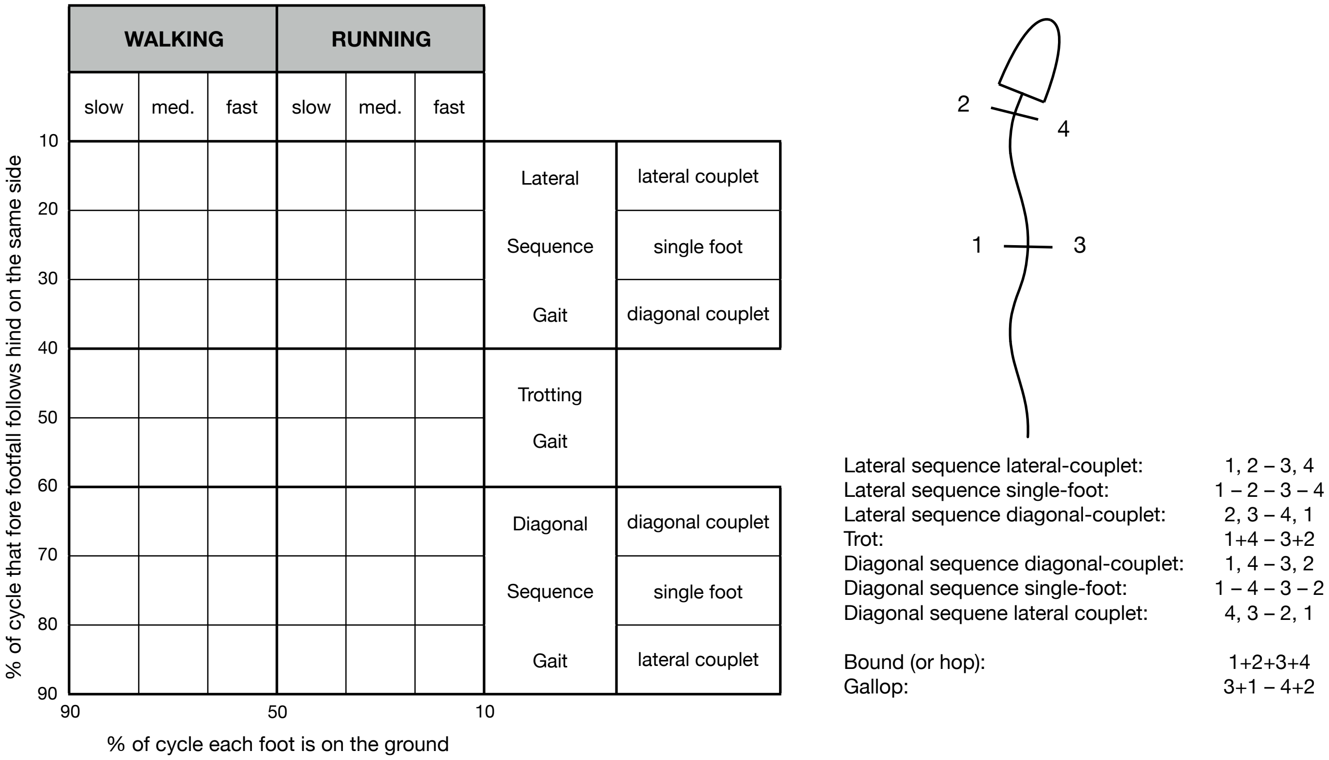
Materials and methods

Gaits.—Hildebrand's work (Hildebrand 1966, 1976, 1977, 1980, 1985) on terrestrial locomotion provided the framework for gait analysis, and I adopt his terminology. In this respect, the terms *walk* and *run* refer to the relative rate of speed within a gait, and describe the amount of time a foot is on the ground when compared to the complete footfall cycle (Hildebrand 1980). For example, if a reference limb contacts the substrate for more than 50% of the footfall cycle, then the animal is walking. However, if it contacts the ground for less than 50% of the cycle, the animal is running (Hildebrand 1985). By contrast, *gaits* diagnose the pattern of footfall, and do not always imply rate (Hildebrand 1976, Reilly et al. 2006). Consequently, because locomotion can be fast or slow, walks and runs can encompass many types of gaits. Gait, not rate, was the primary focus of this analysis. Footfall patterns studied include the lateral sequence diagonal-couplet gait, the lateral sequence lateral-couplet gait, the diagonal sequence diagonal-couplet gait, the diagonal sequence singlefoot, the trot, the bound (which I equate with the hop), and the gallop. See Figure 4.2 for a description of each. It should be noted, however, that the term gait also diagnoses patterns of locomotor shift and muscle recruitment in actinopterygians (Lauder and Madden 2006, Lauder and Tytell 2005), but for clarity, I will use this term only as defined above.

Studied taxa include crown-gnathostomes (jawed vertebrates), specifically chondrichthyans (sharks), actinopterygians (ray-fins), actinistians (coelacanths), dipnoans (lungfishes), lissamphibians (crown-amphibians), chelonians (turtles), lepidosaurs (lizards), and pseudosuchians (crocodiles). Results were informed by a survey of the published literature as well as slow motion videography (⅛-¼ the rate of real-time footage) captured by the British Broadcasting Corporation's *Life* and *Life in Cold Blood* series (Attenborough et al. 2008, Attenborough et al. 2010). Particular gaits were scored as present or absent depending upon reported observations in the primary literature. However, excluding anurans (which data suggest use only hopping and/or lateral sequence diagonal-couplet gaits (Ahn et al. 2004, Anderson et al. 1991, Attenborough et al. 2008, Attenborough et al. 2010, Walton et al. 1994)), when comparing trotting and lateral sequence diagonal-couplet gaits among videographed salamanders, turtles, lizards, and crocodiles, taxa were only scored as 'present' for an observed gait, and not scored as 'absent' for an unobserved gait. That is, even though a trot is accepted as the near simultaneous contact of contralateral limb pairs (Reilly et al. 2006), because a slight difference in timing can transform a lateral sequence diagonal-couplet walk into a walking trot, and because many of these taxa are known to use both gaits, I erred on the side of caution and did not score them as unable to engage in either gait if unobserved. Such 'absences' were used only when noted from the primary literature. In addition, because the foot (or fin-)fall pattern of the epaulette shark, *Hemiscyllium ocellatum*, was often at the boundary between trotting and diagonal sequence diagonal-couplet gaits, it was scored as using both gait types. However—and excluding the squamate *Amevia*'s n=1 sample size (White and Anderson 1994)—because *Hemiscyllium* was the only taxon to use the diagonal sequence diagonal-couplet gait (Pridmore 1995), this gait was excluded from the comparative analysis. In the following analysis, and unless qualified otherwise, the phrase "diagonal-couplet" always refers to the lateral sequence diagonal-couplet gait. Moreover, because the diagonal sequence singlefoot was rare among the tetrapods examined (White and Anderson 1994), it was also excluded from the comparative analysis.

All data were scored using the phylogenetics software Mesquite v. 2.74 (Maddison and Maddison 2010), mapped onto a supertree complied from the primary literature (Brusatte et al. 2010, Cao et al. 2000, Conrad 2008, deBraga and Rieppel 1997, Duellman 1975, Edwards 1976, Emerson 1988, Feng et al. 2007, Ford and Cannatella 1993, Fu 2000, Fujita et al. 2004, Geurgas et al. 2008, Hay et al. 1995, Hedges and Poling 1999, Hillis and Davis 1987, Hugall et al. 2008, Inoue et al. 2001, Krenz et al. 2005, Larson and Dimmick 2007, Larson et al. 2003, Le et al. 2006, Lee 2005, Lyson et al. 2011, Marracci et al. 1996, Miya et al. 2003, Reeder 1995, 2003, Ruvinsky and Maxson 1996, Schuett et al. 2009, Sever 1991a, b, Spinks et al. 2004, Stephens and Wiens 2003, Titus and Frost 1996, Titus and Larson 1995, Townsend and Larson 2002, Townsend et al. 2004, Vidal and Hedges 2005, Weisrock et al. 2005, Wiens et al. 2005, Wilgenbusch and de Queiroz 2000, Winchell 2004, Zhang et al. 2008), and ancestral states reconstructed using both parsimony and likelihood-based methods (Maddison and Maddison 2010). References for the supertree were used to place studied taxa within larger clades and to order the topology of those clades. See supplementary information for the taxon-by-character gait matrix of examined taxa.

Myology.—The primary aim of the myological analysis was to compare axial musculature among coelacanths, lungfishes, and salamanders; the latter are hypothesized to be our best living models for locomotor mechanics



Lateral sequence lateral-couplet:	1, 2 – 3, 4
Lateral sequence single-foot:	1 – 2 – 3 – 4
Lateral sequence diagonal-couplet:	2, 3 – 4, 1
Trot:	1+4 – 3+2
Diagonal sequence diagonal-couplet:	1, 4 – 3, 2
Diagonal sequence single-foot:	1 – 4 – 3 – 2
Diagonal sequene lateral couplet:	4, 3 – 2, 1
Bound (or hop):	1+2+3+4
Gallop:	3+1 – 4+2

Figure 4.2. A scheme for naming the symmetrical gaits used by gnathostomes. Trotting and lateral sequence diagonal-couplet gaits were of primary interest; however, other symmetrical gaits are included here for completeness. The bound (or hop) and gallop are asymmetrical gaits, and are listed to illustrate how their patterns of footfall compare with other gaits. The cadence of footfalls is distinguished by a "+" (for feet that strike the ground nearly simultaneously), a comma (for couplet patterns), and/or a dash (for uncoupled delays, pauses, or evenly spaced patterns in footfall). Modified after Hildebrand (1980).

in the earliest terrestrial vertebrates (Reilly et al. 2006). However, to polarize the data, it was necessary to look several outgroups outside crown-group sarcopterygians, and to work broadly within crown-group chordates. Firsthand dissection, computed tomography (CT), nuclear magnetic resonance imaging (nMRI), and comparison to published works informed the reconstructions of axial sections. Chondrichthyan and actinopterygian dissections were undertaken at the University of California, Berkeley, and coelacanth dissections at the Muséum National d'Histoire Naturelle, Paris, and at the California Academy of Sciences. Myxinids (hagfish), petromyzontids (lampreys), chondrichthyans, and actinopterygians were purchased from the Connecticut Valley Biological Supply Company (Southampton, MA) and the Chinatown Fish Market in San Francisco, California. Chondrichthyan, actinopterygian, coelacanth, lungfish, and salamander specimens were CT- and nMRI-scanned at the University of California, San Francisco, Medical Center (China Basin) and at the Large Animal Clinic at the University of California, Davis, School of Veterinary Medicine. Depending upon specimen size, density, and scanning method, slice thickness varied from 625 µm to 2 mm. Data were reconstructed using the imaging program OsiriX v3.7.1 64-bit (Rosset et al. 2004), and all images, whether dissection photographs or rendered scans, were traced in Adobe Illustrator CS3 using an Intuos3 Wacom tablet. Illustrations were visually mapped onto a cladogram compiled from accepted interrelationships among crown-group chordates (excluding urochordates) (Block et al. 1993, Bourlat et al. 2006, Collin et al. 2009, Delsuc et al. 2006, Inoue et al. 2001, Janvier 1996, 2008, Winchell 2004). For the most part, early-diverging chondrichthyans and actinopterygians were included to avoid the confusion of derived and autapomorphic conditions, especially among fast-swimming, pelagic members of each clade that might obscure informative gnathostome symplesiomorphies (Donley et al. 2004). See supplementary information for the list of included taxa and specimens.

Fossils.—Numerous fossil taxa were examined to gain insight into the origin and early evolution of terrestrial locomotion. The focus was primarily upon stem-tetrapods, although it also included stem-dipnoans, stem-amphibians, and stem-amniotes. Parsimony and Bayesian analyses (Huelsenbeck 2001, Ronquist and Huelsenbeck 2003, Swofford 2002) were used to structure the characters related to the origin of life on land, and to 'fill-in' a tetrapod-stem bracketed by both myological and gait data. Because of the rich fossil record, the aim of including paleontological data was to document a picture otherwise lost by a sole focus on the Recent.

Tetrapodomorpha here defines total-group tetrapods, and I restrict the use of the term tetrapod to the crown-group. I use the monophyletic definition of Elpistostegalia (Daeschler et al. 2006, Downs et al. 2008), but apply it as a stem-based name to any tetrapodomorph more crownward than tristichopterids. In addition, following from the phylogenetic result presented below, I use Canowindridae as a stem-based name to refer to the clade constituting *Marsdenichthys*, *Canowindra*, *Koharalepis*, and *Beelarongia*, I use the stem-based Megalichthyiformes (Coates and Friedman 2010) to refer to the formerly paraphyletic 'osteolepidids' (here recovered as monophyletic, see character optimizations in the supplementary information), and I apply the stem-based Tristichopteridae to define any taxon more closely related to *Tristichopterus* than to *Elpistostege*. Specimen observations derive from the primary literature and firsthand observation of fossil material. See supplementary information for the taxon-by-character matrix and the list of examined taxa and specimens.

Results

Gaits.—Three cladograms were constructed to test hypotheses about the evolution of gnathostome gaits. Their topologies vary only in the placement of included amniotes, to fairly credit competing (although not entirely mutually exclusive) molecular and morphological datasets. Their main differences lie in the phylogenetic position of chelonians and in the interrelationships among squamates. However, and irrespective of topology, the following patterns emerge with parsimony and likelihood-based reconstructions: (1) the trot has evolved in parallel three times in gnathostome evolution; (2) the trot diagnoses crown-group sarcopterygians; (3) the trot was lost in modern anurans; (4) the lateral sequence diagonal-couplet gait diagnoses crown-group tetrapods; (5) the lateral sequence diagonal-couplet gait evolved independently in the angler fish, *Antennarius commerson*, and appears to have been lost in extant pseudosuchians; and (6) the gallop evolved independently in *Antennarius commerson* and *Crocodylus johnstoni*. See Figure 4.3 for a phylogenetic overview of these patterns.

Parsimony-based methods nearly unambiguously reconstruct these patterns. The only ambiguity lies in the scored 'unknown' diagonal-couplet potential of the Australian lungfish *Neoceratodus* and of the pseudosuchian *Gavialis gangeticus*. In other words, even though lungfishes trot, because there are few detailed observations of *Neoceratodus* (Edwards 1989, Rosen et al. 1981), I found it safest to score the diagonal-couplet gait here as unknown. In this respect, even though likelihood ambiguously reconstructs dipnoans as lateral sequence diagonal-couplet walkers, parsimony reconstructs this state as entirely absent. However, both parsimony and likelihood (95%) nearly unambiguously estimate that the diagonal-couplet gait evolved by the tetrapod-crown node. Moreover, following the methodology of not scoring videographed taxa as unable to use unobserved trotting or diagonal-couplet gaits, because the videographed *Gavialis* falls out as the earliest diverging pseudosuchian, its diagonal-couplet prospect is ambiguous as well. However, likelihood measures still estimate a 97-99% probability that the diagonal-couplet gait was lost in remaining pseudosuchian taxa.

Galloping, bounding (or hopping), lateral sequence lateral-couplet, and diagonal sequence singlefoot gaits were of lesser interest, but because they were observed, it is necessary to comment on their distribution. As mentioned, galloping is present only in the aquatic *A. commerson* and *C. johnstoni*. Interestingly enough, even though we associate galloping with high speeds, *A commerson* is reported to gallop at slow speeds (Edwards 1989). The bound (or hop) is present primarily in anurans, although certain taxa such as *Oreophrynella* have lost the ability to hop repeatedly (e.g., *O. macconnelli*) or entirely (e.g., *O. nigra*) (Attenborough et al. 2008). However, as diagnosed by a footfall pattern in which all pedes strike the ground together, even though gavials are not airborne, instead sliding on their bellies, *G. gangeticus* may use a bounding gait to propel itself downhill to a nearby body of water (Attenborough et al. 2008). Other pseudosuchians, such as *Alligator mississippiensis* and *Crocodylus johnstoni*, also use this method of locomotion (Reilly and Elias 1998, Renous et al. 2002). Thus, not only has the gallop evolved independently in certain crocodylids, but as in anurans and some mammals, the (sliding) bound has evolved in pseudosuchians as well. Lateral sequence lateral-couplet and diagonal sequence singlefoot gaits are used less frequently in non-mammals, but were observed in a few squamate groups. In particular, teiids and lacertids use this method of locomotion, albeit infrequently, especially when compared to their frequency of trotting and diagonal-couplet alternatives (Avery and Bond 1989, McElroy et al. 2008, White and Anderson 1994).

Parsimony unambiguously reconstructs trotting and diagonal-couplet gaits as a symplesiomorphic feature of all urodeles, chelonians, and squamates. However, following the scoring methodology noted above, question marks abound among these clades and obscure whether they do or do not use both gaits. A slight difference in timing can transform the sequence of footfalls from one gait into the other, and so it is risky to hypothesize explicitly that the noted taxa are incapable of using either gait if unobserved. If the locomotor patterns are instead perceived as an issue of relative frequency, and are used to treat unobserved gaits not as real unknowns but as *de facto* absences, then re-scoring the above noted groups yields likelihood reconstructions that estimate at least ten parallel origins of the diagonal-couplet gait. As originally scored, the basic likelihood patterns among tetrapods include: (1) the trot is ambiguous at the base of sampled urodeles,

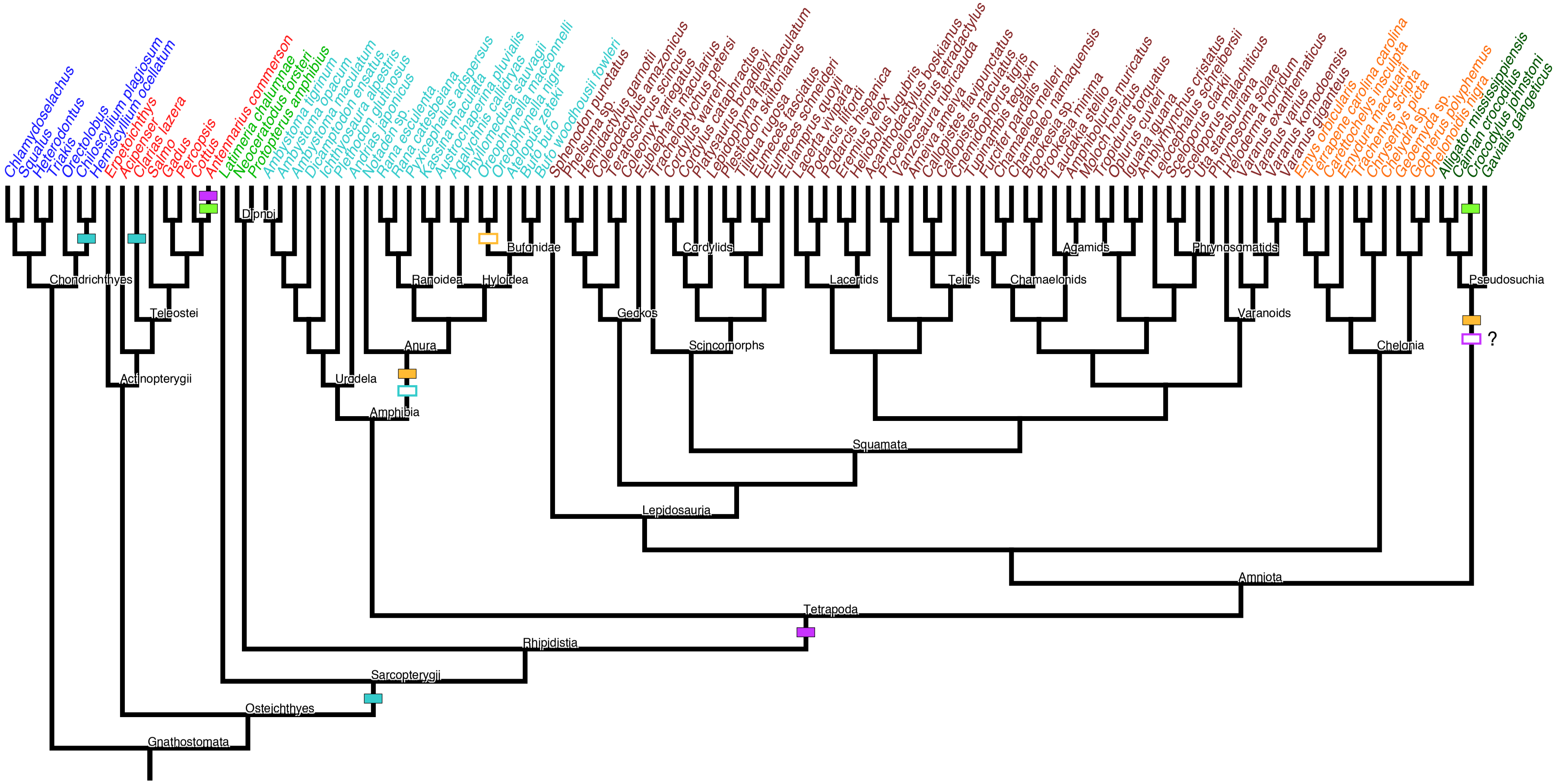


Figure 4.3. The evolution of gnathostome gaits. Supertree topology structured primarily from molecular sequence data. See references in text. A solid teal bar = trotting gait present; open teal bar = trotting gait lost. Solid purple bar = lateral sequence diagonal-couplet gait present; open purple bar = lateral sequence diagonal-couplet gait lost. Solid orange bar = bounding or hopping gait present. Green bar = galloping gait present. For the distribution of other gaits, including the lateral sequence lateral-couplet, the lateral sequence singlefoot, and the diagonal sequence diagonal-couplet, see description in text and in the character matrix of Part B in the supplementary information. See Figures S4.1 and S4.2 for alternative molecular and morphological topologies, though neither change the pattern of gait evolution depicted here.

chelonians, and geckos, even though it is plesiomorphic for lissamphibians and amniotes (99% and 97%, respectively); (2) the trot unambiguously diagnoses lepidosaurs broadly, and squamates specifically (99%, each); (3) the diagonal-couplet gait ancestrally characterizes chelonians and squamates (99%, each) but is ambiguous at the base of Lepidosauria; and (4) within squamates, teiids, some lacertids (*Lacerta vivivapa*), some cordylids (*Cordylus cataphractus*), some scincomorphs (*Tiliqua rugosa*), and some varanids (*Varanus varius*) use the diagonal-couplet gait frequently enough to permit observation; in fact, patterns in many taxa are often at the boundary between diagonal-couplet and trotting gaits (White and Anderson 1994). This broad distribution (especially among squamates) of the diagonal-couplet gait strongly suggests that the original methodology (i.e., scoring unobserved gaits as tentative unknowns) more likely explains the data. It follows that diagonal-couplet or trotting gaits are not truly absent when unobserved, but either (a) present at a lesser relative frequency; and/or (b) both used in a kind of 'hybrid' gait, with footfall often at the boundary between the two. In this sense, most lepidosaurs except teiids and chamaeleonids (which use a combination of trotting and diagonal-couplet gaits depending upon tree- or ground-based locomotion) appear to be *de facto* trotters and have generally phased out the distinct diagonal-couplet gait that ancestrally diagnosed tetrapods.

Myology.—The myological work focused on patterns in the axial musculature among crown-group chordates, in particular among sarcopterygians. The orientation of myomeres and myosepta, not of collagen fibers, was of primary interest. Several authors (Brainerd and Simons 2000, Carrier 1993, Gemballa and Ebmeyer 2003, Gemballa et al. 2006) have already undertaken extensive analyses of collagen fiber orientation among crown-vertebrates, and collagen fiber and (especially) hypaxial function in salamanders. The aim here is to build upon their results.

Chordate myomeres maintain a variety of elaborate three-dimensional shapes that include Vs, Ws, and regions with hollow cones that reflect their overlap with neighboring myomeres and extension alongside medial axial elements. Although the details of these shapes may represent ecomorphotypes, the orientation of myomeres relative to the body axis appears to carry a phylogenetic signal. Figure 4.4 depicts the evolution of axial musculature among crown-group chordates. Epaxial and hypaxial muscles (shaded blue and red, respectively), are divided by horizontal septa, collagen-dense divisions likely apomorphic for gnathostomes. Considering lampreys, which possess W-shaped concentric myomeres, this might predict that gnathostomes radically re-orient their axial muscles in association with the first appearance of the epaxial/hypaxial division. However, the condition in cephalochordates and myxinids suggests that this is not the case. Even though horizontal septa divide epaxial and hypaxial bundles in crown-gnathostomes (Kusakabe and Kuratani 2005), positionally (and etymologically), lancelets and hagfishes still possess myaxial regions dorsal and ventral to their notochords with laterally oriented myosepta. This suggests two hypotheses: (1) that concentrically arranged myosepta in lampreys are autapomorphic, not plesiomorphic; and (2) that elaborate, cone-shaped epaxial myomeres evolved in the gnathostome-stem. This is not surprising, considering the many autapomorphies already recognized in petromyzontids, as well as the numerous traits (e.g., three semicircular canals, paired appendages, jaws, &c.) that enhance a (stem-)gnathostome's predatory mode (Janvier 1996). However, despite cone-shaped (or 'spiraled') epaxial myosepta, it appears that gnathostome hypaxial trunk bundles retain their plesiomorphic lateral (or horizontal) orientation. This pattern persists in early-diverging chondrichthyans and actinopterygians, although it changes radically with later evolving pelagic, predatory ecomorphs such as lamnid sharks and scombrid teleosts that incorporate various degrees of complexity into their hypaxial trunk (Donley et al. 2004, Gemballa et al. 2006). Even *Clarias*, the walking catfish, despite its trotting gait, still maintains the simple ancestral hypaxial pattern. *Trichurus*, a scombroid, shows some degree

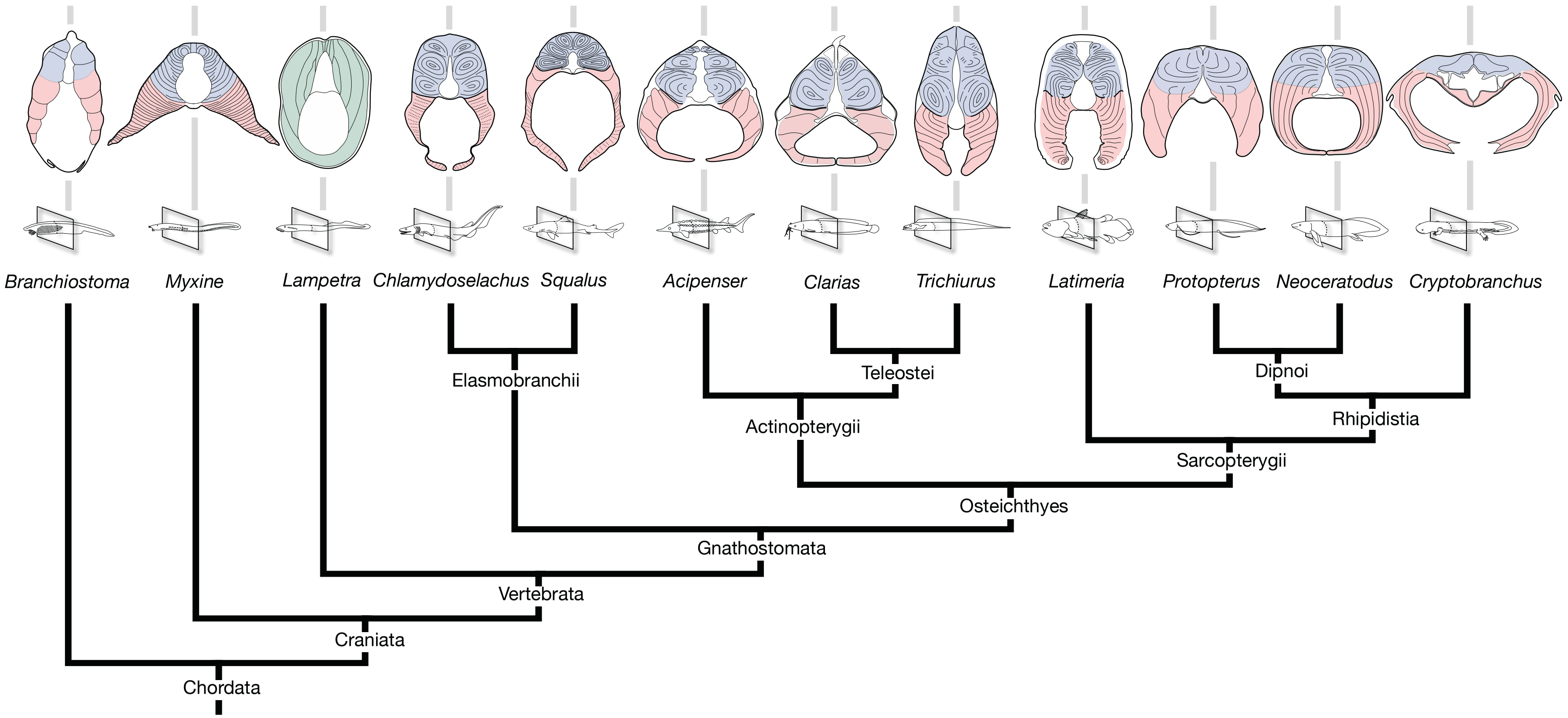


Figure 4.4. The evolution of axial musculature in the trunk region of crown-group chordates. Epaxial and hypaxial divisions are shaded blue and red, respectively, and are divided by horizontal septa represented by thick black lines. This collagen dense division is likely apomorphic for gnathostomes, although (based on the etymology of terms) the blue and red color scheme is also maintained for cephalochordates and myxinids which possess horizontally oriented myosepta dorsal and ventral to the notochord. *Lampetra* is shaded green because of its likely autapomorphic condition. Epaxial spiraling may be apomorphic for craniates, although it is clearly more elaborate in crown-gnathostomes. Horizontal septa are incomplete in *Latimeria* and lost in rhipidistians. Horizontal hypaxial myosepta are symplesiomorphic for sarcopterygians specifically and gnathostomes broadly. Rhipididistians reorient their hypaxial muscles circumferentially, and tetrapods specialize their lateral–medial divisions for torsion resistance and expiration, in addition to lateral flexion present in rhipidistians primitively. See text for additional details.

of hypaxial spiraling, a condition more heavily elaborated upon by scombrids(Donley et al. 2004, Shadwick 2005).

Similar to depicted sharks and ray-fins, sarcopterygians such as *Latimeria* have a strong degree of epaxial spiraling, with three primary (rostrocaudal) re-orientations of epaxial bundles. Each cone-shaped spiral reflects such a change: the larger two ventral spirals are likely apomorphic for gnathostomes, and the dorsal one is possibly present in hagfish. However, *Latimeria* also exhibits a partial loss of horizontal septa, seen by the communication of epaxial and hypaxial myosepta across the missing midpoint of this region on either side. Horizontal septa are still present laterally, below *Latimeria*'s extensive subcutaneous fat deposits, and medially, on either side of its notochord. Epaxial and hypaxial myosepta connect to the remaining horizontal septa at these points, and epaxial myosepta passing through, continue in to the hypaxial division and connect to the extensive tissue network lining the body cavity. Dipnoans take this partial reduction one step further and lose their horizontal septa altogether. In contrast with *Latimeria*, which maintains some degree of ventral myoseptal wrapping, lungfish trunk myosepta maintain a near-completely circumferential arrangement. Although superficially similar to lampreys, the details are more akin to salamanders. Both *Protopterus* and *Neoceratodus* retain a degree of epaxial spiraling, although it is much less extensive than the primitive gnathostome condition. Moreover, and similar to extant urodeles, which vary in their number of lateral hypaxial muscles (from one to four layers, depending upon ecology and function (Brainerd and Simons 2000)), dipnoans exhibit a variable number of ventrally wrapping hypaxials as well. Several convergent (or parallel) traits are known among lungfishes and tetrapods (e.g., elaborate air breathing, choanae, loss of the intracranial joint, &c. (Janvier 1996)), and so this raises the question whether their trunk muscles reflect the influence of ecology or phylogeny. Considering *Latimeria*, with its partial horizontal septa and degree of ventral wrapping, it appears that the lungfish-tetrapod morphology may reflect common ancestry, but see discussion for additional details.

Fossils.—A phylogenetic analysis of 203 morphological characters using PAUP (Swofford 2002) recovered a single most parsimonious tree. A Bayesian analysis (Huelsenbeck 2001, Ronquist and Huelsenbeck 2003) of the same data provided an additional metric. There are no major polytomies, and the major clades, Rhizodontidae, Canowindridae, Megalichthyiformes, and Tristichopteridae form successive sister taxa to more crownward groups. The stem-based Elpistostegalia includes all taxa more closely related to crown-tetrapods than to tristichopterids. See Figure 4.5 for the phylogenetic result. Mapping relevant crown-tetrapod plesiomorphies onto this tree yields the following patterns: (1) pectoral appendages in total-group tetrapods are primitively larger than corresponding pelvics; (2) the humerus (ball) and scapulocoracoid (socket = glenoid fossa) diagnose tetrapodomorphs primitively (in contrast with the reverse polarity in dipnomorphs [total-group lungfishes]); (3) for well-known canowindrids, megalichthyiforms, and tristichoptrids, pectoral and pelvic limbs are about the same size; (4) associated with a flattening of the proximal humerus, the glenoid fossa becomes elongate in the first elpistostegalians; (5) *Panderichthys* and crownward taxa lose their dorsal and anal fins; (6) *Tiktaalik* has a ventrally directed accessory glenoid that, in combination with its flexible elbow, 'wrist', and 'hand' regions, appears to provide support when its limbs are pulled under its body; (7) as a tetrapodomorph, *Tiktaalik* has the first physical neck, that is, a disconnect between its shoulders and head associated with the partial loss of the operculogular series; (8) *Acanthostega* has the first known digits but retains gills and undifferentiated atlantal and axial arches; (9) *Acanthostega* and crownward taxa have at least a rib pair associated with a sacrum; (10) *Ichthyostega* and crownward taxa have buttressed infraglenoids that support the caput humeri, possibly associated with weight-bearing limbs; and (11) colosteids such as *Greererpeton* have the first differentiated atlas. See supplementary materials for the

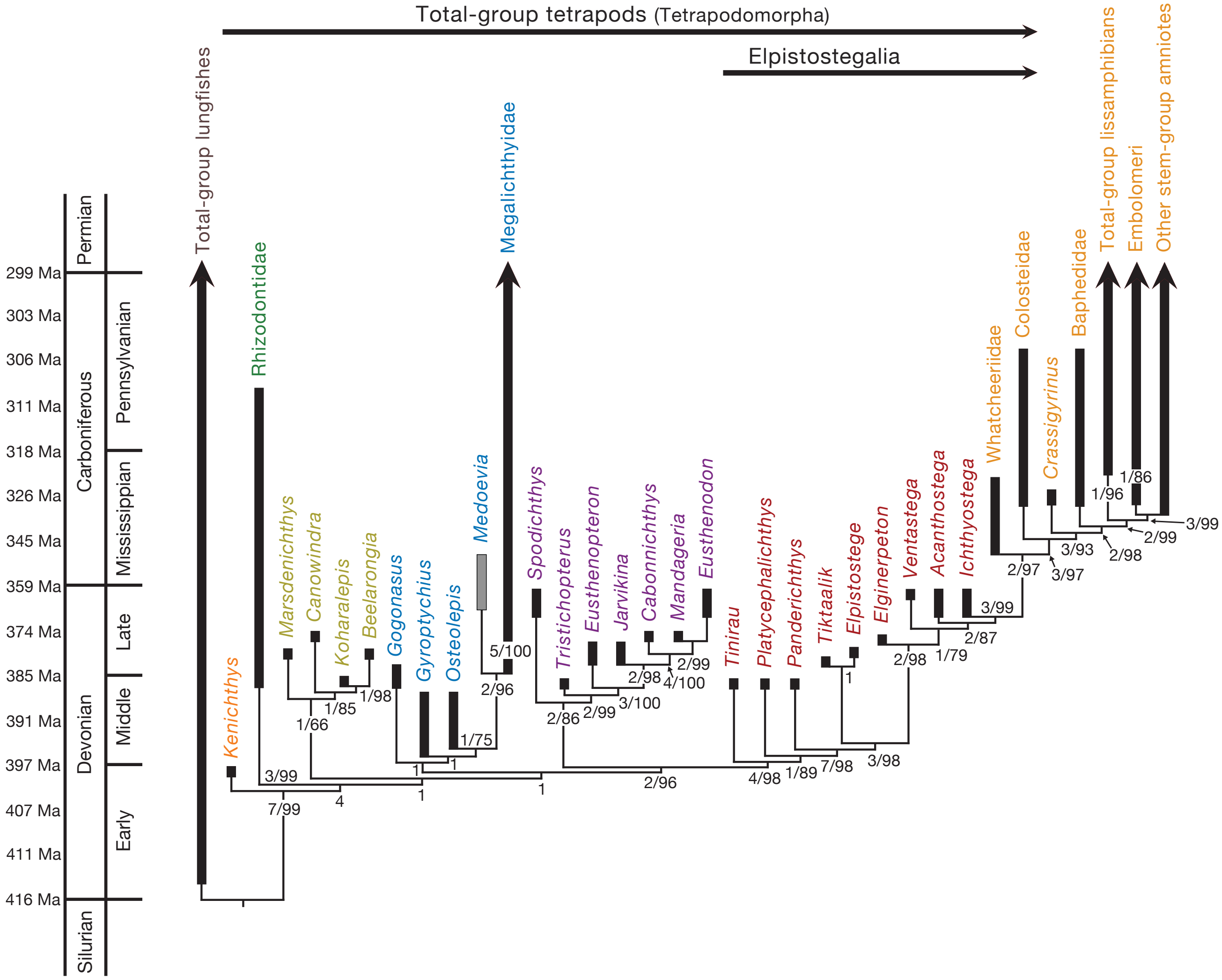


Figure 4.5. Interrelationships among Devonian and select Carboniferous tetrapodomorphs. Analysis includes 46 taxa and 203 characters. Tree length=459, consistency index=0.5468, retention index=0.8423; consistency index excluding the four autapomorphic (uninformative) characters=0.5428, retention index=0.8423. Numbers corresponding to respective nodes represent: Bremer decay value / Bayesian posterior probability. Ghost ranges are calibrated after the early Middle Devonian (Eifelian) Zachełmie footprints (Niedźwiedzki et al. 2010) and recent estimates for the stratophylogenetic position of this trackmaker (Friedman and Brazeau 2011). Tetrapodomorphs include all taxa that are not total-group lungfishes. Rhizodonts are in green, canowindrids are in yellow, megalichthyiforms are in blue, tristichopterids are in purple, Devonian elpistostegalians are in red, and Carboniferous elpistostegalians are in orange. The character list and data matrix are available as supplementary information.

taxon-by-character matrix and character optimizations.

Discussion

There is a long of history of debate about the relative role and determination of structure and function in morphology (Appel 1987, Cuvier 1805, Geoffroy 1818, Goethe 1790, Gould 2002, Padian 1995, Russell 1916, Thompson 1942, Wake 1991, Wake and Larson 1987). The aim here is to incorporate the origin of tetrapod locomotion into a heuristic device that reinforces the interrelationship of structuralist and functionalist thinking.

Following the contributions of a few key authors (Gould 2002, Gould and Vrba 1982, Lauder 1981, Raup 1972, Seilacher 1970, Wake 1991), Figure 4.6 traces the conceptual flow of evolutionary traits across historical, functional, and constructional space-time. No individual component here is fundamentally new, but collectively, it synthesizes a key set of tools for thinking about evolutionary problems, and illustrates the continuity and synergy of all three historically important approaches to understanding natural history. Biological information will unavoidably pass through historical (phylogenetic), functional (ecological), and constructional (physical and developmental) filters over evolutionary time, and despite popular views (Dobzhansky 1941, Mayr 1942, 1963, Simpson 1944, 1953, Wallace 1909, Weismann 1893, 1909) that might otherwise relegate most of biology to a chink in a functionalist corner, a pluralistic view is here considered to be the more fruitful prospect for considering evolutionary questions.

Traits may be described to come in two 'flavors', those that are not produced by natural selection for their current roles, and those that are fit for the environment and are produced by natural selection. The former are termed nonaptations and the latter called aptations (Gould and Vrba 1982) (Figure 4.6). To consider any trait in this respect, one must first recognize that both lineages and the states that diagnose them each have their own histories. Thus, distinguishing aptations from nonaptations will involve tracing the origins and functions of both character states and state combinations, within a phylogenetic context.

The Origin and Early Evolution of Terrestrial Locomotion

Insights from Extant Groups.—Chondrichthyans such as epaulette sharks, teleosts such as *Clarias*, and lungfish such as *Neoceratodus* and *Protopterus* all use trotting gaits when engaged in substrate-based locomotion. By contrast, anglerfish such as *Antennarius commerson* use (lateral sequence) diagonal-couplet and galloping gaits (Edwards 1989), the epaulette shark, *Hemiscyllium ocellatum*, uses a diagonal sequence diagonal-couplet gait in addition to its walking trot (Pridmore 1995), and 'bipedal' pelvic strolls have also been observed in the African lungfish *Protopterus annectens* (King et al. 2011). In the water column, sarcopterygians such as *Latimeria* may trot while maintaining their position or during forward locomotion (Fricke 1987). Similarly, urodeles such as *Taricha torosa* (Ashley-Ross and Bechtel 2004), *Ichthyosauria alpestris* (Attenborough et al. 2008), and *Triturus taeniatus* (Faber 1956), and chelonians such as *Chrysemys picta* (Attenborough et al. 2008) also use trotting gaits during forward swimming.

In terms of primacy, history and construction more likely explain substrate-based gaits, although suspended gaits are probably an immediate function of ecology. Crown-gnathostomes inherited their laterally bending musculoskeletal system and paired appendages from stem-group gnathostomes (Janvier et al. 2004). Appendicular mobility is primitively limited, however, chondrichthyans have lost the dermatocranium that ancestrally bound the shoulder with head (Donoghue and Sansom 2002). Specifically, epaulette sharks are members of crown-group Chondrichthyes, for which lateral bending and the head-shoulder disconnect (i.e., a

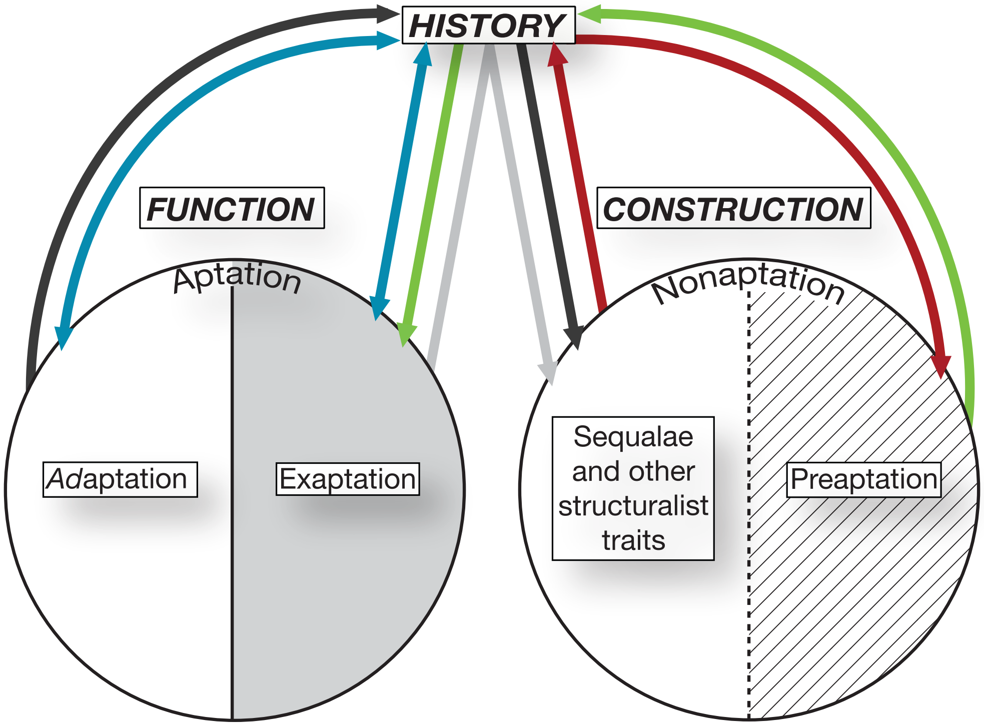


Figure 4.6. The relationships among construction, function, and the attainment of biological traits over evolutionary time. Aptations consist of traits that are fit for the environment and are produced by natural selection; they include primary adaptations and coopted traits that become exaptations. Nonaptations include characters that are not produced by natural selection for their current roles, and consist of any one of a number of structuralist traits. Preaptations are potential but unrealized aptations, in particular, exaptations; they become (ex)aptations when acted upon by the complex interplay of the environment, developmental channeling, and natural selection. "History" encapsulates these interactions within a phylogenetic context. The colored arrows trace the conceptual flow of these relationships. Aptations such as ad- and ex-apations, may become part of the nonaptive structuralist pool when their functions become vestigial. For clarity, note that the only term with the prefix ad- includes adaptation. Modified from concepts in Gould (2002), Gould and Vrba (1982), Lauder (1981), Raup (1972), Seilacher (1970), and Wake (1991).

physical neck) are symplesiomorphies. In addition, *Hemiscyllium ocellatum*, as a hemiscyliid, shares limb and girdle characters with other taxa (e.g., elongate basal cartilages, distally projecting coracoid condyles, an expanded fossa for the depressor pectoralis, a levator pectoralis inferior—traits that it might use in a walking trot) that are not all specific to substrate-based locomotion (Goto et al. 1999). While trotting, *H. oscellatum* uses a combination of lateral flexion, girdle rotation, and limb movement to progress across reef substrates. Body undulation is restricted to a standing wave (unless moving at faster speeds, between trotting and swimming), pectoral girdles rotate more than pelvic girdles, and limb motion is primarily in the plane of yaw (side-to-side). In this respect, *H. oscellatum* uses directly or has coopted many ancestral, structuralist traits for the bulk of its substrate-based repertoire. Similarly, *Clarias*, the walking catfish, uses its complement of plesiomorphies for locomotion as well. Because it retains the neckless osteichthyan condition, with its cleithrum and other dermal elements situated immediately behind its head, its shoulders remain immobile (in contrast to *H. oscellatum*), and substrate-based trotting is assisted by standing waves. In addition, as a siluriform, *Clarias* retains a pair of pre-pectoral spines that it can lock in the outward position, that it uses like levers against the substrate during locomotion. It is primarily through these two actions—lateral undulation and pre-pectoral leverage, both products of phylogeny and construction—that *Clarias* is able to trot. However, in this context, and similar to *H. oscellatum*, these types of traits are now exaptations for gait-based mobility. By contrast, in suspension, because water is a dense fluid that constrains biomechanical systems, synchronous contralateral limb movements (i.e., a trotting gait) will more effectively balance and propel an animal forward than the asymmetries imposed by the staggered limb movements of the diagonal-couplet gait. It does not matter whether an axial system is bound in a bony box (e.g., *Chrysemys*), free for enhanced lateral flexion (e.g., *Latimeria*), or decoupled from a rotating shoulder (e.g., *Taricha*), the biomechanical rules are much the same. Of course, all examples in this case are sarcopterygians, which have four rotating appendages that predispose their utility, but within that phylogenetic range and in this ecological context, it appears that function dictates the most productive use of coordinated limbs. Phylogeny, construction, and ecology collectively work to explain the distribution of observed patterns, and taxa work within their biological means to contend with environmental challenges.

Similar to *Hemiscyllium ocellatum*, an integral part of locomotion in urodeles includes the physical neck, that is, the space between the shoulders and head. During the diagonal-couplet walk, 10% of propulsive effort is supplied by girdle rotation (the remaining 90% being provided by limb retraction, rotation, and elbow extension), although this nearly doubles to 18% while trotting (Edwards 1977). That is, one of the key functions of the physical neck is not so that the head can move independently of the body, but so that the shoulders can move free of the head. Thus, to turn a hypothesis on its head, it follows that the first physical neck in tetrapodomorphs was likely more critically tied to the origin of terrestrial locomotion than to any requirement for head/neck mobility. A counterexample is that sharks, *Latimeria* (partially), and extant lungfishes all maintain discrete, disconnecting regions between their shoulders and heads yet do not engage in elaborate forms of terrestrial locomotion. However, *Clarias*, the walking catfish, does not maintain such a disconnect, and is much more amphibious with its trotting habits. Similar to substrate-based and suspended trotting in these respective clades, even though all taxa (except *Clarias*) have physical necks, trotting in piscine sarcopts appears to derive primarily from limbs that pivot at the base of relatively immobile girdles.

Comparing limb musculature among chondrichthyans, ray-fins, and lobe-fins supports this view (Figure 4.7). Primitively, gnathostomes have only abductor and adductor muscles that lie above and below their paired appendages, and that move them up and down, respectively; though as mentioned, hemiscyliid sharks have modified this pattern slightly. However, *Latimeria* (Millot and Anthony 1958) and *Neoceratodus* (Boisvert 2009) not only maintain the ancestral extensors and flexors, but below them, have angled pronators

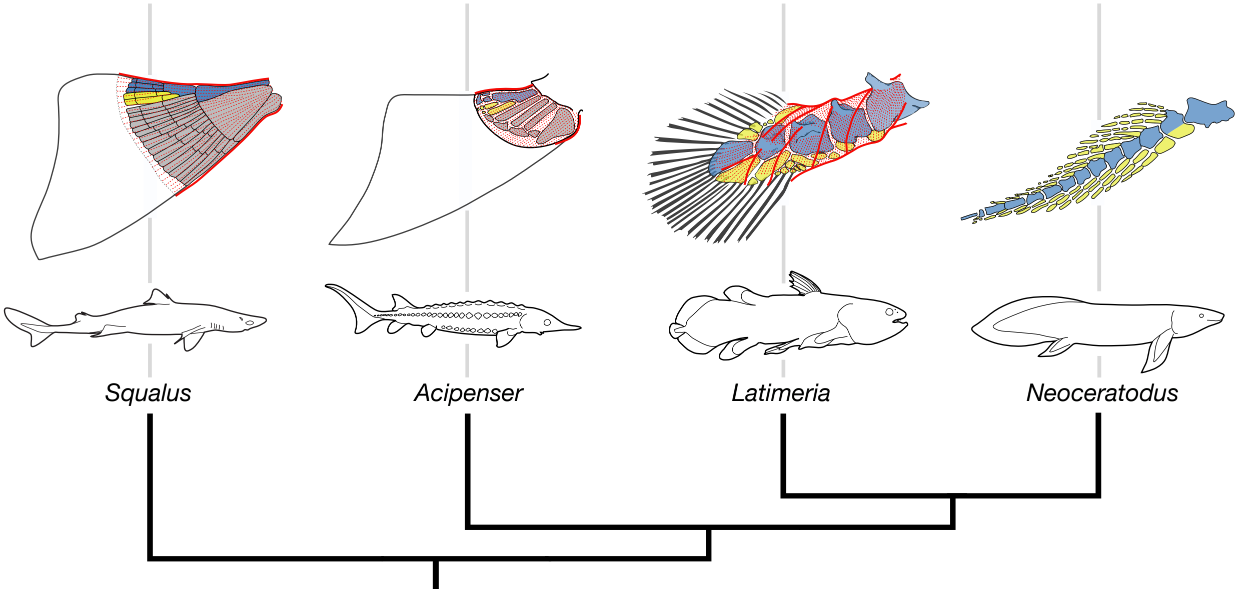


Figure 4.7. Pectoral fin musculature of select piscine gnathostomes. Abductor and adductor muscles positioned dorsal and ventral to the paired appendages characterizes crown-gnathostomes primitively. This condition is present in all above taxa. However, sarcopterygians have a series of pronators and supinators that underlie these ancestral extensors and flexors. Abductors have been removed in the *Latimeria* appendage, which shows only the underlying supinators in dorsal view. Dr. Catherine Boisvert at Monash University is currently reconstructing the appendicular system of *Neoceratodus*, thus these data have been excluded so as not to preempt her work. Muscle boundaries are illustrated with solid red lines, whereas the thinner dashed lines represent myofibrils. Blue elements highlight the metapterygial component of the gnathostome limb; yellow illustrates post and preaxial radials; gray represents pro- and mesopterygial components that have been lost in sarcopterygians. Illustrations are based on firsthand dissection and comparison to the published literature. See text for additional details.

and supinators (in immediate contact with the humerus, radius, and ulna), that, based on their orientation, permit forward and backward rotation as well. In this sense, it is understandable how a synchronized 'abduction/adduction' and 'pronation/supination' of all muscles can produce the rotating trotting pattern seen in taxa such as *Latimeria* (Fricke 1987). The phylogenetic positions of coelacanths and lungfishes relative to tetrapods suggests that this appendicular condition was plesiomorphic for tetrapodomorphs, and since all stem-tetrapods except *Tiktaalik* on crownward maintained the primitive neckless condition seen in *Clarias*, making the transition to a neck-bearing state did not involve inheriting any of the (convergent) conditions seen in modern groups. Instead, it meant losing the operculogular complement that ancestrally characterized osteichthyans. Thus, not only did early stem-tetrapods likely inherit the proximal appendicular musculature common to extant coelacanths and dipnoans, but they also retained the immobile shoulder present in teleosts such as *Clarias*.

Laterally flexing axial muscles are also symplesiomorphic for stem-tetrapods. The details of the muscles, their shapes, patterns, and divisions have changed greatly throughout gnathostome evolution, but lateral bending is symplesiomorphic for most groups. As inferred from the distribution of lateral hypaxial muscles among extant taxa, it appears that their function in lateral undulation is not an adaptation for terrestrial locomotion. The standing wave is likely a terrestrial apomorphy—though parallel in above-mentioned chondrichthyans and actinopterygians, modified in certain (*de facto*) limbless terrestrial groups (Gans 1985, Gillis 1997), and in part possibly just a biomechanical consequence of gait- and substrate-based locomotion whether in water or on land—but lateral flexion is a symplesiomorphy. Instead, this motion, an exaptation, is derived from aptive, nonaptive, and historical pools. Although sinusoidal swimming was likely adaptive for the first stem-chordates, for the first terrestrial vertebrates, it appears that history and construction channeled this locomotor strategy along phyletic lines. Extant dipnoans and urodeles share similar patterns in their lateral hypaxial musculature: these structures are used for expiration and stabilizing torsion in salamanders but not in lungfishes. Considering this, these two tetrapod specializations are likely exaptations coopted from the aptive swimming function of these ancient rhipidistean muscles—but also from nonaptive sources, given their history as gnathostome (possibly even chordate) axial bundles of the ancient somitic, mesodermal, Pax3 program (Kusakabe and Kuratani 2005, 2007).

In addition, considering their phylogenetic distribution, stem-tetrapods likely possessed the wrapped and layered hypaxial bundles common to modern dipnoans and urodeles. Given their structure and orientation, these 'obliques' perform different functions in lungfishes and salamanders (Brainerd and Simons 2000, Gemballa and Ebmeyer 2003, O'Reilly et al. 2000); the traveling wave used in swimming is common to both groups, but expiration and torsion stabilization during terrestrial locomotion is a tetrapod apomorphy (O'Reilly et al. 2000). Nonetheless, despite specializations in function, this general, layered hypaxial structure appears to diagnose rhipidistians primitively. Certain aspects of this arrangement may have been enhanced in parallel. Modern salmonids also exhibit a degree of anterior hypaxial wrapping, although this pattern disappears and returns to the ancestral gnathostome condition posterior to the pectoral fins, albeit with a bit of additional hypaxial spiraling similar to lamnids and scombrids (Shadwick 2005, personal observations). By contrast, the pattern in lungfishes persists throughout the trunk and only begins to spiral in the more typical posterior fish-like fashion caudal to the pelvic girdle (Figure 4.8). Thus, in combination with incomplete horizontal septa and partial hypaxial wrapping throughout the trunk of *Latimeria,* this rhipidistian pattern may be ancestral. If total-group lungfishes and total-group tetrapods diverged in the Upper Silurian (~415 Ma) (Zhu et al. 2006), then the tetrapod-like myaxial condition first evolved in water ~35 million years before amphibious grade stem-tetrapods even appeared. Not only does this imply that stem-tetrapods retained this hypaxial setup and used it for lateral bending, but it also means that they evolved specialized layers for

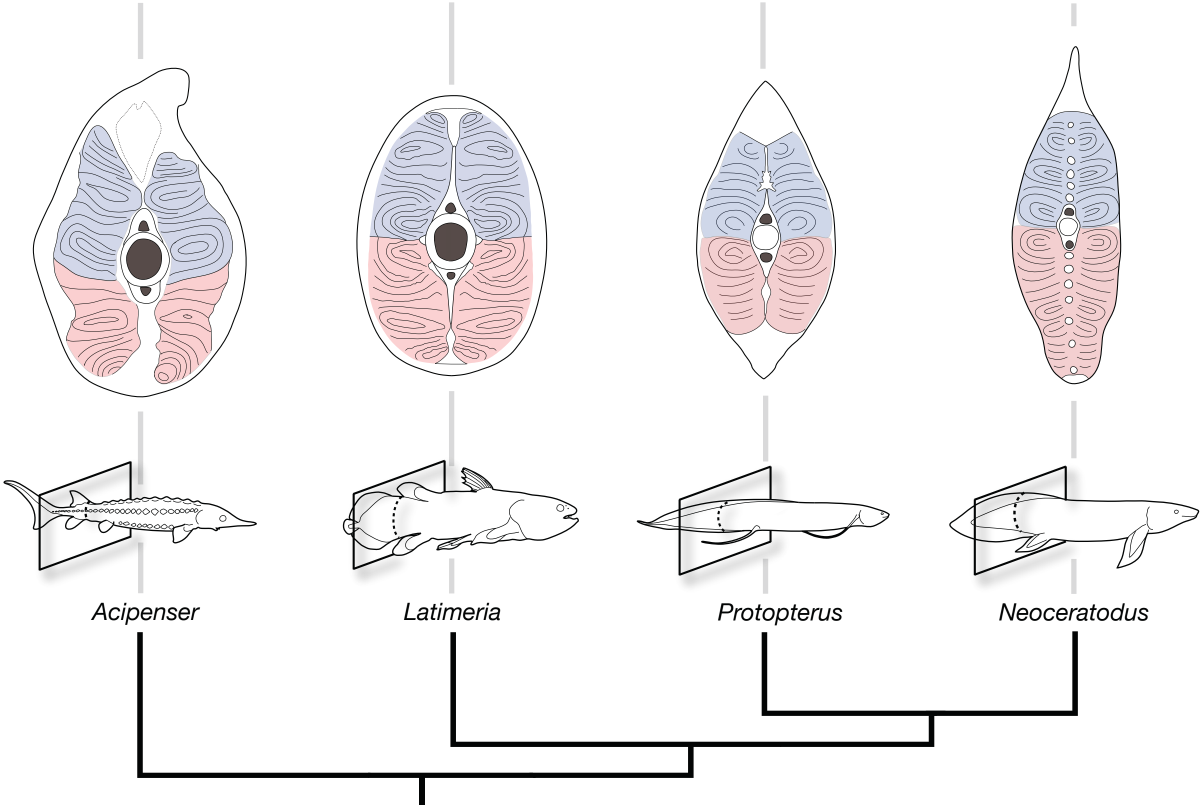


Figure 4.8. Axial musculature in the caudal region of select osteichthyans. In lungfishes, epaxial and hypaxial muscles posterior to the pelvic girdle spiral in the more typical osteichthyan fashion. This contrasts with the trunk region, whereby hypaxial muscles are more similar to tetrapods, suggesting that the tetrapod-like myaxial condition began anteriorly and migrated posteriorly over evolutionary time.

respiration and terrestrial locomotion on the road to land.

Insights from fossils.—Overall, the pectoral fins of the first stem-tetrapods were larger than the pelvics (Garvey 2005, Johanson and Ahlberg 2001); however, this may be exaggerated by convergent or parallel evolution in rhizodonts (Jeffery 2001). By contrast, many 'osteolepiform-grade' taxa (i.e., those 'between' rhizodonts and elpistostegalians, see Figure 4.5) have pectoral and pelvic limbs roughly equal in size, and this difference may suggest a deemphasis of pectoral-enhanced swimming. These taxa also maintain the primitive ostechthyan conditions of lacking necks and sacra. The first elpistostegalians flattened their proximal humeri, a state thought to be associated with further differentiation of proximal dorsal and ventral limb musculature (Shubin et al. 2004). Some humeral flattening seems more taphonomic than biological, but at least the proximal humerus, in association with the glenoid fossa, appears to be changing shape (Figure 4.9).

The Late Devonian *Tiktaalik*, for the first time in the evolution of total-group tetrapods, lost the extrascapulars, posttemporals, opercula, and subopercula to produce a space between its head and shoulders (Daeschler et al. 2006). If the original function of the neck was to move the head independently of the body, one might predict that its origin would be associated with the first atlas. However, this is not the case; the first recognizable atlas is found in the Carboniferous colosteid *Greererpeton* (Godfrey 1989) (figure 8, pg. 89). In fairness, the vertebral skeleton of *Tiktaalik* is not preserved (it is presumed to have been cartilaginous (Daeschler et al. 2006)), but even in *Acanthostega*, atlantal and axial arches remain undifferentiated (Coates 1996). Their primary difference is only one of size, and in this case, the atlas precursor is only a little smaller than more posterior elements. By contrast, if a primary function of the original neck were girdle rotation, based on knowledge of living animals, we would not expect it to be mobile or to incorporate vertebral arches. Not only does this appear to be the case, but in association with this physical space, *Tiktaalik* also exhibits a series of limb specializations that suggest that it was engaged in some degree of body propping and/or substrate-based mobility (Shubin et al. 2006). In a plausible hypothesis that incorporates inferred pectoralis muscles from the clavicle, their insertion onto the ventral ridge of the humerus, an accessory glenoid to accommodate the flexed humerus (see Figure 4.9), and transverse joints to brace the pectoral limb, Shubin et al. (2006) detail how an animal such as *Tiktaalik* could have supported itself. Even though *Tiktaalik* may possess some pectoral autapomorphies linked to its method of support, it exhibits a series of traits that suggest elpistostegalians were more actively engaged than their predecessors in substrate-based locomotion. However, this does not explain why the neck evolved in the first place, especially considering that the operculogular series is intimately tied to gill-based respiration. A loss of these elements suggests a decreased reliance on gill breathing. Splanchnocranial elements are certainly reduced in association with the partial loss of the operculogular series. However, *Tiktaalik* and *Acanthostega* retain well-ossified deeply grooved ceratobranchials that indicate the prevalence of branchial function (Coates and Clack 1991, Downs et al. 2008). Thus, even though respiratory shifts may have been linked to the origin of the elpistostegalian neck, it appears that not long afterward, certain taxa capitalized on this newfound space for girdle rotation and enhanced locomotion.

Quirky functional shifts (Gould 2002), the difference between current utility and historical origin, are intimately linked to many changes that involved disconnecting and attaching appendicular and axial skeletons. If taxa such as *Tiktaalik* were becoming less reliant on gill-based respiration, and if this functional association with the operculogular series is what drove its partial loss, then even though the origin of the physical neck may have been adaptively linked to energy efficiency and respiratory demands, adaptation alone does not explain the observed changes. *Tiktaalik*, as an elpistostegalian, is a broader member of the Osteichthyes (and total-group gnathostomes), which are diagnosed by an anterior dermatocranium.

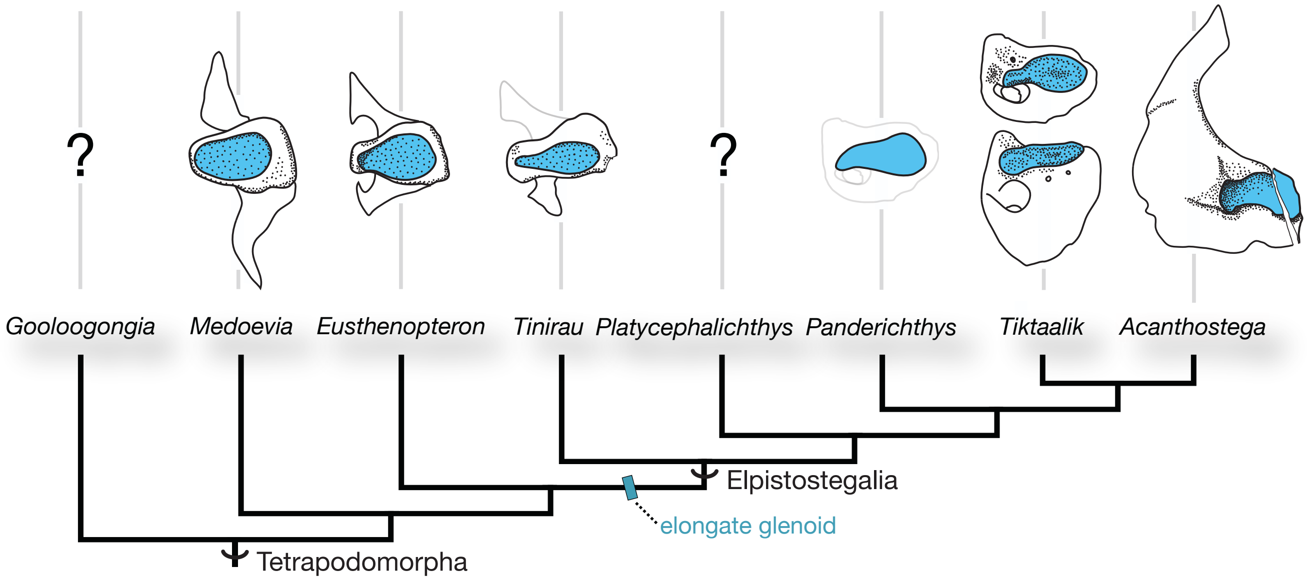


Figure 4.9. Glenoid fossae of Devonian stem-tetrapods. Glenoids are illustrated in posterior view and highlighted in blue. The glenoid of *Tiktaalik* is depicted from two different perspectives, posterior view (above) and posteroventral view (below). Its accessory glenoid is easily recognizable in posterior view, extending medial (left) to the primary glenoid fossa. The glenoid of *Panderichthys* is based on the shape of its caput humerus. The in-plane glenoid measurement (height at maximum extent divided by maximum length) diagnoses an elongate glenoid fossa: *Medoevia* = 0.60; *Eusthenopteron* = 0.60; *Tinirau* = 0.42; *Panderichthys* = 0.48; *Tiktaalik* = 0.44; *Acanthostega* = 0.45.

Osteichthyans maintain a mostly dermal shoulder that is located at the very back of the dermal skull, and a loss of the bones anterior to this shoulder will unavoidably produce a space—i.e., a physical neck. That is, even if the bones that once filled this space were lost for adaptive reasons, the patterned congregation of neural crest cells, and therefore the retained dermal roof, cheek, and shoulder bones that were still located in their symplesiomorphic positions, also contributed to the formation of a space between the remaining components of the dermal skull. Because few traits perform single functions, this new space, although linked to gill-breathing but also taking a nonaptive structural origin, shifted from preaptation to exaptation as girdle rotation enhanced the first steps of a (likely) trotting gait. Moreover, the same pattern has evolved in parallel in the chondrichthyan, *Hemiscyllium oscellatum*. Like *Tiktaalik*, *H. oscellatum* is a total-group gnathostome and hails from a neckless ancestry, but because chondrichthyans lost their dermatocranium yet retained the scapulocoracoid (Donoghue and Sansom 2002), a physical neck evolved in them as well. Thus, this space, a structuralist plesiomorphy for *H. oscellatum*, also shifted from preaptation to exaptation in association with substrate-based mobility.

The Late Devonian *Acanthostega gunnari* has the first known sacrum in vertebrate history, and it evolved by bracing a single modified rib against a dorsal process from the hip on each side (Coates 1996). *Ichthyostega*, the next more crownward taxon, incorporated additional axial elements into its rostrocaudally elongate pelvis. Considering that both of these stem-tetrapods likely retained both laterally flexing axial- and rotating appendicular conditions, connecting hip with vertebral column, for the first time in history, coupled and translated the motion of lateral bending with appendicular trotting. Thus, even though (a) lateral undulation predated terrestrial locomotion, and (b) the first sacrum consisted of recycled gnathostome symplesiomorphies, exapting these nonaptations by connecting hip with rib established for the first time a synapomorphy that relayed axial and appendicular motions. *Ichthyostega*, in particular, maintains a series of heavily ossified, imbricate ribs, and so much of its flexion would have been concentrated in its lumbar and sacral regions. Despite remarks that *Ichthyostega*'s procumbent and recumbent neural spines suggest dorsoventral undulation (Ahlberg et al. 2005) (a spinal pattern common in some marine mammals), alternating neural spines are also found in mososaurs (Lindgren et al. 2007, Lindgren et al. 2011), and in this respect, *Ichthyostega* probably used more of an elaborate sinusoidal motion than a modified aquatic gallop. In addition, for the first time, *Ichthyostega* also exhibits substantial infraglenoid buttressing that constitutes a degree of ventral footing for its proximal humerus. This condition is also present in more crownward Devonian taxa such as *Hynerpeton* (Daeschler et al. 1994) and *Tulerpeton* (Lebedev and Coates 1995), and several post-Devonian forms (Clack and Finney 2005, Godfrey 1989), and suggests that the more typical sprawling tetrapod-like stance had begun to evolve.

Combining this new posture with the ancestral trotting gait and the stem-tetrapod trackways record(Clack 1997, Niedźwiedzki et al. 2010) raises the question whether stem-tetrapods evolved the lateral sequence diagonal-couplet gait before the Carboniferous. Comparison of extant and fossil salamander trackways with fossil stem-tetrapod trackways reveals that the patterns in both groups are strikingly similar. There is much variation among trackways, primarily related to whether the steps are evenly spaced or clustered in doublets, but both patterns emerge in each record (Figure 4.10). Thus, considering that salamanders use both trotting and lateral sequence diagonal-couplet gaits (Bennett et al. 2001), and also produce both trackway patterns (Peabody 1959), stem-tetrapods may have already evolved the diagonal-couplet gait. The primary difference between these two gaits is one of timing of footfall (see Figure 4.2). Trotting is also often associated with faster speeds in tetrapods, and so it could be hypothesized that trots always produce one pattern and diagonal couplets produce the other. The problem, however, is that walking trots are common in many groups (Hildebrand 1985, Reilly 1998), and ultimately, if what distinguishes these

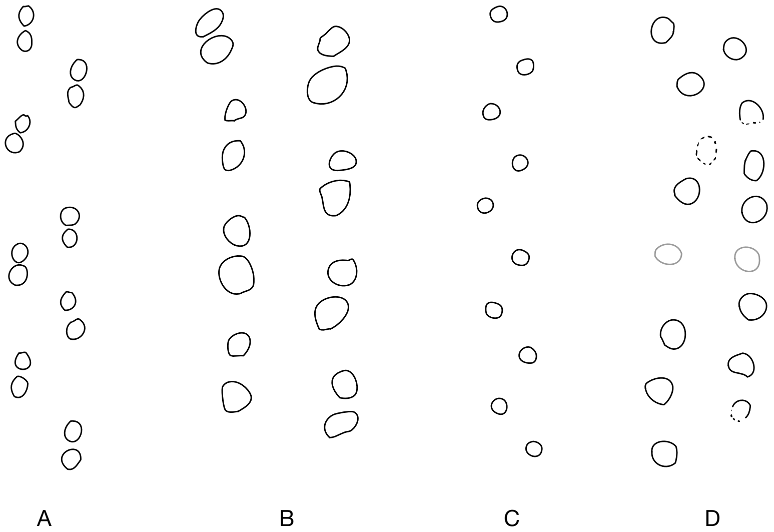


Figure 4.10. Doublet and alternating trackway patterns from crown-group urodeles and stem-tetrapods. A. Lower Pliocene age doublet trackways from California, USA, produced by the salamandrid, *Taricha* sp. (Peabody 1959); B. Middle–Late Devonian age doublet trackways from Valentia Island, Eire, southwest Ireland (Stössel 1995); C. Lower Pliocene age alternate trackways from California, USA, produced by the plethodontid, *Batrachoseps* sp. (Peabody 1959); D. early Middle Devonian (Eifelian) age Zachełmie trackways from Poland. Alternating tracks are in black, the one opposite pair of prints are in gray (Niedźwiedzki et al. 2010). The original length of the tracks are doubled for illustrative purposes in A and C.

gaits is timing only, then what a track reflects will not necessarily derive from the type of gait. Instead, it will more immediately reflect body length, limb length, distance between girdles, girdle rotation and stride length, and degree of lateral undulation, all traits that vary depending upon an animal's morphology (Peabody 1959, figure 3, pg. 10). However, Devonian elpistostegalians are known in reasonable detail, and do not vary as extensively as living salamanders do. That is, independent of whether these animals were using the traveling wave trot (Edwards 1977, 1989) in a nearly fully submerged setting or a standing wave gait on an open mudflat, they may have operated biomechanically like living salamanders. Studies of *Ambystoma tigrinum* (Frolich and Biewener 1992) demonstrate that independent of a traveling or standing wave, a trotting gait produces a body wavelength about twice the girdle separation distance. Thus, assuming that this relationship among trotting, body wavelength, and intergirdle distance also applies to stem-tetrapods, then knowing intergirdle distances and assuming trotting gaits will permit a calculation of body wavelength (Figure 4.11). By contrast, measuring intergirdle distance and doubling it for an estimate of body wavelength will not resolve whether a trotting pattern produced these trackways or even if early elpistostegalians could trot. Such a calculation simply draws upon this mathematical relationship, and any doubled measurement of intergirdle distance in any gnathostome will make them appear capable of trotting. Unfortunately, both intergirdle distance *and* body wavelength need to be measured directly to know whether a trotting or lateral sequence diagonal-couplet gait produced these trackways.

Summary.—The trot evolved at least three times in gnathostome evolution. Environmental circumstances and pectoral autapomorphies certainly contributed to the trotting abilities of sharks, teleosts, and sarcopts, but the symplesiomorphic retention of numerous traits, especially as related to axial and appendicular systems, also predisposed these outcomes. In this case, only some of the features specific to substrate-based mobility have evolved from non-homologous ancestral states—that is, convergently (Wake 1991).

'Constraint', as a term, is often used as a negative construct primarily related to limits of morphological variation and the consequences of the struggle for existence, and only secondarily as a positive promotor or supplier of evolutionary direction (Gould 2002). To be clear, I here use the term 'channeling' to refer to the latter, more positive meaning. Much of what it means to trot as a gnathostome has been channeled along phyletic lines. Lateral undulation and shoulder position are stem-chordate and stem-gnathostome apomorphies, respectively, even though they are critical to locomotion in certain sharks and tetrapods. In this respect, function alone does not explain why the shoulder was coopted for girdle rotation in these groups, even if the physical neck originated for different reasons in each clade. There are probably only so many ways for a gnathostome bauplan to locomote effectively across particular substrates, and this bauplan channeled biomechanical rules into what are and are not feasible means of locomotion. *Hemiscyllium oscillatum*, as a chondrichthyan epaulette shark, uses its axial muscles, rotating girdle, and appendicular autapomorphies to contend with this issue; whereas *Clarias*, an osteichthyan and catfish, also employs axial flection, but because it is neckless it must use its pre-pectoral spines for additional leverage. Stem- and crown-group tetrapods use(d) a similar combination of evolutionary tools, functionally more similar to *H. oscillatum* than to *Clarias*, but nonetheless, an integrated system of historical, constructional, and functional traits. The origin of sacra in stem-tetrapods cobbled axial and appendicular symplesiomorphies into an elpistostegalian synapomorphy that forever changed their locomotor potential. Despite the new integrated system, many early taxa were mostly if not entirely aquatic, and so any relay of function between axial and appendicular motions likely already existed because the pelvic girdle and limbs were already moving with an undulating body. However, because a girdle suspended in the body wall lacks the support provided by one attached to the axial skeleton, whatever the reasons behind this initial connection, once in existence, it helped initiate a functional outcome

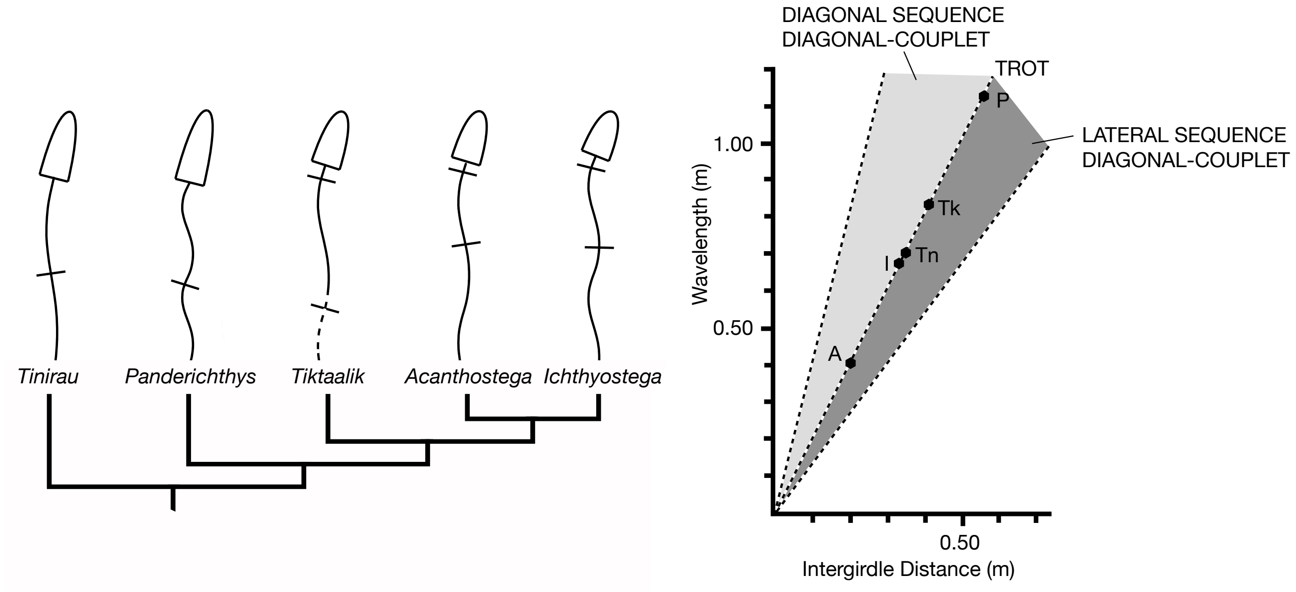


Figure 4.11. The relationships among intergirdle distance, wavelength, and select locomotor gaits. A trotting gait produces a body wavelength about twice the girdle separation distance. By contrast, a lateral sequence diagonal-couplet gait produces a body wavelength less than twice the girdle separation distance, and a diagonal sequence diagonal-couplet gait produces a body wavelength more than twice the girdle separation distance. Unfortunately, because gait and wavelength cannot be measured directly in stem-tetrapods, only wavelength can be calculated when assuming a particular gait given a known intergirdle distance. Taxa not to drawn to scale. Wavelengths illustrated in all taxa are based on a trotting gait. Graph modified after Pridmore (1995).

that permitted terrestriality.

Despite this history, numerous crown-tetrapods such as urodeles, caecilians, several squamate groups, sauropterygians, pinnipeds, and cetaceans have gone on to reduce or lose many traits primitively used in locomotion, from limbs and girdles to employing traveling (and not standing) waves in terrestrial and even secondarily aquatic environments. By contrast, for many other groups such as anurans, birds, and mammals, these plesiomorphies have been essential for exploiting new adaptive zones and modifying axial and appendicular components far removed from earlier conditions. The interplay of aptive and nonaptive transformations has been essential for these changes, and quantifying their contributions to quirky functional shifts will (1) bridge the three historically important modes for thinking about organismal form; and (2) integrate and refine their relative influences to explain diversity and disparity over evolutionary time more adequately.

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SUPPLEMENTARY INFORMATION FOR:

THE ORIGIN AND EARLY EVOLUTION OF TERRESTRIAL LOCOMOTION

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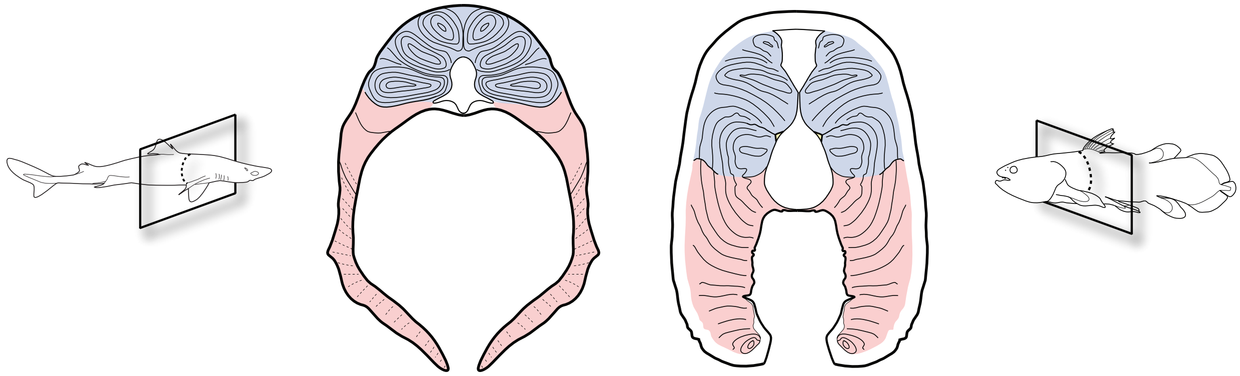

Supplementary Information

Supporting Text

Figures S4.1, 4.2

References

Supporting Text

Part A.

Taxa and characters used in the phylogenetic analysis of gnathostome gaits.—Gaits were studied and analyzed in chondrichthyans (sharks), actinopterygians (ray-fins), actinistians (coelacanths), dipnoans (lungfishes), lissamphibians (crown-amphibians), chelonians (turtles), lepidosaurs (lizards), and pseudosuchians (crocodiles). Results were informed by a survey of the published literature as well as slow motion videography (⅛-¼ the rate of real-time footage) captured by the British Broadcasting Corporation's *Life* and *Life in Cold Blood* series (Attenborough et al. 2008, Attenborough et al. 2010). Particular gaits were scored as present or absent depending upon their observation in the primary literature. However, excluding dipnoans (whose published accounts that are more anecdotal than rigorous (Rosen et al. 1981)) and anurans (which data suggest only use hopping and/or lateral sequence diagonal-couplet gaits (Ahn et al. 2004, Anderson et al. 1991, Attenborough et al. 2008, Attenborough et al. 2010, Walton et al. 1994)), when comparing trotting and diagonal-couplet gaits among videographed salamanders, turtles, lizards, and crocodiles, taxa were only scored as "present" for an observed gait, and not scored as "absent" for an unobserved gait. That is, even though a trot is accepted as the near simultaneous contact of contralateral limb pairs (Reilly et al. 2006), because a slight difference in timing can transform a diagonal-couplet walk into a walking trot, and because many of these taxa are known to use both gaits, I erred on the side of caution and did not score them as unable to engage in either gait if unobserved. Such "absences" were only used when noted from the primary literature.

Examined taxa include:

Acanthodactylus boskianus (McElroy et al. 2008)
Acipenser (Liao and Lauder 2000, Wilga and Lauder 1999)
Agalychnis callidryas (Attenborough et al. 2008)
Alligator mississippiensis (Reilly and Elias 1998)
Amblyrhynchus cristatus (Attenborough et al. 2008)
Ambystoma maculatum (Deban and Schilling 2009)
Ambystoma opacum (Attenborough et al. 2008)
Ambystoma tigrinum (Frolich and Biewener 1992, Reilly et al. 2006)
Ameiva ameiva (McElroy et al. 2008, White and Anderson 1994)
Amphibolurus muricatus (Attenborough et al. 2008)
Andrias japonicus (Attenborough et al. 2008)
Antennarius commerson (Edwards 1989)
Atelopus zeteki (Attenborough et al. 2008)
Austrochaperina pluvialis (Attenborough et al. 2008)
Brookesia minima (Attenborough et al. 2008)
Brookesia sp. (Attenborough et al. 2008)
Bufo bufo (Nauwelaerts and Aerts 2002)
Bufo woodhousii fowleri (Anderson et al. 1991)
Caiman crocodilus (Attenborough et al. 2008)
Callopistes flavipunctatus (White and Anderson 1994)

Callopistes maculatus (White and Anderson 1994)
Carettochelys insculpta (Attenborough et al. 2010)
Chamaeleo melleri (Attenborough et al. 2008, Attenborough et al. 2010)
Chamaeleo namaquensis (Attenborough et al. 2010)
Chelonoidis nigra (Zani 2005)
Chelydra sp. (Jayes and Alexander 1980)
Chiloscyllium plagiosum (Wilga and Lauder 2001)
Chlamydoselachus
Chrysemys picta (Attenborough et al. 2008, Attenborough et al. 2010, Walker 1971)
Clarias lazera (Johnels 1957)
Cnemidophorus tigris (White and Anderson 1994)
Coleodactylus amazonicus (Attenborough et al. 2010)
Coleonyx variegatus (McElroy et al. 2008)
Cordylus cataphractus (Attenborough et al. 2008)
Cordylus warreni (McElroy et al. 2008)
Cottus (Webb et al. 1996)
Crocodylus johnstoni (Renous et al. 2002)
Dicamptodon ensatus (Ashley-Ross and Bechtel 2004)
Emydura macquarii (Baudinette et al. 2000)
Emys orbicularis (Walker 1963)
Eremius velox (Sukhanov 1974)
Erpetoichthys (McKenzie et al. 2007, Pace and Gibb 2011)
Eublepharis macularius (Attenborough et al. 2008)
Eulamprus quoyii (McElroy et al. 2008)
Eumeces fasciatus (Attenborough et al. 2010)
Eumeces schneideri (McElroy et al. 2008)
Furcifer pardalis (Attenborough et al. 2008)
Gadus (Soofiani and Priede 1985, Videler 1981)
Gavialis gangeticus (Attenborough et al. 2008)
Geoemyda sp. (Jayes and Alexander 1980)
Gopherus polyphemus (Attenborough et al. 2008)
Heliobolus lugubris (Attenborough et al. 2010)
Heloderma horridum (Attenborough et al. 2008)
Hemidactylus garnotii (McElroy et al. 2008)
Hemiscyllium ocellatum (Pridmore 1995)
Heterodontus (Simons 1970)
Ichthyosaura alpestris (Attenborough et al. 2008)
Iguana iguana (Attenborough et al. 2008, Carrier 1990)
Kassina maculata (Ahn et al. 2004)
Lacerta vivipara (Avery and Bond 1989)
Latimeria chalumnae (Fricke 1987)
Laudakia stellio (McElroy et al. 2008)

Leiocephalus schreibersii (McElroy et al. 2008)
Lepidophyma flavimaculatum (McElroy et al. 2008)
Moloch horridus (Attenborough et al. 2008)
Neoceratodus forsteri (Rosen et al. 1981)
Notaden sp. (Attenborough et al. 2008)
Oplurus cuvieri (McElroy et al. 2008)
Orectolobus
Oreophrynella macconnelli (Attenborough et al. 2010)
Oreophrynella nigra (Attenborough et al. 2010)
Percopsis
Phelsuma sp. (Attenborough et al. 2008)
Phrynosoma solare (Attenborough et al. 2008)
Phyllomedusa sauvagii (Attenborough et al. 2008)
Platysaurus broadleyi (Attenborough et al. 2008)
Plestiodon skiltonianus (McElroy et al. 2008)
Plethodon glutinosus (Attenborough et al. 2008)
Podarcis hispanica (Van Damme et al. 1998)
Podarcis lilfordi (Attenborough et al. 2008, Peréz-Mellado and Casas 1997)
Procellosaurinus tetradactylus (Renous et al. 2008)
Protopterus amphibius (Greenwood 1986)
Pyxicephalus adspersus (Attenborough et al. 2008)
Rana catesbeiana (Attenborough et al. 2010)
Rana esculenta (Nauwelaerts and Aerts 2002)
Salmo (Mellas and Haynes 1985)
Sceloporus clarkii (Reilly 1998, Reilly and Delancey 1997a, Reilly and Delancey 1997b)
Sceloporus malachiticus (McElroy et al. 2008)
Sphenodon punctatus (Reilly et al. 2006)
Squalus (Simons 1970)
Teratoscincus scincus (Sukhanov 1974)
Terrapene carolina carolina (Attenborough et al. 2008)
Tiliqua rugosa (Attenborough et al. 2008)
Tracheloptychus petersi (McElroy et al. 2008)
Trachemys scripta (Landberg et al. 2009)
Triakis (McKenzie et al. 2007)
Tropidurus torquatus (McElroy et al. 2008)
Tupinambis teguixin (McElroy et al. 2008, White and Anderson 1994)
Uta stansburiana (Attenborough et al. 2008)
Vanzosaura rubricauda (Renous et al. 2008)
Varanus exanthematicus (McElroy et al. 2008)
Varanus giganteus (Attenborough et al. 2008)
Varanus komodoensis (Attenborough et al. 2010)
Varanus varius (Attenborough et al. 2010)

Characters.

1. Trot
    - 0 absent
    - 1 present

2. Lateral sequence diagonal-couplet
    - 0 absent
    - 1 present

3. Lateral sequence lateral-couplet
    - 0 absent
    - 1 present

4. Gallop
    - 0 absent
    - 1 present

5. Bound (Hop)
    - 0 absent
    - 1 present

Part B.

Taxon-by-character matrix and character optimizations for the gait analysis.

	1	**2**	**3**	**4**	**5**
Acanthodactylus boskianus	1	?	0	0	0
Acipenser	0	0	0	0	0
Agalychnis callidryas	0	1	0	0	1
Alligator mississippiensis	1	0	0	0	1
Amblyrhynchus cristatus	1	1	0	0	0
Ambystoma maculatum	1	?	0	0	0
Ambystoma opacum	?	1	0	0	0
Ambystoma tigrinum	1	1	0	0	0
Ameiva ameiva	1	1	1	0	0
Amphibolurus muricatus	1	1	0	0	0
Andrias japonicus	?	1	0	0	0
Antennarius commerson	0	1	0	1	0
Atelopus zeteki	0	1	0	0	1
Austrochaperina pluvialis	0	1	0	0	1
Brookesia minima	1	1	0	0	0
Brookesia sp.	?	1	0	0	0

	1	**2**	**3**	**4**	**5**
Bufo bufo	0	1	0	0	1
Bufo woodhousii fowleri	0	1	0	0	1
Caiman crocodilus	1	0	0	0	?
Callopistes flavipunctatus	1	1	?	0	0
Callopistes maculatus	1	1	1	0	0
Carettochelys insculpta	1	?	0	0	0
Chamaeleo melleri	1	1	0	0	0
Chamaeleo namaquensis	1	1	0	0	0
Chelonoidis nigra	?	1	0	0	0
Chelydra sp.	?	1	0	0	0
Chiloscyllium plagiosum	1	0	0	0	0
Chlamydoselachus	0	0	0	0	0
Chrysemys picta	1	1	0	0	0
Clarias lazera	1	0	0	0	0
Cnemidophorus tigris	1	1	1	0	0
Coleodactylus amazonicus	1	1	?	0	0
Coleonyx variegatus	1	?	0	0	0
Cordylus cataphractus	1	1	?	0	0
Cordylus warreni	1	?	0	0	0
Cottus	0	0	0	0	0
Crocodylus johnstoni	1	0	0	1	1
Dicamptodon ensatus	1	1	0	0	0
Emydura macquarii	?	1	0	0	0
Emys orbicularis	?	1	0	0	0
Eremius velox	1	?	0	0	0
Erpetoichthys	0	0	0	0	0
Eublepharis macularius	?	1	0	0	0
Eulamprus quoyii	1	?	0	0	0
Eumeces fasciatus	1	?	0	0	0
Eumeces schneideri	1	?	0	0	0
Furcifer pardalis	1	1	0	0	0
Gadus	0	0	0	0	0
Gavialis gangeticus	1	?	0	0	1
Geoemyda sp.	?	1	0	0	0
Gopherus polyphemus	?	1	0	0	0
Heliobolus lugubris	1	?	?	0	0
Heloderma horridum	1	?	?	0	0
Hemidactylus garnotii	1	?	0	0	0
Hemiscyllium ocellatum	1	0	0	0	0
Heterodontus	0	0	0	0	0
Ichthyosaura alpestris	1	1	0	0	0

	1	2	3	4	5
Iguana iguana	1	1	0	0	0
Kassina maculata	0	1	0	0	1
Lacerta vivipara	1	1	1	0	0
Latimeria chalumnae	1	0	0	0	0
Laudakia stellio	1	?	0	0	0
Leiocephalus schreibersii	1	?	0	0	0
Lepidophyma flavimaculatum	1	?	0	0	0
Moloch horridus	**1**	**1**	**?**	**0**	**0**
Neoceratodus forsteri	1	?	?	?	?
Notaden sp.	0	1	0	0	1
Oplurus cuvieri	1	?	0	0	0
Orectolobus	0	0	0	0	0
Oreophrynella macconnelli	0	1	0	0	0
Oreophrynella nigra	0	1	0	0	0
Percopsis	0	0	0	0	0
Phelsuma sp.	?	1	0	0	0
Phrynosoma solare	1	?	?	0	0
Phyllomedusa sauvagii	0	1	0	0	1
Platysaurus broadleyi	1	?	0	0	0
Plestiodon skiltonianus	1	?	0	0	0
Plethodon glutinosus	?	1	0	0	0
Podarcis hispanica	1	?	0	0	0
Podarcis lilfordi	1	?	0	0	0
Procellosaurinus tetradactylus	1	?	0	0	0
Protopterus amphibius	1	0	0	0	0
Pyxicephalus adspersus	0	1	0	0	1
Rana catesbeiana	0	1	0	0	1
Rana esculenta	0	1	0	0	1
Salmo	0	0	0	0	0
Sceloporus clarkii	1	?	0	0	0
Sceloporus malachiticus	1	?	0	0	0
Sphenodon punctatus	1	?	0	0	0
Squalus	0	0	0	0	0
Teratoscincus scincus	1	?	0	0	0
Terrapene carolina carolina	?	1	0	0	0
Tiliqua rugosa	?	1	?	0	0
Tracheloptychus petersi	1	?	0	0	0
Trachemys scripta	?	1	0	0	0
Triakis	0	0	0	0	0
Tropidurus torquatus	1	?	0	0	0
Tupinambis teguixin	1	1	0	0	0

	1	**2**	**3**	**4**	**5**
Uta stansburiana	1	?	?	0	0
Vanzosaura rubricauda	1	?	0	0	0
Varanus exanthematicus	1	?	0	0	0
Varanus giganteus	1	?	?	0	0
Varanus komodoensis	1	?	?	0	0
Varanus varius	1	1	0	0	0

Part C.

Taxa and specimens studied in the myological analysis.—Firsthand dissection, computed tomography (CT), nuclear magnetic resonance imaging (nMRI), and comparison to published works informed the reconstructions of axial sections. Chondrichthyan and actinopterygian dissections were undertaken at the University of California, Berkeley, and coelacanth dissections at the Muséum national d'Histoire naturelle, Paris, and at the California Academy of Sciences. Jawless craniates, chondrichthyans, and actinopterygians were purchased from the Connecticut Valley Biological Supply Company (Southampton, MA) and the Chinatown Fish Market in San Francisco, California. Chondrichthyan, actinopterygian, coelacanth, lungfish, and salamander specimens were CT- and nMRI-scanned at the University of California, San Francisco Medical Center (China Basin) and at the University of California, Davis School of Veterinary Medicine. Depending upon specimen size, density, and scanning method, slice thickness varied from 625µm to 2mm. Data were reconstructed using the imaging program OsiriX v3.7.1 64-bit (Rosset et al. 2004), and all images, whether dissection photographs or rendered scans, were traced in Adobe Illustrator CS3 using an Intuos3 Wacom tablet. Illustrations were visually mapped onto a cladogram complied from accepted interrelationships among crown-group chordates (excluding urochordates) (Block et al. 1993, Bourlat et al. 2006, Collin et al. 2009, Delsuc et al. 2006, Inoue et al. 2001, Janvier 1996, 2008, Winchell 2004). For the most part, early-diverging chondrichthyans and actinopterygians were included to avoid the confusion of derived and autapomorphic conditions, especially among fast-swimming, pelagic members of each clade that might obscure informative gnathostome symplesiomorphies (Donley et al. 2004). Specific specimens are noted where appropriate, following each taxon below: California Academy of Sciences (CAS, SU), Muséum national d'Histoire naturelle, Paris (MNHN), Museum of Vertebrate Zoology, Berkeley Natural History Museums (MVZ).

Branchiostoma lanceolatum (Gemballa et al. 2003, Ruppert et al. 2004)
Myxine glutinosa (Flood 1998) (Connecticut Valley Biological Supply)
Lampetra tridentata (Kusakabe and Kuratani 2005, 2007) (Connecticut Valley Biological Supply)
Squalus acanthias (CAS 19159; Connecticut Valley Biological Supply)
Chlamydoselachus anguineus (SU 12922)
Triakis semifasciata (Chinatown Fish Market)
Carcharhinus limbatus (Savary 1994b)
Sphyrna lewini (Nakaya 1995)
Isurus oxyrinchus (Gemballa et al. 2006)
Alopias vulpinus (Savary 1994a)

Acipenser (*medirostris*) (Chinatown Fish Market; SU 14844)
Clarias (SU 52578)
Oncorhynchus (*keta*) (Chinatown Fish Market)
Trichiurus lepturus (Chinatown Fish Market)
Sebastes (Chinatown Fish Market)
Latimeria chalumnae (Millot and Anthony 1958) (CAS 24862; MNHN-C6, 7, 12)
Neoceratodus forsteri (Maurer 1912) (SU 18139)
Protopterus (*aethiopicus*) (Maurer 1912) (SU 52574)
Andrias davidianus (CAS 26787; MVZ 67810, 202290, 204246)
Cryptobranchus alleganiensis (Brainerd and Simons 2000, Simons and Brainerd 1999) (MVZ 25548-25541, 205729-30, 205736)
Amphiuma tridactylum (Simons and Brainerd 1999)
Ambystoma tigrinum (Simons and Brainerd 1999)
Siren lacertina (Simons and Brainerd 1999)

Part D.

Taxa and characters used in the phylogenetic analysis of fossil taxa.—The following 203 morphological characters were used to reconstruct the interrelationships among total-group lungfishes, stem-tetrapods, stem-amphibians, and stem-amniotes. Primary character sources (Ahlberg et al. 2008, Ahlberg and Johanson 1998, Ahlberg et al. 2000, Coates and Friedman 2010, Daeschler et al. 2006, Zhu and Ahlberg 2004) are indicated parenthetically following each character description. Numbers following the citations refer to the character number in the original source. Characters modified from their original source are noted where applicable. Very few characters are shared between this analysis and Coates and Friedman (2010); this was maintained intentionally to demonstrate how nearly independent data sets converge on a similar result. This analysis also recovered a monophyletic Megalichthyiformes, with 'osteolepidid'-grade tetrapodomorphs not simply emerging as lone lineages aligned as successive plesions to crownward forms. *Glyptopomus* was included in a separate analysis to test its influence on the phylogenetic result. Although its inclusion disrupted a monophyletic Canowindridae and pulled *Gyroptychius* and *Gogonasus* from Megalichthyiformes, it had no bearing on the phylogenetic position of any eotetrapodiform.

Characters were polarized by comparison to outgroup taxa such as *Porolepis*, *Glyptolepis*, *Powichthys*, *Youngolepis*, *Diabolepis*, and *Dipterus*. These taxa were selected because they represent a range of total-group lungfish that are known from reasonable material, are well studied, and generally accepted as sister to total-group tetrapods.

Characters were coded based on a combination of published descriptions, specimen illustrations, and firsthand examination of fossil material. Care was taken to avoid simply recycling codings in the published literature. Specimens from the following museums were examined, and are noted following each taxon below: Australian Museum, Sydney (AMF), Australian National University (ANU), Geologisk Museum, Copenhagen, Denmark (MGUH), Latvian Museum of Natural History (LDM), Muséum national d'Histoire naturelle, Paris (MNHN), Museum Victoria, Melbourne, Australia (NMV), The Natural History Museum, London (MNH), Palaeontological Institute of the Russian Academy of Sciences, Moscow (PIN), National Museums of Scotland (NMS), Nunavut Fossil Vertebrate

Collection (NUFV), Swedish Museum of Natural History, Stockholm (NR), University of California Museum of Paleontology (UCMP), University Museum of Zoology Cambridge (UMZC).

Acanthostega (Ahlberg and Clack 1998, Clack 1988, 1989, 1994, 1998a, 2002a, Coates 1996) (MGUH f.n. 157, 255, 1227, 1258; UMZC T1291, T1300)
Balanerpeton (Milner and Sequeira 1993) (UMZC T1312, T1313)
Baphetes (Beaumont 1977, Milner and Lindsay 1998, Owen 1854, Watson 1929)
Barameda (Garvey 2005, Long 1989, Long and Ahlberg 1999) (NMV P10277, P160880, P160885, P212715)
Beelarongia (Long 1987) (NMV P160875, P160972)
Cabonnichthys (Ahlberg and Johanson 1997) (AMF96856, F96858a, F96863, F96902, F98037, F98038)
Canowindra (Long 1985a, Thomson 1973) (BMNH P.34420)
Cladarosymblema (Fox et al. 1995)
Crassigyrinus (Clack 1998b, Panchen and Smithson 1990) (BMNH R10000; UMZC T1250)
Dendrerpeton (Godfrey et al. 1987, Holmes et al. 1998, Owen 1853, Robinson et al. 2005) (UCMP 102367)
Diabolepis (Chang 1995, Chang and Yu 1984, Smith and Chang 1990)
Dipterus (Ahlberg and Trewin 1995, White 1965) (BMNH P.17410, P.33165, P.34544, P.53507; MNHN GBP71, P72; NR P.3108, P.4827; UCMP 43714, 43727, 43728, 43729, 43730, 93066, 93067, 93068, 93069, 93070, 93071, 93072, 115246; UMZC GN1043)
Ectosteorhachis (Thomson 1964)
Elginerpeton (Ahlberg 1991b, 1995, 1998)
Elpistostege (Schultze and Arsenault 1985) (BMNH P.60526 a,b)
Eoherepton (Andrews et al. 1977, Smithson 1985)
Eusthenodon (Jarvik 1952) (NR P.1475, P.1693)
Eusthenopteron (Andrews and Westoll 1970a, Jarvik 1980) (BMNH P.60386, P.60388, P.60397; NR P.222, P.223, P249, P.287, P.290, P.330, P322 a,b, P.326b, P.382, P.2197, a,b, P2609, P.4611, P.6383; UMZC GN.790, GN.791, GN.797, GN.799)
Glyptolepis (Ahlberg 1989, Ahlberg 1991a, Jarvik 1972) (NR P.180, P.2503 a,b, P.8635)
Glyptopomus (Jarvik 1950a)
Gogonasus (Long et al. 1997, Long et al. 2006) (ANU 21885, 49259; NMV P221807)
Gooloogongia (Johanson and Ahlberg 2001)
Greererepton (Bolt and Lombard 2001, Godfrey 1989, Romer 1969, Smithson 1982) (UMZC T1220)
Gyroptychius (Jarvik 1950b, c, 1985) (MNHN GBP44, P63, P107, P138, P209, P264, P265, P307; NR P.1679, P.1698, P.4116, P.4220; UMZC GN.240, GN.939)
Ichthyostega (Ahlberg et al. 2005, Jarvik 1996) (MGUH 6055, 6064, 6081, MGUH f.n. 200, 300, 301)
Jarvikina (Vorobyeva 1977)
Kenichthys (Chang and Zhu 1993, Zhu and Ahlberg 2004)
Koharalepis (Young et al. 1992)
Mandageria (Johanson and Ahlberg 1997, Johanson et al. 2003) (AMF96508, F96855a, F96857a,b,c, F98592c, F98593 a,b, F98594)
Marsdenichthys (Holland et al. 2010, Long 1985b) (NMV P179619, P186572)
Medoevia (Lebedev 1995)

Megalichthys (Andrews and Westoll 1970b, Jarvik 1948, 1967, Romer 1937, Thomson 1964, Watson 1926) (NR P.6157; UMCZ GN.638)
Osteolepis (Andrews and Westoll 1970b, Jarvik 1948, Jarvik 1980, Thomson 1965) (MNHN GBP67, P186, P188, P195, P269 a,b, P277, P280, P284; NR P.1675, P.4110, P.4139, P.11116; UCMP 43711, 43717, 43718, 43719, 43720, 43721, 43733, 58496, 58498, 58499)
Panderichthys (Ahlberg and Clack 1998, Ahlberg et al. 1996, Boisvert 2005, Boisvert et al. 2008, Brazeau and Ahlberg 2006, Vorobyeva 1995, Vorobyeva 2000, Vorobyeva and Schultze 1991) (NR P.6427; PIN 3547 [high resolution photograph]; LDM 60/123 [high resolution photograph])
Pederpes (Clack 2002b, Clack and Finney 2005)
Platycephalichthys (Coates and Friedman 2010, Vorobyeva 1962, 1977) (PIN 54/155, 54/156, 54/158, 54/159, 54/160, 54/160a, 54/161, 54/162, 54/163, 54/164, 54/165, 54/166, 54/183, 54/191, 54/192, 54/193, 54/194, 54/195 [high resolution photographs])
Porolepis (Clément 2004, Jarvik 1972) (MNHN SVD2001, 2034, 2158; NR A28633, A30483)
Powichthys (Clément and Janvier 2004, Jessen 1975, 1980)
Proterogyrinus (Holmes 1984, Romer 1970)
Silvanerpeton (Ruta and Clack 2006) (UMZC T1317, T1351)
Spodichthys (Jarvik 1985, Snitting 2008b) (MGUH VP 6705 (P.1659), VP 6708 (P.1662), VP 6714 (P.1668), VP 6715 (P.1669))
Tiktaalik (Daeschler et al. 2006, Downs et al. 2008, Shubin et al. 2006) (NUFV 108, 110)
Tristichopterus (Egerton 1861, Snitting 2008a) (BMNH 66653, 66660, 66661, 66664, 66666, 66670; NMS.G. 1875.29.220, G.1875.29.221, G.1875.29.224, G.1875.29.225, G.1995.4.28; NR P.4196)
Ventastega (Ahlberg et al. 1994, Ahlberg et al. 2008)
Whatcheeria (Lombard and Bolt 1995, Lombard and Bolt 2006)
Youngolepis (Chang 1982, 1991, 2004, Chang and Smith 1992)

Characters.

1. Ethmoid region
(Ahlberg et al. (2008): Character 25)

0 fully ossified
1 partly or wholly unossified

2. Rostral tubuli
(Coates & Friedman (2010): Character 1)

0 absent
1 present

3. Profundus foramen in postnasal wall
(Zhu & Ahlberg (2004): Character 81)

0 small
1 large

4. Fenestra ventrolateralis
(Coates & Friedman (2010): Character 5)

0 ventral to ethmoid articulation, in posterior view
1 extends dorsal to ethmoid articulation, in posterior view (post nasal wall unossified)

5. Pituitary vein exit
(Coates & Friedman (2010): Character 11)

0 anterior to basipterygoid process
1 dorsal to basipterygoid process

6. Extent of crista parotica
(Zhu & Ahlberg (2004): Character 33)

0 does not reach posterior margin of tabular
1 reaches posterior margin of tabular

7. Endoskeletal intracranial joint
(Coates & Friedman (2010): Character 14)

0 absent
1 present

8. Basicranial fenestra
(Zhu & Ahlberg (2004): Character 76)

0 absent
1 present

9. Processus descendens of sphenoid
(Zhu & Ahlberg (2004): Character 78)

0 absent
1 present

10. Posterior carotid opening in parasphenoid
(Zhu & Ahlberg (2004): Character 80)

0 large
1 small
2 absent

11. Tectum orbitale

(Zhu & Ahlberg (2004): Character 83)

0 narrow
1 extensive

12. Basipterygoid process

(Ahlberg et al. (2008): Character 24)

0 not strongly projecting with concave anterior face
1 strongly projecting with flat anterior face

13. Hypophysial region

(Ahlberg et al. (2008): Character 26)

0 solid side wall pierced by small foramina for pituitary vein and other vessels
1 single large foramen

14. Otic capsule lateral commissure bearing hyomandibular facets

(Ahlberg et al. (2008): Character 27)

0 present
1 absent

15. Relative positions of the hyomandibular facets

(Coates & Friedman (2010): Character 20)

0 dorsal directly above ventral
1 ventral anterior to dorsal
2 dorsal anterior to ventral

16. Parasymphysial plate

(Zhu & Ahlberg (2004): Character 1). *Platycephalichthys* scored after Snitting (2008b).

0 long, sutured to coronoid, denticulated or with tooth row
1 short, not sutured to coronid, denticulated
2 carrying tooth whorl

17. Parasymphysial plate dentition
(Modified from Ahlberg et al. (2008): Character 89)

0 Carrying a tooth whorl
1 shagreen or irregular tooth field
2 organised dentition aligned parallel to jaw margin

18. Parasymphsial fangs
(Modified from Ahlberg et al. (2008): Character 90)

0 absent
1 present

19. Parasymphysial plate: detachable whorl
(Zhu & Ahlberg (2004): Character 7)

0 detachable whorl
1 sutured plate with denticles or teeth

20. Lateral parasymphysial foramen
(Daeschler et al. (2006): Character 66)

0 absent
1 present

21. Mesial parasymphysial foramen
(Daeschler et al. (2006): Character 67)

0 absent
1 present

22. Length of dentary
(Zhu & Ahlberg (2004): Character 10)

0 long
1 short with lip fold

23. Dentary teeth
(Ahlberg et al. (2008): Character 85)

0 same size as maxillary teeth

1 larger than maxillary teeth
2 smaller than maxillary teeth

24. Accessory tooth rows on dentary
(Daeschler et al. (2006): Character 64)

0 present
1 absent

25. Dentary tooth row reaches symphysis
(Zhu & Ahlberg (2004): Character 11)

0 yes
1 no

26. Dentary fangs
(Modified from Zhu & Ahlberg (2004): Character 12)

0 absent
1 1 pair
2 1 unpaired (no replacement pit)

27. Dentary ventral edge
(Ahlberg et al. (2008): Character 55)

0 smooth continuous line
1 abruptly tapering or 'stepped' margin

28. Splenial
(Modified from Zhu & Ahlberg (2004): Character 2)

0 not sutured to prearticular
1 sutured to prearticular
2 postsplenial obstructing splenial-prearticular contact

29. Postsplenial suture with prearticular present
(Modified from Ahlberg et al. (2008): Character 69)

0 no
1 yes but interrupted by Meckelian foramina or fenestrae
2 uninterrupted suture

30. Postsplenial with mesial lamina
(Ahlberg et al. (2008): Character 67)

0 no
1 yes

31. Meckelian foramina/fenestrae, dorsal margins formed by
(Ahlberg et al. (2008): Character 63)

0 Meckelian bone
1 prearticular
2 infradentary

32. Meckelian foramina/fenestrae, height
(Ahlberg et al. (2008): Character 64)

0 much lower than adjacent prearticular
1 equal to or greater than depth of adjacent prearticular

33. Meckelian exposure in precoronoid fossa
(Daeschler et al. (2006): Character 65)

0 present
1 absent

34. Posterior coronoid longer than more anterior coronoids
0 no
1 yes

35. Posterior coronoid one-third longer than more anterior coronoids
(Modified from Zhu & Ahlberg (2004): Character 8)

0 no
1 yes

36. Coronoid fangs larger than marginal teeth
(Daeschler et al. (2006): Character 70)

0 yes
1 no

37. Coronoids: at least one carries shagreen

(Ahlberg et al. (2008): Character 80)

0 no
1 yes

38. Coronoids with a row of very small teeth or denticles lateral to tooth row
(Ahlberg et al. (2008): Character 81)

0 yes
1 no

39. Coronoids: size of teeth (excluding fangs) on anterior and middle coronoids relative to dentary tooth size
(Ahlberg et al. (2008): Character 82)

0 about the same
1 half height or less

40. Coronoid (anterior) contacts splenial
(Ahlberg et al. (2008): Character 49)

0 no
1 yes

41. Coronoid (middle) separated from splenial
(Ahlberg et al. (2008): Character 50)

0 yes, by prearticular
1 no
2 yes, by postsplenial

42. Coronoid (posterior) posterodorsal process
(Ahlberg et al. (2008): Character 52)

0 no
1 yes

43. Coronoid (posterior) posterodorsal process visible in lateral view
(Ahlberg et al. (2008): Character 53)

0 no
1 yes

44. Number of fang pairs on posteriormost coronoid
(Zhu & Ahlberg (2004): Character 13)

0 one
1 two
2 none

45. Non-fanged teeth on posterior coronoid
0 absent
1 organized tooth row
2 shagreen

46. Prearticular
(Zhu & Ahlberg (2004): Character 3)

0 not forked
1 forked

47. Prearticular sutures with mesial lamina of splenial
(Ahlberg et al. (2008): Character 71)

0 no, mesial lamina of splenial absent
1 yes
2 no, mesial lamina of splenial separated from prearticular by postsplenial

48. Prearticular-angular contact
(Ahlberg et al. (2008): Character 48)

0 separated by ventral exposure of Meckelian element
1 prearticular contacts angular edge to edge
2 mesial lamina of angular sutures with prearticular

49. Prearticular sutures with surangular
(Ahlberg et al. (2008): Character 70)

0 no
1 yes

50. Prearticular shagreen field, distribution
(Ahlberg et al. (2008): Character 92)

0 gradually decreasing from dorsal to ventral
1 well defined dorsal longitudinal band
2 scattered patches or absent

51. Prearticular with mesially projecting flange on dorsal edge along posterior border of adductor fossa
(Ahlberg et al. (2008): Character 73)

0 no
1 yes

52. Adductor crest
(Ahlberg et al. (2008): Character 47)

0 absent
1 peak anterior to adductor fossa, dorsal margin of fossa concave
2 peak above anterior part of adductor fossa, dorsal margin of fossa convex

53. Premaxillary tooth proportions
(Modified from Ahlberg et al. (2008): Character 38)

0 all approximately same size
1 enlarged anterior tooth
2 posteriormost teeth at least twice height of anteriormost teeth

54. Maxilla extends behind level of posterior margin of orbit
(Ahlberg et al. (2008): Character 12)

0 yes
1 no

55. Maxilla makes interdigitating suture with vomer
(Ahlberg et al. (2008): Character 10)

0 no
1 yes

56. Posterodorsal process of maxilla
(Zhu & Ahlberg (2004): Character 51)

0 present
1 very weak or absent

57. Vomer proportions
(Zhu & Ahlberg (2004): Character 22)

0 not much broader than long
1 much broader than long

58. Vomerine fangs
(Zhu & Ahlberg (2004): Character 24)

0 absent
1 present

59. Vomerine fang pairs noticeably smaller than other palatal fang pairs
(Ahlberg et al. (2008): Character 41)

0 no
1 yes

60. Vomerine row of small teeth
(Ahlberg et al. (2008): Character 43)

0 present
1 absent

61. Anterior wall of vomer (forming posterior margin of palatal fossa) bears tooth row meeting in midline
(Ahlberg et al. (2008): Character 42)

0 yes
1 no

62. Vomerine shagreen field
(Ahlberg et al. (2008): Character 44)

0 absent
1 present

63. Anteromedial process of vomer
(Zhu & Ahlberg (2004): Character 21)

0 absent, vomers separated
1 present

2 absent, vomers in close contact

64. Posterior process of vomers
(Zhu & Ahlberg (2004): Character 20)

0 absent
1 short
2 long

65. Relationship of vomer to parasphenoid
(Zhu & Ahlberg (2004): Character 23)

0 no contact (via small gap) or simple abutment
1 overlap
2 no contact via blockage by pterygoid elements

66. Parasphenoid, denticulated field
(Ahlberg et al. (2008): Character 29)

0 present
1 absent

67. Posterior end of parasphenoid
(Zhu & Ahlberg (2004): Character 26)

0 denticulated field extends into spiracular groove
1 denticulated field does not extend into spiracular groove

68. Parasphenoid
(Ahlberg et al. (2008): Character 28)

0 does not overlap basioccipital
1 overlaps basioccipital

69. Proportions of entopterygoid
(Zhu & Ahlberg (2004): Character 18)

0 anterior end level with processus ascendens
1 anterior end considerably anterior to processus ascendens

70. Entopterygoids meeting in midline
(Zhu & Ahlberg (2004): Character 19)

0 no
1 yes

71. Entopterygoid-quadrate ramus margin in the subtemporal fossa
(Ahlberg et al. (2008): Character 20)

0 concave
1 with some convex component

72. Dentition of palatoquadrate complex
(Zhu & Ahlberg (2004): Character 16)

0 marginal teeth
1 tooth plates

73. Entopterygoid shagreen
(Ahlberg et al. (2008): Character 37)

0 dense
1 a few discontinuous patches or absent

74. Anterior palatal fenestra
(Ahlberg et al. (2008): Character 93)

0 single
1 double
2 absent

75. Interentopterygoid vacuities
(Ahlberg et al. (2008): Character 95)

0 absent
1 at least 2 x longer than wide
2 < 2 x longer than wide

76. Dermopalatine exposure
(Modified from Ahlberg et al. (2008): Character 2)

0 more or less confined to margins of the tooth row
1 medial exposure in addition to the tooth row

77. Dermopalatine/ectopterygoid denticle row
(Ahlberg et al. (2008): Character 33)

0 present
1 absent

78. Dermopalatine/ectopterygoid shagreen field
(Ahlberg et al. (2008): Character 34)

0 absent
1 present

79. Ectopterygoid reaches subtemporal fossa
(Ahlberg et al. (2008): Character 4)

0 no
1 yes

80. Number of fangs on ectopterygoid
(Zhu & Ahlberg (2004): Character 17)

0 one pair
1 two pairs
2 none
3 one unpaired

81. Ectopterygoid row (3+) of smaller teeth
(Ahlberg et al. (2008): Character 32)

0 present
1 absent

82. Subterminal mouth
(Daeschler et al. (2006): Character 73)

0 absent
1 present

83. Number of nasals
(Zhu & Ahlberg (2004): Character 44)

0 many

1 one or two

84. Anterior tectal/septomaxilla
(Ahlberg et al. (2008): Character 1)

0 anterior tectal (external bone, dorsal to nostril)
1 septomaxilla (external or internal bone, posterior to nostril)
2 absent

85. Lateral rostral present
(Ahlberg et al. (2008): Character 9)

0 yes
1 no

86. Median postrostral
(Zhu & Ahlberg (2004): Character 43)

0 absent (postrostral mosaic)
1 present
2 absent (nasals meet in midline)

87. Dorsal fontanelle on snout
(Ahlberg et al. (2008): Character 94)

0 absent
1 present

88. Internasal pits
(Zhu & Ahlberg (2004): Character 25)

0 undifferentiated
1 strong midline ridge but shallow pits
2 deep pear-shaped pits

89. External nostrils
(Zhu & Ahlberg (2004): Character 29)

0 two pairs
1 one pair

90. Premaxilla forms part of choanal margin

(Ahlberg et al. (2008): Character 17)

0 broadly
1 point
2 not, excluded by vomer

91. Position of anterior external nostril
(Zhu & Ahlberg (2004): Character 30)

0 facial
1 edge of mouth

92. Lacrimal
(Ahlberg et al. (2008): Character 8)

0 contributes to orbital margin
1 excluded from margin

93. Contact between lacrimal and posterior supraorbital [postfrontal]
(Zhu & Ahlberg (2004): Character 56)

0 absent
1 present

94. Jugal
(Ahlberg et al. (2008): Character 7)

0 does not extend anterior to orbit
1 extends anterior to orbit

95. Jugal extends anterior to middle of orbit
(Daeschler et al. (2006): Character 78)

0 no
1 yes

96. Jugal-quadratojugal contact
(Zhu & Ahlberg (2004): Character 52)

0 absent
1 present

97. Position of orbits

(Zhu & Ahlberg (2004): Character 59)

0 lateral and widely separated
1 dorsal and close together

98. Postorbital bone

(Zhu & Ahlberg (2004): Character 54)

0 contributes to orbital margin
1 excluded from orbital margin

99. Contact between postorbital and lacrimal

(Daeschler et al. (2006): Character 84)

0 absent
1 present

100. Quadratojugal, squamosal and preopercular fused

(Zhu & Ahlberg (2004): Character 62)

0 no
1 yes

101. Subsquamosals

(Zhu & Ahlberg (2004): Character 61)

0 absent
1 present

102. Preoperculosubmandibular

(Zhu & Ahlberg (2004): Character 60)

0 absent
1 present

103. Width of ethmoid relative to its length, from snout tip to the posterior margin of the parietals

(Modified from Zhu & Ahlberg (2004): Character 32)
States based on clumped morphospace.

0 greater or = 80%
1 75%-45%

2 less than or = 35%

104. Proportion of skull roof (measured as length from tip of snout to posterior margin of postparietals) lying anterior to middle of orbits

(Modified from Daeschler et al. (2006): Character 75)
States based on clumped morphospace.

0 20-30%
1 33-40%
2 45-48%
3 >53%

105. B-bone

(Zhu & Ahlberg (2004): Character 46)

0 absent
1 present

106. Prefrontal (anterior supraorbital)

(Ahlberg et al. (2008): Character 15)

0 twice as long as broad, or less
1 three times as long as broad

107. Prefrontal (anterior supraorbital)

(Ahlberg et al. (2008): Character 16)

0 transverse anterior suture with tectal (or opens broadly into external nostril)
1 tapers to point anteriorly

108. Relative size of prefrontal [anterior supraorbital] and posterior supraorbital [postfrontal]

(Daeschler et al. (2006): Character 76)

0 similar
1 prefrontal much bigger

109. Postfrontals [posterior supraorbitals] extend anterior of orbits

(Daeschler et al. (2006): Character 86)

0 no
1 yes

110. Shape of postfrontals (posterior supraorbitals)
(Zhu & Ahlberg (2004): Character 58)

0 posterior process shorter than orbital margin
1 posterior process much longer than orbital margin

111. Contact between intertemporal and postfrontal (posterior supraorbital)
(Zhu & Ahlberg (2004): Character 55)

0 present
1 absent

112. Contact between parietal and postfrontal (posterior supraorbital)
(Zhu & Ahlberg (2004): Character 57)

0 present
1 absent

113. Frontals
(Zhu & Ahlberg (2004): Character 45)

0 absent
1 present

114. Parietals surround pineal foramen/eminence
(Zhu & Ahlberg (2004): Character 38)

0 yes
1 no

115. Pineal foramen
(Zhu & Ahlberg (2004): Character 36)

0 present
1 absent

116. Position of pineal foramen/eminence
(Zhu & Ahlberg (2004): Character 37)

0 level with posterior margin of orbits
1 well posterior to orbits

117. Shape of pineal series
(Zhu & Ahlberg (2004): Character 39)

0 round or oval
1 kite-shaped with distinct posterior corner. (non-applicable for Kenichthys)

118. Intemporal
(Ahlberg et al. (2008): Character 6)

0 present
1 absent

119. Dermal intracranial joint
(Zhu & Ahlberg (2004): Character 71)

0 present
1 absent

120. Postparietals narrow to a point posteriorly
(Zhu & Ahlberg (2004): Character 41)

0 no
1 yes

121. Proportions of postparietal shield
(Zhu & Ahlberg (2004): Character 40)

0 not extremely wide posteriorly
1 extremely wide posteriorly

122. Supratemporal
(Modified from Ahlberg & Johanson (1998): Character 49)

0 recognizable as a distinct bone
1 fused with postparietal

123. Posterior margin of tabulars
(Modified from Zhu & Ahlberg (2004): Character 42)

0 anterior to the posterior margin of postparietals
1 level with the posterior margin of postparietals
2 posterior to the posterior margin of the postparietals

124. Postspiracular (extratemporal)
(Zhu & Ahlberg (2004): Character 50)

0 present
1 absent

125. Position of the postspiracular (extratemporal)
0 anterior
1 posteriorly displaced

126. Contact between postspiracular [extratemporal] and supratemporal
(Zhu & Ahlberg (2004): Character 48)

0 absent
1 present

127. Premaxilla canal-bearing
(Zhu & Ahlberg (2004): Character 68)

0 yes
1 no

128. Infraorbital canal follows premaxillary suture
(Zhu & Ahlberg (2004): Character 69)

0 no
1 yes

129. Postotic sensory canal
(Zhu & Ahlberg (2004): Character 66)

0 runs through skull roof
1 follows edge of skull roof

130. Postorbital junction of supraorbital and infraorbital canals
(Zhu & Ahlberg (2004): Character 67)

0 absent
1 present

131. Mandibular sensory canal

(Ahlberg et al. (2008): Character 57)

0 prsesnt
1 absent

132. Mandibular canal exposure
(Ahlberg et al. (2008): Character 58)

0 entirely enclosed, opens through lines of pores
1 mostly enclosed, short sections of open grooves
2 mostly open, short sections with lines of pores
3 entirely open

133. Mandible: oral sulcus/surangular pit line
(Ahlberg et al. (2008): Character 59)

0 present
1 absent

134. Foramina (similar to infradentary foramina) on cheekplate
(Zhu & Ahlberg (2004): Character 63)

0 absent
1 present

135. Submandibulars and gulars
(Daeschler et al. (2006): Character 80)

0 present
1 absent

136. Large median gular
(Modified from Daeschler et al. (2006): Character 81)

0 absent
1 present

137. Preopercular
(Daeschler et al. (2006): Character 88)

0 large
1 small

138. Preopercular
(Ahlberg et al. (2008): Character 18)

0 present
1 absent

139. Opercular
(Ahlberg et al. (2008): Character 14)

0 present
1 absent

140. Spiracular notch
(Daeschler et al. (2006): Character 87)

0 absent
1 small opening
2 narrow groove
3 wide notch

141. Anterior margin of median extrascapular
(Zhu & Ahlberg (2004): Character 65)

0 long
1 very short

142. Extrascapular bones
(Zhu & Ahlberg (2004): Character 64)

0 median overlaps laterals
1 laterals overlap median

143. Extrascapular bones
(Daeschler et al. (2006): Character 77)

0 present
1 absent

144. Posttemporal
(Ahlberg et al. (2008): Character 109)

0 present
1 absent

145. Supracleithrum
0 present
1 absent

146. Anocleithrum
(Zhu & Ahlberg (2004): Character 85)

0 exposed
1 subdermal

147. Anocleithrum
(Ahlberg et al. (2008): Character 99)

0 oblong with distinct anterior overlap area
1 drop-shaped with no anterior overlap area
2 absent

148. Orientation of cleithrum
(Daeschler et al. (2006): Character 105)

0 vertically oriented: tilted less than 10 degrees caudally
1 angulated: tilted over 10 degrees caudally

149. Cleithrum, postbranchial lamina
(Ahlberg et al. (2008): Character 101)

0 present
1 absent

150. Contact margin for clavicle on cleithrum
(Zhu & Ahlberg (2004): Character 84)

0 straight or faintly convex
1 strongly concave

151. Scapulocoracoid
(Ahlberg et al. (2008): Character 115)

0 small and tripodal

1 large plate pierced by large coracoid foramen
2 very large plate without large coracoid foramen

152. Coracoid plate

(Daeschler et al. (2006): Character 103)

0 absent
1 present and extends ventromedially

153. Scapular blade

(Ahlberg et al. (2008): Character 114)

0 absent
1 small with narrow top
2 large with broad top

154. Shoulder joint polarity

(Zhu & Ahlberg (2004): Character 87)

0 caput humeri concave
1 caput humeri convex

155. Glenoid position

(Daeschler et al. (2006): Character 104)

0 elevated from plane formed by clavicles
1 offset ventrally to lie at same level as clavicular plane

156. Glenoid orientation

(Daeschler et al. (2006): Character 110)

0 posterior orientation
1 lateral component to glenoid orientation

157. Glenoid proportions

Measured in plane with glenoid orientation. Height at maximum extent divided by maximum length: *Medoevia* = 0.60; *Eusthenopteron* = 0.60; *Tinirau* = 0.42; *Panderichthys* = 0.48; *Tiktaalik* = 0.44; *Acanthostega* = 0.45; *Ichthyostega* = 0.44; *Greererpeton* = 0.44; *Proterogyrinus* = 0.40; *Eoherpeton* = 0.47.

0 height/width ratio 60% or greater
1 height/width ratio 40-50%

158. Interclavicle

(Ahlberg et al. (2008): Character 106)

0 small and concealed (unornamented) or absent
1 large and exposed (ornamented)

159. Interclavicle shape

(Ahlberg et al. (2008): Character 107)

0 ovoid
1 kite-shaped
2 with posterior stalk

160. Archipterygial pectoral fin

(Zhu & Ahlberg (2004): Character 86)

0 no
1 yes

161. Humerus

(Ahlberg et al. (2008): Character 103)

0 narrow tapering entepicondyle
1 square or parallelogram-shaped entepicondyle

162. Body of humerus

(Zhu & Ahlberg (2004): Character 89)

0 cylindrical
1 flattened rectangular

163. Deltoid and supinator process on humerus

(Zhu & Ahlberg (2004): Character 90)

0 absent
1 present

164. Anterior termination of ventral ridge

(Daeschler et al. (2006): Character 96)

0 adjacent to the caput humeri
1 offset distally toward the proximodistal mid-region of anterior margin of humerus

165. Ectepicondylar process
(Daeschler et al. (2006): Character 100)

0 terminates proximal to epipodial facets
1 extends distal to epipodial facets

166. Radius and ulna
(Ahlberg et al. (2008): Character 110)

0 radius much longer than ulna
1 approximately equal length

167. Radial facet
(Daeschler et al. (2006): Character 98)

0 faces distally
1 has some ventrally directed component

168. Area proximal to radial facet
(Daeschler et al. (2006): Character 102)

0 short, cylindrical leading edge, with no muscle scars
1 enlarged, sharp leading edge, with areas for muscle attachments

169. Shape of radius
(Daeschler et al. (2006): Character 94)

0 bladelike
1 subcylindrical

170. Radial length
(Daeschler et al. (2006): Character 101)

0 longer than humerus
1 shorter than humerus

171. Ulnar facet
(Daeschler et al. (2006): Character 99)

0 faces distally
1 has some ventrally directed component

172. Olecranon process on ulna
(Daeschler et al. (2006): Character 95)

0 absent
1 present

173. Transverse joint at the level of the ulnare, intermedium and radius
(Daeschler et al. (2006): Character 89)

0 absent
1 present

174. Articulations for more than two radials on ulnare
(Daeschler et al. (2006): Character 90)

0 absent
1 present

175. Postaxial process on ulnare
(Daeschler et al. (2006): Character 91)

0 absent
1 present

176. Branched radials distal to the ulnare
(Daeschler et al. (2006): Character 93)

0 absent
1 present

177. Radials
(Zhu & Ahlberg (2004): Character 91)

0 jointed
1 unjointed

178. Digits
(Ahlberg et al. (2008): Character 102)

0 absent
1 present

179. Lepidotrichia in paired appendages
(Ahlberg et al. (2008): Character 108)

0 present
1 absent

180. Basal segments of lepidotrichia elongated
(Zhu & Ahlberg (2004): Character 92)

0 no
1 yes

181. Expanded ribs
(Daeschler et al. (2006): Character 113)

0 absent
1 present

182. Imbricate ribs
(Daeschler et al. (2006): Character 114)

0 absent
1 present

183. Ribs, trunk
(Ahlberg et al. (2008): Character 111)

0 no longer than diameter of intercentrum
1 longer

184. Ribs, trunk
(Modified from Ahlberg et al. (2008): Character 112)

0 all straight
1 at least some ventral component

185. Ribs, trunk
(Ahlberg et al. (2008): Character 113)

0 all cylindrical
1 some or all bear flanges from posterior margin which narrow distally

2 some or all flare distally

186. Supraneural spines

(Zhu & Ahlberg (2004): Character 99)

0 present
1 absent

187. Ilium, iliac canal

(Ahlberg et al. (2008): Character 104)

0 absent
1 present

188. Ilium, posterior process

(Ahlberg et al. (2008): Character 105)

0 oriented posterodorsally
1 oriented approximately horizontally posteriorly

189. Postaxial process on fibula
0 present
1 absent

190. Postaxial process on fibula, size
0 large
1 small

191. Dorsal and anal fins

(Zhu & Ahlberg (2004): Character 93)

0 present
1 absent

192. Posterior radials in posterior dorsal fin

(Zhu & Ahlberg (2004): Character 94)

0 not branched
1 branched

193. Caudal fin

(Zhu & Ahlberg (2004): Character 95)

0 heterocercal
1 diphycercal

194. Epichordal radials in caudal fin

(Zhu & Ahlberg (2004): Character 96)

0 absent
1 present

195. Nature of dermal ornament

(Ahlberg et al. (2008): Character 97)

0 tuberculate
1 fairly regular pit and ridge
2 irregular
3 absent or almost absent

196. Nature of ornament: "starbursts" of radiating ornament on at least some bones

(Ahlberg et al. (2008): Character 98)

0 no
1 yes

197. Cleithral ornamentation

(Daeschler et al. (2006): Character 106)

0 present
1 absent

198. Basal scutes

(Zhu & Ahlberg (2004): Character 97)

0 absent
1 present

199. Body scale morphology

(Zhu & Ahlberg (2004): Character 98). *Platycephalichthys* scored after Snitting (2008b).

0 rhomboid with internal ridge
1 round

200. Squamation
(Ahlberg et al. (2008): Character 117)

0 complete body covering of scales
1 ventral armour of gastralia

201. Tooth folding
(Zhu & Ahlberg (2004): Character 14)

0 none
1 generalized polyplocodont
2 labyrinthodont
3 dendrodont

202. Cosmine
(Zhu & Ahlberg (2004): Character 34)

0 present
1 absent

203. Westoll lines
(Zhu & Ahlberg (2004): Character 35)

0 absent
1 present

Part E.

Taxon-by-character matrix and character optimizations for the phylogenetic analysis of fossil taxa.—The data matrix was subjected to a maximum parsimony analysis in the software package PAUP (Swofford 2002) and a Bayesian analysis using the software package Mr. Bayes(Huelsenbeck 2001, Ronquist and Huelsenbeck 2003). All characters were assigned an equal weight, multistate characters were run unordered, and a heuristic search algorithm was used in PAUP to search for the shortest networks—rooted on *Porolepis*, *Glyptolepis*, *Powichthys*, *Youngolepis*, *Diabolepis*, and *Dipterus*. Bremer decay indices were calculated using PAUP(Swofford 2002) and TNT(Goloboff 1999, Nixon 1999), and Bayesian posterior probabilities were calculated with Mr. Bayes following an analysis that included 500,000 mcmc generations, sampling every 1,000 generations, and with 20 samples discarded as burnin. Character evolution was examined in MacClade(Maddison and Maddison 2000), which was also used to produce the character state distributions below. *Eusthenopteron* is scored as *E. foordi* and *Platycephalichthys* scored as *P. bischoffi*.

A = 0 & 1; **B** = 0 & 2	**1**		**11**		**21**		**31**		**41**	
Acanthostega	100-?	00002	0111?	02110	10010	10100	10100	10011	00-21	11001
Balanerpeton	10?-?	?0002	01???	-?1-0	00110	21221	20100	11-11	2??22	02202
Baphetes	10?-?	?0002	0111?	?111?	?0??0	0????	?????	1????	?????	?????
Barameda	00???	?1???	?????	?????	?0000	10???	?????	?????	?????	?????
Beelarongia	?0???	?????	?????	?????	?0???	?0???	?????	?????	?????	?????
Cabonnichthys	?0???	?1?02	0????	1????	?0000	101??	??0-1	00000	??-10	0???0
Canowindra	?0???	?????	?????	?????	?0???	?0???	?????	?????	?????	?????
Cladarosymblema	00000	01102	00000	01010	00000	10100	00000	00000	?0-00	00000
Crassigyrinus	?0???	?0002	0????	?2110	00110	?1100	10111	11-10	0???2	?1202
Dendrerpeton	10?-?	?0002	0111?	?????	?011?	?1?11	11???	?1-?1	?11??	??212
Diabolepis	01???	?0?0?	10?0?	?---?	?1?-?	0-?--	?????	-????	?????	?????
Dipterus	010??	?00?0	10???	?---?	?1?-?	0-0--	?????	-????	?????	??0??
Ectosteorhachis	00???	01102	?0??0	01010	00?00	10100	??000	00000	?0-00	00000
Elginerpeton	?????	?????	?????	?2111	10?00	10?00	001??	10000	0???1	11001
Elpistostege	?0???	?????	?????	?????	?????	?0???	?????	?????	?????	?????
Eoherepton	10?-?	?0002	01?1?	?????	??01?	?1111	10100	11011	0??22	01?12
Eusthenodon	?????	?????	0????	1??1?	?0?00	101??	???-1	0?00?	??10	0????
Eusthenopteron	00000	11102	00001	11010	00000	00100	000-1	00000	00-10	00000
Glyptolepis	00101	11101	00???	20-00	00001	00?00	??000	00000	??00	00000
Glyptopomus	?????	?1???	?????	?????	?00??	?????	?????	?????	?????	?????
Gogonasus	00000	01102	00000	01010	00000	00000	00000	000A0	??01	?0000
Gooloogongia	?0???	?1???	?????	01010	00000	1????	??0??	0???0	?????	?????
Greererepton	10?-?	?0002	0111?	?2110	00110	21100	111??	11111	01122	11202
Gyroptychius	?0???	01102	0??02	01010	00000	?0???	??00	00000	?0-00	?0?0?
Ichthyostega	10?-?	?0002	01?1?	02110	10210	10100	00100	10111	00-21	11102
Jarvikina	???0?	11102	00??1	1????	?0?00	001??	???-1	0????	?001?	0????
Kenichthys	000??	?1?02	10???	01010	00000	00000	??000	010A0	?0-00	000??
Koharalepis	?0???	?????	?????	?????	?000?	?0???	?????	?????	?????	?????
Mandageria	00???	11102	??02	?????	?0000	101??	?????	0?00?	?????	0????
Marsdenichthys	?????	?????	?????	?????	?0??0	00???	??00	0?0??	?????	?????
Medoevia	00000	01102	00000	01010	000?0	0?100	00000	00000	00-00	00000
Megalichthys	00???	?1102	00000	01010	00000	10100	??000	00000	?0-00	0000?
Osteolepis	00???	01102	00000	01010	00000	00?00	??0??	0????	?????	?????
Panderichthys	00010	01102	00000	01010	00000	10100	000-1	00000	00-01	00100
Pederpes	?0???	?0??2	01?1?	?????	?????	?????	?????	?????	?????	?????
Platycephalichthys	0??1?	?1???	?0???	01010	000?0	10???	000?1	00??0	00-01	000?0
Porolepis	?0101	11101	10?0?	20-00	00001	000??	??00	?0000	??00	00000
Powichthys	011?1	?1111	10?0?	20-0?	?0?01	0?0??	??00	??0??	??00	0?0??
Proterogyrinus	10?-?	?0002	01???	??110	00010	?1111	111??	11-11	??22	??212
Silvanerpeton	?0???	?0002	01???	?????	?0010	?1??1	101?0	11-1?	0??22	????2
Spodichthys	00???	11102	00001	1??1?	?0000	00100	00010	00??0	00-00	0000?
Tiktaalik	000-?	01102	00?00	0?010	00000	101?0	?00-1	00100	00-21	00100
Tinirau	0000?	?1102	00001	?????	?0000	10000	???-1	00000	00-01	00000
Tristichopterus	?0???	1110?	?0?01	1???0	00000	00?00	??010	00000	?0-00	?0???
Ventastega	10?-1	?0?02	?101?	?2011	100?0	10100	001-1	00111	00-21	11101
Whatcheeria	?????	?0002	01?1?	?2110	00210	20100	00100	10111	01021	11101
Youngolepis	01001	10010	10001	20-00	00?01	00000	??000	010A0	?0-00	00000

	5		**6**		**7**		**8**		**9**	
	1		**1**		**1**		**1**		**1**	
Acanthostega	00200	10100	00202	01011	00010	00012	00101	21011	11011	11000
Balanerpeton	01001	?0101	11200	0?110	10022	11110	1?121	20–12	00001	1100–
Baphetes	??000	?0101	11202	0?111	00020	11110	1?111	20–11	00001	1100–
Barameda	??10?	??1??	????0	????0	?0???	?????	?0100	00?1?	00000	?000?
Beelarongia	???0?	?????	?????	?????	?????	?????	?0???	10?1?	00?0?	001?0
Cabonnichthys	0?100	10100	00221	010?0	00000	00?01	00000	10010	00000	00100
Canowindra	???0?	?????	?????	?????	?????	?????	?00??	?0?1?	00000	00100
Cladarosymblema	00100	01100	00100	010?0	?0000	?????	?0010	10010	00000	00000
Crassigyrinus	?0001	?0100	10202	0?1?1	00010	11003	00111	21?12	00001	1100–
Dendrerpeton	0?00?	?0011	11200	??110	10022	1111?	10111	20–1?	00001	1100–
Diabolepis	?00?–	?00––	–1000	000?0	01?0?	–??–?	–?0??	?000–	1????	?0???
Dipterus	?0?––	?0?––	––20–	0?011	01?–?	–??–?	–00??	0000–	10?00	10000
Ectosteorhachis	00100	011?0	00100	010?0	?0?0?	?????	??010	10010	00000	0000?
Elginerpeton	??0??	?????	?????	?????	?????	?0???	?????	???1?	1????	?????
Elpistostege	??000	?????	?????	0????	?????	?????	?1000	00???	?0011	0101?
Eoherepton	1201?	?????	?????	1?11?	101?0	110?0	10121	21–1?	01011	1100–
Eusthenodon	?0100	10100	00221	???10	00?0?	000??	00000	10?10	00100	00100
Eusthenopteron	00000	00100	00221	01010	00000	00001	00000	10010	00000	00000
Glyptolepis	00000	10100	00000	00000	00000	10010	00000	0020–	00000	00000
Glyptopomus	??00?	00100	??2??	??10	0??00	???1?	??000	10?1?	00000	00000
Gogonasus	00000	001?0	00200	01000	00000	00010	00000	10010	00000	00000
Gooloogongia	???0?	0????	?????	?????	?0???	?????	?0100	00?1?	00001	00000
Greererepton	02200	??11	10??2	0?111	00011	1101?	00121	21?11	10001	1100–
Gyroptychius	00000	00100	00100	010?0	?0000	000?0	00000	10010	00000	00010
Ichthyostega	00201	10100	10202	01011	00100	1101B	0010?	20012	11011	11000
Jarvikina	?00?0	?010?	??221	?1??0	?0???	?????	??000	1001?	00000	000?0
Kenichthys	00000	0????	????0	010??	?0?0?	?00?0	00?00	?000–	00000	00001
Koharalepis	???0?	0?10?	?????	??10	?????	?????	?00??	?0?1?	00000	00100
Mandageria	??100	10100	00221	01010	00000	00001	00000	10010	00100	00110
Marsdenichthys	???0?	1010?	???0?	010?0	?00?0	0??0?	?0000	10?1?	00000	00?00
Medoevia	00100	00100	00100	01000	00000	00010	00???	?0?10	00000	00000
Megalichthys	00100	011?0	00100	01000	?0000	?00?0	00010	10010	00000	00000
Osteolepis	00000	0????	?????	010?0	00000	000?0	00000	10?10	00000	00000
Panderichthys	00000	10100	00211	01010	00000	00010	01000	00010	10000	110A0
Pederpes	??00	?????	????2	0???1	?00?0	11113	0???1	?????	?0001	11000
Platycephalichthys	0010?	101?0	002?1	?????	??00	?????	??000	10?10	00?00	0???1
Porolepis	00000	101??	??000	00000	00000	????0	?00??	0020–	00000	00000
Powichthys	?00?0	?0??0	00002	0000?	?0000	0????	??0??	0020–	0?0??	?0???
Proterogyrinus	12010	??0??	????2	1?111	100?0	11000	10121	20–1?	1?001	1100–
Silvanerpeton	02010	??001	11??2	0?111	10020	1??0?	?0121	20–1?	00001	1100–
Spodichthys	00?0?	00???	??22?	??10	000?0	0???0	?????	1??1?	0????	?0???
Tiktaalik	00000	1010?	0?211	01010	00000	00010	00?00	?001?	10011	11010
Tinirau	00000	10100	00221	01010	00000	00010	000––	10?10	00000	00??1
Tristichopterus	00000	0?100	00221	0?0?0	?0???	0????	?0???	10?10	00000	00000
Ventastega	00200	1?100	?0???	0?0?1	00000	010??	?01?1	21??1	?1011	11000
Whatcheeria	0020?	??01	10??2	??1?1	000?0	11000	00121	20?11	?1011	11000
Youngolepis	00000	001?–	–1000	000?0	?0?0?	001?0	0?0??	?010–	0?000	000?1

	101		111		121		131		141	
Acanthostega	00230	11100	-0100	1-110	0021-	-0000	01101	01013	--111	01101
Balanerpeton	00220	11000	00100	1-010	0021-	-????	1-101	0-113	--111	-2?1?
Baphetes	00230	11100	00100	1-010	0011-	-0000	03?01	0-113	--111	-2?1?
Barameda	??000	00000	00000	00001	00000	10001	?????	???0?	110??	????0
Beelarongia	00000	???00	00000	00000	11000	???0?	???0?	?0001	110??	??000
Cabonnichthys	00110	00001	00000	11000	00101	0000?	???00	00001	01000	00001
Canowindra	00100	???00	00000	10?00	11000	???0?	??00?	?000?	110??	000??
Cladarosymblema	00010	00000	00011	--000	00000	00001	00000	00001	01000	00000
Crassigyrinus	00230	11100	00100	1-010	0021-	-0000	03101	0-113	--111	-201?
Dendrerpeton	00230	11000	00100	1-010	0021-	-????	1-101	0-113	--111	-211?
Diabolepis	??001	????0	01011	0-?10	000??	?1110	?????	?????	?????	?????
Dipterus	0??11	0?000	01011	?-?10	0011-	-??01	00?0?	???00	00000	10001
Ectosteorhachis	0?010	????0	00011	--000	00???	?0001	00???	?????	010??	?????
Elginerpeton	????0	?????	?????	?????	?????	?????	000??	?????	?????	???1?
Elpistostege	??23?	10110	??1??	1-1?0	0?21-	-????	00??0	1????	?????	?????
Eoherepton	00230	01?00	00100	1-010	0021-	-????	1-101	0-11?	?????	?????
Eusthenodon	00110	00001	10000	11000	00101	0000?	???00	0000?	01000	0000?
Eusthenopteron	00110	00000	00000	00000	00101	00001	00000	00001	01000	00001
Glyptolepis	11000	???00	??011	0-000	1-000	00101	00000	00000	00000	10000
Glyptopomus	00100	00000	00000	00000	00000	0??0?	0???0	00001	0100?	????1
Gogonasus	00100	00000	00000	0-000	00000	00001	00000	00002	01000	000?0
Gooloogongia	00100	00000	00000	00001	00000	1000?	???00	00000	11000	100??
Greererepton	00220	10110	-0100	1-?10	0011-	-0000	01101	0-11?	-?111	-210?
Gyroptychius	00100	0??00	00000	10000	00000	00001	00000	00001	01000	00001
Ichthyostega	00230	11100	-0100	0-110	0021-	-0000	02101	01013	--111	-2101
Jarvikina	00110	????1	00000	10?00	001??	???0?	???0?	?????	010??	?????
Kenichthys	00000	???00	?0?10	0-?00	00000	01101	00?1?	?????	010??	????0
Koharalepis	00000	0?000	00000	10000	11000	???01	00000	00001	11000	??0??
Mandageria	00110	00001	10000	11000	01101	?000?	???00	0000?	11000	00001
Marsdenichthys	00110	????0	00000	00000	10000	0????	????0	?0002	11000	??0??
Medoevia	00010	0?110	00000	00000	01000	?????	????0	00001	01000	0?000
Megalichthys	00??0	???00	00011	--000	000??	?0001	???00	00001	010??	000?0
Osteolepis	00110	0?000	00000	00000	00000	00001	0000?	?0001	01000	00000
Panderichthys	00220	00010	00100	1-010	0011-	-0001	00000	1?002	01000	00101
Pederpes	00??0	01?0?	??1??	??0??	?011-	-????	???0?	?1013	--111	-211?
Platycephalichthys	??1?0	00???	??000	--0??	?????	?0?0?	0?0??	?00??	?????	?????
Porolepis	11000	????0	?1011	0-000	1-100	00101	00000	00001	00000	10000
Powichthys	?1000	????0	01010	10010	001??	?1101	?????	?????	00000	????0
Proterogyrinus	00230	11000	00100	0-010	0021-	-????	1-101	0-113	--111	-201?
Silvanerpeton	00230	01000	00100	0-010	0021-	-????	1-101	0-113	--111	-201?
Spodichthys	??100	???0?	00000	00000	00100	00?0?	0?000	???0?	??0??	??001
Tiktaalik	00230	1?1?0	-0100	0-?10	0011-	-??00	00000	10013	--110	00101
Tinirau	00100	0000?	?0000	1-000	00100	00001	00000	00001	0?0??	??001
Tristichopterus	00110	00000	00000	0-000	00101	???0?	?0?00	00001	010??	00001
Ventastega	00230	1??00	001??	1-010	0?11-	?0???	0000?	??013	-?111	01?11
Whatcheeria	00230	???00	00100	0-010	0011-	-????	01001	01013	--111	-2?0?
Youngolepis	00000	?????	?1?11	0-010	001??	?1110	???1?	?????	?????	????0

	151		161		171		181		191	
Acanthostega	21011	11110	11111	00111	00???	0011-	10102	1001-	1-111	11-01
Balanerpeton	21?11	1?110	111??	11111	110?0	0011-	10102	1001-	1-??1	11-?1
Baphetes	???11	1???0	11110	11111	11???	?????	?????	?001-	????1	11?01
Barameda	???1?	????0	0010?	00001	00010	?0001	?????	?????	????0	0??1?
Beelarongia	?????	?????	001??	?????	?????	???00	?????	?????	????0	00?0?
Cabonnichthys	???1?	????0	0010?	00000	00001	01000	?????	?????	0?100	00110
Canowindra	?????	?????	?????	?????	?????	?????	?????	?????	0?0?0	0?01?
Cladarosymblema	??010	0????	?????	?????	?????	???00	?????	?????	????3	00?00
Crassigyrinus	???1?	??110	11111	11111	11???	0011-	10110	1??1-	1-??2	11-?1
Dendrerpeton	21211	1?110	1111?	11111	11000	0011-	10110	1001-	1-??1	11-?1
Diabolepis	?????	?????	?????	?????	?????	?????	?????	?????	????3	0????
Dipterus	???0?	????1	?????	?????	?????	?0001	00100	0????	010?3	000?0
Ectosteorhachis	?????	?????	?????	?????	?????	???00	?????	?????	????3	0??0?
Elginerpeton	??01?	?????	111??	?????	?????	?????	?????	?11??	????1	11???
Elpistostege	?????	?????	?????	?????	?????	?????	?????	?????	????0	?????
Eoherepton	21211	11??0	111-0	1111?	1????	?????	10110	1001-	1-??1	0?-??
Eusthenodon	?????	?????	?????	?????	?????	?????	?????	?????	0???0	00?10
Eusthenopteron	00010	00000	00100	00000	00001	01000	00000	10-00	00100	00110
Glyptolepis	00000	0?0?1	000??	?????	?????	?0001	00000	0????	01003	00010
Glyptopomus	?????	?????	?????	?????	?????	???00	?????	?????	0?100	0?000
Gogonasus	???1?	????0	00100	00000	000?1	01000	?????	?????	????3	00?0?
Gooloogongia	?0???	??0?0	?????	00000	00010	???01	00???	???00	000?0	00010
Greererepton	21111	11110	11111	11111	11???	0011-	10111	1001-	1-??1	11-01
Gyroptychius	?????	?????	?????	?????	?????	???00	00000	1????	0?103	00100
Ichthyostega	21010	11120	11111	11111	11???	0011-	11111	1111-	1-111	11-??
Jarvikina	?????	?????	?????	?????	?????	?????	?????	?????	????0	0??1?
Kenichthys	?????	?????	?????	?????	?????	?????	?????	?????	????3	0?10?
Koharalepis	?????	?????	?????	?????	?????	???00	?????	?????	????0	00?0?
Mandageria	???1?	????0	001?0	00000	00001	01000	?????	?????	00100	00010
Marsdenichthys	?????	?????	?????	?????	?????	?????	?????	?????	0???0	00?10
Medoevia	00010	0000?	00100	?0???	?????	?????	?????	?????	0???3	00100
Megalichthys	00010	0?0?0	00100	00000	00001	01000	-----	1????	00003	00100
Osteolepis	?????	????0	?????	?????	?????	???00	-----	1????	00003	00100
Panderichthys	11011	110?0	01100	00100	00000	0?000	00101	1??01	1-1?0	00-00
Pederpes	21111	1?120	1111?	11111	11???	?011-	11111	1011-	1-??1	11-?1
Platycephalichthys	00???	0????	?????	?????	?????	?????	?????	?????	????0	0??0?
Porolepis	?????	?????	?????	?????	?????	?????	?????	?????	??0?3	00?00
Powichthys	?????	?????	?????	?????	?????	?????	?????	?????	????3	0??0?
Proterogyrinus	21211	11110	11110	11111	11???	0011-	10110	1001-	1-??1	11-01
Silvanerpeton	21211	1?120	111??	11111	11???	0011-	10110	1011-	1-??1	11-?1
Spodichthys	000??	?????	?????	?????	?????	?????	?????	?????	????0	00???
Tiktaalik	11011	110?0	01101	01101	00110	10001	11?01	?0-??	1-??0	00-00
Tinirau	00?10	01??0	?????	0??0?	??001	01000	00000	10-01	0?000	00?10
Tristichopterus	???1?	????0	00100	00000	00001	01000	?????	1????	00000	00110
Ventastega	210??	??110	?????	?????	?????	?????	?????	?00??	????1	11???
Whatcheeria	2121?	??120	111?1	?11??	1????	?????	11111	101??	1-??3	11-??
Youngolepis	000?0	0????	?????	?????	?????	?????	?????	?????	????3	0??0?

	201
Acanthostega	210
Balanerpeton	210
Baphetes	210
Barameda	?1?
Beelarongia	?00
Cabonnichthys	110
Canowindra	?1?
Cladarosymblema	100
Crassigyrinus	210
Dendrerpeton	?10
Diabolepis	?01
Dipterus	?01
Ectosteorhachis	?00
Elginerpeton	???
Elpistostege	???
Eoherepton	?10
Eusthenodon	110
Eusthenopteron	110
Glyptolepis	31?
Glyptopomus	?10
Gogonasus	100
Gooloogongia	?1?
Greererepton	210
Gyroptychius	100
Ichthyostega	210
Jarvikina	11?
Kenichthys	100
Koharalepis	100
Mandageria	110
Marsdenichthys	?1?
Medoevia	?00
Megalichthys	100
Osteolepis	100
Panderichthys	210
Pederpes	?10
Platycephalichthys	?1?
Porolepis	300
Powichthys	100
Proterogyrinus	210
Silvanerpeton	?10
Spodichthys	???
Tiktaalik	210
Tinirau	?10
Tristichopterus	?10
Ventastega	???
Whatcheeria	?10
Youngolepis	100

Character optimizations.

Rhizodonts + other tetrapodomorphs:

- 89, 0→1 = one pair of external nostrils
- 114, 1→0 = parietals surround a parietal foramen/eminance
- 127, 1→0 = premaxilla is canal bearing
- 128, 1→0 = infraorbital canal does not follow the premaxillary suture
- 195, 3→0 = tuberculate ornament
- 199, 0→1 = round body scales
- 202, 0→1 = loss of cosmine

Rhizodonts:

- 26, 0→1 = 1 pair of dentary fangs
- 83, 0→1 = 1 or 2 nasal bones
- 120, 0→1 = postparietals narrow to a point posteriorly
- 126, 0→1 = contact between postspiracular and supratemporal

'Osteolepiforms' + elpistostegalians:

- 86, 0→1 = median postrostral present
- 140, 0→1 = small opening to spiracular notch
- 146, 1→0 = exposed anocleithrum
- 180, 1→0 = basial lepidotrichial segments not elongate

Canowindrids:

- 121, 0→1 = PP shield extremely wide posteriorly

Canowindrids (minus *Marsdenichthys*):

- 122, 0→1 = supratemporal fused with postparietals

Canowindrids (*Koharalepis* + *Beelarongia* only):

- 103, 1→0 = width of ethmoid ≥80%
- 199, 1→0 = rhomboid body scales
- 202, 1→0 = cosmine present

Megalichthyiforms + eotetrapodiforms:

- 198, 0→1 = basal scutes present

Megalichthyiforms:

- 15, 1→0 = dorsal directly above ventral hyomandibular facet
- 69, 1→0 = anterior end of entopterygoid level with processus ascendens
- 195, 0→3 = ornament absent or almost absent
- 199, 1→0 = rhomboid body scales
- 202, 1→0 = cosmine present

Megalichthyiforms (minus *Gogonasus*):

- 63, 2→1 = anteromedial process of vomer present

Megalichthyiforms (minus *Gyroptychius*):

- 104, 0→1 = 33-40% of skull roof lies anterior to orbits

Osteolepidids (*Medoevia* + megalichthyids):

- 53, 0→1 = enlarged premaxillary tooth
- 103, 1→0 = width of ethmoid ≥80%

Megalichthyiforms (megalichthyids only)

- 26, 0→1 = 1 pair of dentary fangs
- 57, 0→1 = vomers much broader than long
- 114, 0→1 = parietals do not surround the pineal foramen
- 115, 0→1 = pineal foramen absent

Eotetrapodiforms:

- 64, 0→2 = long posterior processes on vomers
- 65, 0→1 = overlap of vomers and parasphenoid
- 123, 0→1 = posterior margin of tabular level with posterior margin of postparietals
- 150, 0→1 = contact margin for clavicle on cleithrum strongly concave

Tristichopterids:

- 16, 0→1 = parasymphyseal plate short not sutured to coronoid
- 34, 0→1 = Posterior coronoid longer than more anterior coronoids

Tristichopterids (minus *Spodichthys*):

- 104, 0→1 = 33-40% of skull roof anterior to orbits
- 125, 0→1 = posteriorly displaced PSP

Tristichopterids (*Eusthenopteron* + remaining tristichopterids):

- 35, 0→1 = posterior coronoid one-third longer than more anterior coronoids
- 44, 0→1 = 2 fang pairs on posteriormost coronoid
- 193, 0→1 = diphycercal caudal fin

Tristichopterids (*Jarvikina* + remaining tristichopterids):

- 110, 0→1 = posterior orbital process much longer than orbital margin
- 116, 0→1 = pineal foramen well posterior to orbital margin

Tristichopterids (*Cabonnichthys* + remaining tristichopterids):

- 26, 0→1 = 1 pair of dentary fangs
- 53, 0→1 = enlarged premaxillary tooth
- 98, 0→1 = postorbital excluded from orbital margin
- 117, 0→1 = pineal series kite-shaped

Tristichopterids (*Mandageria* + *Eusthenodon* only):

- 93, 0→1 = contact between lacrimal and posterior supraorbital
- 111, 0→1 = no contact between intertemporal and posterior supraorbital

Tinirau + [*Platycephalichthys* + Elpistostegalia]:

- 26, 0→1 = 1 pair of dentary fangs
- 35, 0→1 = posterior coronoid one-third longer than more anterior coronoids
- 45, 0→1 = organized tooth row on posterior coronoid
- 56, 0→1 = posterodorsal maxillary process weak/absent
- 116, 0→1 = pineal foramen posterior to orbits
- 157, 0→1 = height/width ratio of glenoid fossa, 40-50%
- 190, 0→1 = highly reduced postaxial process on fibula

Platycephalichthys + Elpistostegalia:

- 4, 0→1 = In posterior view, the fenestra ventrolateralis extends dorsal to the ethmoid articulation

- 199, 1→0 = rhomboid scales

Elpistostegalia:

- 48, 0→1 = prearticular contacts angular edge-to-edge
- 86, 1→0 = median postrostral absent
- 91, 0→1 = anterior nostril at edge of mouth
- 96, 0→1 = jugal/quadratojugal contact
- 103, 1→2 = ethmoid proportions ≤35%
- 113, 0→1 = frontals present
- 151, 0→1 = scapulocoracoid, large plate pierced by coracoid foramen
- 152, 0→1 = coracoid plate present
- 156, 0→1 = lateral component to glenoid orientation

Elpistostegalia minus *Panderichthys*:

- 44, 0→2 = no fang pairs on posterior-most coronoid
- 94, 0→1 = jugal extends anterior to front of orbit
- 95, 0→1 = jugal extends anterior to middle of orbit
- 106, 0→1 = anterior supraorbital 3x longer than broad
- 108, 0→1 = prefrontal much bigger than postfrontal
- 130, 1→0 = no fusion of supra and infraorbital canals
- 139, 0→1 = loss of opercular
- 143, 0→1 = loss of extrascapular bones
- 144, 0→1 = lost of posttemporals
- 165, 0→1 = ectepicondytlar processes extends distal to epipodial facets
- 170, 0→1 = radius is shorter than the humerus
- 181, 0→1 = expanded ribs present

Elpistostege + *Tiktaalik*:

- 99, 0→1 = contact between postorbital and lacrimal

Elginerpeton + remaining elpistostegalians:

- 21, 0→1 = mesial parasymphyseal foramen present
- 33, 0→1 = loss of Meckelian exposure in precoronoid fossa
- 46, 0→1 = forked prearticular
- 47, 0→1 = prearticular sutured to mesial lamina of splenial (i.e., mesial lamina of the splenial present)
- 50, 0→1 = well-defined dorsal longitudinal band of shagreen on prearticuular
- 161, 0→1 = square/parallelogram-shaped entepicondyle on humerus
- 195, 0→1 = fairly regular pit and ridge derma ornament
- 196, 0→1 = starbursts radiating on at least some bones
- 197, 0→1 = loss of cleithral ornamentation

Ventastega + remaining elpistostegalians:

- 39, 0→1 = anterior and middle coronoid teeth ≤½ the height of dentary teeth
- 40, 0→1 = anterior coronoid contacts splenial
- 53, 0→2 = posterior teeth ≥2x height of anterior teeth

Acanthostega + remaining elpistostegalians:

- 13, 0→1 = single large foramen in the hypophyseal region of braincase
- 35, 1→0 = posterior coronoid not substantially longer than anterior coronoids
- 132, 0→1 = mandibular line canal mostly enclosed but short sections with open grooves
- 133, 0→1 = no surangular pit line

Ichthyostega + remaining elpistostegalians:

- 23, 0→2 = dentary teeth smaller tan maxillary teeth
- 61, 0→1 = anterior wall of vomer lacks teeth along the ridge
- 76, 0→1 = medial exposure of dermopalatine, in addition to tooth roow
- 147, 1→2 = loss of anocleithrum
- 159, 1→2 = interclavicle with a posterior stalk
- 166, 0→1 = radius and ulna about equal in length
- 171, 0→1 = ulnar facet has some ventrally directed component
- 172, 0→1 = olecranon process present
- 184, 0→1 = at least some ventral component to ribs

Whatcheeria + remaining elpistostegalians:

- 21, 1→0 = no mesial parasymphyseal foramen
- 26, 1→2 = 1 unpaired dentary fang (i.e., no replacement pit)
- 42, 0→1 = posterodorsal process of posterior coronoid
- 60, 0→1 = no row of small teeth on the vomer
- 68, 0→1 = parasphenoid overlaps basioccipital
- 84, 0→2 = loss of anterior tectal

Pederpes + remaining elpistostegalians:

- 92, 1→0 = lacrimal contributes to orbital margin
- 94, 1→0 = jugal does not extend anterior to the anterior orbital margin

Greererpeton + remaining elpistostegalians:

- 138, 0→1 = loss of preoperculum
- 159, 2→1 = kite-shaped interclavicle (i.e., no posterior stalk)
- 182, 1→0 = loss of imbricate ribs
- 188, 1→0 = posterior process on ileum oriented posterodorsally

Crassigyrinus + remaining elpistostegalians:

- 53, 2→0 = all premaxillary teeth all the same size
- 91, 1→0 = facial position of anterior external nostril (not edge of mouth)
- 132, 1→3 = entirely open mandibular line canal
- 185, 1→0 = all ribs cylindrical

Baphetes + remaining elpistostegalians:

- 62, 0→1 = vomerine shagreen field present
- 74, 1→2 = anterior palatal fanestra absent
- 81, 0→1 = no row of 3+ smaller teeth on ectopterygoid
- 165, 1→0 = ectepicondylar process terminates proximal to epipodial facets

Stem-lissamphibians + stem-amniotes + embolomeres:

- 71, 0→1 = convex component to the ectopterygoid/quadratojugal in the subtemporal fossa
- 108, 1→0 = anterior and posterior surpraorbitals of similar size

- 131, 0→1 = loss of mandibular sensory line canal

Stem-lissamphibians (*Balanerpeton* + *Dendrerpeton*):

- 65, 2→0 = no contact (via gap – or simple abutment) between vomers and parasphenoid
- 70, 1→0 = entopterygoids do not meet at midline
- 75, 0→2 = interentopterygoid vacuities < 2x longer than wide

Stem-amniotes (*Sylvanerpeton* + embolomeres):

- 23, 1→0 = De teeth same size as Mx teeth
- 54, 0→1 = Mx does not extend behind posterior orbital margin
- 79, 1→0 = ectopterygoid does not reach subtemporal fossa

Embolomeres (*Proterogyrinus* + *Eoherpeton*):

- 51, 0→1 = Prearticular with mesially projecting flange on dorsal edge along posterior border of adductor fossa
- 66, 0→1 = denticulated field of parasphenoid absent

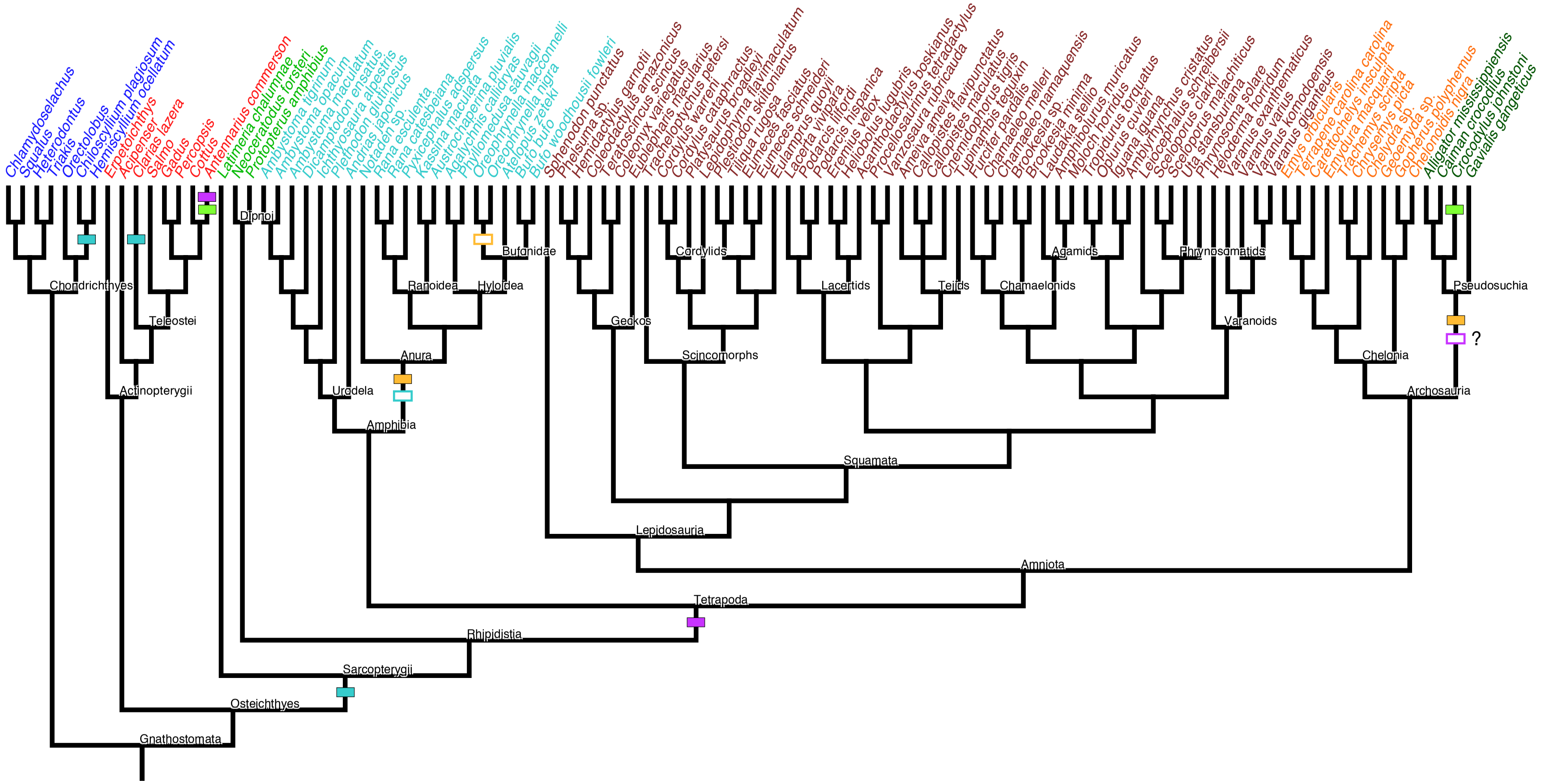

Figure S4.1. The evolution of gnathostome gaits. Supertree topology structured primarily around molecular sequence data, including the archosaurian position of turtles. See references in main text. A solid teal bar = trotting gait present; open teal bar = trotting gait lost. Solid purple bar = lateral sequence diagonal-couplet gait present; open purple bar = lateral sequence diagonal-couplet gait lost. Solid orange bar = bounding or hopping gait present. Green bar = galloping gait present. For the distribution of other gaits, including the lateral sequence lateral-couplet, the lateral sequence singlefoot, and the diagonal sequence diagonal-couplet, see description in main text and in the character matrix of Part B in the supplementary information. See Figures 4.3 and S4.2 for alternative molecular and morphological topologies, though neither change the pattern of gait evolution depicted here.

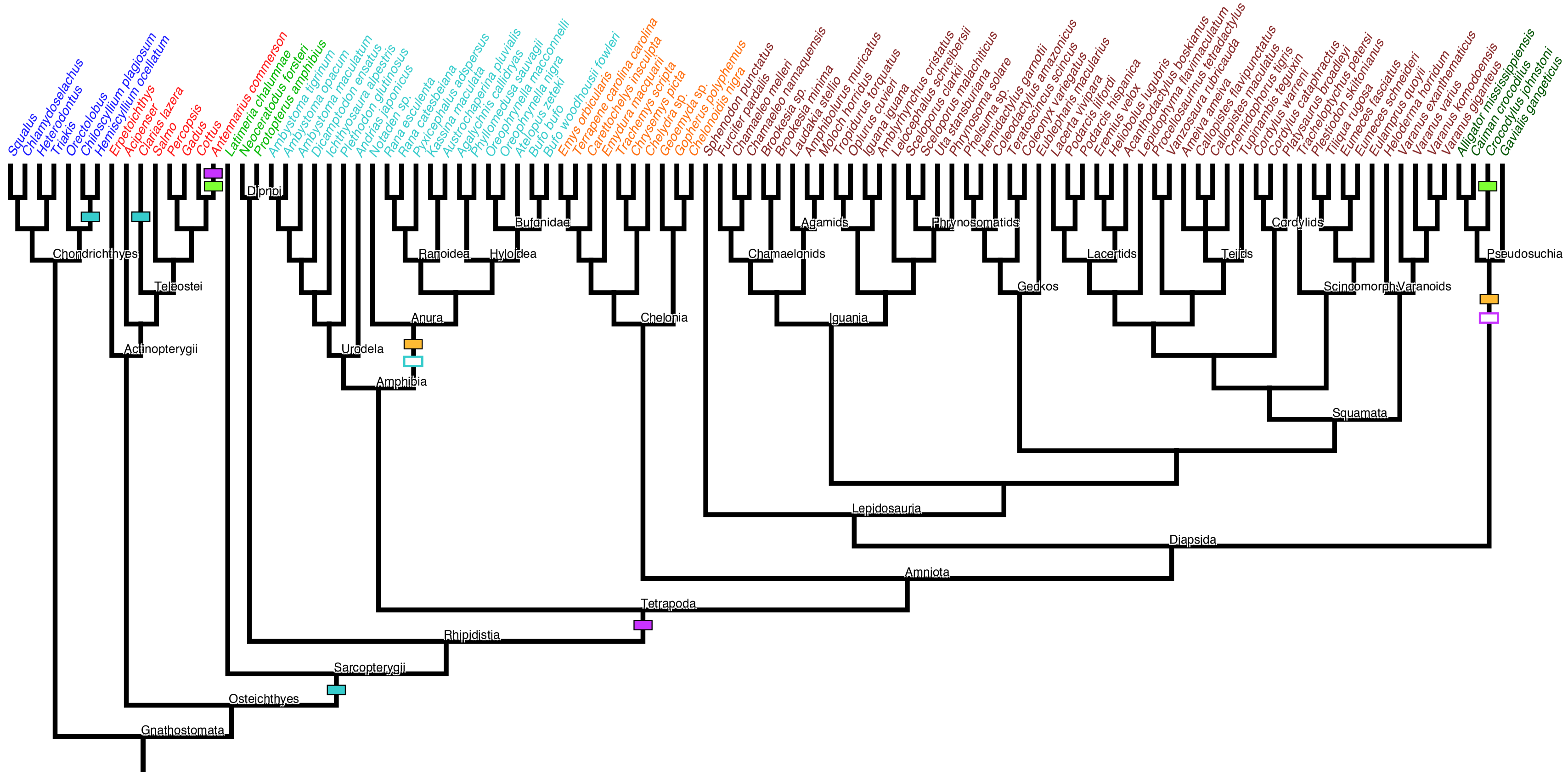

Figure S4.2. The evolution of gnathostome gaits. Supertree topology structured primarily around morphological data, including the traditional position for turtles. See references in main text. A solid teal bar = trotting gait present; open teal bar = trotting gait lost. Solid purple bar = lateral sequence diagonal-couplet gait present; open purple bar = lateral sequence diagonal-couplet gait lost. Solid orange bar = bounding or hopping gait present. Green bar = galloping gait present. For the distribution of other gaits, including the lateral sequence lateral-couplet, the lateral sequence singlefoot, and the diagonal sequence diagonal-couplet, see description in main text and in the character matrix of Part B in the supplementary information. See Figures 4.3 and S4.1 for alternative molecular topologies, though neither change the pattern of gait evolution depicted here.

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CHAPTER FIVE: CONCLUDING DISCUSSION

Summary of research: the origin of terrestrial vertebrates

I set out to answer four interconnected questions at the interface of paleontology, neontology, evolutionary morphology, and evolutionary theory: (1) what are the traits that underpin the tetrapod condition?; (2) how well do current phylogenies explain the distribution of character-states among Devonian and Carboniferous stem-tetrapods?; (3) how do the environments of stem-tetrapods inform and contextualize these evolutionary changes?; and (4) given the distribution of synapomorphies, and what is known about how modern and fossil sarcopterygians (including tetrapods) negotiate their aquatic and terrestrial environments, how do insights from evolutionary morphology and evolutionary theory inform the origin of walking on land? The aim here is to summarize the answers to these questions, both individually and collectively.

A Marine Stem-tetrapod from the Devonian of Western North America

Tinirau clackae is a well-preserved fossil sarcopterygian from the Middle Devonian of Nevada that helps to resolve the temporal and anatomical framework of tetrapod origins. New data from *Tinirau* were included in constructing the most extensive phylogenetic analysis of Devonian and Carboniferous tetrapodomorphs to date. The cladistic result provides a great degree of phylogenetic resolution among Devonian taxa. There are no polytomies (Figure 5.1), and rhizodontids, canowindrids, megalichthyiforms, and tristichopterids form successive sister taxa to more crownward groups. In turn, *Tinirau* is sister to *Platycephalichthys* and other elpistostegalians, one step crownward of tristichopterids. When combined with the early Middle Devonian (Eifelian) age Polish trackways data, the late Middle Devonian (Givetian) age of *Tinirau*, its phylogenetic position as stem to the first digited forms, and its many symplesiomorphies, suggest a rich early tetrapodomorph record still to be discovered. In addition, *Tinirau* documents substantial parallelism among early stem-tetrapods (with many tristichopterid synapomorphies evolving in parallel during the early history of eotetrapodiforms); shows that incipient stages of the terrestrial appendicular condition (e.g., elongate glenoid fossae) began when sarcopterygians still retained their median fins and occupied aquatic habitats; and that conventional crown-group limb characteristics first originated in the pelvic fins.

The extensive list of crown-tetrapod symplesiomorphies that evolved among Devonian and Carboniferous tetrapodomorphs are available as supplementary information (see Chapters 2 and 4), but the primary changes, especially those that relate to the origin of terrestrial locomotion, involved mosaic rounds of modifying, decoupling, and linking components of the axial and appendicular skeletons. Examples include: the pectoral appendages in total-group tetrapods are primitively larger than the corresponding pelvics, though this may be autapomorphic; the humerus (ball) and scapulocoracoid (socket = glenoid fossa) diagnose tetrapodomorphs primitively (in contrast with the reverse polarity in dipnomorphs); for well-known canowindrids, megalichthyiforms, and tristichoptrids, pectoral and pelvic limbs are about the same size; associated with a flattening of the proximal humerus, the glenoid fossa becomes elongate in the first elpistostegalians (possibly related to

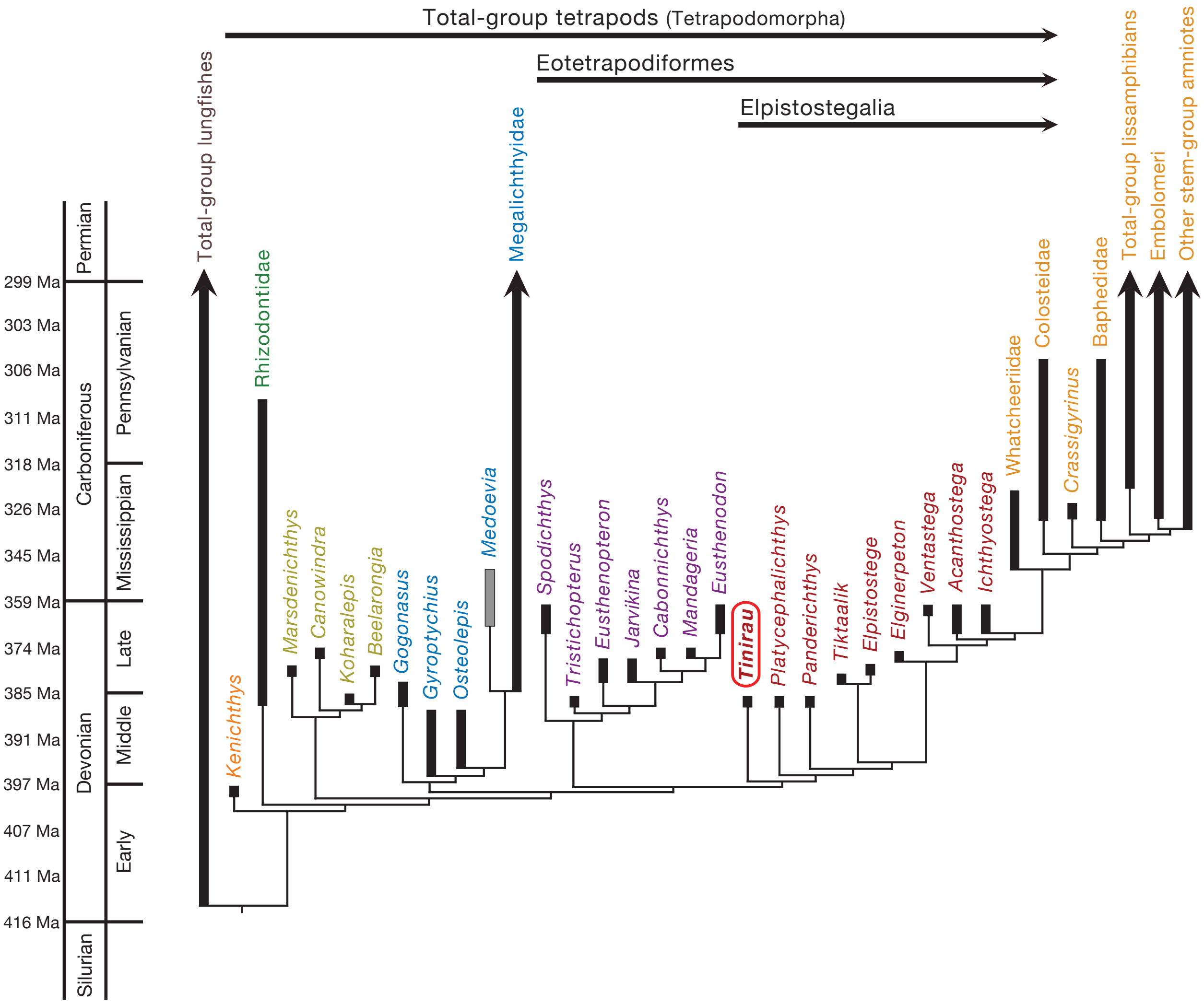

Figure 5.1. Interrelationships among Devonian and select Carboniferous tetrapodomorphs including new data from ***Tinirau clackae*****.** Analysis includes 46 taxa and 203 characters. Ghost ranges are calibrated after the early Middle Devonian (Eifelian) Zachełmie footprints (Niedźwiedzki et al. 2010) and "scenario 1" from Friedman and Brazeau (2011). Tetrapodomorphs include all taxa that are not total-group lungfishes. Rhizodonts are in green, canowindrids are in yellow, megalichthyiforms are in blue, tristichopterids are in purple, Devonian elpistostegalians are in red, and Carboniferous elpistostegalians are in orange.

the differentiation of dorsal and ventral limb musculature); *Panderichthys* and crownward taxa lose their dorsal and anal fins but retain their paired fins; *Tiktaalik* has a ventrally directed accessory glenoid that, in combination with its flexible elbow, 'wrist', and 'hand' regions, appears to provide support when its limbs are pulled under its body; *Tiktaalik* loses some of its operculogular bones to create a physical neck (possibly associated with girdle rotation and walking); *Acanthostega* has the first known digits but retains gills and an undifferentiated atlas and axis (suggesting that the physical neck did not evolve 'for' neck mobility); *Acanthostega* and crownward taxa have at least a rib pair associated with a sacrum; *Ichthyostega* and crownward taxa have buttressed infraglenoids that support caput humeri (possibly associated with weight bearing limbs); and colosteids such as *Greererpeton* have the first differentiated atlas (sugesting that the mobile neck evolved much later, and that the first function of the physical neck was related to terrestrial locomotion). Interestingly, even though the phylogenetic resolution among canowindrids, megalichthyiforms, and tristichopterids (the so called 'osteolepiforms') is well-resolved (see Figure 5.1), the utility of their traits to underscore main stem changes that underpin the tetrapod condition still remains ambiguous. This is also in part why understanding the morphology of *Tinirau* is so helpful, because even though it superficially appears much like a tristichopterid, the details of its anatomy (apomorphies: a pair of dentary fangs, a posterior coronoid that is much longer than the anterior coronoids, an organized tooth row on the posterior coronoid, a weak posterodorsal maxillary process, a pineal foramen that lies posterior to the orbits, an elongate glenoid fossa, and a reduced postaxial fibular process; versus plesiomorphies: a single fang pair on the posterior coronoid, an anteriorly positioned postspiracular, a single ectopterygoid fang pair, about 25% of the dermatocranium anterior to the orbits, and a heterocercal caudal fin skeleton) help to resolve the history of the elpistostegalian condition and document the transition from 'osteolepiform' to the first digit-bearing sarcopterygians. Moreover, the combination of *Tinirau*'s phylogenetic position and coastal marine preservation were critical for testing hypotheses about the evolution of stem-tetrapod paleoenvironments.

The Paleoenvironmental History of Stem-tetrapods

To test the paleoenvironmental origins question, I traced the relationship between the phylogenetic and paleoenvironmental histories of Devonian stem-tetrapods. I analyzed sedimentological, assemblage, and isotopic data to elucidate how the Devonian rock record informs the evolution of tetrapodomorph habitats, and reconstructed the ancestral environments of the first digit-bearing sarcopterygians. Results suggest that: tetrapodomorphs took either a freshwater or marginal marine origin; both freshwater and marginal environments pervaded the early history of major groups even though members of each clade were more often freshwater than not; the first elpistostegalians moved into coastal marine environments (established by the analysis of *Tinirau* in Chapter 2, and the modified phylogenetic result in Chapter 3) (see Figure 5.2); later diverging elpistostegalians moved shoreward (including the likely phylogenetic position of the Polish trackmaker); and the first digited sarcopterygian body fossils appeared following at least four cladogenetic events where extramontane freshwater habitats were the ancestral environment. This conforms nicely with Thomson's (1980) hypothesis for the marine origin of elpistostegalians, which predicts that part of their diversification included taxa that invaded extramontane freshwater environments. By contrast, it dispels with

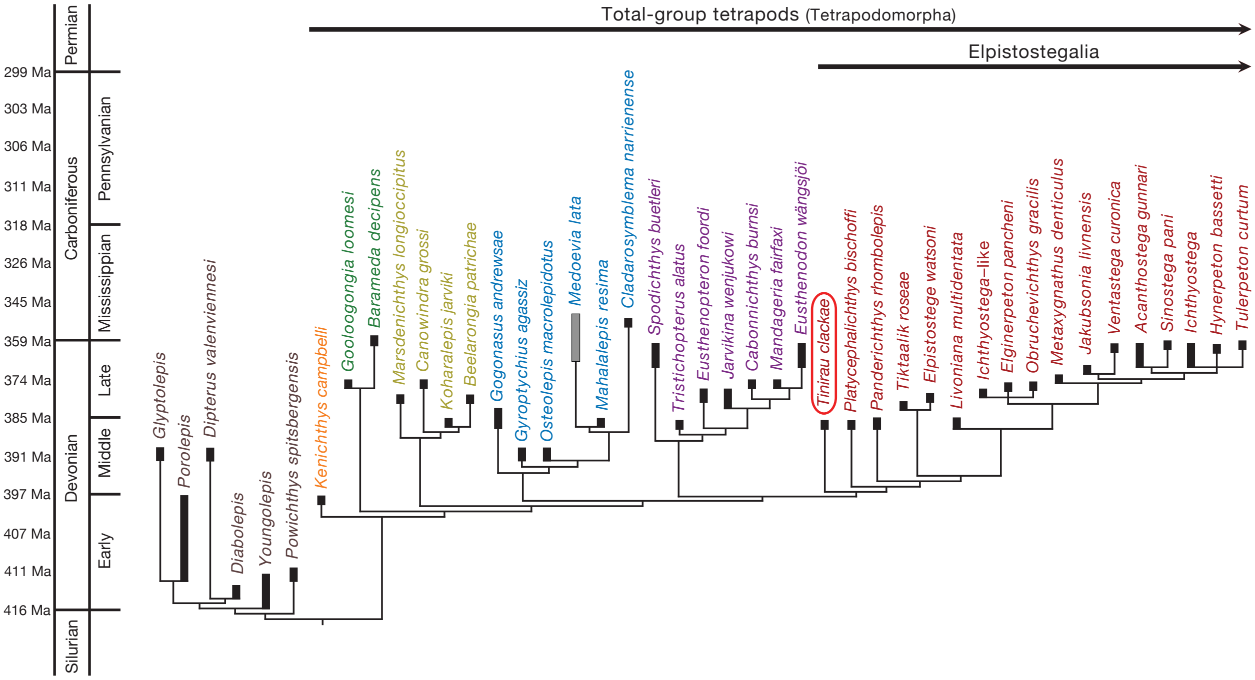

Figure 5.2. Interrelationships among Devonian and select Carboniferous stem-tetrapods used to test the paleoenvironmental origin of elpistostegalians. Analysis includes 43 taxa and 175 characters. Ghost ranges are calibrated after the early Middle Devonian (Eifelian) Zachełmie footprints (Niedźwiedzki et al. 2010) and "scenario 1" from Friedman and Brazeau (2011). Rhizodonts are in green, canowindrids are in yellow, megalichthyiforms are in blue, tristichopterids are in purple, and elpistostegalians are in red.

classical notions of digited forms evolving in continental interiors where drying ponds drove the origin of terrestriality and air breathing. Moreover, this result raises interesting questions about the all-encompassing importance of *Tiktaalik* in the vertebrate water-to-land transition. If *Tiktaalik* is a secondarily freshwater taxon, then what does this suggest about autapomorphies specific to its adaptive zone? There is little doubt that *Tiktaalik* shares many synapomorphies with crownward forms (e.g., the partial loss of the operculogular series, a physical neck, anteriorly imbricate ribs, frontal bones, &c.), but renewed effort should be made to consider traits (especially related to its pectoral propping mechanisms) that may be less revealing to terrestrial vertebrates origins than conditions present in other taxa that at this point in history still inhabited marine-influenced environments. Conversely, as an early elpistostegalian, and following from the paleoenvironmental analyses in Chapter 3 (Figure 5.3), the likely phylogenetic position of the Eifelian age Zachełmie trackmaker fits beautifully with the predictions of Thomson (1980). In combination with these data, it helps to confirm that the first digited members of the body fossil record descended from elpistostegalians that ancestrally inhabited marine-influenced environments.

Unfortunately, none of these taxa reveal why elpistostegalians invaded freshwater environments during the Middle and Late Devonian extinction events. Insights may be drawn from patterns in other groups—such as gastropods and bivalves, which also colonized freshwater at this time—but until the re-analysis of vertebrate diversity dynamics in freshwater-influenced ecosystems, it remains only suggestive that extramontane freshwater environments functioned as refugia for sarcopterygians during these Devonian events.

The Origin and Early Evolution of Terrestrial Locomotion

In a phylogenetic assessment of over 150 modern and fossil taxa, I analyzed osteological, myological, and locomotor data to test how gaits evolved in gnathostome evolution, and how variation in the historical, constructional, and functional components of the axial and appendicular systems underpins the origin of terrestrial locomotion. Results showed that: the trot evolved at least three times in gnathostome evolution; the tetrapod myaxial condition evolved in water ~35 million years before the origin of amphibious sarcopterygians; trackways data from modern and fossil records cannot verify whether the lateral sequence diagonal-couplet gait evolved by the end-Devonian; the original function of the physical neck was likely related to the origin of terrestrial locomotion; and distinguishing aptations and nonaptations in a continuum of historical, constructional, and functional influences is critical to elucidating evolutionary transformations.

Again, the phylogenetic result from Chapter 1 (Figure 5.1) was essential to teasing apart relevant crown-tetrapod plesiomorphies. However, bracketing these paleontological data within a comparative neontological framework of gait and myological analyses also helped structure and resolve patterns related to the origin of terrestrial locomotion. In particular, tracing axial and appendicular changes among extant and extinct taxa helped show that much of what it means to trot as a gnathostome was channeled along phyletic lines. That is, even though critical to the origin of terrestrial locomotion, lateral undulation and shoulder position are stem-chordate and stem-gnathostome apomorphies, respectively. Figure 5.4 helped structure thinking about these changes in a comparative, integrative, and historical framework. In this respect, 'adaptive' puzzles that might otherwise appear

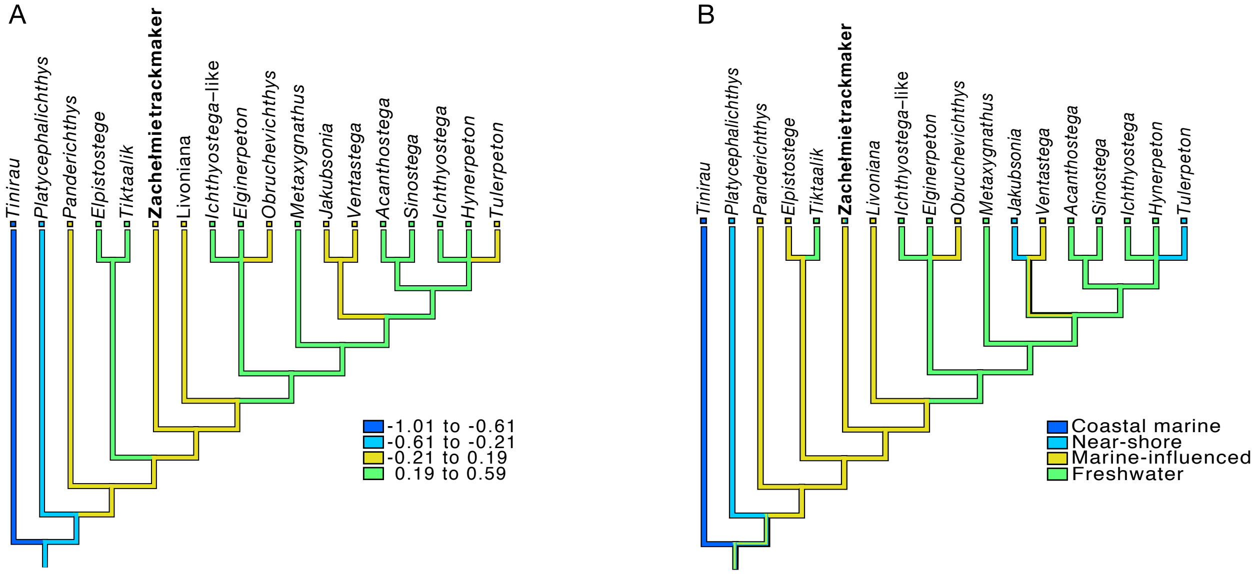

Figure 5.3. The likely phylogenetic position of the Polish, Zachełmie trackmaker following the 95% credibility estimate from ‟scenario 1” after Friedman and Brazeau (2011). (A) The pattern following the results of the assemblage analysis in Chapter 3, Figures 3.2 and 3.3; (B) The pattern following the analysis of sedimentological data in Chapter 3. The Zachełmie trackmaker was scored as polymorphic, marine-influenced/nearshore. *Elginerpeton* was scored as ‘freshwater’ following the local sedimentological signal from Scat Craig.

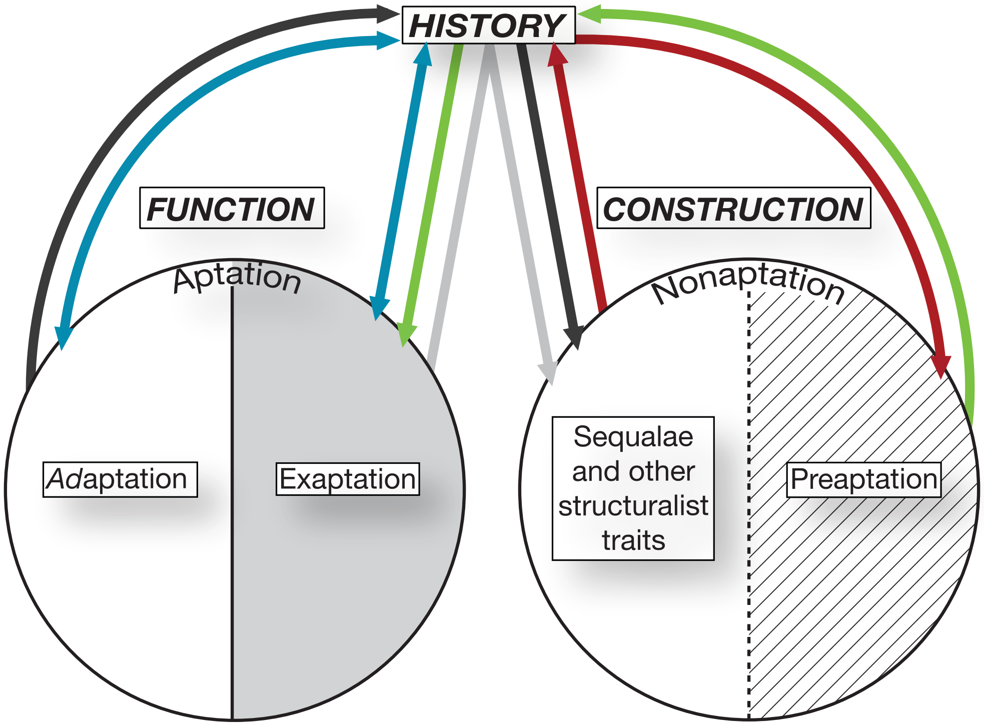

Figure 5.4. The relationships among construction, function, and the attainment of biological traits over evolutionary time. Aptations consist of traits that are fit for the environment and are produced by natural selection; they include primary adaptations and coopted traits that become exaptations. Nonaptations include characters that are not produced by natural selection for their current roles, and consist of any one of a number of structuralist traits. Preaptations are potential but unrealized aptations, in particular, exaptations; they become (ex)aptations when acted upon by the complex interplay of the environment, developmental channeling, and natural selection. "History" encapsulates these interactions within a phylogenetic context. The colored arrows trace the conceptual flow of these relationships. Aptations such as ad- and ex-apations, may become part of the nonaptive structuralist pool when their functions become vestigial. For clarity, note that the only term with the prefix ad- includes adaptation. Modified from concepts in Gould (2002), Gould and Vrba (1982), Lauder (1981), Raup (1972), Seilacher (1970), and Wake (1991).

obscure, such as the origin of the neck and its original utility, begin to make sense. Stem-tetrapods are simply broader members of total-group gnathostomes which are diagnosed by an anterior dermatocranium, and a loss of the bones anterior to the dermal shoulder will unavoidably produce a space. Thus, even if these bones were lost for adaptive reasons, the patterned congregation of neural crest cells, and retained dermal roof, cheek, and shoulder bones still located in their symplesiomorphic positions, also contributed to the existence of a space between the remaining components of the dermal skull. In following, this structuralist space shifted from preaptation to exaptation as girdle rotation enhanced the first steps of a walking gait. History, construction, and function all contribute to biological design, and phylogenetic methods can help distinguishing their relative contributions to organismal form.

Summary

The description and analysis of *Tinirau* established a phylogenetic backbone for testing hypotheses about the origin of terrestrial vertebrates. This phylogeny helped structure the traits that diagnose crown-tetrapods, their paleoenvironmental history, and the origin of their locomotory strategies. Without this result, the early history of elpistostegalians would still begin with *Panderichthys*, and Thomson's (1980) marine origins hypothesis (variant II) would remain uncorroborated. Moreover, the integration of these paleontological data with the neontological analyses in Chapter 4 helped build a framework for testing hypotheses about macroevolutionary transformations. We have moved far beyond the neo-Darwinian functionalism that embodies classical depictions of evolutionary transitions. It is hoped that a deeper consideration of integrative biology, and the three historic modes for thinking about organismal form, will further underscore the utility of pluralism and its bearing on reconstructing the evolutionary history of biological diversity.

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