University of Alberta

Lower Triassic Coelacanths of the Sulphur Mountain Formation (Wapiti Lake) in British Columbia, Canada

by

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To my father,

ABSTRACT

The coelacanths from the Lower Triassic Sulphur Mountain Formation (Wapiti Lake) have been known for nearly 100 years, though they remained undescribed. Preliminary works identified them as belonging to a single undescribed species of *Whiteia*; however, six distinct coelacanths were identified: six new species, four new genera and a new family were erected thus bringing the total of known Lower Triassic coelacanths to near twenty-five, the highest recorded in the fossil record. Additionally, two of the new coelacanths, *Rebellatrix*, gen. nov., and *Everticauda*, gen. nov., have body forms that are new and distinct from forms previously attributed to coelacanths. These specimens represent the first major change in the coelacanth body form in 75 million years (since the Mississippian). These coelacanths are the first piece of evidence that morphological diversity may have actually peaked in the Lower Triassic. Finally, the various caudal morphotypes are examined to determine functional differences (related to locomotion) and the lifestyles (niches) that they suggest.

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CHAPTER ONE

GENERAL INTRODUCTION

Coelacanths (actinistians) are among the most basal members of Sarcopterygii, the clade that gives rise to tetrapods (Forey, 1998). They first appear in the Early Devonian (Johanson, 2006) prior to the appearance of the first recorded amphibians (Blieck et al., 2010; Friedman and Brazeau, 2010). The fossil record of coelacanths extends to the end of the Cretaceous (Maastrichtian), with the last known fossil coelacanth, *Megalocoelacanthus* (Schwimmer et al., 1994), being also the largest known coelacanth, reaching lengths of up to three meters. It was thought that coelacanths had gone extinct until, in 1938, after a seventy-five million year gap, a living coelacanth was caught off the coast of South Africa sending the scientific world into a frenzy. *Latimeria chalumnae* Smith, 1939, looked nearly identical to fossil forms previously described in the hundred years before its discovery; it was dubbed a living fossil for this uncanny appearance to fossil forms. Since then, dozens more fossil coelacanths have been described (Forey, 1998), as well as a second species of living coelacanth, *Latimeria menadoensis* (Erdmann, 1998; Pouyaud et al., 1999).

Coelacanths of Sulphur Mountain Formation (Wapiti Lake)

The Lower Triassic fossils of the Wapiti Lake area have been known since Laudon et al. (1949) described large and well-preserved articulated fishes that were found within what is now Wapiti Lake Provincial Park, BC. Schaeffer and Mangus (1976) were the first to critically examine the diverse ichthyofauna and gave preliminary identifications to a dozen kinds of fishes, including one coelacanth that was identified as an undescribed species of *Whiteia* (Moy-Thomas, 1935). A quarter of a century later, there was a resurgence of interest in Wapiti Lake fossils as many new fish were described (Mutter, 2004; Neuman and Mutter, 2005; Mutter and Neuman, 2006; Mutter et al., 2006, 2007, 2008a, 2008b; Mutter and Neuman, 2008a, 2008b, 2009); however, the coelacanths still remained undescribed. The chapters herein provide descriptions of six distinct coelacanths (1 new family, 4 new genera and 6 new species) present within the Sulphur Mountain Formation. This extraordinary diversity makes the Wapiti Lake area home to the most morphologically diverse and species-rich coelacanth fauna in the fossil record to date.

Fins of a Coelacanth

Coelacanths, both fossil and extant, are characterized by several unusual features in the post-cranium. Arguably, the most unique feature of a coelacanth is its diphycercal tail. Two rounded dorsal (d.l) and ventral lobes (v.l) (principal lobes) comprise the majority of the tail and a small caudal extension, referred to as the supplementary lobe (s.l), reaches past the posterior margin of the principal lobes (Fig. 1.1). The shape and size of these caudal features were thought to have varied little since the Mississippian, though several coelacanths described within this thesis exhibit radical changes to their caudal fins (Chapters 2, 4 and 5).

Sarcopterygian fishes are sometimes referred to as lobe-finned fishes. This unique feature is caused by their large fleshy fins that eventually evolve into limbs (i.e., *Tiktaalik*). In a coelacanth, the paired fins (pectoral, Pc.f, and pelvic, P.f) as well as the posterior dorsal (D2.f) and anal fins (A.f) are lobed (Fig. 1.1). The anterior dorsal fin (D1.f), unlike the lobed fins, is a large sail-like fin (Fig. 1.1). The median fins (anterior and posterior dorsal and anal fins) are ‘anchored’ by bones called basal plates (i.e. D1.b, D2.b). The anterior dorsal fin abuts against its basal plate, whereas the posterior dorsal and anal fins are set apart from the basal plates. In *Latimeria* (and *Laugia*, see Chapter 6), a series of cartilage supports called axial mesomeres articulate with the lobed portion of the fin (Forey, 1998:fig. 8.3a–d) in the posterior dorsal and anal fins. The shape and length of these fins vary drastically in the coelacanths of the Sulphur Mountain Formation.

Evolution of the Coelacanth Body Form

Most fossil coelacanths are diagnosed based on cranial material with very little description dedicated to the post-cranium. This is ironic because the coelacanth story is heavily invested in the post-cranium, particularly in the caudal fin. The first coelacanth was described by Agassiz in 1839. He described a peculiar isolated caudal fin found in the Permian Marl Slate of England. Agassiz noted the unique shape of the tail, unusual caudal extension, and what he interpreted as hollow fin rays supporting the majority of the caudal fin. On account of the latter feature, he named the specimen *Coelacanthus*, meaning hollow spine. This description of the first coelacanth fossil predated the discovery of *Latimeria* by exactly one-hundred years. Had the caudal fin changed drastically in form, J. L. B. Smith might not have recognized the importance of Ms. Latimer's discovery (Smith, 1956). Although many coelacanths retain their 'typical' coelacanth body form, not all coelacanths stay true to this body plan.

Few well-preserved specimens of the earliest coelacanths (Devonian–Mississippian) are known, though the ones that are known exhibit a wide array of body forms: from eel-like (Friedman and Coates, 2006) to dacriform (Melton, 1969; Lund and Lund, 1984, 1985) to having a heterocercal tail (Schultze, 1973; Long, 1999) and finally a *Latimeria*-like form (Schaeffer, 1962; Jessen, 1966, 1973) (Fig. 1.2). These drastic morphological differences led some to believe that early in their history coelacanths underwent periods of rapid morphological evolution (Schaeffer, 1952; Cloutier, 1991; Friedman and Coates, 2006) (Fig. 1.2), but Forey (1998) reported a relatively gradual rate of evolution through time with two peaks in their diversity: one in the Early Triassic and the other in the Late Jurassic. In spite of their differing conclusions, many authors noted that the species diversity appeared to have peaked in the Early Triassic (Schaeffer, 1952; Forey, 1988; Cloutier, 1991). Forey (1998) suggested that the increase in the rate of morphological diversity coincided with the peak in species diversity in the Early Triassic. The addition of six taxa from the Sulphur Mountain Formation brings the total of known coelacanths from the Lower Triassic to approximately twenty-four species (Forey, 1998:fig. 9.9; Tong et al, 2006; Geng et al., 2009; Chapters 2–5). Furthermore, two of the coelacanths described herein, *Rebellatrix divaricerca*, gen. et sp. nov., and *Everticauda pavoidea*, gen. et sp. nov. (Chapters

2 and 4), have body and caudal fin forms completely new to coelacanths. These coelacanths not only contribute to the known species diversity during the Lower Triassic but also represent the first major departure in the coelacanth body form since the Mississippian coelacanth *Allenypterus* (Melton, 1969; Lund and Lund, 1984, 1985). The discovery of these coelacanths challenges the view that coelacanths are amongst the most evolutionary conservative of all vertebrates.

Introduction to Chapter Two

This chapter describes an unusual fork-tailed coelacanth from the Lower Triassic Sulphur Mountain Formation of British Columbia, Canada, marking the first considerable departure in actinistian body form since the Mississippian Period. *Rebellatrix divaricerca*, gen. et sp. nov., is unique among coelacanths in its possession of a bifurcated caudal fin, reduced segmentation of fin rays, and fusion of caudal fin elements. The family Rebellatricidae is erected to include only *R. divaricerca*, gen. et sp. nov. This novel body shape of the new coelacanth raises questions concerning the idea that coelacanths were morphologically static following the Mississippian. *Rebellatrix divaricerca*, gen. et sp. nov. also emphasizes the morphological diversity of coelacanths during the Early Triassic, a time when species diversity of coelacanths was also highest. The slender, fork-tailed body form suggests fast swimming and an active lifestyle, unique among known fossil and extant coelacanths.

Introduction to Chapter Three

This chapter describes *Whiteia lepta*, sp. nov., and *Whiteia durabilis*, sp. nov., two new species of the most diverse Triassic coelacanth genus *Whiteia* (Moy-Thomas, 1935). This extends the geographical range of this genus to include Western Canada. Previously, species of *Whiteia* were only known from Madagascar, Greenland and South Africa (Broom, 1905; Moy-Thomas, 1935; Lehman, 1952; Forey, 1998). The new species are the largest members of the Whiteiidae, reaching total lengths of at least 60 cm (and perhaps to 1 meter). The difference in preservation in the new Canadian species gives the opportunity to examine previously unknown features in this genus. *Whiteia lepta*, sp. nov., is preserved as articulated flattened specimens, whereas *W. durabilis*, sp. nov., is preserved as three-dimensional skulls. The two species possess sickle-shaped lachrymojugals, a parietonasal shield that is twice the length of the postparietal shield, and saddle-shaped coronoids, features that are found only in species of *Whiteia,* and at the same time display unique features, such as the presence of a calcified ‘swim bladder’, lack of denticles on the anterior dorsal fin, and raised areas of the skull roof. These two new species add to the growing list of coelacanths of the Early Triassic, a time during which coelacanth diversity peaked not long after the Permo-Triassic extinction event.

Introduction to Chapter Four

This chapter describes two deep-bodied coelacanths, *Everticauda pavoidea*, gen. et sp. nov., and *Wapitia robusta*, gen. et sp. nov. *Everticauda*, gen. nov., is unique among coelacanths in its possession of elongate dorsal and ventral caudal lobes that extend well past the supplementary lobe as well as an elongate anterior dorsal fin, whereas *Wapitia*, gen. nov., is distinctive in its combination of derived features, expanded occipital neural arches, with primitive features, reduced number of neural arches and high number of anterior dorsal fin rays. Additionally, the new caudal fin form of *Everticauda*, gen. nov., adds to the growing list of body forms attributed to coelacanths in their overall history as well as adding to the diversity of forms from the Early Triassic, a time in which coelacanth species diversity peaked. Furthermore, ontogenetic variation is examined within *Everticauda*, gen. nov.

Introduction to Chapter Five

This chapter describes the western-most occurrence of the family Laugiidae (Berg, 1940) based on *Belemnocerca prolata*, gen. et sp. nov. The family Laugiidae has a temporal range from the Early Triassic to the Late Jurassic and members of this family have been described from Madagascar, Greenland and Germany (Quenstedt, 1858; Stensiö, 1932; Lehman, 1952; Lambers, 1991; Forey, 1998; Clément, 1999). In particular, *B. prolata*, sp. nov., is most similar to one member of this family, *Laugia groenlandica* (Stensiö, 1932), in the asymmetry and shape of the caudal fin, though it differs in caudal fin ray count and anal fin position as well as in the size and shape of the supplementary lobe.

Introduction to Chapter Six

This chapter discusses the broad range of morphological diversity in the caudal fins of coelacanths present within the Sulphur Mountain Formation. Several of the coelacanths described in the preceding chapters exhibit unusual caudal fin shapes. Four distinct tail morphotypes were observed amongst the six new species of coelacanth: 1) a general broadly rounded *Latimeria*-like tail, 2) a forked tail, 3) an everted tail and 4) a tapering tail with a broad, extended supplementary lobe. Little is known about how coelacanths used their tails, which exhibit a wide array of morphologies in the fossil record. Based on direct observations of modern coelacanths (*Latimeria*), it is known that some of them are slow moving, only using the caudal fin for rapid acceleration to catch prey (Fricke et al., 1987; Fricke and Hissmann, 1992). The forked-tailed coelacanth is interpreted as being a relatively active, fast predator, while the other three forms suggest variations in ambush predator lifestyles. The wide span of the caudal fin and the unsegmented fin rays in the fork-tailed coelacanth suggest a stiff, high-aspect-ratio tail adapted for rapid swimming that has not been previously attributed to coelacanths. In the other three morphotypes, the aspect ratio is much lower. These tails have segmented fin rays as is present in the majority of coelacanths. The segmented fin rays create a more flexible tail that allows for greater acceleration from rest. These morphological differences in the caudal fin denote a more diverse locomotory repertoire than was previously known in coelacanths, supporting Forey’s (1998) idea that coelacanth morphological diversity coincides with the peak in species diversity in the Early Triassic.

LITERATURE CITED

Agassiz, L. 1839. Recherches sur les Poissons Fossiles. Vol. 2. Neuchâtel.

Berg, L. 1940. Classification of fishes, both recent and fossil Trudy Zoologicheskogo Instituta, Akademiya Nauk SSSR 5:1–141.

Blieck, A., G. Clément and M. Steel. 2010. The biostratigraphical distribution of earliest tetrapods (Late Devonian): a revised version with comments on biodiversification. Geological Society of London, Special Publications 339:129–138.

Broom, R. 1909. The fossil fishes of the Upper Karoo Beds of South Africa. Annals of the South African Museum, East London 7:251–269.

Clément, G. 1999. The Actinistian (Sarcopterygii) *Piveteauia madagascariensis* Lehman from the Lower Triassic of Northwestern Madagascar: A redescription on the basis of new material. Journal of Vertebrate Paleontology 19(2):234–242.

Cloutier, R. 1991. Patterns, trends and rates of evolution within the Actinistia. Environmental Biology of Fishes 32:23–58.

Erdmann, M. V., R. L. Caldwell and M. K. Moosa. 1998. Indonesian 'king of the sea' discovered. Nature 395:335.

Forey, P. L. 1998. History of the Coelacanth Fishes. Chapman and Hall, London, U.K., pp. 248-260.

Friedman, M. and M. D. Brazeau. 2010. Sequences, stratigraphy and scenarios: what can we say about the fossil record of the earliest tetrapods? Proceedings of the Royal Society: B 278:432–439.

Friedman M. and M. I. Coates. 2006. A newly recognized fossil coelacanth highlights the early morphological diversification of the clade. Proceedings of the Royal Society: B 273:245-250.

Fricke, H., O. Reinicke, H. Hofer and W. Nachtigall. 1987. Locomotion of the coelacanth *Latimeria chalumnae* in its natural environment. Nature 329:331–333.

Fricke, H. and K. Hissmann. 1992. Locomotion, fin coordination and body form of the living coelacanth *Latimeria chalumnae*. Environmental Biology of Fishes 34:329–356.

Geng, B.-H., M. Zhu and J. Fan. 2009. A revision and phylogenetic analysis of *Guizhoucoelacanthus* (Sarcopterygii, Actinistia) from the Triassic of China. Vertebrata Palasiatica 47:165–177.

Jessen, H. L. 1966. Die Crossopterygier des Oberen Plattenkalkes (Devon) der Bergisch-Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge) unter Berücksichtung von amerikanischem und europäischem Onychodus–Material. Arkiv för Zoologi 18:305–389.

Jessen, H. L. 1973. Weitere Fischreste aus dem Oberen Plattenkalk der Bergisch-Gladbach-Paffrather Mulde (Oberdevon, Rheinisches Schieferbebirge). Palaeontographica 143:159–187.

Johanson, Z., J. A. Long, J. A. Talent, P. Janvier and J. W. Warren. 2006. Oldest coelacanth, from the Early Devonian of Australia. Biology Letters 2:443–446.

Lambers, P. H. 1991. The identity of the type specimen of *Coelacanthus harlemensis* Winkler (Pisces, Actinistia) from the lithographic limestone of Solnhofen (Tithonian), Bavaria. Paläontologische Zeitschrift 65:173–189.

Laudon, L. R., E. Deidrick, E. Grey, W. B., Hamilton, P. J. Lewis, W. McBee, A. C. Spreng, and R. Stoneburner. 1949. Devonian and Mississippian stratigraphy, Wapiti Lake area, northeastern British Columbia. American Association of Petroleum Geology Bulletin 33:1502–1552.

Lehman, J. P. 1952. Etude complémentaire des poisons de l'Eotrias du Nord-Ouest de Madagascar. Kungliga Svenska Vetenskapsakademiens Handlingar 2:1–201.

Long, J. A. 1999. A new genus of fossil coelacanth (Osteichthyes: Coelacanthiformes) from the Middle Devonian of southeastern Australia. Records of the Western Australian Museum 57:37–53.

Lund, R. and W. Lund. 1984. New Genera and Species of Coelacanths from the Bear Gulch Limestone (Lower Carboniferous) of Montana (U.S.A.). Geobios 17:237-244.

Lund, R. and W. L. Lund. 1985. Coelacanths from Bear Gulch limestone (Namurian) of Montana and the evolution of Coelacanthiformes. Bulletin of the Carnegie Museum of Natural History 25:1–74.

Melton, W. G. 1969. A new dorypterid fish from central Montana. Northwest Science, Cheney 43:196–206.

Mutter, R. J. 2004. Fossile Fische aus den kanadischen Rocky Mountains. Vierteljahrschrift der Naturforschenden Gesellschaft in Zürich 149:51–58.

Mutter, R. J., and A. G. Neuman. 2006. An enigmatic chondrichthyan with Palaeozoic affinities from the Lower Triassic of western Canada. Acta Palaeontologica Polonica 51:271–282.

Mutter, R. J., A. G. Neuman, and K. de Blanger. 2007. Elasmobranchs from the Lower Triassic Sulphur Mountain Formation near Wapiti Lake (BC, Canada). Zoological Journal of the Linnean Society 149:309–337.

Mutter, R. J., and A. G. Neuman. 2008a. New eugeneodontid sharks from the Lower Triassic Sulphur Mountain Formation near Wapiti Lake (BC, Canada). Zoological Journal of the Linnean Society 149:309–337.

Mutter, R. J., and A. G. Neuman. 2008b. Jaws and dentition in an Early Triassic, 3-dimensionally preserved eugeneodontid skull (Chondrichthyes). Acta Geologica Polonica 58(2):223-227.

Mutter, R. J., A. G. Neuman, and K. de Blanger. 2008a. *Homalodontus* nom. nov., a replacement name for *Wapitiodus* Mutter, de Blander and Neuman, 2007 (Homalodontidae nom. nov., ?Hybodontoidea), preoccupied by

Wapitiodus Orchard, 2005. Zoological Journal of the Linnean Society 154:419–420.

Mutter, R. J., J. Cartanyà, and S. A. U. Basaraba. 2008b. New evidence of *Saurichthys* from the Lower Triassic with an evaluation of early saurichthyid diversity. In: G. Arratia, H.-P. Schultze, and M. V. H. Wilson (eds.), Mesozoic Fishes 4—Homology and Phylogeny. Verlag Dr. Friedrich Pfeil, Munich, pp. 103–127.

Mutter, R. J., and A. G. Neuman. 2009. Recovery from the end-Permian extinction event: Evidence from “Lilliput *Listracanthus*.” Palaeogeography, Palaeoclimatology, Palaeoecology 284:22–28.

Neuman, A. G., and R. J. Mutter. 2005. *Helmolepis cyphognathus*, sp. nov., a new platysiagid actinopterygian from the Lower Triassic Sulphur Mountain Formation (British Columbia, Canada). Canadian Journal of Earth Sciences 42:25–36.

Pouyaud, L., S. Wirjoatmodjo, I. Rachmatika, A. Tjakrawidjaja, R. K. Hadiaty and W. Hadie. 1999. Une nouvelle espèce de coelacanthe, preuves génétiques et morphologiques. Comptes Rendus de l’Académie des Sciences 322:261–267.

Quenstedt, F. A. 1858. Der Jura. Tubingen. 823 pp.

Schaeffer, B. 1952. The Triassic coelacanth fish *Diplurus*, with observations on the evolution of the Coelacanthini. Bulletin of the American Museum of Natural History 99(2):25–78.

Schaeffer, B. 1962. A coelacanth fish from the Upper Devonian of Ohio. Scientific Publications of the Cleveland Museum of Natural History, New Series 1:1–13.

Schaeffer, B., and M. Mangus. 1976. An early Triassic fish assemblage from British Columbia. Bulletin of the American Museum of Natural History 156:515–564.

Schultze, H.-P. 1973. Crossopterygier mit heterozerker Schwanzflose aus dem Oberdevon Kanadas, Nebst einer Beschreibung von Onychodontida-Resten aus dem Mittledevon Spaniens und dem Karbon der USA. Palaeontographica 143A:188208.

Schwimmer, D. R., J. D. Stewart and G. D. Williams. 1994. Giant fossil coelacanths of the Late Cretaceous in the eastern United States. Geology 22:503–506.

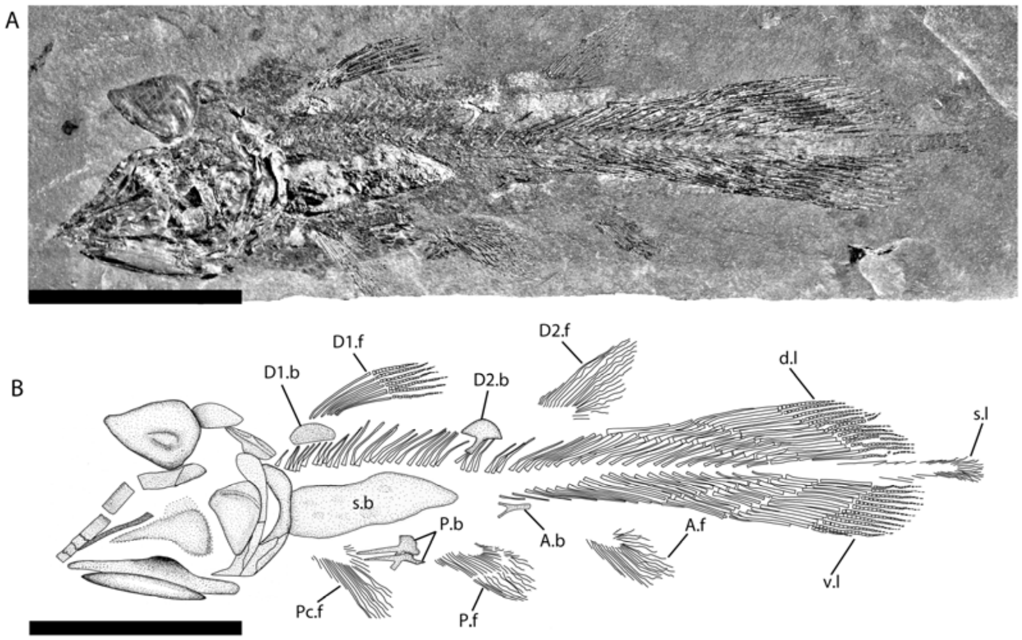
Smith, J. L. B. 1939. A living fish of Mesozoic type. Nature 143:455-456.

Smith, J. L. B. 1956. Old Four Legs: the story of the Coelacanth. London: Longman Green, 260 pp.

Stensiö, E. 1932. Triassic fishes from East Greenland collected by the Danish expedition 1929-1931. Meddelelser om Grønland 83(3):1–305.

Tong, J., X. Zhou, D. H. Erwin, J. Zuo and L. Zhao. 2006. Fossil fishes from the Lower Triassic of Majiashan, Chaohu, Anhui Province, China. Journal of Paleontology 80(1):146–161.

FIGURE 1.1. UALVP 24228, *Wapitia robusta*, left lateral view. Abbreviations: **A.b**, anal basal plate; **A.f**, anal fin; **D1.b**, anterior dorsal basal plate; **D1.f**, anterior dorsal fin; **D2.b**, posterior dorsal basal plate; **D2.f**, anterior dorsal fin; **d.l**, dorsal lobe of caudal fin; **P.b**, pelvic bone; **Pc.f**, pectoral fin; **P.f**, pelvic fin; **s.b**, ‘swim bladder’; **s.l**, supplementary lobe of caudal fin; **v.l**, ventral lobe of caudal fin. Scale bar equals 5 cm.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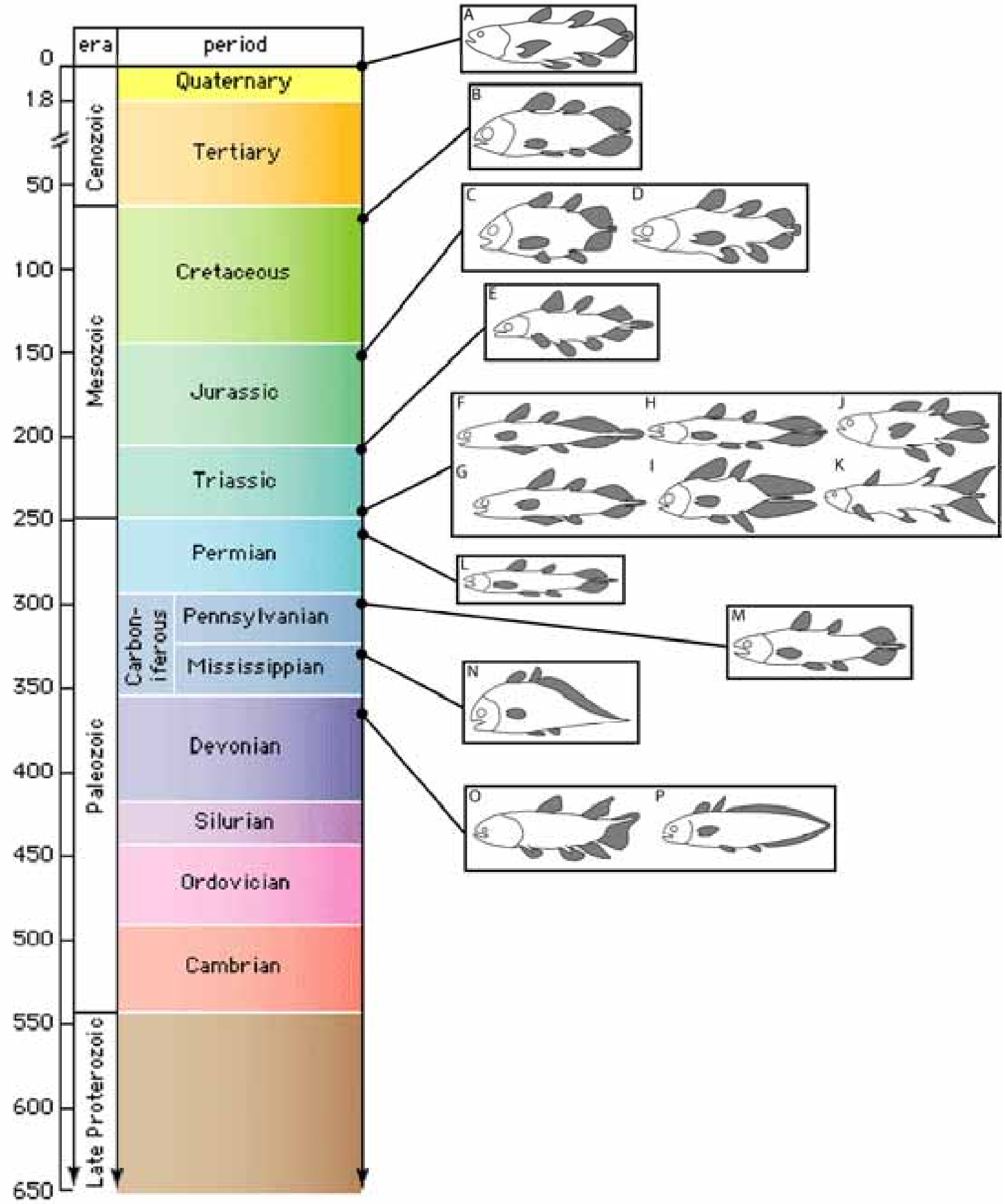
Pc.f
P.f

FIGURE 1.2. Comparison of the coelacanth body form from their first appearance through to the extant form. **A**, *Latimeria chalumnae*; **B**, *Macropomoides orientalis*; **C**, *Libys polypterus*; **D**, *Holophagus gulo*; **E**, *Diplurus newarki*; ***F***, *Belemnocerca prolata*; **G**, *Laugia groenlandica*; **H**, *Whiteia lepta*; **I**, *Everticauda pavoidea*; **J**, *Wapitia robusta*; **K**, *Rebellatrix divaricerca*; **L**, *Coelacanthus granulatus*; **M**, *Rhabdoderma elegans*; **N**, *Allenypterus montanus*; **O**, *Miguashaia bureau*; **P**, *Holopterygius nudus*. Outlines of B, D, E, G, M, N and O were modified from Forey (1998:fig. 8.2) and A, C and P are modified from Friedman and Coates (2006:fig. 2.b). Images are not to scale.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CHAPTER TWO

A fork-tailed coelacanth, *Rebellatrix divaricerca,* gen. et sp. nov. (Actinistia: Rebellatricidae, fam. nov.), from the Lower Triassic of Western Canada

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INTRODUCTION

Coelacanths are traditionally thought of as an evolutionarily conservative group of sarcopterygian fishes that have changed little over geological time (Huxley, 1861; 1935; Schaeffer, 1948, 1952; Moy-Thomas and Miles, 1971; Jarvik, 1980; Forey, 1984; Lund and Lund, 1985; Schultze, 1987; Balon et al., 1988 Cloutier, 1991; Schultze, 2004). However, early in their evolutionary history, they exhibit a wide array of caudal fin forms from tapering to heterocercal (Schultze, 1973; Forey, 1998; Long, 1999; Friedman and Coates, 2006), but after the Mississippian, they are believed to have been morphologically static (Schaeffer, 1948, 1952; Moy-Thomas and Miles, 1971; Lund and Lund, 1985; Schultze, 1987; Cloutier, 1991; Schultze, 2004), adhering closely to a body plan comparable to that of the extant coelacanth *Latimeria* Smith, 1939. A number of authors have suggested that peak species diversity of coelacanths occurs in the Lower Triassic (Schaeffer, 1948, 1952; Forey, 1984, 1988; Cloutier, 1991; Cloutier and Forey, 1991; Forey, 1991, 1998); however, there is disagreement over the implications of this peak. As Cloutier (1991) noted, there is no correlation between peak species diversity and rate of morphological change. While Schaeffer (1952) determined that the rate of morphological diversity was highest in the Devonian, Forey (1988) argued that morphological diversity peaked along with species diversity in the Lower Triassic. Forey (1988) asserted that arguments to the contrary may be skewed based on early deviations in Devonian to Mississippian forms.

Here we describe the first major divergence in coelacanth body form since the Mississippian coelacanth *Allenypterus* Melton, 1969, from the Bear Gulch limestone of Montana. *Rebellatrix divaricerca*, gen. et sp. nov., is the first morphologically divergent body form consistent with Forey's (1988, 1998:245) claim that the highest number of species is correlated with the highest rate of morphological change. The unusual caudal fin and associated elements of *R. divaricerca*, sp. nov., show that coelacanths were likely still capable of great anatomical change. By adding to the ever-growing record of anatomical diversity seen in fossil coelacanths, it further supports the idea that coelacanths are not as morphologically conservative as widely believed.

GEOLOGY

Coelacanths have been known from the Lower Triassic of Western Canada since 1916, when Lambe described a partial specimen as belonging to the genus *Coelacanthus* Agassiz, 1839. Since that time, a more productive locality, commonly referred to as Ganoid Ridge within the Sulphur Mountain Formation, was found in British Columbia within and around the area of what is now Wapiti Lake Provincial Park (Laudon, 1949; Callaway and Brinkman, 1989; Neuman, 1992; Neuman and Mutter, 2005). A preliminary description of the fossil fishes by Schaeffer and Mangus (1976) included a brief synopsis of the coelacanths, attributing them to an undescribed species of *Whiteia* (Moy-Thomas, 1935).

The Sulphur Mountain Formation consists (from lowest in stratigraphic succession to highest) of the Vega, Meosin, Phroso, Whistler and Llama Members (Gibson, 1975; Orchard and Zonneveld, 2009). The formation spans the Lower to Middle Triassic and sits on a Permian unconformity (McGugan and Rapson-McGugan, 1976; Neuman, 1992). The majority of the fossils have not been collected in situ, but rather were found along skree slopes well below the exposures, causing problems for determining the exact fossil-producing beds and the exact age of the fossiliferous horizons. Additionally, most of the fossils collected are fragmentary.

Neuman (1992) noted that there are at least three fossil-producing layers within the Sulphur Mountain Formation in Wapiti Lake Provincial Park. The main fossil bed is approximately 30 to 70 meters above the Permian unconformity and produces the majority of the fossil fishes including the coelacanths from this study. These specimens are from the Vega-Phroso member (Meosin Member not present), and are preserved in a dark-grey to brownish-grey calcareous siltstone (Gibson, 1968; Neuman, 1992) (for detailed accounts of the geology see Neuman, 1992; Neuman and Mutter, 2005; Orchard and Zenneveld, 2009).

The specimens described here were collected from skree slopes within several different cirques along the Ganoid Ridge. The preservation of the fossils is such that they appear at first glance to be well preserved but upon closer inspection the bone detail is poor. The age of the Sulphur Mountain Formation has been determined to be Griesbachian to Ladinian (Lower to Middle Triassic) based on conodont and ammonoid biostratigraphic markers (Orchard and Zonneveld, 2009). The most productive cirque within the park is referred to as cirque C (map in Callaway and Brinkman, 1989:fig. 1;Orchard and Zonneveld, 2009:fig. 1) where TMP 1989.138.33 was found. The age of the fossils recovered from this cirque was identified as ranging from Dienerian (Late Induan) to the earliest Smithian (Early Olenekian) based on ammonoid and conodont markers (Mutter and Neuman, 2009; Orchard and Zonneveld, 2009); though, Mutter and Neuman (2009) noted overlap between the fauna present at Wapiti Lake and the Dienerian localities in Spitsbergen and Madagascar.

The paleoenvironment of Wapiti Lake represents a continental shelf (Neuman, 1992; Mutter, de Blanger and Neuman, 2007). As *Rebellatrix divaricerca*, gen. et sp. nov., is a rare member of this fauna, this may suggest that it was present within a more open water environment.

MATERIALS AND METHODS

Informative silicon peels of TMP 2006.10.001, the holotype, were prepared by immersing the specimen in a dilute solution of hydrochloric acid (5%

by volume) to dissolve the bone and create a negative mold. The specimen was then sprayed with a silicon oil (releasing agent) to minimize damage from the casting process. A layer of liquid silicone, Smooth-On Dragon Skin®, was poured on to the specimen in a grid pattern to prevent bubbles from forming, and allowed to dry. Once dried, the peel was slowly peeled off and represents a detailed positive cast of the specimen. The skull cast of the holotype was dusted with ammonium chloride and photographed for maximum detail using a Canon Rebel XS digital SLR (Figs. 2.1A, E, 2.2A–F, 2.3A). Close ups were dusted with ammonium chloride and photographed using a Nikon DXM 1200C digital camera mounted on a Zeiss Discovery V8 stereo microscope (Figs. 2.1B, C, 2.3B–D). Outline drawings were made using Adobe Photoshop CS4. Drawings were hand stippled and then scanned back into Photoshop. Phylogenetic analyses were performed using Phylogenetic Analysis Using Parsimony (PAUP*) version 4 b10 (Swofford, 2002).

Institutional Abbreviations—PRPRC, Peace Region Palaeontology Research Centre, Tumbler Ridge, British Columbia, Canada; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

SYSTEMATIC PALEONTOLOGY

Class OSTEICHTHYES Huxley, 1880

Subclass SARCOPTERYGII Romer, 1955

Order ACTINISTIA Cope, 1871

Family REBELLATRICIDAE, fam. nov.

Diagnosis—As for the type genus *Rebellatrix*.

REBELLATRIX, gen. nov.

Type and Only Known Species—*Rebellatrix divaricerca*, sp. nov.

Diagnosis—As for the type and only species.

Etymology—From the Latin noun *Rebellatrix,* meaning ‘rebel,’ in reference to the unique caudal fin, which goes against the norm for actinistians, gender feminine.

REBELLATRIX DIVARICERCA, sp. nov.

(Figs. 2.1–2.4)

Holotype—PRPRC 2006.10.001, a nearly complete and articulated specimen, missing the pectoral and pelvic fins and much of the skull, the caudal margin being truncated at the end of the block (Fig. 2.1), length 54 cm, collected in 2006 outside Wapiti Lake Provincial Park by members of the collecting party from the PRPRC.

Paratypes—PRPRC 2004.10.001, consisting of the posterior half of the skeleton from pelvic fin to caudal fin (Fig. 2.2), length 69 cm, collected by a private collector in the 1950s in the vicinity of Wapiti Lake Provincial Park and recently donated to the PRPRC—no other information available; PRPRC 2007.11.108, consisting of the posterior half of the skeleton from the pelvic girdle to the caudal fin (not figured), length 25.5 cm long, collected along the Hart Ranges at latitude 54° 56' 28"N, longitude 122° 23' 51"W; TMP 1989.138.33, an isolated caudal fin (Fig. 2.3), length 15.5 cm, collected within what is now the park area at Cirque C.

Stratigraphic Horizon and Type Locality—Sulphur Mountain Formation, Vega-Phroso Siltstone Member. Lower Triassic. Hart Ranges, latitude 54° 54' 58"N, longitude 122° 28' 14"W.

Etymology—From the Latin verb *divarico*, to spread or fork, and the Greek noun *kerkos*, tail, Latinized in feminine adjectival form as *cerca*, referring to the unique shape of the caudal fin.

Diagnosis—Large, slender coelacanth reaching estimated lengths up to 1.30 meters. Apomorphies of taxon: caudal fin bifurcated; dorsal and ventral margins of tail tapering to a point; perfectly symmetrical caudal fin; reduction of segmented fin rays to the distal margins of the tail; caudal fin supported primarily by unsegmented thickened fin rays; fusion of the radials to unsegmented fin rays; thickened dorsal and ventral rays at the outer margin of the caudal fin; shortest caudal fin ray one-eighth the length of the longest caudal fin ray; reduction of the supplementary lobe; notochord four-times the width of the thinnest portion in caudal fin; narrow caudal peduncle; asymmetrically tapering anal, posterior dorsal and pelvic fins; posterior location of anal fin in relation to posterior dorsal fin; high number of anterior dorsal fin rays; simple pelvic bone lacking an acetabulum.

DESCRIPTION AND COMPARISONS

Skull

The skull is only preserved on the holotype (PRPRC 2006.10.001) and due to the disarticulated nature of the specimen, several bones are incomplete and/or indeterminate (Fig. 2.1C, D). The operculum (Op) and a partial lower jaw are identifiable. The right operculum is displaced and flipped, making its exact position uncertain, but it is likely that the straight margin faces anteriorly (Fig. 2.1E, F). The curved margin of the operculum likely faced posteriorly, allowing the pectoral girdle to tightly fit the curved shape. The operculum is a very deep bone with a height nearly twice its width. There is a small patch of tubercles on the anterodorsal margin, the only ornamentation on this bone. Additionally, this is the only ornamentation present on this specimen as the typical bones that carry ornamentation (i.e., postorbital, squamosal, preoperculum, lachrymojugal and suboperculum) are not present.

The right lower jaw consists of an angular (Ang), articular (Art) and a retroarticular (Rart). The angular is large, though incomplete, with radiating ridges and an off-center, posterior oral pit line (o.p.l) (Fig. 2.1D). Many coelacanths have a pit line located at the center of ossification and an off-center pit line is considered by Forey (1998) to be a derived feature.

Pectoral Girdle

The left and right pectoral girdles are preserved on the holotype but are displaced. The pectoral fins are not preserved on any specimen. The pectoral girdle is preserved in external view and lacks ornamentation. The right girdle is best preserved. It is slightly dorsally displaced and preserves the cleithrum (Cl), clavicle (Cla), and extracleithrum (Ecl). The anocleithrum (Acl) is located posterior to it (Fig. 2.1C, D). The cleithrum is a long, curved bone with an expanded dorsal head. The clavicle makes up well over 2/3 of the lower half of the pectoral girdle whereas the extracleithrum is reduced to a tiny sliver. The anocleithrum is a long, unornamented structure with a thin, ventral process and a rounded dorsal end. It is not forked and articulates with the dorsal end of the cleithrum, wrapping around the curved dorsal margin of the operculum. The left pectoral girdle is disassociated ventrally from the rest of the skull. None of the sutures between the cleithrum, clavicle, and extracleithrum can be discerned.

Pelvic Girdle and Fin

The pelvic fins are preserved in PRPRC 2004.10.001 (Fig. 2.2A, G) and PRPRC 2007.11.108; however, they are best preserved in the former. The pelvic fins are abdominal and terminate opposite the posterior dorsal basal plate. Each pelvic fin has 22 long fin rays that taper to a slender point, much like the anal and posterior dorsal fins. Both the right and left pelvic fins are preserved; however, they are slightly disarticulated. The pelvic girdle in the form of paired pelvic bones (P.b) is complete and well preserved in lateral view on this specimen as well (Fig. 2.2F). The pelvic bones are large, robust, but simple, and have expanded anterior and posterior ends with a slightly larger and thicker posterior end. The pelvic bones do not seem fused at the midline as with all coelacanths except for *Laugia groenlandica* (Stensiö, 1932) and *Coccoderma suevicum* (Quenstedt, 1858). Additionally, *L. groenlandica* and *C. suevicum* have simple pelvic bones with a single anterior process (Forey, 1998), but *R. divaricerca* has fairly symmetrical pelvic bones without a distinct anterior process. The pelvic bones of coelacanths typically have the acetabulum preserved on the posterior end (Forey, 1998). However, this feature is not visible on the available specimens.

Anterior Dorsal Fin

The anterior dorsal fin is only preserved in the holotype, PRPRC 2006.10.001, and is slightly disarticulated (Fig. 2.1A, D). There are 12 to 13 fin rays approximately of the same length that are smooth and completely lacking ornamentation or denticles. The fin rays articulate with the straight anterodorsal margin of the anterior dorsal basal plate (D1.b). The basal plate is rounded, with a smooth ventral margin that sits above the neural spines (Fig. 2.1D). It has a thickened ridge oriented dorsoventrally that widens ventrally, similar to *Diplurus newarki* Bryant, 1934 and *Undina penicillata* Münster, 1834.

Posterior Dorsal and Anal Fins

In most coelacanths, the anal and posterior dorsal fins are opposite or only slightly offset from each other. However, the posterior dorsal fin of *R. divaricerca* is almost a full fin length anterior to the anal fin (Fig. 2.2A, G). The posterior dorsal fin has 25 to 26 long, segmented fin rays that taper to a slender point (e.g., PRPRC 2007.11.108, PRPRC 2004.10.001, and PRPRC 2006.10.001) (Fig. 2.2C). There are an additional 8 to 10 shortened rays that outline the posterior margin of the fin lobe (Fig. 2.2B). The posterior dorsal basal plate (D2.b) (Fig. 2.2D) is similar in shape to the one found in *Caridosuctor populosum* (Lund and Lund, 1984). The distal end is greatly expanded to form a large semi-circle, where the anterodorsal facing process of the distal end is more slender than the posteroventral process. There is a long, slender rod-like proximal process that is anchored along a neural spine.

Aside from their different positions, the posterior dorsal and anal fins are mirror images of each other. Both are tapered and have approximately the same fin-ray count (Fig. 2.2B, C). The anal basal plate (A.b) does not have the long proximal process seen in the posterior dorsal, although it may be buried under the matrix (Fig. 2.2E). The distal end of the plate in the anal fin is expanded to a more robust semi-circle than the basal plate of the posterior dorsal fin and the anterior and posterior ends are not thinned to form processes.

Axial Skeleton and Caudal Fin

Directly posterior to the skull, neural spines are shortest and neural arches are closest together (Fig. 2.1). The first 2 arches, known as the occipital neural arches (occ.n.a), are slightly anteroposteriorly expanded, similar to those in members of the Latimerioidei Schultze, 1993 (see also Forey, 1998) (Fig. 2.1E). The neural arches are most widely separated from each other at the mid-point of the body and become more closely spaced towards the caudal fin. There are no ossified ribs present anterior to the haemal arches in neither PRPRC 2004.10.001 nor PRPRC 2007.11.109. Ribs are present in *Chinlea* Schaeffer, 1967, and *Diplurus* Newberry, 1878, both of which are Triassic coelacanths from North America. There are approximately 40 to 41 haemal arches in total, based on PRPRC 2004.10.001 (Fig. 2.2A, G). The anterior most of these haemal arches inserts anterior to the anal basal plate. In the tail, both the neural and haemal spines are longest anterior to the caudal fin as they articulate with the radials marking the beginning of the caudal region. The shape of the tail and high number of fin rays mean that the neural and haemal spines are close together and in places are stacked upon one another.

The notochord is very broad below the posterior dorsal basal plate in PRPRC 2004.10.001 for a coelacanth and tapers relatively quickly towards the caudal fin (Fig. 2.2A, G). The notochord is nearly four-times the width of the thinnest part in the caudal fin (Fig. 2.2A, G). Conversely most coelacanths maintain a fairly consistent notochord diameter throughout the body that then tapers quickly through the caudal fin (Uyeno, 1991:fig. 1b; Forey, 1998). There are possible remnants of an ossified ‘swim bladder’ in specimen PRPRC 2004.10.001 (Fig. 2.2G). If this feature is indeed a so-called ‘swim bladder’, then this structure in *R. divaricerca* is similar in size to that known in other coelacanths.

PRPRC 2004.10.001 is the largest specimen of *R. divaricerca* and represents approximately the posterior half of the entire body length. Based on this specimen, we estimate that this coelacanth reached lengths of 1.30 m or more. An estimate of the total number of neural arches is based on a composite reconstruction of PRPRC 2004.10.001 and PRPRC 2006.10.001. There are approximately 74 to 75 neural arches in the axial skeleton (Fig. 2.1A, D), creating a long and slender profile. This high neural arch count is even greater than that of another slender coelacanth, *Coelacanthus*, which possesses 70 neural arches (Forey, 1998; Clément, 1999). There are very few fossil coelacanths that reach a length in excess of one meter, making *R. divaricerca* one of the largest, although it is clearly dwarfed by *Megalocoelacanthus* Schwimmer et al., 1994, and *Mawsonia* Maisey, 1986, that possibly reached lengths of 3 meters.

The caudal fin is preserved in the holotype and all three paratypes; however, the isolated tail of paratype TMP 1989.138.33 is the best preserved (Fig. 2.3A–E). The tail is bifurcated at the supplementary lobe with the dorsal and ventral tips of the tail each terminating at a point, forming a fork. This is a significant departure from the typical lobe-shaped tail and has not been recorded in the coelacanth fossil record to date. The distal tips of the ‘lobes’ of the caudal fin make an angle of about 60º with the body axis near the supplementary lobe in TMP 1989.138.33 (Fig. 2.3A, E), however, the distal rays along the caudal dorsal and ventral margins are comparatively longer and makes a shallower angle to the body axis.

The posterior margin of the fin is concave rather than V-shaped. In conjunction with the tail shape and angle, the caudal fin has a wide span that is at least twice the depth of the caudal peduncle. Most coelacanths, in contrast, have a broad caudal peduncle that is only slightly less than the span of the caudal fin (Fricke and Hissmann, 1992).

The caudal fin is symmetrical, with 22 fin rays each in the dorsal and ventral (principal) lobes (Fig. 2.3A, E, F). Coelacanths generally have 16 to 24 fin rays (Forey, 1998), with *R. divaricerca* being near the higher end of the range. The dorsal lobe of the caudal fin usually has 1 or 2 more rays than the ventral, but

R. divaricerca has a completely symmetrical tail with the same number of rays in each half. Fin rays 6, 7, and 8 (counting anterior to posterior) are significantly thickened and support the tips of the main lobes (Fig. 2.2A, G). The fin rays anterior to the thickened rays decrease in size rapidly anteriorly, creating a stepped leading edge.

A typical coelacanth tail is comprised of distinct elements: neural and haemal spines, radials, unsegmented fin rays and segmented fin rays (Forey, 1998). In *R. divaricerca,* the segmented portions of the fin rays are absent or reduced to a minimum and the radials are fused to the unsegmented portions of the rays (Fig. 2.3C). Three of the four specimens, as preserved, completely lack segmented fin rays. However, the best-preserved specimen of a caudal fin, TMP 1989.138.33 has segmented fin rays only at the distal tips of the five longest dorsal and ventral rays (Fig. 2.3B). The longest ray in each half of the tail also has the longest segmented tip. The segmentation is reduced in each subsequent ray until it is completely absent by the sixth fin ray. The rest of the fin rays are completely unsegmented (Fig. 2.3C). While the reduction and loss of segmented fin rays is unusual, it is not unheard of in coelacanths. *Allenypterus* from the Mississippian Bear Gulch Limestone has completely lost its segmented fin rays in the tail (Melton, 1969; Lund and Lund, 1984; 1985; Friedman and Coates, 2006). *Rebellatrix divaricerca* differs from *Allenypterus* in that it does not show a complete loss of segmented fin rays, but rather displays a significant reduction of them in the caudal region. Additionally, the fin rays of *R. divaricerca* are thick, unlike the typical slender rays associated with most coelacanths, and are much shorter closer to the supplementary lobe. The shortest ray is approximately one-eighth the length of the longest one.

The apparent fusion of the fin rays and the radials is a feature never seen before in coelacanths (Fig. 2.3C). All known specimens of *R. divaricerca* preserve the tail and all show this fusion between the unsegmented fin rays and the radials. Each unsegmented fin ray fused to a radial would have formed a single functional unit.

The supplementary lobe is reduced and squared off (Fig. 2.3D). The longest fin rays of the principal lobes extend posterior to it, whereas the shortest rays of the caudal fin end anterior to it. The supplementary lobe in TMP 1989.138.33 (Fig. 2.3) is 2 cm long; its length is only 2.5 cm in PRPRC 2004.10.001 (Fig. 2.2), a specimen representing a significantly larger fish. This suggests that the supplementary lobe exhibits negative allmoetric growth, becoming proportionally smaller through ontogeny. This is not an uncommon occurrence as Schultze (1972) reported that in *Rhabdoderma elegans* (Newberry, 1856) the supplementary lobe was proportionally larger in the specimens deemed juvenile, whereas it was much smaller proportionally in larger individuals (Cloutier, 2010).

Scales

Scales are best preserved on the holotype, where they are characterized by a series of radiating ridges (Fig. 2.1C). Scales can be useful in diagnosing species (Forey, 1998). Such is the case for two Lower Triassic coelacanths: *Whiteia woodwardi* and *W. tuberculata* (Moy-Thomas, 1935). The latter species is characterized by tubercles (as the specific epithet suggests) and the former by longitudinal ridges. The most derived coelacanth scales, like those found on *Latimeria*, are characterized by clustered rugose denticles (Forey, 1998:fig. 11.9b), while the more plesiomorphic scales are characterized by closely spaced tubercles or ridges (Forey, 1998).

The holotype of *R. divaricerca* preserves an intricate lateral line system (Fig. 2.1B). There is a series of bony tubes that are distributed in a line along the mid-section of the body and represent portions of the lateral line system. These tubes only open at a single pore in the anterior part of the scale. In other coelacanths with similar tubes (e.g., *Macropoma* Agassiz, 1835), these usually open at two or more pores (Forey, 1998:fig. 11.12b). These pores are found from behind the shoulder girdle to the tip of the supplementary lobe in *R. divaricerca*.

PHYLOGENETIC ANALYSIS

Analytical Methods

We used a taxon-character matrix (Appendix II) modified from Clément (2005), Friedman and Coates (2006) and Yabumoto (2008), ultimately based on Forey's (1998) matrix. Forey (1998) created a matrix consisting of 30 ingroup and 2 outgroup taxa (Porolepiformes and Actinopterygii) and 108 characters. Because of missing data, Forey deleted 6 genera (% data missing): *Euporosteus* (85%), *Wimania* (81%), *Axelia* (78%), *Lualabaea* (94%), *Indocoelacanthus* (81%) and *Ticenepomis* (65%). Clément's (2005) revision of the character matrix fixed the miscoding of character 31 (preoperculum absent [0], present [1]) and added the taxon *Swenzia* Clément, 2006. Friedman and Coates (2006) revised the matrix by adding character 109 (ventral keel scales absent [0], present [1]) and an additional taxon, *Holopterygius* (Jessen, 1973; Friedman and Coates, 2006). Yabumoto (2008) added the taxon *Parnaibaia,* along with the changes from Clément (2005), but not those from Friedman and Coates (2006). Here we add a new taxon, *Rebellatrix divaricerca,* gen. et sp. nov. Our final data set includes 29 taxa and 109 characters. *Rebellatrix divaricerca* is coded for 23 out of 109 characters. Cladograms were generated using PAUP v4.0 b10 (Swofford, 2002) employing heuristic search with TBR and 100 random-addition-sequence replicates. Characters were unordered and unweighted, and character transformations were mapped onto the phylogeny using MacClade (Maddison and Maddison, 2005) using Acctran character state optimization.

Results

Maximum parsimony analysis yielded 3 most-parsimonious trees of 246 steps each (CI = 0.463, HI = 0.537, RI = 0.701). The 50% majority rule tree (Fig. 2.5) shows a polytomy within the suborder Latimerioidei (sensu Clément, 2005) between (*Chinlea* (*Parnaibaia* (*Mawsonia* + *Axelrodichthys*))), (*Diplurus* + *Libys* (Latimeriidae)) and *Garnbergia* (Martin and Wenz, 1984). *Diplurus* and *Libys* are traditionally considered members of the Mawsoniidae sensu Forey (1998) are here resolved as a sister taxon to the Latimeriidae sensu Clément, 2005. The clade (*Whiteia* (*Rebellatrix* (Latimerioidei))) is supported by six synapomorphies, two of which are coded for *R. divaricerca*: (1) retroarticular and articular separate (character 53) and (2) oral pit line removed from the center of ossification (character 59). *Rebellatrix divaricerca* is resolved as the sister to the Latimerioidei, as supported by a single synapomorphy: occipital neural arches expanded (Character 91).

Discussion

The addition of *Rebellatrix divaricerca* yielded a cladogram that provides more resolution to the ingroup of the Latimerioidei, which is traditionally recovered as a large polytomy (Clément, 2005:fig. 7). Two genera, *Diplurus* and *Libys*, that have been classically considered members of the Mawsoniidae sensu Forey (1998), were here resolved as a sister clade to the Latimeriidae. Five synapomorphies support the monophyly of the clade *Diplurus* + *Libys* (23, 27, 49, 50 and 59). Characters 9, 17, 47 and 98 support the clade (*Diplurus* + *Libys* (Latimeriidae)); however, only character 98, denticles on the anterior dorsal fin, is coded for *Libys*. *Garnbergia* occupies three alternate positions within the three most parsimonious topologies: sister to the Latimerioidei, sister to (*Chinlea* (*Parnaibaia* (*Mawsonia* + *Axelrodichthys*))), and sister to ((*Diplurus* + *Libys*) (Latimeriidae)). This uncertain position of *Garnbergia* within this clade has been noted before by both Clément (2005) and Forey (1998) and has been suggested by these authors to be the result of missing key characters that unite the clade.

The separation of the retroarticular and articular (Character 53) is considered a derived feature in coelacanths (Forey, 1998); though, it is also present in within the Whiteiidae (see Chapter 3). Character 59 is not a reliable character, because it is highly homoplastic. This character state present in Rebellatrix is also shared by *Miguashaia*, *Hadronector, Allenypterus, Whiteia*, *Undina*, *Macropoma*, *Swenzia* and *Latimeria*. Deleting this character yields 3 most-parsimonious trees with a length of 241 (CI = 0.469, HI = 0.531, and RI = 0.704). These three topologies were not different from the previous three. These results support the idea that character 59 is homoplastic and therefore not a phylogenetically reliable character.

Rebellatrix divaricerca is resolved as the sister taxon to Latimerioidei based on a single synapomorphy (character 91). This character concerns the expansion of the occipital neural arches, a character that Forey (1998) considered to be found only in the most derived coelacanths. Previously, only Latimerioidei and Laugiidae (sensu Forey, 1998) had expanded occipital arches. *Rebellatrix divaricerca* is excluded from the Latimerioidei in having greater than 10 anterior dorsal fin rays (character 96). Derived coelacanths have a tendency to reduce their anterior dorsal fin rays, whereas *R. divaricerca* retains the plesiomorphic condition of 10 or more anterior dorsal fin rays. Presence of a single lateral line pore (character 105) may also exclude *R. divaricerca* from Latimerioidei (Forey, 1998:fig. 11.19b single pore; fig. 11.12b multiple pores). This character is not coded for most coelacanths; in fact it is only coded for 36% of the coelacanths in this matrix. Multiple pore openings are found in *Whiteia*, *Undina*, *Coccoderma*, *Macropoma* and *Latimeria*, whereas single lateral line pores are present in *Miguashaia* Schultze, 1973, *Diplocercides* Stensiö, 1922, *Rhabdoderma* Reis, 1888, and *Allenypterus* Melton, 1969. Single pore openings in the lateral line may represent the primitive condition (based on its distribution in the resulting cladograms), in which case its presence in *R. divaricerca* likely indicates a reversal of character 105.

The post-cranium of *R. divaricerca* is well known based on the specimens described here; however, the skull is very poorly preserved. Unfortunately, of the 109 characters used in the phylogenetic analysis, only 22 of these concern the post-cranium. Given the paucity of cranial characters coded for *R. divericerca*, the presence of several primitive character states (character 96 and 105) as well as the derived character 91 make the position of *R. divaricerca* uncertain.

EVOLUTION OF BODY FORM IN COELACANTHS

Two aspects of the form of *Rebellatrix divaricerca* are especially unusual among coelacanths: (1) the long, slender body (increased number of neural arches) with a posterior displacement of the posterior dorsal and anal fins, and (2) the tail shape (forked caudal fin with relatively high aspect ratio, reduced fin-ray segmentation and fusion of caudal elements). Both features raise questions about long-held ideas concerning the evolution of coelacanth body forms and the mode of locomotion. It is particularly interesting that this unusual form appeared relatively early in the Triassic, following the Permo-Triassic extinction event, at a time when other groups of fishes perhaps were not dominating the fast-swimming piscivorous niches.

Coelacanths are usually thought to have changed little after the Mississippian, adhering to the typical *Latimeria*-like body form (Moy-Thomas, 1939; Schaeffer, 1948, 1952; Moy-Thomas and Miles, 1971; Lund and Lund, 1985; Schultze, 1987; Balon et. al, 1988; Cloutier, 1991). Prior to the discovery of *Rebellatrix divaricerca*, the most unusual body forms in Mesozoic coelacanths were *Laugia*, with its expanded thoracic pelvic fins, and *Libys*, with its wide body form; however, these coelacanths for all of their differences were clearly still following the overall traditional coelacanth body plan. There is an approximately 70-million-year gap (Lund, 1990; Orchard and Zonneveld, 2009) between the distinct body forms from the Mississippian (e.g., *Allenypterus*) to the new Early Triassic form *R. divaricerca*. One possibility is that there is a great deal of anatomical diversity that has yet to be discovered in the Late Paleozoic and Early Mesozoic fossil record. Another possibility is that there was something unusual about competition and selection in the earliest Triassic.

Schaeffer (1952) was the first to critically examine the rate of evolutionary change in a temporal context for coelacanths. He concluded that after the first radiation of species with diverse body forms, the rate of evolutionary change (morphological) dropped and then leveled off. It is understandable to think that coelacanths experienced a rapid period of morphological evolution early in their history, during and after the appearance of primitive coelacanths such as *Holopterygius*, *Gavinia*, *Miguashaia*, and *Allenypterus* that all have bodies that diverge from what is thought to be the 'standard' coelacanth form (Schultze, 1973; Lund and Lund, 1984, 1985; Long, 1999; Friedman and Coates, 2006). However, the idea that coelacanth evolution proceeded at a slower pace later in their history is not supported by fossil evidence on taxonomic diversity, which shows that diversity of species of coelacanths reached a peak in the Early Triassic (Schaeffer, 1952; Forey, 1988, 1998). Cloutier and Forey (1991) noted that the apparent peak in diversity could have been influenced by preservational bias owing to global geological events such as a marine transgression, which might have generated conditions appropriate for many of the marine Lagerstätten in the Early Triassic, whereas conditions were not as conducive to preservation at other times (Schaeffer and Mangus, 1976).

The shape of the caudal fin in *R. divaricerca* is unique among coelacanths. This departure in tail shape shows that actinistians were more diverse in body form than previously thought and suggests that the Early Triassic peak in diversity of species may also have coincided with a peak in morphological diversity. Additionally, the change in caudal form of *R. divaricerca* suggests a major change in lifestyle, one previously unknown in any coelacanth.

With a few exceptions, coelacanths generally have a broad, rounded tail with a low span and high surface area yielding a low aspect ratio, a type of tail that is generally used for short bursts of speed, powerful acceleration, and low-speed swimming (Nursall, 1958). The segmented fin rays that support the caudal fin allow for a great amount of flexibility. Fricke and Hissmann (1992) noted that this flexibility allows for the tail to move through larger lateral amplitude for quick acceleration. They noted that the caudal fin in *Latimeria* was so flexible that it could flex 90° lateral to the body axis. The forked, high-span caudal fin with relatively high aspect ratio, along with the reduced segmentation of the fin rays, thickening of the unsegmented fin rays, fusion of rays to radials, and the presence of a narrow caudal peduncle denote a major shift in the locomotory habits of *R.*

divaricerca, in which the caudal fin must have been used in a distinctly different manner. The loss of segmented rays, thickened unsegmented rays, and fusion of the radials to the unsegmented fin rays likely increased rigidity of the tail for high-frequency tail movement typical of fast swimmers. Additionally, the thicker notochord anterior to the caudal fin in *R. divaricerca* likely reduced flexibility anterior to the caudal fin. The narrowing of the caudal peduncle is evidence that lateral motion was largely restricted to the caudal fin. A similar feature is seen in tuna and relatives in the family Scombridae, which are notoriously fast swimmers with high-span caudal fins and narrow caudal peduncles (Morikawa et al., 2008). In scombrids, lateral motion is restricted to the caudal fin, which oscillates at a high frequency. In *Latimeria* (and presumably most fossil coelacanths with similar body form), the whole body moves in s-shape undulations when using the caudal fin (Fricke et al., 1987; Fricke and Hissmann, 1992). Extant coelacanths only use their caudal fin for lunging at prey or quick escapes (Fricke and Hissmann, 1992). The 'general' locomotion of *Latimeria* does not entail the use of their caudal fin; rather they use all of their other fins. Primary thrust is achieved through the collaborative effort of the posterior dorsal and anal fins, which move in a sculling motion (Locket and Griffith, 1972; Fricke and Hissmann, 1992). The paired fins, which have coordinated movement like those of a tetrapod, are used primarily for stability (Locket and Griffith, 1972). Direct observations of modern coelacanths show that they are slow-moving fish only using the caudal fin for rapid acceleration to catch prey (Fricke and Hissmann, 1992). All of the features of the caudal fin in *R. divaricerca* point to reduction of flexibility. *Latimeria* *chalumnae* is thought to be a benthic drifter that lunges when prey nears its mouth using its caudal fin for quick acceleration, relying on flexibility in its tail for high-amplitude movements (Uyeno, 1991; Fricke and Hissmann, 2000). *Rebellatrix divaricerca* would not have been an effective lunger in light of its high-span, low surface-area tail (Nursall, 1958), and was more likely a cruising, active predator. In addition to the changes in caudal fin, the paired fins as well as the dorsal and anal fin have departed from shapes appropriate for sculling motions. Instead they are streamlined. Whereas posterior dorsal and anal fins are opposite each other in most coelacanths to minimize unwanted pitch and roll, in *R. divaricerca* these fins are not opposite each other. Therefore, the new coelacanth was not using its posterior dorsal and anal fins for sculling. Rather, the streamlined, tapered, and asymmetrical fins of *R. divaricerca* suggest their use for precise control in a fast-swimming predator.

CONCLUSION

The several specimens of *Rebellatrix divaricerca*, gen. et sp. nov., described here represent a unique deviation from the traditional coelacanth body form. The presence of a bifurcated caudal fin alone represents a major deviation from the traditional lobed tail of most coelacanths. Stiffening of the tail via thickening of the supporting elements of the caudal fin (in this case the notochord anterior to the tail and fin rays) and reduction of segmentation of rays, along with the narrowing of the caudal peduncle and the forked shape with high aspect ratio are features usually attributed to fast-swimming fishes, such as tuna. Paired fins and posterior dorsal and anal fins also depart in shape and relative position from the usual coelacanth pattern. All of these features demonstrate that *R. divaricerca* is the first fast-swimming, actively predatory coelacanth to be discovered.

The approximately 70-million-year gap between *Rebellatrix* in the very Early Triassic and *Allenypterus*, the next earlier great deviation in coelacanth body form from the Late Mississippian, suggests either that preservational issues are the explanation and additional unusual coelacanths remain to be discovered from Late Paleozoic or Mesozoic formations, or else that the Early Triassic represented an adaptive radiation of fast swimming fishes with forked tails (i.e. *Birgeria* and *Saurichthys*), a niche that was previously only occupied by sharks. Regardless of the explanation, not all coelacanths were slow-swimming lurk-and-lunge predators, and the group was not composed entirely of morphologically stagnant lineages.

LITERATURE CITED

Agassiz, L. 1835. Recherches sur les Poissons Fossiles. Vol. II. 4th Livraison. Feuilleton, pp. 35–64. Neuchâtel.

Agassiz, L. 1839. Recherches sur les Poissons Fossiles. Vol. 2. Neuchâtel.

Balon, E. K., M. N. Bruton, and H. Fricke. 1988. A fiftieth anniversary reflection on the living coelacanth, *Latimeria chalumnae*: some new interpretation of its natural history and conservation status. Environmental Biology of Fishes 23:241–280.

Bryant, W. L. 1934. New fishes from the Triassic of Pennsylvania. Proceedings of the American Philosophical Society, Philadelphia 73:319–326.

Callaway, J. M., and D. B. Brinkman. 1989. Ichthyosaurs (Reptilia, Ichthyosauria) from the Lower and Middle Triassic Sulphur Mountain Formation, Wapiti Lake area, British Columbia, Canada. Canadian Journal of Earth Sciences 26:1491–1500.

Clément, G. 1999. The Actinistian (Sarcopterygii) *Piveteauia madagascariensis* Lehman from the Lower Triassic of Northwestern Madagascar: A redescription on the basis of new material. Journal of Vertebrate Paleontology 19(2):234–242.

Clément, G. 2005. A new coelacanth (Actinistia, Sarcopterygii) from the Jurassic of France, and the question of the closest relative fossil [sic] to *Latimeria*. Journal of Vertebrate Paleontology 25:481–491.

Clément, G. 2006. *Swenzia*, n. nov., a replacement name for the preoccupied coelacanth genus *Wenzia* Clément, 2005. Journal of Vertebrate Paleontology 26:461.

Cloutier, R. 1991. Patterns, trends and rates of evolution within the Actinistia. Environmental Biology of Fishes 32:23–58.

Cloutier, R. 2010. The fossil record of fish ontogenies: insights to developmental patterns and processes. Seminars in Cell Developmental Biology 21:400–413.

Cloutier, R. and P. L. Forey. 1991. Diversity of extinct and living actinistian fishes (Sarcopterygii). Environmental Biology of Fishes 32:59–74.

Cope, E. D. 1871. Contribution to the ichthyology of the Lesser Antilles. Transactions of the American Philosophical Society 14:445–483.

Forey, P. L. 1984. The coelacanth as a living fossil. pp. 166–169. In: N. Eldredge and S. M. Stanley (eds.), Living Fossils. Springer, New York.

Forey, P. L. 1988. Golden jubilee for the coelacanth *Latimeria chalumnae*. Nature 336:727–732.

Forey, P. L. 1991. *Latimeria chalumnae* and its pedigree. Environmental Biology of Fishes 32:75–97.

Forey, P. L. 1998. History of the coelacanth fishes. Chapman and Hall, London, 419 pp.

Friedman, M., and M. I. Coates. 2006. A newly recognized fossil coelacanth highlights the early morphological diversification of the clade. Proceedings of the Royal Society B 273:245–250.

Fricke, H., and K. Hissmann. 1992. Locomotion, fin coordination and body form of the living coelacanth *Latimeria chalumnae*. Environmental Biology of Fishes 34:329–356.

Fricke, H., and K. Hissmann. 2000. Feeding ecology and evolutionary survival of the living coelacanth *Latimeria chalumnae*. Marine Biology 136:379–386.

Fricke, H., O. Reinicke, H. Hofer, and W. Nachtigall. 1987. Locomotion of the coelacanth *Latimeria chalumnae* in its natural environment. Nature 329:331–333.

Gibson, D. W. 1968. Triassic stratigraphy between the Athabasca and Smoky Rivers of Alberta. Geological Survey of Canada, Paper 67-65:1–114.

Gibson, D. W. 1975. Triassic rocks of the Rocky Mountain Foothills and Front Ranges of northeastern British Columbia and west-central Alberta. Geological Survey of Canada, Bulletin 247:1–61.

Huxley, T. H. 1861. Preliminary essay upon the systematic arrangement of the fishes of the Devonian epoch. Memoirs of the Geological Survey of the United Kingdom 10:1–40.

Huxley, T. H. 1880. On the applications of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. Proceedings of the Zoological Society 1880:649–662.

Jarvik, E. 1980. Basic structure and evolution of vertebrates. Volume I. 575 pp., London: Academic Press.

Jessen. H. 1973. Weitere Fischreste aus dem Oberen Plattenkalk der Bergische-Gladbach-Paffrather Mulde (Oberdevon, Rheinisches Schiefergebirge). Palaeontographica A 143:159-187.

Lambe, L. M. 1916. Ganoid fishes from near Banff. Transactions of the Royal Society of Canada 10:35–44.

Laudon, L. R., E. Deidrick, E. Grey, W. B., Hamilton, P. J. Lewis, W. McBee, A. C. Spreng, and R. Stoneburner. 1949. Devonian and Mississippian stratigraphy, Wapiti Lake area, northeastern British Columbia. American Association of Petroleum Geology Bulletin 33:1502–1552.

Locket, N. A. and R. W. Griffith. 1972. Observations on a living coelacanth. Nature 237:175.

Long, J. A. 1999. A new genus of fossil coelacanth (Osteichthyes: Coelacanthiformes) from the Middle Devonian of southeastern Australia. Records of the Western Australian Museum Supplements 57:37–54.

Lund, R. 1990. Chondrichthyan life history styles as revealed by the 320 million years old Mississippian of Montana. Environmental Biology of Fishes 27:1–19.

Lund, R. and W. L. Lund. 1984. New genera and species of coelacanths from the Bear Gulch Limestone (Lower Carboniferous) of Montana (USA). Geobios 17:237–244.

Lund, R. and W. L. Lund. 1985. Coelacanths from Bear Gulch limestone (Namurian) of Montana and the evolution of Coelacanthiformes. Bulletin of the Carnegie Museum of Natural History 25:1–74.

McGugan, A., and J. E. Rapson-McGugan. 1976. Permian and Carboniferous stratigraphy, Wapiti Lake area, northeastern British Columbia. Bulletin, Canadian Petroleum Geology, 24(2):193–210.

Maddison, W. P. and D. R. Maddison. 2005. MacClade: Analysis of Phylogeny and Character Evolution, version 4.08. Sunderland, Massachusetts.

Maisey, J. G. 1986. Coelacanths from the Lower Cretaceous of Brazil. American Museum Novitates 2866:1–30.

Martin, M. and S. Wenz. 1984. Découverte d'un nouveau Coelacanthidé, *Garnbergia ommata* n. gen., n. sp., dans le Muschelkalk supérieur du Baden-Württemberg. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) 105:1–17.

Melton, W. G. 1969. A new dorypterid fish from central Montana. Northwest Science, Cheney 43:196–206.

Morikawa, H., K. Yusa and S. Kobayashi. 2008. Mechanical properties of the caudal fin resulting from the caudal skeleton structure of the Bluefin Tuna; pp. 67–77 in N. Kato and S. Kamimura (eds.), Bio-mechanics of Swimming and Flying. Springer Press, Japan.

Moy-Thomas J. A. 1935. The coelacanth fishes from Madagascar. Geology Magazine 72:213–227.

Moy-Thomas, J. A. 1939. Palaeozoic fishes. Methuen, London. 149 pp.

Moy-Thomas, J. A. and R.S. Miles. 1971. Palaeozoic Fishes. 2nd ed. Chapman and Hall, London. 259 pp.

Münster, G. von. 1834. Mitteilungen an Professor Bronn gerichtet. Neues Jahrbuch für Mineralogie Geognosie. Geologie und Petrefakten-Kunde, Stuttgart 1834:538–542.

Münster, G. von. 1842. Beitrag zur Kenntniss einiger neuen seltenen Versteinerungen aus den Lithographischen Schiefern in Baiern. Neues Jahrbuch für Mineralogie Geognosie. Geologie und Petrefakten-Kunde, Stuttgart 1842:35-46.

Mutter, R. J., K. de Blanger, A. G. Neuman. 2007. Elasmobranchs from the Lower Triassic Sulphur Mountain Formation near Wapiti Lake (BC, Canada). Zoological Journal of the Linnean Society 149:309–337.

Neuman, A. G. 1992. Lower and Middle Triassic Sulphur Mountain Formation, Wapiti Lake, British Columbia: Summary of Geology and Fauna. Contributions to Natural Science, Royal British Columbia Museum 16:1–12.

Neuman, A. G. and R. J. Mutter. 2005. *Helmolepis cyphognathus*, sp. nov., a new platysiagid actinopterygian from the Lower Triassic Sulphur Mountain Formation (British Columbia, Canada). Canadian Journal of Earth Sciences 42:25–36.

Newberry, J. S. 1856. Descriptions of several genera and species of fossil fish from Carboniferous strata of Ohio. Proceedings of the Academy of Natural Sciences Philadelphia 8:96–100.

Newberry, J. S. 1878. Descriptions of new fossil fishes from the Trias. Annals of the New York Academy of Sciences. 1:127–128.

Nursall, J. R. 1958. The caudal fin as a hydrofoil. Evolution 12:116–120.

Orchard, M. J., and J.-P. Zonneveld. 2009. The Lower Triassic Sulphur Mountain Formation in the Wapiti Lake area: Lithostratigraphy, conodont biostratigraphy, and a new biozonation for the lower Olenekian (Smithian). Canadian Journal of Earth Sciences 46:757–790.

Quenstedt, F. A. 1858. Der Jura. Tubingen. 823 pp.

Romer, A. S. 1955. Herpetichthyes, Amphibioidei, Choanichthyes or Sarcopterygii? Nature 176: 126.

Schaeffer, B. 1948. A study of *Diplurus longicaudatus* with notes on the body form and locomotion of the Coelacanthini. American Museum Noviates 1378: l–32.

Schaeffer, B. 1952. Rates of evolution in the coelacanth and dipnoan fishes. Evolution 6:101–111.

Schaeffer, B. 1967. Late Triassic fishes from the western United States. Bulletin of the American Museum of Natural History 135:285–342.

Schaeffer, B., and M. Mangus. 1976. An Early Triassic fish assemblage from British Columbia. Bulletin, American Museum of Natural History 156:519–563.

Schultze, H.-P. 1972. Early growth stages in coelacanth fishes. Nature New Biology 236:90–91.

Schultze, H.-P. 1973. Crossopterygier mit heterozerker Schwanzflose aus dem Oberdevon Kanadas, Nebst einer Beschreibung von Onychodontida-

Resten aus dem Mittledevon Spaniens und dem Karbon der USA. Palaeontographica 143A:188208.

Schultze, H.-P. 1987. Dipnoans as sarcopterygians; pp. 39–74 in W.E. Bemis, W.W. Burggren and N.E. Kemp (eds.) The Biology and Evolution of Lungfishes, Centennial Supplement. 1, Journal of Morphology, Alan R. Liss, New York.

Schultze, H.-P. 1993. Osteichthyes: Sarcopterygii; pp. 657–663 in M. J. Benton (ed.), The Fossil Record 2. Chapman and Hall, London.

Schultze, H.-P. 2004. Mesozoic sarcopterygians; pp. 463–492 in Arratia, G., Tintori, A. (eds.), Mesozoic Fishes 3 — Systematics, Paleoenvironments and Biodiversity. Verlag Dr. Friedrich Pfeil, München.

Schwimmer, D. R., J. D. Stewart and G. D. Williams. 1994. Giant fossil coelacanths of the Late Cretaceous in the eastern United States. Geology 22:503–506.

Smith, J. L. B. 1939. A living fish of Mesozoic type. Nature 143:455–456.

Stensiö, E. A. 1922. Über zwei Coelacanthiden aus dem Oberdevon von Wildungen. Paläontologischen Zeitschrift 4:167–210.

Stensiö, E. A. 1932. Triassic fishes from East Greenland. Meddelelser Grønland 83(3):l–305.

Swofford, D. L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Uyeno, T., 1991. Observations on locomotion and feeding of released coelacanths, *Latimeria chalumnae*. Environmental Biology of Fishes 32:267–273.

Woodward, A. S. 1909. The fossil fishes of the English Chalk. Part 5. Monograph of the Palaeontographical Society, London: 153–184.

Woodward, A.S. 1942. Some new and little-known Upper Cretaceous fishes from Mount Lebanon. Annals and Magazine of Natural History 9:537–568.

Yabumoto, Y. 2008. A new Mesozoic coelacanth from Brazil (Sarcopterygii, Actinistia). Paleontological Research 12:329–342.

FIGURE 2.1. *Rebellatrix divaricerca*, gen. et sp. nov., holotype, PRPRC 2006.10.001, Lower Triassic, Sulphur Mountain Formation, British Columbia, Canada. **A,** photograph of holotype in right lateral view; **B**, close up of lateral line system of holotype; **C**, close up of a scale, dotted line represents scale margin; **D**, line drawing of holotype; **E**, ammonium chloride dusted silicone peel of the skull, image flipped horizontally; **F**, line drawing of skull. **Abbreviations: Acl**, anocleithrum; **A.f**, anal fin; **Ang**, angular; **Art**, articular; **Cl**, cleithrum; **Cla**, clavicle; **D1.b**, anterior dorsal basal plate; **D1.f**, anterior dorsal fin; **D2.b**, posterior dorsal basal plate; **D2.f**, posterior dorsal fin; **Ecl**, extracleithrum; **lPG**, left pectoral girdle; **occ.n.a**, occipital neural arches; **Op**, operculum; **o.p.l**, oral pit line; **Rart**, retroarticular. Scale bar equals 10 cm (A, D); 2 mm (B, C); 2 cm (E, F).

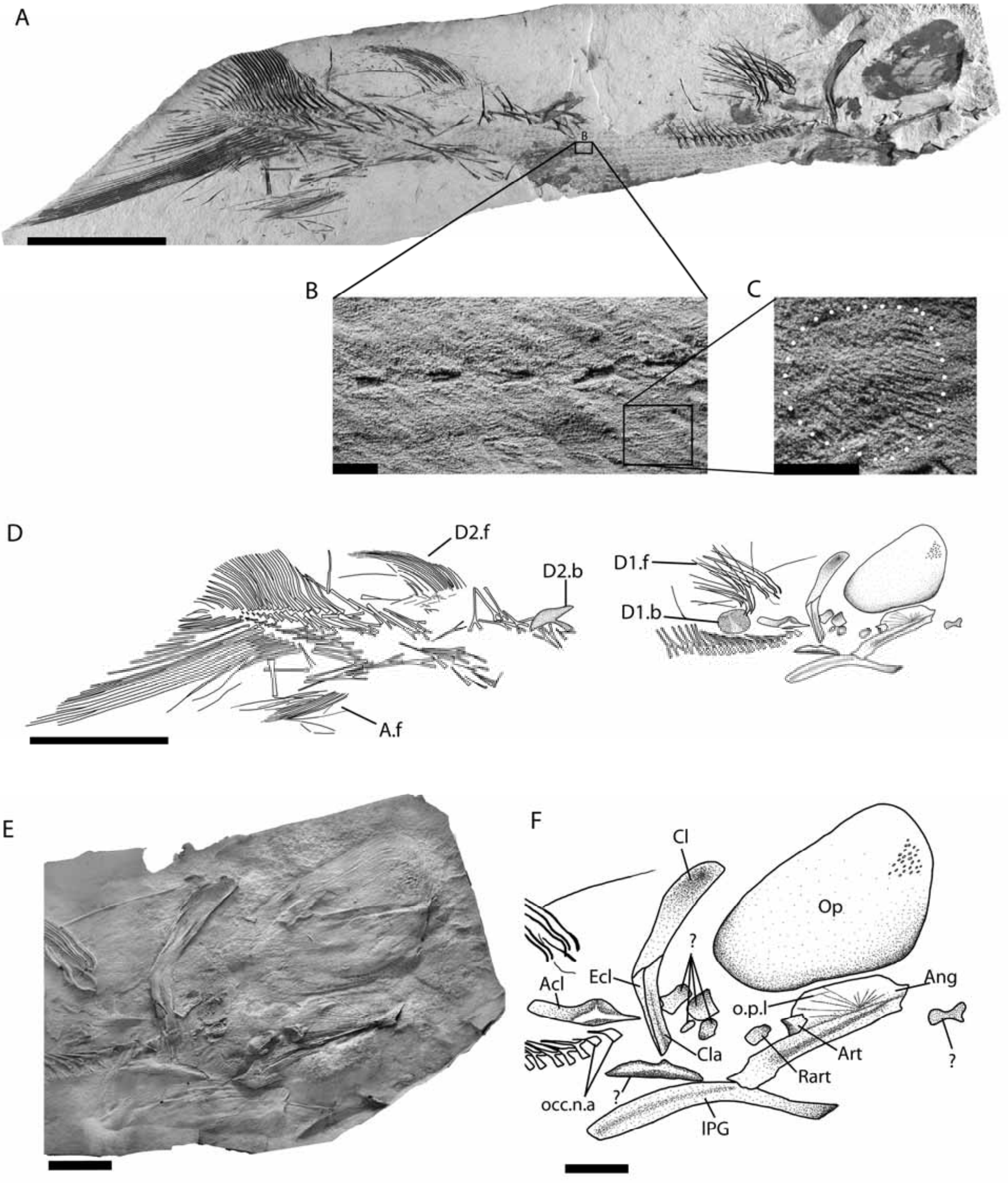

A
B
B
C
D
D2.f
D2.b
D1.f
D1.b
A.f
E
F
Cl
Op
?
Ecl
Acl
Ang
o.p.l
Art
Cla
Rart
?
?
occ.n.a
IPG

FIGURE 2.2. *Rebellatrix divaricerca*, gen. et sp. nov., paratype, PRPRC 2004.10.001. **A**, photograph of complete specimen; **B**, lobed base of posterior dorsal fin; **C**, tapered anal fin; **D**, posterior dorsal basal plate; **E**, anal basal plate; **F**, left and right pelvic plates (pelvic girdle); **G**, line drawing of complete specimen. **Abbreviations**: **A.b**, anal basal plate; **A.f**, anal fin; **D2.b**, posterior dorsal basal plate; **D2.f**, posterior dorsal fin; **P.b**, pelvic bone; **P.f**, pelvic fins; **sb**, swim bladder; **s.l**, supplementary lobe. Scale bar equals 10cm (A, G); 2cm (B-F).

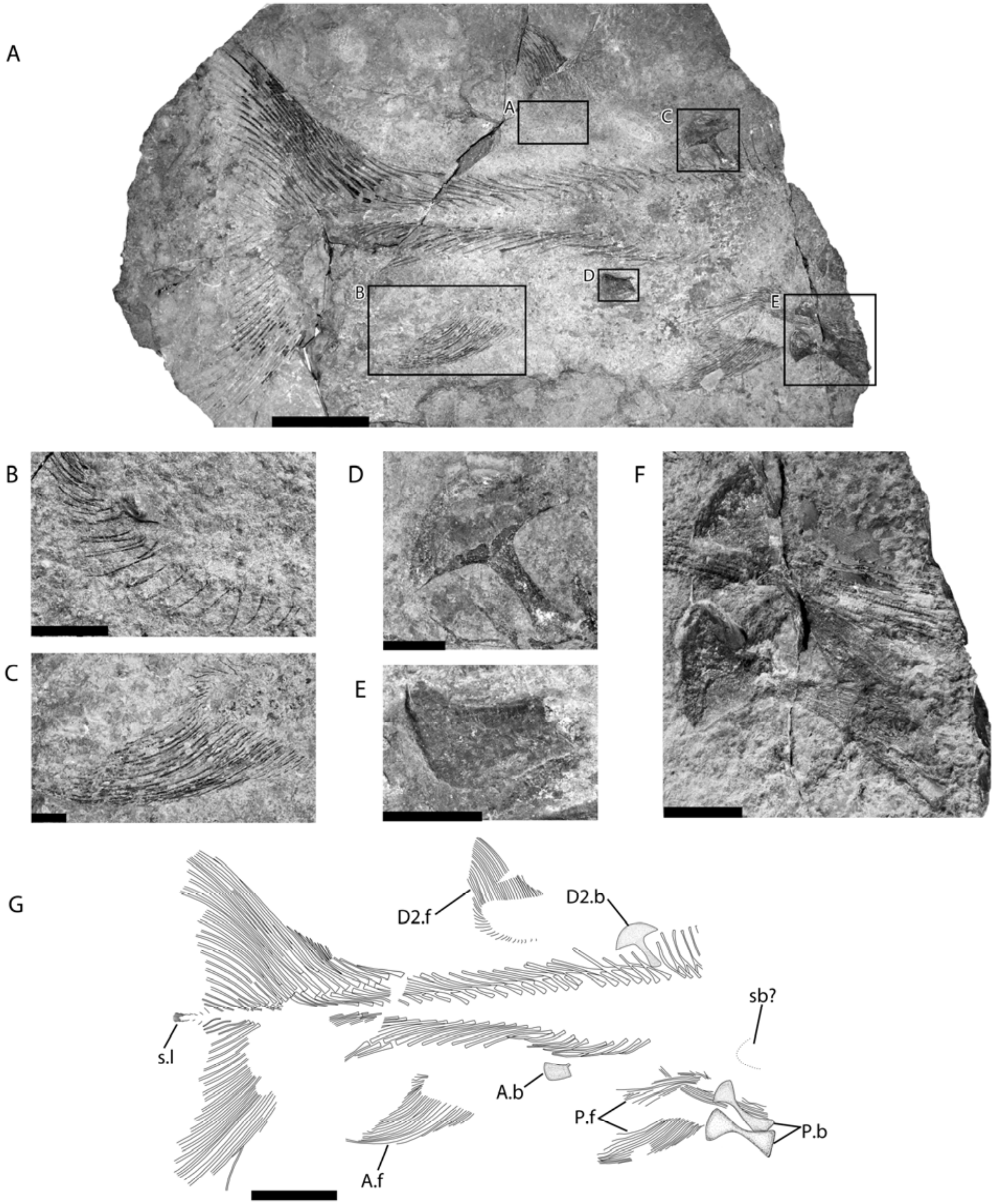

A
A
C
D
B
E
B
C
D
E
F
G
D2.f
D2.b
sb?
s.l
A.b
A.f
P.f
P.b

FIGURE 2.3. Caudal fin of *Rebellatrix divaricerca*, gen. et sp. nov., paratype, TMP 1989.138.33 (**A**–**E**) and reconstruction (**F**). **A**, photograph of entire specimen as preserved; **B**, segmented caudal fin rays; **C**, radials fused to unsegmented caudal fin rays; **D**, supplementary lobe; **E**, line drawing; **F**, reconstructed caudal fin based on TMP 1989.138.33 and PRPRC 2004.10.001. Scale bar equals 5 cm (A, E); 1 cm (B–D).

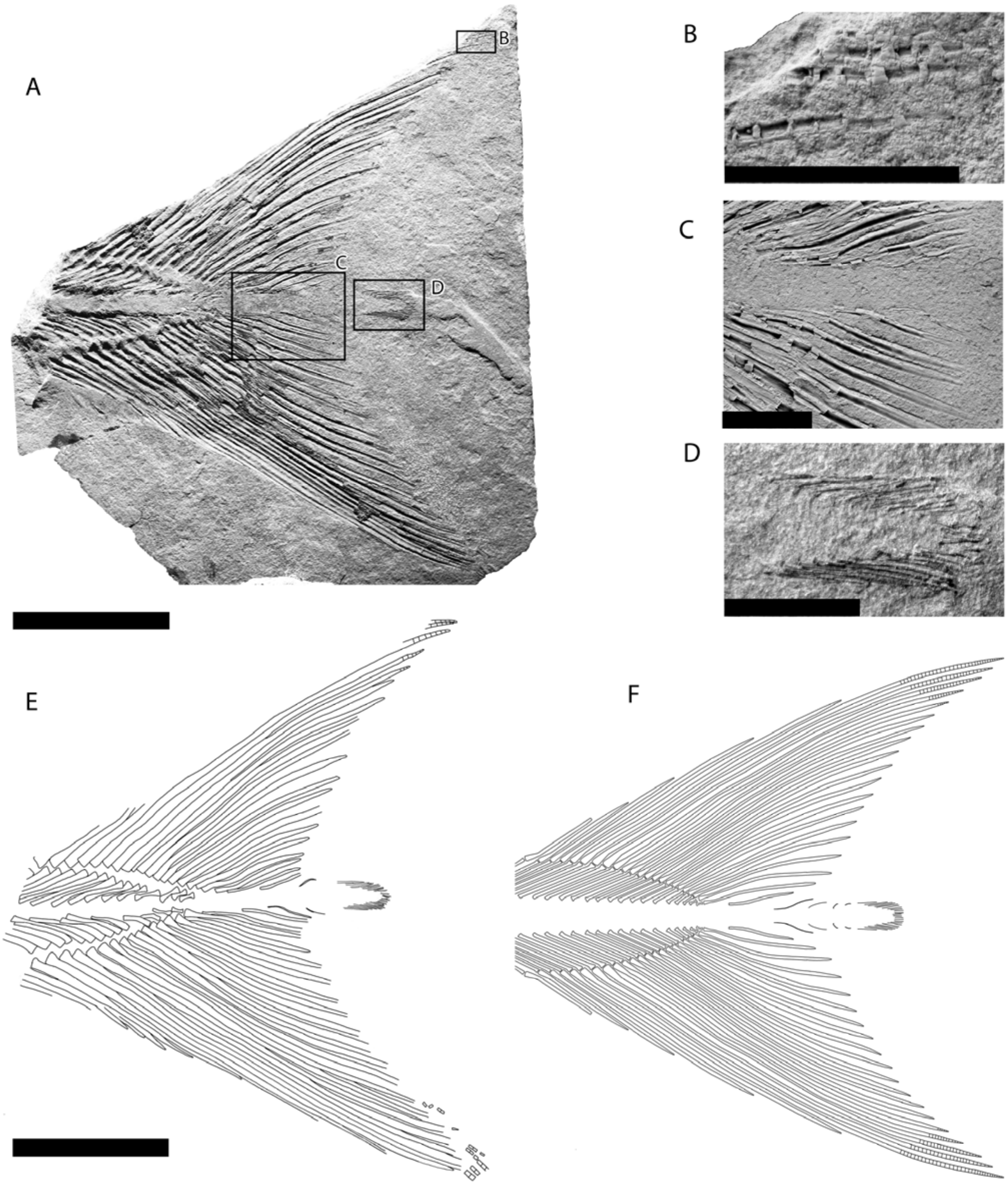

A
B
C
D
B
C
D
E
F

FIGURE 2.4. Reconstruction of *Rebellatrix divaricerca*, gen. et sp. nov., based mainly on PRPRC 2006.10.001 (holotype), PRPRC 2004.10.001 and TMP 1989.138.33 (paratypes). Size based on largest specimen PRPRC 2004.10.001. Scale bar equals 30 cm.

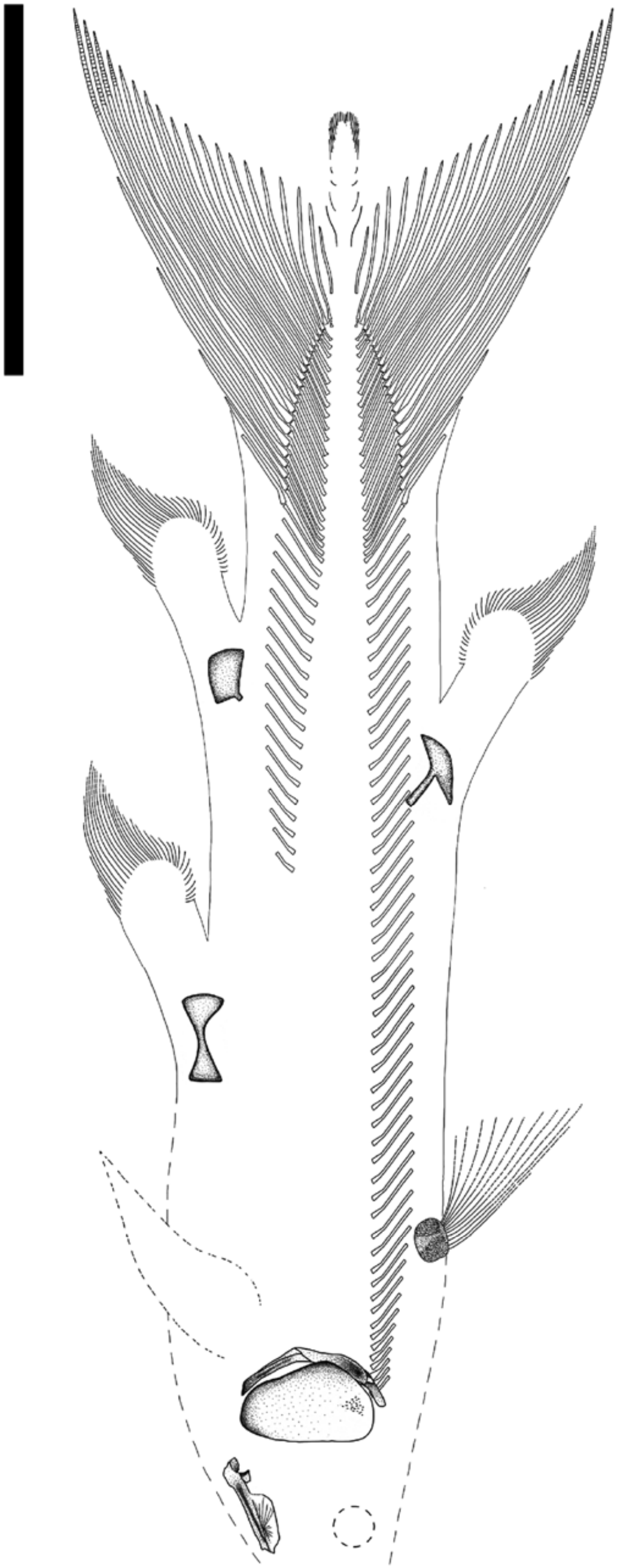
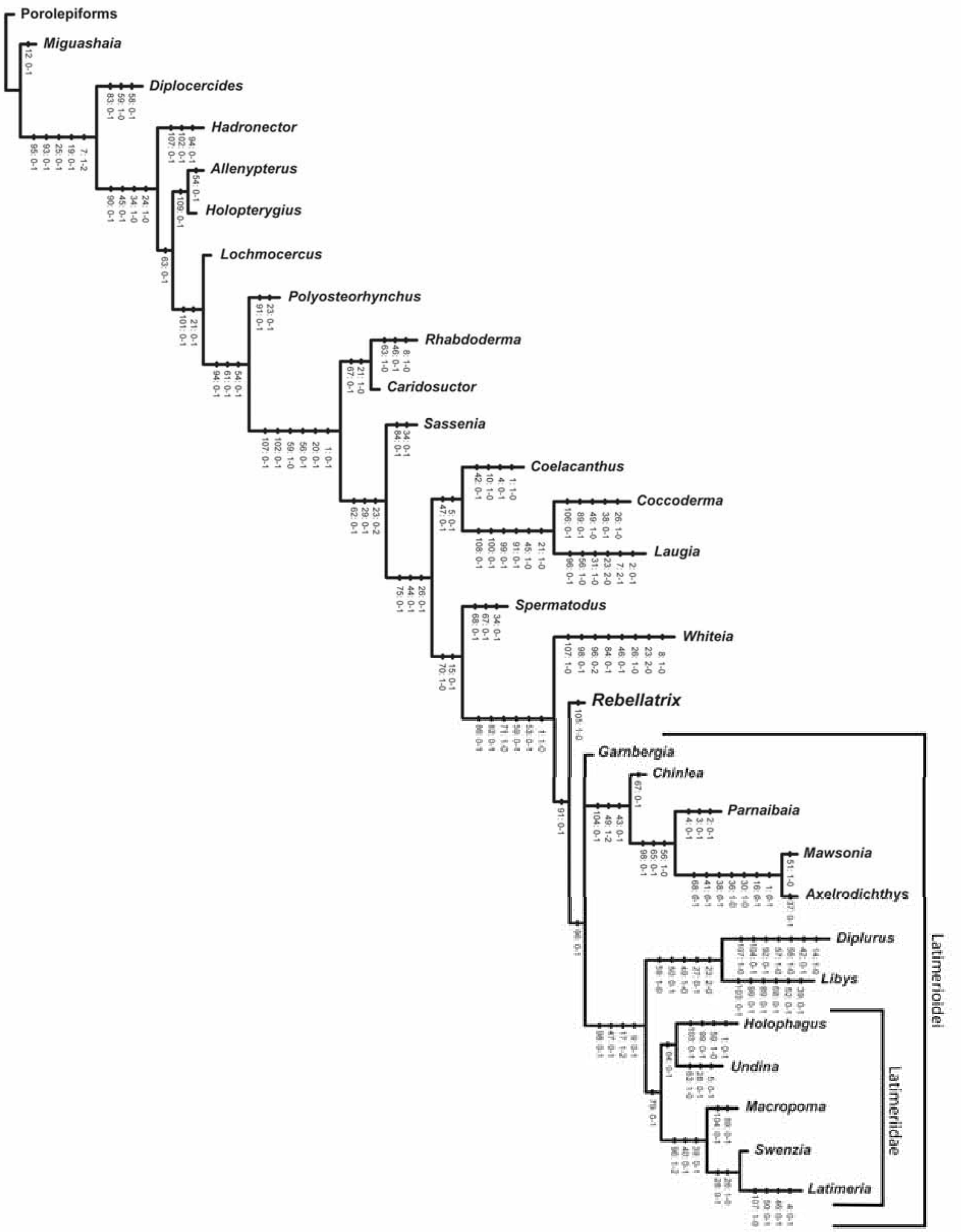


FIGURE 2.5. 50% majority rule cladogram resulting from three most-parsimonious trees (length = 246; CI = 0.463; HI = 0.537; RI = 0.701) resulting from a heuristic maximum-parsimony analysis using TBR and 100 random-addition-sequence replicates on an updated version of the character-taxon matrix of Forey (1998).


Porolepiforms
Miguashaia
Diplocercides
Hadronector
Allenypterus
Holopterygius
Lochmocercus
Polyosteorhynchus
Rhabdoderma
Caridosuctor
Sassenia
Coelacanthus
Coccoderma
Laugia
Spermatodus
Whiteia
Rebellatrix
Garnbergia
Chinlea
Parnaibaia
Mawsonia
Axelrodichthys
Diplurus
Libys
Holophagus
Undina
Macropoma
Swenzia
Latimeria
Latimerioidei
Latimeriidae

APPENDIX I

Character descriptions taken directly from Forey (1998) with the addition of character 109 from Friedman and Coates (2006).

1. Intracranial joint margin straight (0), strongly interdigitate (1).
2. Snout bones lying free from one another (0), snout bones consolidated.
3. Single median rostral (0), several median rostrals (internasals) (1).
4. Paired premaxillae (0), fragmented premaxillae (1).
5. Premaxilla with dorsal lamina (0), without dorsal lamina (1).
6. Anterior opening of the rostral organ contained within premaxilla (0), within separate rostral ossicle (outgroup taxa which lack a rostral organ must be scored as non applicable [N]).
7. One pair of parietals (1), two pairs (2)
8. Anterior and posterior pairs of parietals of similar size (0), dissimilar size (1) (non applicable coding used for those taxa with only a single pair).
9. Number of supraorbitals/tectals; fewer than eight (0), more than 10 (1).
10. Preorbital absent (0), present (1).
11. Parietal descending process absent (0), present (1).
12. Intertemporal absent (0), present (1).

13. Postparietal descending process absent (0), present (1).

14. Supratemporal descending process absent (0), present (1).

15. Extrascapulars sutured with postparietals (0), free (1).

16. Extrascapulars behind level of neurocranium (0), forming part of skull roof (1).

17. Number of extrascapulars: three (0), five (1), more than seven (2).

18. Posterior margin of the skull roof straight (0), embayed (1).

19. Supraorbital sensory canal running through centres of ossification (0), following a sutural course (1).

20. Medial branch of otic canal absent (0), present (1).

21. Otic canal joining supratemporal canal within lateral extrascapular (0), in supratemporal (1).

22. Anterior branches of supratemporal commissure absent (0), present (1).

23. Supraorbital sensory canals opening through bones as single large pores (0), bifurcating pores (1), many tiny pores (2).

24. Anterior pit line absent (0), present (1).

25. Middle and posterior pit lines within posterior half of postparietals (0), within anterior third (1).

26. Pit lines marking postparietals (0), not marking postparietals (1).

27. Parietals and postparietals ornamented with enamel-capped ridges/tubercles (0), bones unornamented (1), bones marked by coarse rugosities (2).

28. Parietals and postparietals without raised areas (0), with raised areas (1).

29. Cheek bones sutured to one another (0), separated from one another (1).

30. Spiracular (postspiracular) absent (0), present (1).

31. Preoperculum absent (0), present (1).

32. Suboperculum absent (0), present (1).

33. Quadratojugal absent (0), present (1).

34. Squamosal limited to mid-level of cheek (0), extending behind the postorbital to reach skull roof (1).

35. Lachrymojugal not expanded anteriorly (0), expanded anteriorly (1).

36. Lachrymojugal ending without anterior angle (0), angled anteriorly (1).

37. Squamosal large (0), reduced to a narrow tube surrounding the jugal sensory canal only (1).

38. Preoperculum large (0), reduced to a narrow tube surrounding the preopercular canal only (1).

39. Preoperculum undifferentiated (0), developed as a posterior tube-like canal-bearing portion and an anterior blade-like portion (1).

40. Postorbital simple, without anterodorsal excavation (0), anterodorsal excavation in the postorbital (1).

41. Postorbital without anterior process (0), with anterior process (1).

42. Postorbital large (0), reduced to a narrow tube surrounding the sensory canal only (1).

43. Postorbital entirely behind level of intracranial joint (0), spanning the intracranial joint (1).

44. Infraorbital canal within postorbital, with simple pores opening directly from the main canal (0), anterior and posterior branches within the postorbital (1).

45. Infraorbital sensory canal running through centre of postorbital (0), running at the anterior margin of the postorbital (1).

46. Jugal sensory canal simple (0), with prominent branches (1).

47. Jugal canal running through centre of bone (0), running along the ventral margin of the squamosal (1).

48. Pit lines marking cheek bones (0), failing to mark cheek bones (1).

49. Ornament upon cheek bones tubercular (1) or absent or represented as coarse superficial rugosity (2).

50. Infraorbital, jugal and preopercular sensory canals opening through many tiny pores (0), opening through a few large pores (1).

51. Lachrymojugal sutured to preorbital and lateral rostral (0), lying in sutural contact with the tectal-supraorbital series (1).

52. Sclerotic ossicles absent (0), present (1).

53. Retroarticular and articular co-ossified (0), separate (1).

54. Dentary teeth fused to dentary (0), separate from dentary (1).

55. Number of coronoids, coded as integers.

56. Coronoid opposite posterior end of dentary not modified (0), modified (1).

57. Dentary simple (0), dentary hook-shaped (1).

58. Oral pit line confined to angular (0), oral pit line reaching forward to the dentary and/or the splenial (1).

59. Oral pit line located at centre of ossification of angular (0), removed from centre of ossification (1).

60. Subopercular branch of the mandibular sensory canal absent (0), present (1).

61. Dentary sensory pore absent (0), present (1).

62. Ridged (0) or granular ornament (1) on the lower jaw.

63. Dentary with ornament (0), without ornament (1).

64. Splenial with ornament (0), without ornament (1).

65. Dentary without prominent lateral swelling (0), with swelling (1).

66. Principal coronoid lying free (0), sutured to angular (1).

67. Coronoid fangs absent (0), present (1).

68. Prearticular and/or coronoid teeth pointed and smooth (0), rounded and marked with fine striations radiating from the crown (1).

69. Orbitosphenoid and basisphenoid regions co-ossified (0), separate (1).

70. Basisphenoid extending forward to enclose the optic foramen (0), optic foramen lying within separate interorbital ossification or cartilage (1).

71. Processus connectens meeting parasphenoid (0), failing to meet parasphenoid (1).

72. Basipterygoid process absent (0), present (1).

73. Antotic process not covered by parietal descending process (0), covered (1).

74. Temporal excavation lined with bone (1), not lined (0).

75. Otico-occipital solid (0), separated to prootic/opisthotic (1).

76. Supraoccipital absent (0), present (1).

77. Vestibular fontanelle absent (0), present (1).

78. Buccohypophysial canal opening through parasphenoid (1), closed (0).

79. Parasphenoid without ascending laminae anteriorly (0), with ascending laminae (1).

80. Suprapterygoid process absent (0), present (1).

81. Vomers not meeting in the midline (0), meeting at midline (1).

82. Prootic without complex structure with the basioccipital (0), with complex suture (1).

83. Superficial ophthalmic branch of anterodorsal lateral line nerve not piercing antotic process (0), piercing antotic process (1).

84. Process on braincase for articulation of infrabranchial 1 absent (0), present (1).

85. Separate lateral ethmoids absent (0), present (1).

86. Separate basioccipital absent (0), present (1).

87. Dorsum sellae small (0), large and constricting entrance to cranial cavity anterior to the intracranial joint (1).

88. Extracleithrum absent (0), present (1).

89. Anocleithum absent (0), present (1).

90. Posterior neural and haemal spines abutting one another (0), not abutting (1).

91. Occipital neural arches not expanded (0), expanded (1).

92. Ossified ribs absent (0), present (1).

93. Diphycercal tail absent (0), present (1).

94. Fin rays more numerous than radials (0), equal in number (1).

95. Fin rays branched (0), unbranched (1).

96. Fin rays in anterior dorsal fin greater than 10 (0), 8 -9 rays (1), less than 8 rays (2).

97. Caudal lobes symmetrical (0), asymmetrical (1).

98. Anterior dorsal fin without denticles (0), with denticles (1).

99. Paired fin rays not expanded (0), expanded (1).

100. Pelvic fins abdominal (0), thoracic (1).

101. Basal plate of anterior dorsal fin with smooth ventral margin (0), emarginated and accommodating the tips of adjacent neural spines (1).

102. Posterior dorsal basal plate simple (0), forked anteriorly (1).

103. Median fin rays not expanded (0), expanded (1).

104. Scale ornament not differentiated (0), differentiated (1).

105. Lateral line openings in scales single (0), multiple (1).

106. Scale ornament of ridges or tubercles (0), rugose (1).

107. ‘Swim bladder’ not ossified (0), ossified (1).

108. Pelvic bones on each side remain separate (0), pelvic bones of either side fused in midline (1).

109. Ventral thickened keel scales absent (0), present (1).

APPENDIX II.

Character-taxon matrix used for phylogenetic analysis (modified from Forey, 1998) with 28 coelacanth taxa including *Rebellatrix divaricerca*, gen. et sp. nov. and Porolepiforms as the outgroup.

The first 108 characters are described in Forey (1998) and character 109 is discussed in Friedman and Coates (2006). Missing data = ‘?’; non-applicable states = ‘N’.

	10	20	30	40	50
Porolepiforms	00100N1??0	0000000000	00210?0001	1111NN0000	0000000010
Diplocercides	001???2101	0000000010	0021100001	1101000000	0000000010
Rhabdoderma	1000002001	1001001011	0000100001	1100000000	0000110010
Caridosuctor	1000002101	?0??001011	0000100001	11??000000	000??00010
Hadronector	00100021?1	?0??000010	0010100001	1100??0000	000?1?0?10
Polyosteorhynchus	00?0002101	???100?010	101???0001	11?0000000	000?1?0010
Allenypterus	0?????2001	?0??000010	000000001?	1100000000	01001??101
Lochmocercus	??????????	????????10	100???0001	11??000000	00?01000?0
Coelacanthus	00?11?2100	10010011?1	10?0?1101?	??00001??0	010?1?1?10
Spermatodus	1000002101	100110?111	?020?1001?	1101000000	00?????010
Whiteia	00?0002001	1001101111	1000100011	1100010000	0001110010
Laugia	11?0??1?01	1001001011	0000?10010	0000000000	0001001110
Sassenia	10????2?01	100100?01?	?020100011	1101000000	0000100010
Chinlea	00?01?2000	10??0011?1	10????2011	100?110000	100100?01?
Diplurus	00001?2110	1010102111	1000?11011	1000100000	0100111101
Holophagus	10?01?2110	101110?111	1?20?10010	1100100000	000?1??110
Undina	00?00?2110	101110211?	1?2???0110	1100??0000	000?101110
Coccoderma	10?011210?	1001001011	0020101010	0001001100	0001001100
Libys	0???1?????	10111??111	1?00?11010	000?1???01	000?1???01
Mawsonia	1?????2100	10100111?1	1020?12010	101?000120	101?000120
Macropoma	01?0?12110	1011102111	1120?10010	0001101110	0001101110
Latimeria	0011112110	1011102111	1100102111	0001111111	0001111111
Miguashaia	00?0001?0?	01??000000	002?00000?	000?000?10	000?000?10
Axelrodichthys	1000112100	101001111?	1020?12010	1011000120	1011000120
Garnbergia	??????21?0	?0?????1??	????????1?	000?????1?	000?????1?
Swenzia	01?0??2???	?011???1??	11?0101111	0001101110	0001101110
Holopterygius	?0?0??????	??????????	??0???????	??????????	??????????
Parnaibaia	0111??2000	?0??0011?1	??2??12011	001?????2?	001?????2?
Rebellatrix	??????????	??????????	??????????	??????????	????????1?

60	70	80	90	100	109
01003000?0	0?00001001	01N000?101	000N0?0000	000000N000	000000000
0100300100	0000000001	1101001101	?010000??0	0010100000	??0000???
0101410000	1001001011	10110?0000	?000101101	0011100000	110000100
0101410000	1010001???	??????????	???????101	?011101000	1100?0100
010???0010	000000????	??????????	???????101	?011100000	010??0100
0101?00010	10??000???	??????????	???????1?1	10111?1000	1000?0000
0101?00010	001000????	??????????	???????101	0010101000	000000001
01?0?00??0	00??000???	??????????	???????101	??10100000	100??0?00
0101410??0	1?110000??	??????????	???????101	0011101000	0100?0100
010141?000	?1???01110	101??0110?	?00?101???	??????????	???0?0???
011141101?	1111000010	00111??00?	11011111?1	0011120100	010010000
0101400000	1111000011	101110110?	?000101101	1011111011	0100?0110
01?1?10??0	111100??01	1011001?01	?0011011??	??????????	???0?0??0
10???11???	1?11001???	??????????	???????1?1	?11111?000	?101?1?00
101??00000	1?11000010	001?11?00?	??0?111101	1111110100	0101?0000
101??11001	1110001???	????11????	?1??1??1?1	101111?110	0110?0100
101??1101?	1100001010	001011?01?	?1??111101	?011110100	010010100
01?1410000	1111000???	??????????	???????111	1011100011	010011110
?1?1411001	1?110001??	??????????	???????111	1011110110	011010100
0011??1??0	1?111101??	??????????	?????????1	??111?0100	0101?1?0?
10114?1011	1111000010	001011?01?	110?111111	1011120100	010110100
1011411011	1N11001010	0010110010	1100111101	1011120100	010010000
?1?0??001?	?0??0000??	??????????	???????1?0	??0000?000	??0000??0
1011401??0	1?11110110	001111?0??	110?1111?1	1111110100	0101?1100
10????????	??????????	??????????	??????????	?????1?0??	0100?0??0
?0?1??101?	1N110??0??	????????1?	?????????1	?011??0??0	01?0?01?0
??00??0???	??????00??	???????00?	???????10?	?111110100	?00???0?1
101??01???	11111?00??	??????????	???????1?1	1011100000	0?01?0100
??1?????1?	??????????	??????????	???????101	1011100000	010000?0?

CHAPTER THREE

Two new species of *Whiteia, W. lepta* and *W. durabilis,* from the Lower Triassic Sulphur Mountain Formation in British Columbia, Canada

To be submitted as: Wendruff, A. J. and M. V. H. Wilson. Two new species of *Whiteia, W. lepta* and *W. durabilis,* from the Lower Triassic Sulphur Mountain Formation in British Columbia, Canada. Journal of Vertebrate Paleontology.

INTRODUCTION

Directly after the Permo-Triassic extinction, coelacanth species diversity peaked (Schaeffer, 1948, 1952; Forey, 1984, 1988; Cloutier, 1991; Cloutier and Forey, 1991; Forey, 1991, 1998). Of the 15 to 16 coelacanth genera found in the Triassic (Forey, 1991, 1998), *Whiteia* is both the most speciose and cosmopolitan, having been found in Madagascar (*W. woodwardi* and *W. tuberculata*), South Africa (*W. africana*), and Greenland (*W. neilseni*) (Broom, 1905; Moy-Thomas, 1935; Stensiö, 1936; Lehman, 1952; Forey, 1998). *Whiteia* has been noted to be present in Western Canada, but no formal description has been done (Schaeffer and Mangus, 1976).

Coelacanths have been known from the Lower Triassic of Western Canada ever since Lambe (1916) described *Coelacanthus banffensis* from Banff, Alberta, Canada, based on a partial specimen consisting of a section of body and a pectoral fin (CNM 756 and 756a, holotype). *Coelacanthus granulatus*, the type species, is characterized by having 17–20 pectoral fin rays and scales with closely spaced tubercles (Forey, 1998). Conversely, the holotype of *C. banffensis* preserves approximately 22–23 pectoral fin rays and scales with 17–19 ridges (the best scale is preserved just below the anterior insertion of the pectoral fin). Neither feature present on *C. banffensis* is diagnostic of the genus. Gardiner (1966) noted that the holotype of *C. banffensis* strongly resembled *Whiteia* Moy-Thomas, 1935; however, Schaeffer and Mangus (1976) as well as Forey (1998) both noted that the specimen may be too fragmentary to make any significant observations. While this specimen can likely be attributed to the genus *Whiteia*, based on the lack of information provided by the specimen, *Coelacanthus banffensis* is currently considered to be a nomen dubium.

Laudon et al. (1949) later reported on a more productive locality, near Wapiti Lake, British Columbia within the Sulphur Mountain Formation, where they found well-preserved and articulated fossil fishes. Schaeffer and Mangus (1976) were the first to actually document the vast faunal diversity of this site, which created great interest in this locality. This report stimulated large-scale collecting of specimens from this locality and years later the descriptions of numerous fishes (Mutter, 2004; Neuman and Mutter, 2005; Mutter and Neuman, 2006; Mutter et al., 2006, 2007, 2008a, 2008b; Mutter and Neuman, 2008a, 2008b, 2009).

Schaeffer and Mangus (1976) briefly described the coelacanths from the Sulphur Mountain Formation and attributed them to *Whiteia*, albeit as an undescribed species. They based their generic assignment on the similarity in basisphenoid form, pelvic plates, and fin-ray counts to *Whiteia woodwardi* Moy-Thomas, 1935. Additionally, they noted that the species reached up to a meter and perhaps as large as 3 meters in length based on a large isolated basisphenoid of similar form (CMN 12317).

However, the coelacanth diversity in the Sulphur Mountain Formation is more likely represented by 4 or 5 distinct genera, including *Whiteia.* Here we describe two new species, *W. lepta* and *W. durabilis,* that represent the largest known members of this genus, with *W. lepta*, sp. nov., reaching nearly a meter in length based on a partial caudal fin (UALVP 43719). *Whiteia lepta*, sp. nov., is exquisitely preserved as articulated, compressed specimens with well-preserved post-crania and crushed skulls, whereas *W. durabilis*, sp. nov., is found as three-dimensionally preserved skulls in large concretions. These species add to the temporal range and diversity of one of the best-known fossil coelacanth genera.

GEOLOGY

The Sulphur Mountain Formation, as it is exposed in cirque C (Wapiti Lake Provincial Park), consists of the Vega-Phroso, Llama, and Whistler Members (oldest to youngest) that span a temporal range from the Early to Middle Triassic (Gibson, 1975; Neuman, 1992). The fossil fishes are concentrated within the Vega-Phroso member, which consists of rust-colored to brownish-grey calcareous siltstones and shales (Gibson, 1972). The fishes of the Sulphur Mountain Formation were likely deposited in a continental shelf environment (Neuman, 1992). Gibson (1975) noted that at one point the environment was significantly shallower, even above wave base, farther up section in the Vega-Phroso member.

All of these specimens were collected along Ganoid Ridge (Range) within the vicinity of Wapiti Lake in British Columbia, Canada. Nearly all of these specimens were collected from cirque C. A single specimen, UALVP 43382, was found in a neighboring cirque F in the Sulphur Mountain Formation (see Callaway and Brinkman, 1989:fig. 1; Neuman, 1992:fig. 1). Other than the holotype of *W. lepta*, sp. nov., RBCM.EH 1986.001.0022, which was collected in a commercial quarry within cirque C, none of the specimens described here were collected in situ. Rather, they were collected in the talus below the exposure of the Sulphur Mountain Formation.

The Vega-Phroso siltstone member within the Sulphur Mountain Formation represents the Lower Triassic. Fossils from this exposure generally cannot be collected in situ, making it difficult to know their exact age. The Ganoid Ridge locality exposes multiple fish-producing beds that likely range from Induan to Ladinian in age (Neumann, 1992; Neuman and Mutter, 2005; Mutter and Neuman, 2006, 2008a). The two new species of *Whiteia* described here are from two different beds within the Sulphur Mountain Formation.

The main fish bed that produces *W. lepta*, sp. nov., represents the lowest concentration of fossil fish remains within the Lower Triassic of the Sulphur Mountain Formation, though it has been difficult to narrow down its stratigraphic origin further (Neuman, 1992). Schaeffer and Mangus (1976) as well as Neuman and Mutter (2005) both noted that the main fish exposure was likely Smithian (lower Olenekian); though, Orchard and Zonneveld (2009) dated the exposure as Dienerian (upper Induan) to early Smithian (lower Olenekian). Additionally, Mutter and Neuman (2009) noted that the similarity in faunas between British Columbia, Spitsbergen, and Madagascar may indicate that the age of the fish bed is more likely Dienerian (upper Induan). Neuman (1992) noted that there are at least three fossil fish-producing zones within the Sulphur Mountain. The main fish producing bed is located approximately 30 to 70 meters above the Triassic-Permian unconformity (Neuman, 1992). This layer is best exposed in cirques C, D, and R, which are those locations where coelacanths are most abundant (Neuman, 1992).

Whiteia durabilis, sp. nov., was preserved in the concretionary layer where the fossil material is three-dimensional and well-inflated. While it is unknown which bed produces the concretions, Neuman (1992) narrowed the occurrence down to a horizon above the lowest concentration of fishes, which produces *W. lepta*, sp. nov. A number of eugeneodontid sharks have been recently described from this concretionary layer (Mutter and Neuman, 2008). The concretion-bearing bed is directly above the lowest concentration of fish and is best exposed in cirques C, D, and T (Mutter and Neuman, 2009). A single specimen of *Fadenia uroclasmoto* (a eugeneodontid shark) has been collected in situ from the concretion-producing beds and has been determined to be lower Olenekian in age (Mutter and Neuman, 2008).

MATERIALS AND METHODS

The post-crania of coelacanths are well preserved at Wapiti Lake localities, while the skulls are usually crushed and poorly preserved.

The specimens of *Whiteia lepta*, sp. nov., are preserved in the 'split layer', where specimens are compressed, as opposed to being three-dimensional concretion specimens. Typically, the post-cranium is exquisitely preserved, though the skulls are crushed flat. In order to reveal more detail, UALVP 43602 and 43382 were both acid prepared in a dilute solution of hydrochloric acid (5% by volume) to dissolve the bone and create a high-fidelity negative mold in the rock. The negative of UALVP 43382 was dusted with ammonium chloride and then photographed, though typically after acid dissolution a silicone peel is made instead, as was done for UALVP 43602. The latter specimen was sprayed with a releasing agent (silicone oil) to prevent damage to the specimen. A layer of liquid silicone, Smooth-On Dragon Skin®, was poured onto the specimen in a grid pattern to prevent bubbles from forming, and allowed to dry over the course of four hours before being carefully peeled off. The final product represents a detailed positive cast of the specimen that can be then dusted with ammonium chloride and photographed. TMP 1983.206.01 and TMP 1983.206.02 were both mechanically prepared at the Royal Tyrrell Museum. TMP 1983.207.02 was not prepared, but rather split open. All specimens were photographed with a Canon Rebel XS digital SLR (Figs. 3.1A, C, 3.2A, 3.3A, 3.5A, 3.6A, E, 3.7A, 3.8A, C, E, 3.9A, D). Close-ups of scales and basal plates were achieved through the use of a Nikon DXM 1200C digital camera mounted on a Zeiss Discovery V8 stereo microscope (Figs. 3.2B–E, 3.3 B–E, 3.5B, 3.6B–D, 3.9B). Outline drawings were made using Adobe Photoshop CS4. Drawings were hand stippled and then scanned back into Photoshop. Phylogenetic analyses were performed using

Phylogenetic Analysis Using Parsimony (PAUP*) version 4 b10 (Swofford, 2002).

Institutional Abbreviations—AMNH, American Museum of Natural History, New York City, New York, United States; **MNHN MNA**, Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris, France; **MGUH,** Geological Museum at the University of Copenhagen, Denmark; **CMN,** Canadian Museum of Nature, Ottawa, Ontario, Canada; **RBCM**, Royal British Columbia Museum, Victoria, British Columbia, Canada; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP,** University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta, Canada.

SYSTEMATIC PALEONTOLOGY

Class OSTEICHTHYES Huxley, 1880

Subclass SARCOPTERYGII Romer, 1955

Order ACTINISTIA Cope, 1871

Family WHITEIIDAE Schultze, 1993

WHITEIA Moy-Thomas, 1935

Type Species—*Whiteia woodwardi* Moy-Thomas, 1935.

Included Species—*W. tuberculata*, *W. neilseni*, *W. africana*, *W. durabilis*, sp. nov., and *W. lepta*, sp. nov.

Emended Diagnosis—Apomorphies of genus: straight intracranial margin; large skull that is approximately one-third the standard length; long, slender snout; parietonasal shield approximately twice the length of the postparietal shield; narrow parietonasal shield in comparison to postparietal shield; descending processes on the parietals and postparietals, but lacking them on supratemporals; posterior margin of skull roof is embayed; two pairs of parietals of similar size; three pairs of nasals; paired premaxillae; elongate lateral rostral with poorly developed ventral process; sickle-shaped lachrymojugal with a thickened anterior process that is angled anteriorly and extends well past the orbit; 4–5 infraorbital pores on lachrymojugal; five supraorbitals; cheek bones that do not overlap, other than the suboperculum; oval suboperculum; small, scale-like spiracular; operculum rounded dorsally with a narrow ventral tip; saddle-shaped principal coronoid; hooked posterior process of dentary; shallow angular; recurved splenial; fourth coronoid is elongate and shallow bearing small needle-like teeth; retroarticular and articular separate; dentary unfused to bone; tubercular ornamentation on lower jaw confined strictly to the angular; two dermopalatines and one ectopterygoid covered in needle-like teeth on ventral surface of pterygoid; 7–9 anterior dorsal fin rays; unfused pelvic plates with two long slender anterior processes and two small posterior processes with a thin sheet of bone between the plates; symmetrical caudal fin with 15 dorsal and 14 ventral fin rays.

Remarks—An emended description for *W. neilseni* is needed as the type description was abridged. The species *W. groenlandica* is likely an error in Forey

(1998) as he used it interchangeably with *W. neilseni*. At one point he referred to a figure in text as belong to *W. groenlandica*; however, the figure was labeled *W. neilseni* in the figure caption. *Whiteia neilseni* is the valid name for these specimens from the Lower Triassic of Greenland. Additionally, Cloutier and Forey (1991) moved *Coelacanthus africanus* (Broom, 1905) to the genus *Whiteia*. According to the rules of the International Code of Zoological Nomenclature (1999) in respect to gender, the specific epithet should reflect the transfer from male to female generic name. Therefore, the correct spelling is *W. africana*.

WHITEIA LEPTA, sp. nov.

(Figs. 3.1–3.4A, 3.6–3.7)

Holotype—RBCM.EH 1986.001.0022, a complete and articulated specimen from the skull to the tip of the supplementary lobe, skull poorly preserved (Fig. 3.1), length 25 cm, collected in the commercial quarry within Cirque C (just SE of fossil fish lake)

Paratypes—UALVP 43602, complete skull in dorsolateral view with partial pectoral fin, cheek bones mostly missing, nearly complete skull roof in dorsal view (Fig. 3.2), length 26 cm, collected in Cirque C (see map in Neuman, 1992:fig. 1; Orchard and Zonneveld, 2009:fig. 1), latitude 54° 30’N, longitude 120° 43’W; UALVP 43382, consisting of the anterior half of the skeleton from the skull to the pelvic girdle (Fig. 3.3), length 19 cm, collected in Cirque F (see

Callaway and Brink, 1989:fig. 1; Orchard and Zonneveld, 2009:fig. 1); AMNH 6249, complete juvenile specimen, skull disarticulated, fins poorly preserved (Fig. 3.6A–D), length 18 cm, locality information unknown other than Sulphur Mountain Formation, specimen cited in Schaeffer and Mangus (1976); TMP 1983.206.48 (Fig. 3.6E), complete juvenile specimen, length 14 cm, collected in Cirque C; TMP 1984.42.02, complete specimen with poorly preserved skull, length 35 cm, collected in Cirque C; TMP 1984.131.28 (Fig. 3.7), consisting of the caudal fin and supplementary lobe, length 12 cm, collected in Cirque C; UALVP 43719, partial caudal fin, 18 cm deep, collected in Cirque C.

Stratigraphic Horizon and Type Locality—Sulphur Mountain Formation, Vega-Phroso Siltstone Member, Lower Triassic, Ganoid Range, Cirque C (S.E. of Fossil Fish Lake), latitude 54° 30’N, longitude 120° 43’W.

Etymology—From the Latin feminine adjective *lepta*, slender, referring to the long, slender body and caudal fin.

Diagnosis—Slender coelacanth reaching lengths up to one meter, although average size is around 25–30 cm. Apomorphies of species: large ventral process of posterior parietal; vaulted skull roof (postparietal and posterior parietal) across intracranial joint; depression behind vaulted area on postparietals; large supratemporal comprising a quarter or more of postparietal shield; small, irregular tubercles on skull roof; unornamented median parietonasal depression; large supratemporal; long, thin parasphenoid; differentiated ornamentation on the cheek bones, operculum, angular and skull roof; scales covered in numerous semi-radial ridges; robust quadrate and symplectic; tridentate dentary processes; robust symplectic; ‘swim bladder’ present; anocleithrum present; 67–70 scales along body from skull to base of supplementary lobe; 49–50 neural arches; absence of denticles on anterior dorsal fin rays; higher fin ray counts of pectoral, pelvic, anal and posterior dorsal fins than other species of *Whiteia*; long, slender caudal fin comprising nearly 40% of the entire body length.

DESCRIPTION AND COMPARISONS

Body Shape

Whiteia lepta is among the longest and most slender coelacanths along with *Coelacanthus granulatus* Agassiz, 1839. It is much more slender than *W. woodwardi* and *W. tuberculata*, although the total length of the caudal fins of the latter two species is unknown due to preservation in nodules. The two most complete specimens of *W. lepta*, RBCM.EH 1986.001.0022, holotype, and TMP 1984.131.28, are approximately 25 and 35 cm (respectively) from the skull to the base of the supplementary lobe (standard length as defined in Forey, 1998). They also have a caudal peduncle depth of 3.5 and 4.5 cm (respectively). Forey (1998) noted that *W. woodwardi* has 45 scales along the lateral line from the skull to the anterior margin of the supplementary lobe (where the posterior-most radial is inserted). Based on the RBCM.EH 1986.001.022 and TMP 1984.131.28, there are 67–70 scales along the lateral line of *W. lepta*. This is nearly a 50% increase in the number of scales compared to *W. woodwardi*, which suggests an elongation of the post-cranium. This elongation is most evident in the caudal region, in which the caudal fin (not including supplementary lobe) makes up nearly 40% of the standard length of *W. lepta*.

Skull

The skull roof of *W. lepta* is preserved on the holotype (RBCM.EH 1986.001.0022), and the paratype (UALVP 43602) (Figs. 3.1, 3.2, respectively). The skull roof in the holotype is preserved in lateral view, while UALVP 43602 preserves the skull dorsolaterally with the skull roof preserved in dorsal view. The parietonasal and half of the postparietal shields are preserved. The intracranial joint is straight across the margin between the two shields (Figs. 3.1D, 3.2F). Forey (1998) considered this to be a plesiomorphic feature because it is also present in the porolepiforms. The majority of the skull roof is covered in irregular, highly raised tubercles (Fig 3.2B). In contrast, most species of *Whiteia* have little ornamentation or ridges. On several of the largest specimens of *W. neilseni* and *W. woodwardi* there are tubercles present, though they are restricted to the postparietal shield (Forey, 1998). The posterior margin of the posterior pair of parietals and the anterior margin of the postparietals are greatly raised yielding a vaulted region across the intracranial joint (i.j.v) (Fig. 3.2F). The skull, in lateral view, has an elongated, slender ‘snout’ that is consistent with all other species of *Whiteia* (Fig. 3.3)

Postparietal Shield—The postparietal shield is preserved in both the holotype and the paratype UALVP 43602 (Figs. 3.1 and 3.2, respectively). In both specimens, only half of the shield is preserved. The postparietal shield as preserved consists of a single postparietal and a supratemporal (Figs. 3.1D, 3.2F). There is a small, circular, depression posterior to the vaulted anterior margin of the postparietal (Fig. 3.2F). The postparietal shield is wider than it is long in *W. durabilis*, sp. nov., *W. neilseni* and *W. woodwardi* (Stensiö, 1921; Moy-Thomas, 1935; Lehman, 1952; Forey, 1998). The supratemporal in *W. woodwardi* is reduced, making up a small portion of the postparietal shield (Forey, 1998:fig. 3.15), whereas in *W. lepta* the supratemporal is very large, extending the total length of the postparietal shield and making up approximately a quarter of the entire postparietal shield. The lateral margin of the supratemporal in *W. lepta* is similar in form to that of *W. neilseni,* although the supratemporal is proportionally larger in *W. lepta*. None of the typical pit lines or sensory canals is visible on this specimen due to poor preservation.

Parietonasal Shield—The parietonasal shield as preserved in the known specimens of *W. lepta* consists of two pairs of parietals, three pairs of nasals, one premaxilla and five supraorbitals (Fig. 3.2A, F). The parietonasal shield is long and narrow in *W. lepta* as it is also in *W. woodwardi*, *W. tuberculata* and *W. neilseni* (Forey, 1998). Both pairs of parietals are the same length, a feature common to all species of *Whiteia* (Stensiö, 1921; Moy-Thomas, 1935; Lehman, 1952; Forey, 1998) (Fig. 3.2F). On the right lateral side of the skull roof, a large ventral process of the posterior parietal is visible in UALVP 43602 (Fig. 3.2F).

There is a median, depression (parietonasal depression) starting in the center of the posterior parietal and continuing until the parietonasal shield begins to disarticulate at the second pair of nasals (Fig. 3.2A, F). This depression is nearly one third the width of the entire shield and completely unornamented. This is the only area on the entire skull roof that is devoid of ornamentation. This structure, which may have been covered in thicker soft tissues in life, is not present on any other known species of *Whiteia*.

There are three pairs of nasals in *W. lepta*, as in all other species of *Whiteia*. The three pairs of nasals are visible in lateral view on the holotype (Fig. 3.1C, D) and in dorsal view on UALVP 43602 (Fig. 3.2A, F). The first pair of nasals on UALVP 43602, which articulate with the anterior pair of parietals, is approximately half the length of the parietals (Fig. 3.2F). The second pair of nasals has begun to disarticulate and is nearly two-thirds the size of the previous nasal. The third and final pair of nasals (anterior most) is disarticulated and broken. None of the median rostrals is preserved on any of the known specimens of *W. lepta*; however, Forey (1998) noted that they are so commonly disarticulated that the total number is not even known for *W. woodwardi*, one of the best-known Triassic coelacanths.

The premaxilla is displaced just above the dentary. Since the teeth are large and curved anteriorly, it is not a displaced dentary tooth plate (Fig. 3.2F). There is a small groove on the median (middle of body) portion of the premaxilla that is consistent with the ethmoid commissure.

The right lateral series of supraorbitals is well preserved on UALVP 43602 (Fig. 3.2F). They flank the parietals from the intracranial joint to the anterior parietal. There are five supraorbitals, a number consistent with that found in all other species of *Whiteia* (Moy-Thomas, 1935; Lehman, 1952; Forey, 1998). In *W. woodwardi*, the farthest posterior supraorbital has a wide, rounded process that reaches past the intracranial joint (Fig. 3.2A, F). This process is preserved on UALVP 43602 on the left lateral side of the skull roof. The next two supraorbitals (second and third) are approximately the same size. The fourth supraorbital is larger and the fifth supraorbital, which is largest in all species of *Whiteia*, is incomplete. The tectals, the series anterior to the supraorbitals that flanks the parietonasal shield, are not preserved. The supraorbital canal follows the sutures between the supraorbitals and the parietals because no pores are visible through the bones.

Cheek Bones and Operculum—The cheek bones are poorly preserved in *W. lepta*, and none is discernable on the holotype, RBCM.EH 1986.001.0022 (see reconstruction, Fig. 3.4A). On UALVP 43602, the ornamentation on the cheek bones is clearly visible, but the boundaries of the postorbital, squamosal and preoperculum are not discernible. Ornamentation on the cheek consists of long, compressed tubercles that are very closely crowded (Fig. 3.2C). This ornamentation has been used to differentiate among species of *Whiteia* in the past (Moy-Thomas, 1935; Lehman, 1952; Forey, 1991, 1998). *Whiteia woodwardi* (Forey, 1998:fig. 4.14) is characterized by having irregular, sporadic tubercles, *W. neilseni* (Fig. 3.5B) by crowded, oval tubercles, and *W. tuberculata* (Lehman

1952: pl. 4, fig. a) by oval tubercles of uniform size and spacing (Forey, 1998). The ornamentation on *W. lepta* is just as crowded as that in *W. neilseni*, but the tubercles in *W. lepta* are significantly longer and compressed.

The suboperculum is present on UALVP 43602 and is located directly below the ventral tip of the operculum (Fig. 3.2F). The suboperculum is ovoid and wider than the one found in *W. durabilis*, sp. nov. In *W. woodwardi* and *W. neilseni*, it is the only cheek bone that does not tightly fit with the others, but rather is overlapped by the preoperculum (Forey, 1998).

The lachrymojugal, the most characteristic cheek bone of *Whiteia*, is well preserved on UALVP 43382 (Fig. 3.3A). It is a very long, highly curved (sickle-shaped) bone under the orbit that is angled anteriorly. The section below the orbit is the same thickness as the posterior section, whereas *W. durabilis*, sp. nov., has a pronounced thickened area of the lachrymojugal below the orbit. The anterior projection of the lachrymojugal in *W. lepta* is slightly thickened but relatively short compared to that in other species of *Whiteia*. The posterior end of the lachrymojugal that articulates with the ventral process of the postorbital is longer in *W. lepta* than in any other species of *Whiteia* other than *W. durabilis*.

Both the left and right opercula are preserved on the holotype (Fig. 3.1C, D). The operculum has the typical shape found in *Whiteia*, with a narrow ventral aspect and a broadly rounded dorsal side. No ornamentation is present on the operculum in the holotype, though UALVP 43382 and UALVP 43602 have ornamentation covering the entire operculum (Fig. 3.2D). The ornamentation consists of rows of elongate tubercles that are more compressed (elongated) than the ones on the cheek bones. Conversely, the operculum in *W. neilseni* is covered in the same crowded, round tubercles found on the rest of its cheek bones (pers. obs.).

Sclerotic ossicles (S.o) are present on UALVP 43602 and UALVP 43382 (Figs. 3.2F, 3.3A). There are approximately 22–25 present within the orbit.

Parasphenoid and Palate—A mostly complete parasphenoid (Par) is present on the holotype (Fig. 3.1C). It is a long, slender bone originating ventral to the intracranial joint and extending to the anterior portion of the skull. The posterior end is slightly expanded. Forey (1998) noted that the ventral surface of the parasphenoid in *W. woodwardi* is covered in teeth, but none is visible in the holotype of *W. lepta*, though it may be in lateral view.

The palate is best preserved in the holotype, in UALVP 43382, and in UALVP 43602. The pterygoid (Pt), quadrate (Q), and metapterygoid (Mtp) are the only palatal bones preserved in these specimens. The holotype preserves the impressions of the pterygoid and metapterygoid (Fig. 3.1C, D). The pterygoid is the classic triangular shape found in coelacanths. The metapterygoid, though incomplete, is very wide and most similar to the one found in *W. woodwardi* (Lehman, 1952:pl. 3, fig. a) and *Rhabdoderma elegans* Newberry, 1856 (see also Forey, 1998). The pterygoid shows two thickened ridges that extend dorsoventrally directly above the quadrate in UALVP 43602 (Fig. 3.2F). These ridges have also been noted in *Rhabdoderma elegans* (Forey, 1998:fig. 7.1e) and

Mawsonia gigas (Maisey, 1986:fig. 10). The quadrate is stout and shows the double-condyle shape typical of coelacanths (Fig. 3.3A).

Lower Jaw and Gular—The lower jaw is very well preserved on UALVP 43382 (Fig. 3.3A). The angular is shallower than the one found on *W. durabilis*, sp. nov., but comparable to those found in *W. woodwardi* and *W. tuberculata* (Lehman, 1952:pl. 2 and 4, respectively). In UALVP 43602, the angular is covered in disorderly, anteroposteriorly elongated tubercles (Fig. 3.2E) that are significantly more crowded than the ornamentation on the smaller UALVP 43382 (Fig. 3.3B). A large, curved, oral pit line (o.p.l), similar in shape to the one found in *W. neilseni* (Forey, 1998:fig. 5.9 d) is preserved on UALVP 43382 (Fig. 3.3B). The oral pit line is confined to the center of ossification on the angular.

The dentary (De) has an unusual three-pronged shape, although this feature may have been caused by crushing of the dentary (Fig. 3.2F). The dentary is hooked posteriorly, a typical feature of *Whiteia*, although it is not as greatly hooked as in *W. neilseni* or *W. durabilis*, sp. nov. No teeth are present on the dentary, but could have been easily displaced. In *W. woodwardi* and *W. neilseni*, the dentary has loosely attached dentary tooth plates, which commonly disarticulate away from the jaw (Forey, 1998). No splenial is preserved.

The enlarged 5th coronoid (principal coronoid, p.Co) and a toothed coronoid (4th coronoid, Co.4) are best preserved on UALVP 43602 (Fig. 3.2F). The principal coronoid has the typical saddle shape found in all species of *Whiteia* other than the largest specimen of *W. durabilis*, sp. nov. The dorsal margin of the principal coronoid is greatly thickened. A small, partial, toothed coronoid is preserved as well, below the anterior process of the pterygoid. It bears 5–6 conical teeth with rounded tips.

The double articulation of the lower jaw with the symplectic (Sy) and quadrate (Q) is well preserved in situ on UALVP 43382 (Fig. 3.3A). Both bones are preserved as impressions. The symplectic is more robust than is known in *W. woodwardi* and articulates with the retroarticular. The articular is not visible in any of the specimens known and thus its fusion to the retroarticular cannot be determined. For all other species of *Whiteia*, the retroarticular is distinctly separate from the articular (Forey, 1998).

The gular plate (Gu) is in place directly below the angular. A straight gular pit line (gu.p.l) is present at the center of the gular (Fig. 3.3C). Ornamentation is only present on the gular in UALVP 43602, perhaps because it is the largest specimen (Fig. 3.2A). It is covered in small, irregular tubercles and there is a small thickened ridge along the outer margin of the bone.

Appendicular Skeleton

Pectoral Fin and Girdle—The pectoral fin (Pc.f) has a total of 21–22 fin rays, 14–15 of which are long, while the rest are short and are at the dorsal and ventral margins of the fin base (Fig. 3.1A, B). Conversely, *W. woodwardi* has 16 pectoral fin rays (Forey, 1998), though it is possible that the smaller fin rays are not preserved. The pectoral girdle of *W. lepta* is best preserved on the holotype (Fig. 3.1C, D). Both the left and right girdles are present; the left is seen from an external view and the right from an internal view. The girdle consists of a cleithrum (Cl), extracleithrum (Ecl), clavicle (Cla) and anocleithrum (Acl). Interclavicles have been reported in *W. woodwardi* (Forey, 1998:fig. 4.15), although none seem to be present on the specimens of *W. lepta*. The cleithrum is a large element consisting of approximately half of the entire girdle. The dorsal end of the cleithrum is broadly rounded. The extracleithrum is closely associated with the clavicle and is small. The clavicle has an anteriorly projecting process similar to the one found in *W. woodwardi* (Forey, 1998:fig. 4.15), but it is not as slender. The anocleithrum is only preserved in the holotype and is slightly displaced dorsally and partially obscured by the pectoral girdles. It is not forked (simple) and has a centrally thickened ridge throughout the bone. All of the pectoral girdle elements are unornamented as they are in *W. neilseni* (pers. obs., e.g MGUH 2335).

Pelvic Fin and Girdle—The pelvic fin (P.f) is situated approximately half-way between the two dorsal fins (Fig. 3.1A, B). There are 23–24 fin rays; 15–16 of these rays are very long, while the rest are short along the dorsal and ventral margins of the fin (outer margin along base of fin). The pelvic plates (P.b) are well preserved in the holotype, and in AMNH 6249, a small, disarticulated specimen (Figs. 3.1B, 3.6A, B). The pelvic plates are situated anterior to the pelvic fin and are unfused at the midline. Each pelvic plate has two long, slender processes that fork anteriorly. Woodward (1935) reconstructed the pelvic girdle of *W. woodwardi* as having a thin plate of bone between the two slender processes. This feature is partially preserved in AMNH 6249 (Fig. 3.6B). There are two shorter posteriorly facing processes. The posteroventral process is expanded whereas the posterodorsal process is a short and slender.

Anterior Dorsal Fin

The anterior dorsal fin (D1.f) consists of 7–8 rays in *W. lepta* (Fig. 3.1A, B), a number that is consistent with both *W. woodwardi* and *W. tuberculuta*; however, *W. neilseni* has 9 anterior dorsal fin rays (pers. obs., e.g. MGUH 2335). The rays are all about the same length and lack ornamentation or denticles, unlike the saw-tooth-like denticles found on the fin rays of *W. woodwardi* and *W. tuberculata*. The ornamentation on the anterior dorsal fin rays of *W. neilseni* is a double-sided series of pointed denticles similar to a saw blade (e.g. MGUH 2335). The more poorly known species, *W. africana*, lacks ornamentation on the anterior dorsal fin (Broom, 1905; Forey, 1998). The anterior dorsal basal plate (D1.b) has been described as triangular in all species of *Whiteia* (Forey, 1998). The anterior dorsal basal plate of *W. lepta* is semi-circular with the anterior margin straight (Fig. 3.1A, B). The plate has a straight, smooth ventral margin that does not articulate with the neural spines below, unlike *Caridosuctor* Lund and Lund, 1984, (see Lund and Lund, 1985; Forey, 1998). The basal plate of *W. neilseni* is similar in shape to that of *W. lepta*, although the anterior end is narrower (pers. obs., e.g. MGUH 2328).

Posterior Dorsal and Anal Fins

The posterior dorsal fin (D2.f) is slightly anterior to the anal fin (A.f). The posterior dorsal fin has 20–22 fin rays; 14–15 are long (middle of fin) and 6–7 are short (along outer edges) (Fig. 3.1A, B). *Whiteia woodwardi* possesses 15 fin rays in the posterior dorsal fin (Moy-Thomas, 1935; Lehman, 1952; Forey, 1998). The anal fin of *W. lepta* has approximately 21–23 fin rays with 13–14 long ones, whereas *W. woodwardi* has 13 rays (Forey, 1998). The posterior dorsal and anal fin-ray counts are unknown for *W. neilseni*. The posterior dorsal basal plate (D2.b) is poorly known in *W. woodwardi* and *W. tuberculata* because of preservation and it is completely unknown in *W. neilseni*. The posterior dorsal basal plate in *W. lepta* is most similar in shape to that of *Caridosuctor* (Lund and Lund, 1985:fig. 19). The distal end of the basal plate is semi-circular, with a slightly narrower anterior end (Fig. 3.1A, B). The proximal end is a slender process that articulates with a neural spine. The posterior dorsal basal plate in AMNH 6249, a juvenile specimen, has an incompletely ossified distal end (Fig. 3.6C). The anal basal plate (A.b) is best preserved in the holotype and in AMNH 6249 (Figs. 3.1B, 3.6D). It is situated posterior to the dorsal basal plate and is a tube-like bone with two small, slender, anteriorly forked processes. This plate is significantly smaller than the posterior dorsal basal plate opposite it.

Axial Skeleton

There are approximately 49–50 neural arches in *W. lepta* based on the holotype, (Fig. 3.1A, B), paratype AMNH 6249 (Fig. 3.6A) and TMP 1984.42.02, a complete unfigured specimen. The neural spines are longest anterior to the caudal fin. The occipital neural arches are not expanded as in all species of *Whiteia*, a feature that Forey (1991, 1998) considered to be plesiomorphic. There are approximately 23–24 haemal arches, which first appear opposite the anal basal plate. As with the neural spines, the haemal spines are longest directly anterior to the caudal fin. No ossified ribs are preserved.

The ossified ‘swim bladder’ is preserved on both TMP 1984.42.02 and RBCM.EH 1986.001.0022, and extends posterior to the pelvic girdle. It has been noted that this feature is not present in *W. woodwardi*, *W. tuberculata*, or in *W. neilseni* (Moy-Thomas, 1935; Forey, 1998; Brito et al., 2010). The assumption is that if the ‘swim bladder’ is not preserved, it was not ossified; however, juvenile specimens of *W. lepta* (Fig. 3.6A, E) do not preserve an ossified ‘swim bladder’ whereas the holotype, a much larger specimen (Fig. 3.1A) does preserve one. This feature may not ossify until a later stage in development (ontogenetic). Furthermore, all current known specimens of *W. woodwardi* and *W. tuberculata* from Madagascar (Brito et al., 2010) do not preserve a ‘swim bladder’ and do not get much larger than the juveniles of *W. letpa* (Fig. 3.6A, E). Lacking an ossified ‘swim bladder’ in a fossil coelacanth may simply be due to preservational and ontogenetic biases in the fossil record.

Caudal Fin

The caudal fin in *W. lepta* is longer and more slender than in other species of *Whiteia* in which the caudal fin is known (Figs. 3.1A, B, 3.7). The caudal fin makes up nearly 40% of the entire body length (not including the supplementary lobe). The fin-ray count is identical to that of *W. woodwardi* (Moy-Thomas, 1935; Lehman, 1952; Forey, 1998) with 15 rays in the dorsal lobe and 14 in the ventral lobe, based on the holotype and TMP 1984.42.02. The posterior margin of the caudal fin is not known in most species of *Whiteia* due to the different preservation at those sites. The caudal fin of *W. lepta* is symmetrical (several radials displaced on holotype), in that the dorsal radials insert directly opposite the ventral radials. In some coelacanths, such as *Coelacanthus* Agassiz, 1839, and *Laugia* Stensiö, 1932, the dorsal radials first insert anterior to the ventral radials, creating an asymmetrical caudal fin (Schaumberg, 1978; Forey, 1998). The fin rays are longest towards the center of the tail near the supplementary lobe and shortest on the dorsal and ventral margins (Fig. 3.7). The supplementary lobe is small, slender and rounded. In the holotype, it extends past the posterior margin of the caudal fin (Fig. 3.1A, B); however, there is some variation in the length of the supplementary lobe. TMP 1984.42.02 and TMP 1984.131.28 both have reduced supplementary lobes. The former has the most reduced supplementary lobe, which barely extends past the posterior margin of the caudal fin (Fig. 3.7A, B). These variations may be attributed to individual variation within the species or perhaps sexual dimorphism, and therefore this feature is not considered enough to divide the species.

Scales

Scales have been used to distinguish between *W. woodwardi* (Lehman, 1952:pl. 5, fig. a) and *W. tuberculata* (Lehman, 1952:pl. 5, fig. b), both of which are found in Madagascar. The scales of *W. woodwardi* are composed of longitudinal ridges, while *W. tuberculata*, as the name suggests, has scales covered in tubercles (Moy-Thomas, 1935; Forey, 1998:fig. 11.9b, c). The scales of *W. lepta* (Fig. 3.3C, D) are covered in densely packed ridges that are arranged fanned out, and most resemble the scales of *W. neilseni* (Forey, 1998:fig. 11.19a), which are also densely covered in ridges, though not as many. In UALVP 43382, there are approximately 15–16 ridges per scale, while scales on the slightly smaller holotype have 12–13 per scale. The lateral line can be easily distinguished in the holotype as a series of pores running along the mid-flank of the body. The lateral line canal opens into multiple pores through the scales.

WHITEIA DURABILIS, sp. nov.

(Figs. 3.8–3.10)

Holotype—TMP 1983.206.02 (Fig. 3.8), complete three-dimensional skull with left, right, dorsal and ventral sides all well preserved (laterally crushed), length: 18 cm.

Paratypes—TMP 1983.206.01 (Fig. 3.9), mostly complete skull, right and left lateral sides preserved, well-preserved lower jaw and palate, mechanically prepared, length: 21 cm, collected in Cirque C; TMP 1983.207.02 (Fig. 3.10), mostly complete right lateral skull, length: 12 cm, exact cirque not recorded.

Stratigraphic Horizon and Type Locality—Sulphur Mountain Formation, Vega-Phroso Siltstone Member, Lower Triassic, Ganoid Range, Cirque C (see map in Neuman, 1992; Orchard and Zonneveld, 2009), latitude 54° 30'N, longitude 120° 43'W.

Etymology—From the feminine form of the Latin adjective *durabilis*, durable or long-lasting, in reference to the three-dimensional preservation of these specimens.

Diagnosis—Coelacanth reaching a maximum skull length of 20 cm. Apomorphies of taxon: v-shaped raised areas on both pairs parietals; radiating ridges across skull roof and lacking any other ornamentation; postorbital expanded anteroposteriorly; squamosal nearly as wide as it is deep; deep preoperculum; large sensory canal along posterior border of preoperculum; lachrymojugal deep below and behind orbit; large posterior process of lateral rostral comprising more than 50% of the bone; large posteriorly hooked dentary; presence of an anterior process of principal coronoid; large triangular autopalatine; pterygoid with multiple longitudinal ridges along the surface; two large dermopalatines; large, slender fourth coronoid with needle-like teeth.

DESCRIPTION AND COMPARISONS

Skull

The skull roof is poorly preserved in the two paratypes, TMP 1983.206.01 and TMP 1983.207.02, but is adequately preserved in the holotype (TMP 1983.206.02). The skull roof has little ornamentation other than radiating ridges that form at the center of ossification across both pairs of parietals (anterior and posterior) as well as the postparietals (Fig. 3.8E, F). Similar radiating lines are present on the skull roof of *Wimania sinuosa* (Stensiö, 1921:pl. 5, fig. 1). Tubercles have been found on the largest specimens of *W. woodwardi* and *W. neilseni* (Forey, 1998), although none have been noted on the largest specimens of *W. durabilis* (TMP 1983.206.01 and 1983.206.02). The intracranial joint (i.j) is clearly discernable between the postparietal shield and the parietonasal shield and is straight (Fig. 3.8E, F). The postparietal shield is significantly shorter than the parietonasal shield.

Postparietal Shield—The postparietal shield is only preserved well enough to provide detail in TMP 1983.206.02 (Fig. 3.8F). A pair of postparietals (Pp) and a single partial supratemporal (Stt) are the only elements preserved from the postparietal shield. While the lateral borders of the postparietals are incomplete, the postparietal shield is still wider than it is long and the postparietal shield is approximately half the length of the parietonasal shield; both features are shared with all species of *Whiteia* (Forey, 1998). The supratemporal is relatively small compared to the postparietals, making up a tiny portion of the total surface area of the postparietal shield.

Coelacanth skulls are covered by sensory lines, pits and pores, which lead to the rostral organ at the front of the skull. These features are also important sources of characters used to diagnose genera. Unfortunately, very few of these are preserved in *W. durabilis.* No visible pit lines or sensory canals are preserved on any of the specimens.

Parietonasal Shield—In *W. woodwardi*, the parietonasal shield generally consists of one to two pairs of parietals, several pairs of nasals and several rostral bones (Moy-Thomas, 1935; Lehman, 1952; Forey, 1998). Additionally, a series of supraorbitals (5) and tectals (4) flank the parietals and nasals (Moy-Thomas, 1935; Lehman, 1952; Forey, 1998)

There is also a series of supraorbitals and tectals that flank the parietals and nasals (approximately 9–10). TMP 1983.206.02 preserves both pairs of parietals (anterior and posterior, Pa), a series of supraorbitals (So), partial tectals (Te) and an undiscernible number of paired nasals (Na) in front of the parietals (Fig. 3.8F). The parietonasal shield is approximately twice the length of the postparietal shield, a typical feature found in all species of *Whiteia* due to their elongated, slender snouts (Forey, 1998). The parietonasal shield of *Whiteia* is generally considered to be one of the narrowest amongst coelacanths (Forey, 1998:fig. 3.15), however, it appears proportionally broader in *W. durabilis.* Nevertheless, it may appear this way because the lateral borders of the postparietals are incomplete or perhaps because these specimens are so much larger than previous described species of *Whiteia*. Both pairs of parietals are the same length and width, compared to each other, and both pairs have raised v-shaped areas (Pa.r) at the anterior portions of the bones (Fig. 3.8F). The area is raised higher on the anterior pair of parietals. This feature has not been noted in any other species of *Whiteia*. There are these raised areas are present on *W. lepta* as well, but they are located on the posterior parietals and postparietals across the intracranial margin.

The supraorbitals and tectals are preserved on the holotype, but the exact number of bones cannot be determined due to poor preservation of the sutures between them. The series extends from the intracranial joint to a point just anterior to the lateral rostral. A small flange projects posterior of the intracranial joint, which is part of the farthest posterior supraorbital (Fig 3.8A, F); this is a feature found on most coelacanths (Forey, 1998:fig. 3.15). TMP 1983.207.02 preserves the best supraorbitals of the known specimens of *W. durabilis* (Fig. 3.10). Five supraorbitals are preserved, the same number found in both *W. woodwardi* and *W. tuberculata* (Moy-Thomas, 1935; Lehman, 1952; Forey, 1998), as well as in *W. neilseni* (pers. obs., e.g., MGUH VP.133). The anterior-most supraorbital is significantly larger than the rest, a condition consistent with at least *W. woodwardi* and *W. neilseni* (Lehman, 1952; Forey, 1998).

All species of *Whiteia* are characterized in having three sets of nasals, but preservation of the known specimens of *W. durabilis* is too poor to see sutures. A partial premaxilla (Pmx) is preserved in TMP 1983.206.01 (Fig. 3.9D, E). The majority of this premaxilla has weathered away, but it is apparent that the premaxillae were paired, not fused, by the presence of smooth symphyseal margins. There are small, sharp teeth born upon the dentigerous portion of the premaxilla. None of the typical premaxillary pores (anterior rostral organ pores) are observed due to poor surface preservation.

The lateral rostral (L.r) is preserved on both the left and right lateral sides of TMP 1983.206.02 and is very long (Fig. 3.8A–D). Forey (1998) noted that the length of this bone may reflect elongation of the skull, particularly in relation to the long, slender snout. The posterior process is long, uniform, and slender. This process comprises more than half the entire lateral rostral. It is much longer in *W. durabilis* than in other known species of *Whiteia*, although once again, this may also be a function of the large size of *W. durabilis*. Adequate comparisons cannot be made with the other specimens of *W. durabilis,* because the lateral rostral is not preserved. The left lateral side of TMP 1983.206.02 preserves a small, ventrally squared-off process on the lateral rostral (Fig. 3.8D). In contrast, *W. woodwardi* has a poorly developed small, rounded ventral process. There are two dorsal processes preserved on the lateral rostral in *W. durabilis*, but only one on either side of the specimen. On the right lateral side, the process is just anterior to the midpoint of the bone (Fig. 3.8B), while on the left lateral side it is located at the anterior tip of the bone (Fig. 3.8D). The posterior dorsal process is more developed than the anterior dorsal process, the same condition seen (Forey, 1998) in *W. woodwardi*. In that species, the dorsal processes of the lateral rostral articulate with a series of tectals leaving two large gaps, which represent the posterior openings of the rostral organ (Forey, 1998). The dorsal processes of the lateral rostral are preserved on *W. durabilis*, but the tectals with which they would articulate are not preserved (Fig. 3.8B, D).

Cheek and Operculum—The cheek in *W. durabilis* is composed of six bones: the lachrymojugal (L.j), postorbital (Po), spiracular (Sp), squamosal (Sq), preoperculum (Pop) and suboperculum (Sop). No ornamentation is preserved on any of these bones in the known specimens. Cheek bones of the various species of *Whiteia* do not differ much in shape, but rather in ornamentation instead (Forey, 1998). The two Madagascar species, *W. woodwardi* and *W. tuberculata*, can be distinguished from each other, since the former has ornamentation characterized by sparse, elongated, irregular tubercles and the latter by closer packed oval tubercles (Lehman, 1952; Forey, 1998). The differences between the shape of the cheek bones in *W. woodwardi* and *W. tuberculata* are nearly indistinguishable. Furthermore, there is much variation within a species as well; Forey (1998) discussed that the proportions in the cheek bones (squamosal and postorbital) of *W. woodwardi* can vary a great deal. Typically, species of *Whiteia* have cheek bones covered in pit lines and pores, though none are preserved on any of the specimens of *W. durabilis*.

In all known species of *Whiteia*, the squamosal contacts the posterior margin of the postorbital, while the ventral process of the postorbital contacts the lachrymojugal. The squamosals of all species of *Whiteia* are triangular, although the proportions do vary from species to species (and within a species). The cheek bones fit tightly together but are not sutured in species of *Whiteia* (Forey, 1998:fig. 4.14).

The postorbital is best preserved on TMP 1983.207.02, the smallest specimen. It is posteriorly expanded with a small ventral process that likely articulated with the lachrymojugal, but has since been displaced. The postorbital is also displaced behind the squamosal in TMP 1983.206.02. The squamosal is very large in *W. durabilis*. Based on TMP 1983.206.01 and TMP 1983.207.02, the squamosal is nearly the same width as its height. It takes up a significantly greater area in the cheek than the postorbital. This condition is also found in *W. tuberculata* and *W. woodwardi*, whereas the postorbital and squamosal are nearly equal in size in *W. neilseni* (pers. obs., MGUH VP.133, 3270 and 2330). *Whiteia tuberculata* has a squamosal that is taller than it is wide, whereas the proportions vary greatly in *W. woodwardi* (Forey, 1998). The squamosal and postorbital proportions in *W. neilseni* are variable as well (pers. obs.).

The shape of the lachrymojugal is the most characteristic feature in the cheek of *Whiteia*. It is a long, sickle-shaped bone that is anteriorly angled (inclined) and located directly below the orbit. While it is preserved on all three specimens, it is best preserved on the two largest specimens, TMP 1983.206.02 and TMP 1983.206.01 (Figs. 3.8, 3.9). The anterior projection is slightly thickened and runs a considerable way in front of the orbit, terminating approximately at the parietal-nasal suture. The anterior tip of the lachrymojugal abuts the posterior end of the lateral rostral, a feature also found on other species of *Whiteia*. The lachrymojugal is thickened considerably below the orbit, similar to the condition in *W. durabilis* and *W. neilseni* (Forey, 1998); however, specimens of both species are larger than those of *W. tuberculata* and *W. woodwardi*, and this feature may vary through ontogeny. No pores are preserved in the lachrymojugal in any of the known specimens of *W. durabilis*.

The preoperculum is a wide bone that abuts the squamosal (TMP 1983.206.01). The shape and size varies with each specimen of *W. durabilis* due to preservation, preparation, and probably intraspecific variation. It appears to be best preserved on the right lateral side of the holotype (TMP 1983.206.02) (Fig. 3.8B). Similarly to other species of *Whiteia*, the preoperculum is squared off and wider than the squamosal. The preoperculum is usually much narrower than the squamosal, but it is nearly the same depth in *W. durabilis*, though the squamosal may be incomplete. In *W. woodwardi, W. tuberculata*, and *W. neilseni,* the dorsal margin of the preoperculum that abuts the squamosal is straight (Lehman, 1952; Forey, 1998). In *W. woodwardi* and *W. neilseni,* there is a small anterior projection of the preoperculum with a curved margin that meets the posteroventral side of the lachrymojugal (Stensiö, 1932; Lehman, 1952; Forey, 1998). In *W. tuberculata*, the preoperculum is reduced to such a degree that it is obscured from the margin of the lachrymojugal (Forey, 1998; Lehman, 1952:pl. 2, figs. a, c; pl. 4, figs. a, c). While the preoperculum is large in *W. durabilis*, it is not possible to determine whether its anterior margin meets the lachrymojugal because of displacement and crushing of the specimen. There is a curved, longitudinal depression along the posterior edge of the preoperculum, which represents the infilling of the preopercular canal (Fig. 3.8B, pop.sc).

All of the cheek bones of *Whiteia* abut one another, but one bone, the suboperculum, is usually overlapped by the preoperculum (Forey, 1998). It is not possible to determine if it is overlapped in *W. durabilis* because the posterior portion of the preoperculum is incomplete. The suboperculum is best preserved on TMP 1983.207.02 (Fig. 3.10). It is a tall, narrow bone with rounded margins with a height that is double its width. The smallest cheek bone, the spiracular (Sp), is preserved on the left lateral side of the holotype (Fig. 3.8D). It is a reduced and rounded element that is not preserved on many coelacanths, either because it is so small and easily obscured in most species, or because it is not present. The spiracular on *W. durabilis* is most similar in shape to the one preserved on *W. neilseni* (Fig. 3.5A).

The operculum (Op) is not completely preserved on any of the specimens known, but it is best preserved on the left lateral side of the holotype (Fig. 3.8C, D). It is a deep bone, spanning almost the entire height of the cheek, and lacks ornamentation.

Palate—The palate of *W. durabilis* preserves the pterygoid (Pt), quadrate (Q), ectopterygoid (Ecpt), dermopalatines (Dpl), and autopalatine (Aup). The toothed elements (ectopterygoid, dermopalatine, and the autopalatine) are best preserved on left lateral side of TMP 1983.206.01. A small section of pterygoid is preserved on the right lateral side of the same specimen. The quadrate is preserved on both the holotype and TMP 1983.207.02 (between the preoperculum and suboperculum) (Figs. 3.8D, 3.10). The characteristic triangular coelacanth palate is not visible in any of these specimens.

The preserved portion of the endodermal palate consists of the quadrate and autopalatine (Forey, 1998). The quadrate is a long bone with a double condyle that articulates with the lower jaw. The autopalatine is preserved on the paratype, TMP 1983.206.01, on both the left and right sides (Fig. 3.9C, E). The autopalatine is incomplete but in place on the left lateral side; it is displaced but complete on the right lateral side. It is a concave, triangular bone that tapers anteriorly.

The dermal palate consists of the pterygoid, ectopterygoid, and dermopalatines as preserved on TMP 1983.206.01. The palatal surface of the pterygoid is covered in narrow, longitudinal ridges (Fig. 3.9A, C). The left lateral side of the specimen shows two dermopalatines (one slightly anteriorly displaced) that articulate with the autopalatine, one in front of the other (Fig. 3.9E). These bones are likely only loosely attached to the autopalatine as they commonly disarticulate in other coelacanths (Forey, 1998). The ectopterygoid is similar in size to the posterior dermopalatine, but has larger teeth (Fig. 3.9E). This is the reverse condition from that of *Latimeria chalumnae* Smith, 1939, and *Macropoma lewesiensis* Mantell, 1822, which have large fangs on their dermopalatines and small conical teeth on their ectopterygoid (Forey, 1998).

Lateral Ethmoid and Parasphenoid—The lateral ethmoids are part of the anterior portion of the neurocranium (ottic-occipital) and are rarely preserved in fossil coelacanths (Maisey, 1986; Forey, 1998). They flank both the right and left lateral side of the basisphenoid. While no basisphenoids are preserved on the specimens described here, Schaeffer and Mangus (1976) made reference to a large, isolated basisphenoid (unfigured) from the Sulphur Mountain Formation. They deduced that it came from a massive specimen of *Whiteia* nearly 3 meters long, though it is not possible to determine from which species of *Whiteia* this came.

The lateral ethmoids are located directly below the paired nasals and as such form the bottom and lateral walls of the nasal capsule (Forey, 1998). Both lateral ethmoids are preserved on TMP 1983.206.01 (Fig. 3.9). The description is, however, based on the right lateral ethmoid, as it is three-dimensional and best preserved (Fig. 3.9C). It is a large bone, approximately the size of the autopalatine. The anterior margin of the lateral ethmoid is incomplete. There are two thickened ridges extending from the dorsal to anteroventral margins of the element. Between these ridges is a triangular depression known as the ventrolateral fossa, which is the point of insertion of the autopalatine (Forey, 1998). There is some ventral swelling on the anterior portion of the lateral ethmoid that is consistent with *Latimeria* (Forey, 1998:fig. 6.1). A large opening in the anterior portion of the left lateral ethmoid corresponds to the buccal canal (bucc.can). The parasphenoid (Par) articulates with the posterior part of the lateral ethmoids. This is the only visible part of the parasphenoid in these specimens. It is relatively thick at nearly half the depth of the lateral ethmoid and is slightly convex. No teeth are preserved.

Lower Jaw—The lower jaw of *W. durabilis* is well preserved and consists of the angular (Ang), gular (Gu), dentary (De), splenial (Spl), prearticular (Part), principal coronoid (p.Co), tooth-bearing 4th coronoid (Co.4), and retroarticular (Rart).

The angular is relatively shallow when compared to that of other coelacanths such as *Axelrodichthys* Maisey, 1986, and *Coelacanthus* Agassiz, 1839. The only ornamentation on the lower jaw is present on the angular, which consists of closely packed oval tubercles covering most of the bone on TMP 1983.206.01 (Fig. 3.9B). The tubercles are similar in shape to those found in *W. neilseni* (Forey, 1998:fig. 5.9d), however, unlike *W. durabilis,* the tubercles are restricted to the center of ossification of the angular in *W. neilseni* (pers. obs., e.g. MGUH 2335). On TMP 1986.206.02, two pores from the mandibular sensory canal (m.s.c) are preserved on the anteroventral portion of the angular (Fig. 3.8B). The pores are large and round, most similar to those found in *W. tuberculata* (Lehman, 1952:pl. 4, fig. c).

The dentary (De) is relatively large and deep in *W. durabilis* with a pronounced posterior hook in the dorsal side (Figs. 3.8D, 3.9C). The dentary is most similar in form to the one found in *W. neilseni* (Forey, 1998:fig. 5.9d). In all known species of *Whiteia*, the dentary has a large posterodorsal hook and a posterior process that reaches back into the angular. *Whiteia woodwardi* has a posterior dentary process that extends farthest posterior to the angular, much farther than in *W. durabilis* and *W. neilseni*. No teeth are preserved on the dentary in *W. durabilis*. Forey (1998) noted that many specimens of *W. woodwardi* and *W. tuberculata* lacked teeth born on the dentary; based on a few specimens that preserve the tooth plates, he stated that they likely displace easily during fossilization.

The splenial (Spl) is preserved on the left lateral side of the holotype and the right lateral side of TMP 1983.206.01 (Figs. 3.8D, 3.9C). The splenial is a long, slender bone below the dentary that is nearly two-thirds the length of the dentary. On the holotype, the splenial appears to have a small ventral lip.

Coelacanths have five coronoids on the lower jaw. Only the 4th coronoid (tooth bearing) and the 5th (principal coronoid) are visible in these specimens. The principal coronoid (p.Co) is preserved on all three specimens and the fourth coronoid (Co.4) is only preserved on the right lateral side of TMP 1983.206.01. In *W. neilseni* and *W. woodwardi*, the first three coronoids are small tooth-bearing plates located on the dentary (Forey, 1998:fig. 5.9c, 5.9e), but they are not preserved in any of the known specimens of *W. durabilis*. The fourth coronoid is a slender, elongate bone that articulates with the prearticular and possesses a series of crowded, small conical teeth. (Fig. 3.9A, C). The principal coronoid is saddle-shaped in all species of *Whiteia* (Forey, 1998); however, TMP 1983.207.01 (Fig. 3.9), the largest specimen of *W. durabilis*, shows an anterior process on the principal coronoid. This process is longer than deep and has the characteristic dorsal thickening found on the principal coronoid present in both *W. woodwardi* and *W. neilseni* (Forey, 1998:fig. 5.9a, 5.9d). It is possible that this anterior process is the result of ontogenetic variation. The labial side of the principal coronoid is characterized by a dorsally thickened ridge that follows the outline of the adductor muscle (Forey, 1998). It is possible that this anterior process, which is only present in the largest specimen, would have affected jaw motion and feeding.

The retroarticular (Rart) is disarticulated from the lower jaw on the left lateral side of the holotype (Fig. 3.8D). The articular is not preserved. Together these two bones form the condyle for the quadrate. Since the retroarticular is found separate from the articular, it is likely that they are not fused. The gular plates (Gu) are best preserved on the holotype, though they nearly overlap each other due to lateral crushing of the specimen. They are elongate with no ornamentation or pit-lines preserved, but with two ridges around the outer margin of the gular plates (Fig. 3.8).

PHYLOGENETIC ANALYSIS

Analytical Methods

A taxon-character matrix (Appendix III) was modified from Clément (2005), Friedman and Coates (2006), and Yabumoto (2008), as well as Wendruff and Wilson (in review and Chapter 2), which is ultimately based on Forey's (1998) matrix. The original matrix from Forey (1998) consisted of 30 ingroup and 2 outgroup taxa (Porolepiformes and Actinopterygii) and 108 characters. Because of missing data, Forey (1998) removed the following genera from his analysis: *Euporosteus*, *Wimania*, *Axelia*, *Lualabaea*, *Indocoelacanthus* and *Ticenepomis* leaving only 24 taxa. Clément (2005) revised the character matrix by fixing a miscoding of character 31 (preoperculum absent [0], present [1]) and added *Swenzia* Clément, 2006. Geng et al. (2009) added *Piveteauia* Lehman, 1952 based on Clément's (1999) description to Forey's (1998) taxon-character matrix, though several inaccuracies are rectified. We excluded *Guizhoucoelacanthus* (Liu et al., 2006; Geng et al., 2009) from the analysis because the cladogram could not be replicated perhaps due to miscodings in the published taxon-character matrix. Friedman and Coates (2006) revised the matrix by adding character 109 (ventral keel scales absent [0], present [1]) as well as an additional taxon, *Holopterygius* (Jessen, 1973; Friedman and Coates, 2006). Yabumoto (2008) later added the taxon *Parnaibaia*. Brito et al. (2010) fixed two miscodings in Forey's (1998) original matrix for character 107 (ossified 'swim bladder' absent [0], present [1]) with respect to *Allenypterus* (Melton, 1969) and *Polyosteorhynchus* (Lund and Lund, 1984). The new genus *Rebellatrix* (Chapter 2) was also included using data from Chapter 2.

Here we add our two new species, *Whiteia durabilis* and *Whiteia lepta*. Our final data set includes 32 taxa and 109 characters. *Whiteia durabilis* is coded for 42 out of 109 characters and *W. lepta* is coded for 55 out of 109 characters.

Cladograms were generated using PAUP v4.0 b10 (Swofford, 2002) employing heuristic search with TBR and 100 random-addition-sequence replicates. Acctran character state optimization was used. Characters were unordered and unweighted. Character transformations were examined using MacClade (Maddison and Maddison, 2005).

Piveteauia

This poorly known genus was described by Lehman (1952) on the basis of a nearly complete specimen with a partial disarticulated skull, that is missing the posterior margin of the caudal fin. It was recognized as unique based on the unusually placed pelvic fin that was situated directly below the pectoral fin. Clément (1999) redescribed *Piveteauia* on the basis of a new specimen with a well preserved skull in lateral relief, though he did not add the new information to Forey’s (1998) taxon-character matrix. Geng et al. (2009) included *Piveteauia* in their phylogenetic analysis based strictly on Clément’s (1999) description; however, several features mentioned by Clément (1999) were left as unknown (?) and several features are contrary to the description in Geng et al.’s (1999) matrix. We recoded *Piveteauia* based on the original description by Lehman (1952), Forey (1991) and a redescription by Clément (1999).

In total, 24 of 109 characters codings were amended (characters 1, 12, 14, 15, 22, 27, 28, 29, 37, 45, 48, 53, 54, 61, 65, 68, 78, 79, 91, 92, 93, 96, 97 and 104). The following characters were specifically addressed by Clément (1999) but were either coded as missing or as another character state in Geng et al. (2009): characters 14, 15, 27, 28, 37, 53, 68, 78, 79, 91 and 96. Characters 12 and 22 were coded for *Piveteauia* in Forey’s (1991) original taxon-character matrix (*Piveteauia* was not included in his 1998 matrix). Geng et al. (2009) coded character 1 as straight, even though Clément (1999) was uncertain whether the intracranial joint margin was straight or interdigitating. Based on the original description and figures of the holotype (Lehman, 1952:fig. 17, pl. 3, fig. 3; Clément, 1999:fig. 4, 5) we changed the character state to reflect the interdigitating anterior margin of the post parietals. Geng et al. (2009) coded the cheek bones as sutured to one another (character 29), however, the only cheek bones known in *Piveteauia* (Clément, 1999:fig.1, 2) are fragmentary and displaced, and thus the character state is changed to missing or unknown (?). The character state of character 45 is reassessed because Clément (1999) showed the infraorbital sensory canal running through the postorbital (Clément, 1999:fig. 1, iosc). The character state for character 48 is changed to reflect the absence of pit lines marking the cheek bones. While the cheek bones are broken, pit lines are not observed on any of those that are preserved (postorbital, squamosal and preoperculum). The character state of character 54 is recoded as having separate tooth plates from the dentary because no fused dentary teeth are observed. While no dentary teeth are preserved on the new specimen of *Piveteauia* (Clément, 1999:fig. 2), Forey (1998) noted a similar occurrence in many specimens of *Whiteia woodwardi* (Moy-Thomas, 1935), which were missing their tooth places because they commonly disarticulated from the lower jaw. Clément (1999) identified a pore in the splenial as the splenial pore (Clément, 1999:fig. 1, spp); however, this is more likely the dentary pore (character 61) in which the suture between the dentary and splenial is poorly preserved. Neither dentary shows signs of a prominent lateral swelling (character 65) (Clément, 1999:fig. 2, lDe, rDe), unlike *Axelrodichthys* (Maisey, 1986) and *Mawsonia* (Woodward, 1907; Maisey, 1986). Ribs are absent in *Piveteauia* (character 92) (Lehman, 1952:pl. 3, fig. c; Clément, 1999:fig. 3, 4). Geng et al. (2009) recorded that a diphycercal tail was present (character 93) in *Piveteauia*; while it is likely that this is true, the posterior margin of the caudal fin is unknown in either the holotype (MNHN MAE 116) or the paratype (MNHN MAE 2392) and as such we coded it as unknown. Geng et al. (2009) also coded the caudal fin as symmetrical (character 97). Clément (1999) did not discuss whether the tail is symmetrical or asymmetrical; however, Forey (1991) coded the tail as asymmetrical in *Piveteauia*. While the tail in the holotype is incomplete (Lehman, 1952:pl. 3, fig. c), the dorsal radials clearly insert farther anterior to the ventral radials, yielding an asymmetrical caudal fin similar to that of *Laugia* Stensiö, 1932. Scales are covered in ridges and are not differentiated (character 104), unlike *Parnaibaia* Yabumoto, 2008 and *Chinlea* Schaeffer, 1967.

The familial placement of *Piveteauia* has been problematic. Forey (1991) and Geng et al. (2009) both placed it as sister to *Whiteia* and within the Whiteiidae (respectively); however, Forey (1998) and Clément (1999) both tentatively place it within the Laugiidae. Clément (1999) noted that the five features (presence of parietal descending processes; presence of a spiracular; retroarticular and articular ossified; medial branch of the otic canal developed and opened within the parietal; caudal fin rays equal to number of radials) that place *Piveteauia* sister to *Whiteia* in Forey (1991) were homoplastic. Furthermore, Clément (1999) observed that the anterior position of the pelvic fin and the shape of the lachrymojugal tie *Piveteauia* closely with *Laugia* (Stensiö, 1932; Forey, 1998) and *Coccoderma* Quenstedt, 1858 (Lambers, 1991). While neither Clément (1999) nor Forey (1991, 1998) noted it, both *Piveteauia* and *Laugia* also have squared-off principal coronoids (Clément, 1999:fig. 1, Co; Forey, 1998:fig. 4.10).

Piveteauia is resolved as a sister to the clade (*Laugia* + *Coccoderma*) within the family Laugiidae Berg, 1940. The family is supported by six synapomorphies: 1) infraorbital sensory canal running through center of postorbital (character 45); 2) optic foramen lying within separate interorbital ossification or cartilage (unknown in *Piveteauia*) (character 70); 3) expanded occipital neural arches (character 91); 4) 8–9 anterior dorsal fin rays (character 96); 5) thoracic abdominals (character 100); 6) pelvic bones on either side fused at midline (unknown in *Piveteauia*) (character 108). The clade (*Laugia* + *Coccoderma*) to (the exclusion of *Piveteauia*) is supported by four synapomorphies: 1) straight posterior margin of skull roof (character 18); 2) spiracular absent (character 30); 3) jugal canal running along the squamosal ventral margin (character 47); 4) paired fin rays expanded (character 99). Five synapomorphies exclude *Piveteauia* from the clade (*Laugia* + *Coccoderma*): 1) postparietal descending process present (character 13); 2) anterior branches of supratemporal present (character 22); 3) jugal sensory canal with prominent branches (character 46); 4) retroarticular and articular separate (character 53); 5) parasphenoid with ascending laminae (character 79).

Results

Maximum-parsimony analysis yielded 46 most-parsimonious trees of 254 steps (CI = 0.449, HI = 0.551, RI = 0.696). The 50% majority rule consensus tree (Fig. 3.11) shows resolution of a polytomy present in Chapter 2 within the suborder Latimerioidei between (*Chinlea* (*Parnaibaia* (*Mawsonia* + *Axelrodichthys*))), (*Diplurus* + *Libys* (Latimeriidae)), and *Garnbergia* Martin and Wenz, 1984 (see Wendruff and Wilson, in review). The clade (Whiteiidae (*Rebellatrix* (Latimerioidei))) is held together by seven synapomorphies, three of which are coded for *W. durabilis* and four that are coded for *W. lepta*. Three of the synapomorphies are shared by both new species: (1) straight intracranial margin (character 1), (2) lachrymojugal anteriorly angled (character 36) and (3) retroarticular and articular separate (character 53). *Whiteia durabilis* and *W. lepta* are resolved as two new members of the monotypic family Whiteiidae Schultze, 1993. The two new species are held within the Whiteiidae by a single synapomorphy: fewer than eight fin rays in the anterior dorsal fin (character 96).

PHYLOGENETIC DISCUSSION

Whiteia is among the most speciose genera within Actinistia Cope, 1871. In contrast, most other coelacanth genera are monospecific. Forey's (1998) phylogenetic analysis did not include species for this reason; however, it creates a problem with diverse genera such as *Whiteia*. The addition of *W. durabilis* and *W. lepta* to the modified dataset from Forey (1998) presented here yields a cladogram that improves our understanding of the evolution of the Whiteiidae.

The clade (*Whiteia (W. durabilis* + *W. lepta* (*Rebellatrix* + Latimerioidei))) is supported by seven synapomorphies (characters 1, 36, 53, 59, 71, 82, and 86). Of these seven characters, *W. durabilis* is coded for three and *W. lepta* for four. Three of the synapomorphies are coded for both *W. durabilis* and *W. lepta*: (1) straight intracranial margin (character 1), (2) lachrymojugal anteriorly angled (character 36) and (3) retroarticular and articular separate (character 53). Whether the intracranial margin is straight or interdigitate (character 1) is fairly homoplasious in that it reverses multiple times. For example, the Latimerioidei are characterized as having a straight intracranial margin; however, it reverses within this clade in three taxa: *Mawsonia*, *Axelrodichthys*, and *Holophagus.* Forey (1998) noted that a straight intracranial margin is plesiomorphic in coelacanths as it is present in both osteolepiforms and porolepiforms. Additionally, the variation between a straight and interdigitate margin has no known functional significance. An anteriorly angled lachrymojugal (character 36) is present in all members of the Whiteiidae as well as *Chinlea* and *Garnbergia*. This is a nearly unique feature in coelacanths, having only evolved once in Whiteiidae and again separately in *Chinlea* and *Garnbergia*. Separation of the retroarticular and articular (character 53) is considered to be a derived feature among coelacanths, only present within (*Whiteia (W. durabilis* + *W. lepta* (*Rebellatrix* + Latimerioidei))) (Forey, 1991, 1998). Character 59 (oral pit line located at the center of ossification) is coded for *W. lepta*, but not for *W. durabilis*; however, Wendruff and Wilson (in review) noted that this character is highly homoplasious and therefore not a phylogenetically informative character.

The family Whiteiidae is held together by a single synapomorphy: anterior dorsal fin with fewer than eight rays (character 96). Forey (1998) did not state for which species he based his coding of *Whiteia*. This character is problematic, because *W. neilseni* has nine anterior dorsal fin rays, meaning that the character state should be 1 for *Whiteia* instead of 0. Forey (1998) noted that *W. woodwardi* and *W. africana* have approximately seven to eight fin rays, which would render the character state assignment for these taxa highly subjective, due to the arbitrary delimitation of the states for this character (i.e. 0: D1 > 10 fin rays, 1: 8–9 fin rays, 2: D1 <8 fin rays). The only species of *Whiteia* known to consistently have fewer than eight anterior dorsal fin rays is *W. tuberculata* (Forey, 1998). These character-state variations are problematic for the resolution of the Whiteiidae.

Two synapomorphies that might potentially exclude *W. lepta* and *W. durabilis* from *Whiteia* are: (1) anterior dorsal fin lacking denticles (character 98) and (2) presence of an ossified ‘swim bladder’ (character 107), although *W. lepta* is the only one of the two new species with post-cranial material preserved. *Whiteia neilseni* (pers. obs., e.g. MGUH 2335), *W. woodwardi,* and *W. tuberculata* all have denticles on the anterior dorsal fin rays, but *W. africana* was noted to lack these denticles (Broom, 1905; Forey, 1998), a condition also found in *W. lepta*. Brito et al. (2010) noted that both species of *Whiteia* (*W. woodwardi* and *W. tuberculata*) from Madagascar does not preserve an ossified ‘swim bladder’, while the two lesser known genera from the same locality, *Piveteauia* Lehman, 1952 and *Rhabdoderma* Reis, 1888 do preserve one. It is possible that the specimens of *Whiteia* from Madagascar are juveniles, compared to the sizes of *W. lepta* and *W. durabilis,* in which case the ‘swim bladder’ may not have ossified yet. Regardless, the presence or absence of an ossified ‘swim bladder’ in coelacanths is highly variable. Deleting this character yields 39 most-parsimonious trees with a length of 249 (CI = 0.454, HI = 0.546, RI = 0.702). The topologies are also the same as the previous ones, supporting the idea that as the character currently stands, it is not phylogenetically useful. It is likely that the majority, if not all, of fossil coelacanths possessed an ossified ‘swim bladder.’ Preservational and ontogenetic variations are more likely explanations for the variability in these codings.

The presence of raised areas in the skull roof (character 28) is exclusive to *W. durabilis* and *W. lepta* within the Whiteiidae, though there are some minor differences in the raised areas of these two species. *Whiteia lepta* has a vaulted area across the intracranial joint. The posterior margin of the posterior parietal is raised and the anterior margin of the postparietal is raised. In *W. durabilis*, both pairs of parietals have raised areas, but the dorsal surface of the postparietal is completely flat. The anterior portion of each parietal has a highly raised triangular area with the anterior parietal having a higher raised area.

DISCUSSION

Following the Permian extinction, species diversity in coelacanths hit a high-point (Schaeffer, 1948, 1952; Forey, 1984, 1988; Cloutier, 1991; Cloutier and Forey, 1991; Forey, 1991, 1998; Wendruff and Wilson, in review and Chapter 2). Currently, there are approximately twenty species of Triassic coelacanths known. The genus *Whiteia* is known from the highest number of species during this time: *W. tuberculata*, *W. woodwardi*, *W. neilseni*, *W. africana*, *W. durabilis* and *W. lepta*. The Whiteiidae, first proposed in 1993 by Schultze, is characterized by many features in the skull correlated with elongation of the snout, such as a long, sickle-shaped lachrymojugal, an extended lateral rostral bone, and a parietonasal shield that is twice as long as the postparietal shield.

A number of phylogenetic issues are raised by these species. One major issue is the disparity in preservation among species of *Whiteia*. The specimens of *W. tuberculata* and *W. woodwardi* from Madagascar are preserved as negative molds (Moy-Thomas, 1935; Lehman, 1952; Beltan, 1996) in which there is excellent skull anatomy known, but relatively little post-cranial anatomy. *Whiteia* *neilseni* from Greenland is preserved in crushed nodules preserving three-dimensional specimens, although this species has been poorly described to date. The two species described here are also preserved differently. *Whiteia durabilis* is preserved inflated in concretions, whereas *W. lepta* is preserved as compressed fossils in layers of siltstone.

Additionally, only a few morphological features differentiate these species (i.e., scales and ornamentation of cheek bones in *W. woodwardi* and *W. tuberculata*). Moreover, Forey (1998) noted that certain species of *Whiteia* (i.e., *W. africana*) may be conspecific with other species of *W. woodwardi*. The differences among these species have often been incompletely described because of differences in preservation or lack of attention to certain features, particularly post-cranial ones, or are at this time tenuous, making the relationships among these species poorly understood at best.

Both *W. lepta and W. durabilis* clearly belong to the family Whiteiidae as it stands, although more complete material may indicate enough differences for a new generic assignment. At present, the following features of the skull and post-cranium indicate that *W. durabilis* and *W. lepta* are both members of the genus *Whiteia.* The lachrymojugal, principal coronoid, and lower jaw are similar throughout all species of *Whiteia*, including *W. lepta* and *W. durabilis*. The unusual sickle-shaped lachrymojugal with an anteriorly angled process is characteristic of the genus *Whiteia* (Stensiö, 1921; Moy-Thomas, 1935; Lehman, 1952; Forey, 1998). The Upper Triassic coelacanth *Chinlea* (Schaeffer, 1967; Elliot, 1987) has an anteriorly angled process as well, but there are two major differences in the lachrymojugal: (1) the portion beneath the orbit is not highly curved as it is in *Whiteia* (2) the anterior process is forked and contacts two tectals and the lateral rostral, whereas in *Whiteia* it just contacts the posterior margin of the lateral rostral. The principal coronoid is saddle-shaped in both *W. lepta* and *W. durabilis*, which is typical of *Whiteia*; however, the largest specimen of *W. durabilis* shows an anterior process not seen in the others. The lower jaw has a characteristically shallow angular and a large posteriorly hooked dentary. The large pores of the mandibular sensory canal present in *W. lepta* are similar to those found in *W. tuberculata*. The curved oral pit line in *W. lepta* is nearly identical to the one in *W. neilseni* (Forey, 1998:fig. 5.9d). These morphological features are indicative of affinities to the genus *Whiteia*.

Whiteia lepta is the only species of *Whiteia* known from complete post-cranial material, which extends all the way to the tip of the supplementary lobe. As such, some features can be compared to previously described species, but a number of the postcranial features cannot be compared due to missing data in the other species. The fin-ray counts in the paired fins of *W. lepta* are much higher than those in most other described species, though the caudal fin ray counts are the same as in *W. woodwardi*. The shape of the basal plate of the anterior dorsal fin is diagnostic for each genus (pers. obs.). In *W. lepta*, it is most similar to the one found in *W. neilseni*. The scales of *W. lepta* are also similar to the ones found in *W. neilseni* in that they are covered in densely crowded ridges, although the presence of ridges on the scales is considered the plesiomorphic condition in coelacanths (Forey, 1991, 1998). The body outline of *W. lepta* is significantly more slender than those of *W. woodwardi* and *W. tuberculata*; the post-cranium of *W. neilseni* is poorly known. Additionally, the body of *W. lepta* may very well be longest, however, the posterior caudal margins are unknown for nearly all known species of *Whiteia* (i.e. *W. woodwardi*, *W. tuberculata*, *W. neilseni* and *W. durabilis*).

Whiteia durabilis and *W. lepta* share features that make them distinct from the other species of *Whiteia*. Both have similar tubercle shape on the angulars and raised areas on the skull roof. Additionally, they are considerably larger than all previous known species of *Whiteia*. *Whiteia woodwardi* reached maximum lengths of 16–20 cm, whereas *W. lepta* and *W. durabilis* are significantly larger, with estimated lengths of one meter and 60 centimeters respectively.

Whiteia durabilis and *W. lepta* are distinct from each other based on several key features: width of the parietonasal shield, shape and length of the lachrymojugal, ornamentation on the skull roof, principal coronoid, and modified fourth coronoid shape, as well as raised areas in the skull roof. The parietonasal shield in *W. durabilis* is nearly as long as it is wide, while the proportions in *W. lepta* are consistent with those in all other species of *Whiteia*. As *W. durabilis* is not currently known from post-cranial material, only cranial comparisons can be made, but *W. durabilis* displays a number of skull bones that *W. lepta* lacks, so many comparisons between the species are not possible. Nevertheless, it is possible to say that the lachrymojugal in *W. durabilis* is significantly thicker below and behind the orbit than in *W. lepta* and that it extends farther anteriorly. Additionally, the anterior projection in *W. durabilis* is wedge-shaped and very large. Conversely, the lachrymojugal of *Whiteia lepta* is slender and the anteroposterior process of the lachrymojugal, which articulates with the ventral process of the postorbital, is much longer proportionally than in *W. durabilis*. A comparison of similar-sized skulls between the two species makes it unlikely that the difference may be due to ontogenetic variation (UALVP 43602, *W. lepta*; TMP 1986.206.02, *W. durabilis*). As previously mentioned ornamentation differs amongst the species of *Whiteia* and can be used to distinguish between them. *W. lepta* is covered in tubercles that differ across the skull (Fig. 2B–E). Additionally, ornamentation present on the angular of *W. lepta* differs altogether from the ornamentation on the cheek bones. *Whiteia durabilis* has little ornamentation preserved on the skull, though both species have tubercles present across the entire angular. The tubercles are similar between *W. durabilis* and *W. lepta*; however, *W. durabilis* has tubercles organized in rows, while the tubercles in *W. lepta* are disorderly. The ornamentation on the jaws of *W. durabilis* and *W. lepta* is distinct even from the other species of *Whiteia*. *Whiteia neilseni* has elongate tubercles similar in shape to those of both *W. durabilis* and *W. lepta,* though they are restricted to the center of ossification of the angular. *Whiteia woodwardi* has scattered tubercles around the oral pit line and *W. tuberculata* lacks ornamentation on the angular (Forey, 1998). Additionally, *W. lepta* differs in possessing an unornamented depression along the center of the skull roof.

CONCLUSION

The exceptional preservation of the Sulphur Mountain Formation coelacanths provides further information about *Whiteia*, the most speciose and cosmopolitan coelacanth genus during the Early Triassic. The two new species *Whiteia lepta* and *Whiteia durabilis* both add to the growing number of coelacanths known to have lived during the Early Triassic, a time in which species diversity of coelacanths peaked (Schaeffer, 1948, 1952; Forey, 1984, 1988; Cloutier, 1991; Cloutier and Forey, 1991; Forey, 1991, 1998). The excellent preservation of the postcranial anatomy of *Whiteia lepta* reveals body, tail, and fin features that have not previously been documented in the genus. The two new species are also significantly larger than all other known species of *Whiteia*. Whether their large sizes are adaptations to their habitat and lifestyle or whether the other known species are represented only by juveniles is difficult to determine on present evidence. Both new species possess a large number of morphological features that occur also within all other species of *Whiteia*, further supporting their inclusion in this genus. They also possess features uniquely shared by both of them that show them to be most closely related to each other within the genus *Whiteia*.

LITERATURE CITED

Agassiz, L. 1839. Recherches sur les Poissons Fossiles. Vol. 2. Neuchâtel.

Beltan, L. 1996. Overview of systematics, paleobiology and paleoecology of Triassic fishes of Northwestern Madagascar; pp. 479–500 in G. Arratia and G. Viohl (eds.), Proceedings of the Symposium of Mesozoic Fishes—Systematics and Paleocology, Verlag Dr. Friedrich Pfeil, München.

Brito, P. M, F. J. Meunier, G. Clément, and D. Geffard-Kuriyama. 2010. The histological structure of the calcified lung of the fossil coelacanth *Axelrodichthys araripensis* (Actinistia: Mawsoniidae). Palaeontology 53:1281–1290.

Broom, R. 1909. The fossil fishes of the Upper Karoo Beds of South Africa. Annals of the South African Museum, East London 7:251–269.

Callaway, J. M., and D. B. Brinkman. 1989. Ichthyosaurs (Reptilia, Ichthyosauria) from the Lower and Middle Triassic Sulphur Mountain Formation, Wapiti Lake area, British Columbia, Canada. Canadian Journal of Earth Sciences 26:1491–1500.

Clément, G. 1999. The Actinistian (Sarcopterygii) *Piveteauia madagascariensis* Lehman from the Lower Triassic of Northwestern Madagascar: A redescription on the basis of new material. Journal of Vertebrate Paleontology 19(2):234–242.

Clément, G. 2005. A new coelacanth (Actinistia, Sarcopterygii) from the Jurassic of France and the question of the closest relative fossil [sic] to *Latimeria*. Journal of Vertebrate Paleontology 25(3):481–491.

Clément, G. 2006. *Swenzia*, n. nov., a replacement name for the preoccupied coelacanth genus *Wenzia* Clément, 2005. Journal of Vertebrate Paleontology 26:461.

Cloutier, R. 1991. Patterns, trends and rates of evolution within the Actinistia. Environmental Biology of Fishes 32:23–58.

Cloutier, R., and P. L. Forey. 1991. Diversity of extinct and living actinistian fishes (Sarcopterygii). Environmental Biology of Fishes 32:59–74.

Cope, E. D. 1871. Contribution to the ichthyology of the Lesser Antilles. Transactions of the American Philosophical Society 14:445–483.

Elliot, D. K. 1987. A new specimen of *Chinlea sorenseni* from the Chinle Formation, Dolores River, Colorado. Journal of the Arizona–Nevada Academy of Science 22:47–52.

Forey, P. L. 1984. The coelacanth as a living fossil; pp. 166–169 in N. Eldredge and S. M. Stanley (eds.), Living Fossils. Springer, New York.

Forey, P. L. 1988. Golden jubilee for the coelacanth *Latimeria chalumnae*. Nature 336:727–732.

Forey, P. L. 1991. *Latimeria chalumnae* and its pedigree. Environmental Biology of Fishes 32:75–97.

Forey, P. L. 1998. History of the Coelacanth Fishes. Chapman and Hall, London, 419 pp.

Friedman, M., and M. I. Coates. 2006. A newly recognized fossil coelacanth highlights the early morphological diversification of the clade. Proceedings of the Royal Society B 273:245–250.

Gardiner, B. G. 1966. Catalogue of Canadian fossil fishes. Contribution to Life Sciences at the Royal Ontario Museum, Toronto 61:1–153.

Geng, B.-H., M. Zhu and J. Fan. 2009. A revision and phylogenetic analysis of *Guizhoucoelacanthus* (Sarcopterygii, Actinistia) from the Triassic of China. Vertebrata Palasiatica 47:165–177.

Gibson, D.W. 1972. Triassic stratigraphy of the Pine Pass–Smoky River area, Rocky Mountain Foothills and Front Ranges of British Columbia and Alberta. Geological Survey of Canada, Paper 71-30:1–108.

Gibson, D. W. 1975. Triassic rocks of the Rocky Mountain Foothills and Front Ranges of northeastern British Columbia and west-central Alberta. Geological Survey of Canada, Bulletin 247:1–61.

Huxley, T. H. 1880. On the applications of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. Proceedings of the Zoological Society 1880:649–662.

International Code of Zoological Nomenclature. 1999. Fourth Edition. The International Trust for Zoological Nomenclature, London, 305 pp.

Jessen, H. 1973. Weitere Fischreste aus dem Oberen Plattenkalk der Bergische-Gladbach-Paffrather Mulde (Oberdevon, Rheinisches Schiefergebirge). Palaeontographica A 143:159-187.

Lambe, L. M. 1916. Ganoid fishes from near Banff. Transactions of the Royal Society of Canada 10:35–44.

Lambers, P. H. 1991. The identity of the type specimen of *Coelacanthus harlemensis* Winkler (Pisces, Actinistia) from the lithographic limestone of Solnhofen (Tithonian), Bavaria. Paläontologische Zeitschrift 65:173–189.

Laudon, L. R., E. Deidrick, E. Grey, W. B., Hamilton, P. J. Lewis, W. McBee, A. C. Spreng, and R. Stoneburner. 1949. Devonian and Mississippian stratigraphy, Wapiti Lake area, northeastern British Columbia. American Association of Petroleum Geology Bulletin 33:1502–1552.

Lehman, J. P. 1952. Étude complémentaire des poisons de l'Éotrias du Nord-Ouest de Madagascar. Kungliga Svenska Vetenskapsakademiens Handlingar 2:1–201.

Liu, H. –T. 1964. A new coelacanth from the marine Lower Triassic of N. W. Kwangsi, China. Vertebrata Palasiatica 8:211–214.

Lund, R. and W. L. Lund. 1984. New genera and species of coelacanths from the Bear Gulch Limestone (Lower Carboniferous) of Montana (USA). Geobios 17:237–244.

Lund, R. and W. L. Lund. 1985. Coelacanths from Bear Gulch limestone (Namurian) of Montana and the evolution of Coelacanthiformes. Bulletin of the Carnegie Museum of Natural History 25:1–74.

Maddison, W. P., and D. R. Maddison. 2005. MacClade: Analysis of Phylogeny and Character Evolution, Version 4.08. Sinauer Associates, Sunderland, Massachusetts.

Maisey, J. G. 1986. Coelacanths from the Lower Cretaceous of Brazil. American Museum Novitates 2866:1–30.

Mantell, G. 1822. The Fossils of the South Downs; or Illustrations of the Geology of Sussex. Lupton Relfe, London, 327 pp.

Martin, M., and S. Wenz. 1984. Découverte d'un nouveau Coelacanthidé, *Garnbergia ommata* n. gen., n. sp., dans le Muschelkalk supérieur du Baden-Württemberg. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) 105:1–17.

Melton, W. G. 1969. A new dorypterid fish from central Montana. Northwest Science 42(4):186–206.

Moy-Thomas, J. A. 1935. Coelacanth Fishes from Madagascar. Geological Magazine 72:213–227.

Mutter, R. J. 2004. Fossile Fische aus den kanadischen Rocky Mountains. Vierteljahrschrift der Naturforschenden Gesellschaft in Zürich 149:51–58.

Mutter, R. J., and A. G. Neuman. 2006. An enigmatic chondrichthyan with Palaeozoic affinities from the Lower Triassic of western Canada. Acta Palaeontologica Polonica 51:271–282.

Mutter, R. J., K. de Blanger, A. G. Neuman. 2007. Elasmobranchs from the Lower Triassic Sulphur Mountain Formation near Wapiti Lake (BC, Canada). Zoological Journal of the Linnean Society 149:309–337.

Mutter, R. J., and A. G. Neuman. 2008a. New eugeneodontid sharks from the Lower Triassic Sulphur Mountain Formation near Wapiti Lake (BC, Canada). Zoological Journal of the Linnean Society 149:309–337.

Mutter, R. J., and A. G. Neuman. 2008b. Jaws and dentition in an Early Triassic, 3-dimensionally preserved eugeneodontid skull (Chondrichthyes). Acta Geologica Polonica 58(2):223-227.

Mutter, R. J., A. G. Neuman, and K. de Blanger. 2008a. *Homalodontus* nom. nov., a replacement name for *Wapitiodus* Mutter, de Blander and Neuman, 2007 (Homalodontidae nom. nov., ?Hybodontoidea), preoccupied by *Wapitiodus* Orchard, 2005. Zoological Journal of the Linnean Society 154:419–420.

Mutter, R. J., J. Cartanyà, and S. A. U. Basaraba. 2008b. New evidence of *Saurichthys* from the Lower Triassic with an evaluation of early saurichthyid diversity; pp. 103–127 in G. Arratia, H.-P. Schultze, and M. V. H. Wilson (eds.), Mesozoic Fishes 4—Homology and Phylogeny. Verlag Dr. Friedrich Pfeil, Munich.

Mutter, R. J. and A. G. Neuman. 2009. Recovery from the end-Permian extinction event: Evidence from “Lilliput *Listracanthus*.” Palaeogeography, Palaeoclimatology, Palaeoecology 284:22–28.

Neuman, A. G. 1992. Lower and Middle Triassic Sulphur Mountain Formation, Wapiti Lake, British Columbia: summary of geology and fauna. Contributions to Natural Science, Royal British Columbia Museum 16:1–12.

Neuman, A. G., and R. J. Mutter. 2005. *Helmolepis cyphognathus*, sp. nov., a new platysiagid actinopterygian from the Lower Triassic Sulphur Mountain Formation (British Columbia, Canada). Canadian Journal of Earth Sciences 42:25–36.

Newberry, J. S. 1856. Descriptions of several genera and species of fossil fish from Carboniferous strata of Ohio. Proceedings of the Academy of Natural Sciences of Philadelphia 8:96–100.

Orchard, M. J., and J.-P. Zonneveld. 2009. The Lower Triassic Sulphur Mountain Formation in the Wapiti Lake area: lithostratigraphy, conodont biostratigraphy, and a new biozonation for the lower Olenekian (Smithian). Canadian Journal of Earth Sciences 46:757–790.

Quenstedt, F. A. 1858. Der Jura. Tubingen. 823 pp.

Romer, A. S. 1955. Herpetichthyes, Amphibioidei, Choanichthyes or Sarcopterygii? Nature 176:126.

Schaeffer, B. 1948. A study of *Diplurus longicaudatus* with notes on the body form and locomotion of the Coelacanthini. American Museum Noviates 1378:l–32.

Schaeffer, B. 1952. Rates of evolution in the coelacanth and dipnoan fishes. Evolution 6:101–111.

Schaeffer, B. 1967. Late Triassic fishes from the western United States. Bulletin of the American Museum of Natural History 135:285–342.

Schaeffer, B. and M. Mangus. 1976. An early Triassic fish assemblage from British Columbia. Bulletin of the American Museum of Natural History 156:515–564.

Schaumberg, G. 1978. Neubeschreiburg von *Coelacanthus granulatus* Agassiz (Actinistia, Pisces) aus dem Kupferschiefer can Richelsdorf (Perm, W.–Deutschland). Paläontologische Zeitschrift 52:169–197.

Schultze, H.-P. 1993. Osteichthyes: Sarcopyerygii; pp. 657–663 in M. J. Benton (ed.), The Fossil Record 2. Chapman and Hall, London.

Smith, J. L. B. 1939. A living fish of Mesozoic type. Nature 143:455–456.

Stensiö, E. 1921. Triassic Fishes from Spitzbergen. Part. 1. Adolf Holzhausen, Vienna, Xxviii + 307 pp.

Stensiö, E. 1932. Triassic fishes from East Greenland collected by the Danish expedition 1929-1931. Meddelelser om Grønland 83(3):1–305.

Stensiö, E. 1936. Some few preliminary remarks on Triassic Fishes from East Greenland. Meddelelser om Grønland 112(3):9–55.

Swofford, D. L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Yabumoto, Y. 2008. A new Mesozoic coelacanth from Brazil (Sarcopterygii, Actinistia). Paleontological Research 12:329–342.

FIGURE 3.1. *Whiteia lepta*, sp. nov. (Holotype RBCM.EH 1986.001.0022), Lower Triassic, Sulphur Mountain Formation, British Columbia, Canada. **A**, complete specimen in left lateral view; **B**, line drawing of holotype; **C**, close up of the skull; **D**, line drawing of skull. **Abbreviations**: **A.b**, anal basal plate; **Acl**, anocleithrum; **A.f**, anal fin; **Ang**, angular; **Cl**, cleithrum; **Cla**, clavicle; **D1.b**, anterior dorsal basal plate; **D1.f**, anterior dorsal fin; **D2.b**, posterior dorsal basal plate; **D2.f**, posterior dorsal fin; **De**, dentary; **Ecl**, extracleithrum; **Gu**, gular; **Mpt**, metapterygoid; **Na**, nasal; **Op**, operculum; **Pa**, parietal; **Par**, parasphenoid; **P.b**, pelvic plate; **Pc.f**, pectoral fin; **P.f**, pelvic fin; **Pt**, pterygoid; **s.b**, swim bladder; **Sop**, suboperculum; **Stt**, supratemporal. Scale bar equals 5 cm (A, B); 2 cm (C, D).

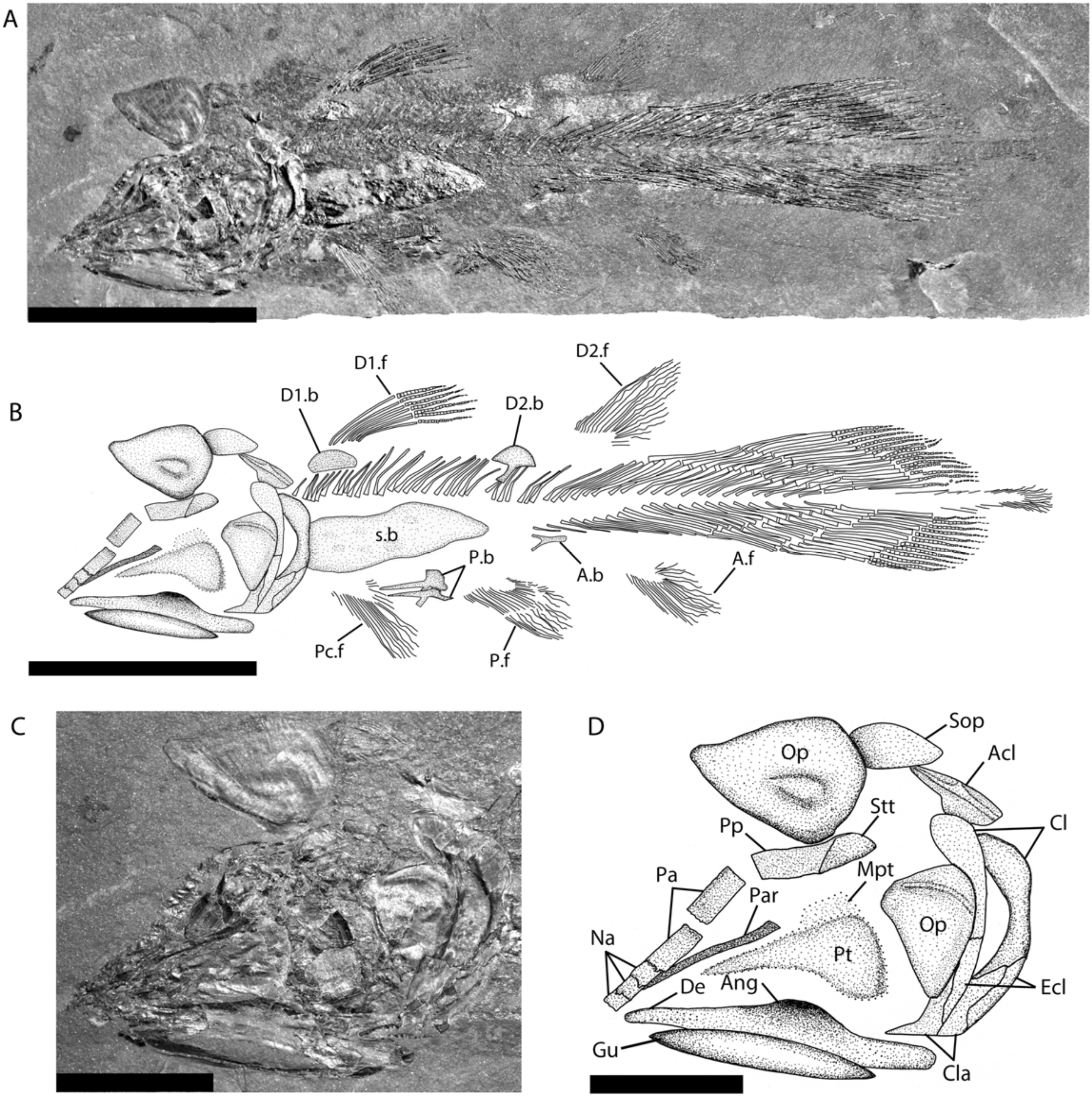

A
B
D1.f
D1.b
D2.f
D2.b
s.b
P.b
A.b
A.f
Pc.f
P.f
C
D
Op
Sop
Acl
Pp
Stt
Cl
Pa
Mpt
Par
Op
Na
Pt
Ecl
De
Ang
Gu
Cla

FIGURE 3.2. *Whiteia lepta*, sp. nov. (Paratype UALVP 43602). **A**, ammonium chloride dusted peel of skull; **B**, anterior parietals; **C**, ornamentation on cheek bones; **D**, ornamentation on operculum; **E**, ornamentation on angular; **F**, line drawing of skull. **Abbreviations**: **Ang**, angular; **Cb**, ceratobranchial; **c.b**, cheek bones; **Ch**, ceratohyal; **Cla**, clavicle; **Co.4**, fourth coronoid; **De**, dentary; **Ecl**, extracleithrum; **Gu**, gular plate; **i.j.v**, vaulted bones along intracranial joint; **L.j**; lachrymojugal; **Mpt**, metapterygoid; **Na**, nasal; **Op**, operculum; **Pa**, parietal; **Pa-Na.d**, parietonasal depression; **p.Co**, principal coronoid; **Pmx**, premaxilla; **Pp**, postparietal; **Pp.d**, postparietal depression; **Pt**, pterygoid; **Q**, quadrate; **So**, supraorbital; **S.o**, sclerotic ossicles; **Sop**, suboperculum; **Stt**, supratemporal; **v.pr.Pa**, ventral process of the (posterior) parietal. Scale bar equals 5 cm (A, F); 5 mm (B–E).

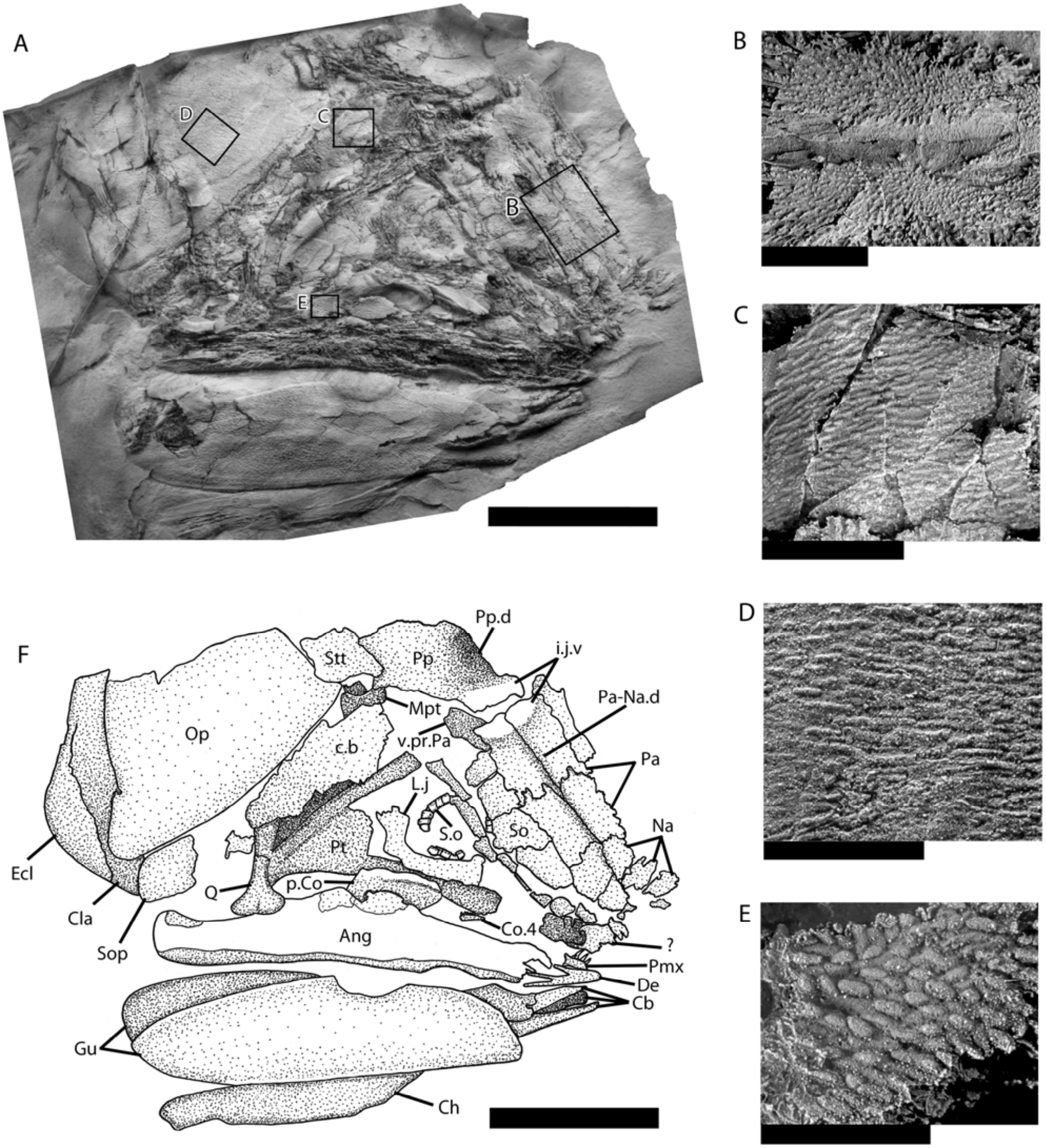

A
D
C
B
E
B
C
D
E
F
Pp.d
Stt
Pp
i.j.v
Mpt
Pa-Na.d
Op
c.b
v.pr.Pa
Pa
L.j
S.o
So
Na
Pt
Ecl
Q
p.Co
Co.4
Cla
Sop
Ang
?
Pmx
De
Cb
Gu
Ch

FIGURE 3.3. *Whiteia lepta*, sp. nov. (Paratype UALVP 43382). **A,** ammonium chloride dusted skull in right lateral view; **B,** close up of the oral pit line and ornamentation on the angular; **C**, close up of the gular pit line on the gular plate; **D**, scales behind the skull; **E**, close up of a single scale. **Abbreviations: gu.p.l,** gular pit line; **L.j**, lachrymojugal; **o.p.l**, oral pit line; **Q**, quadrate; **Sy**, symplectic. Scale bar equals 5 cm (A); 2 mm (B, C, E); 5 mm (D).

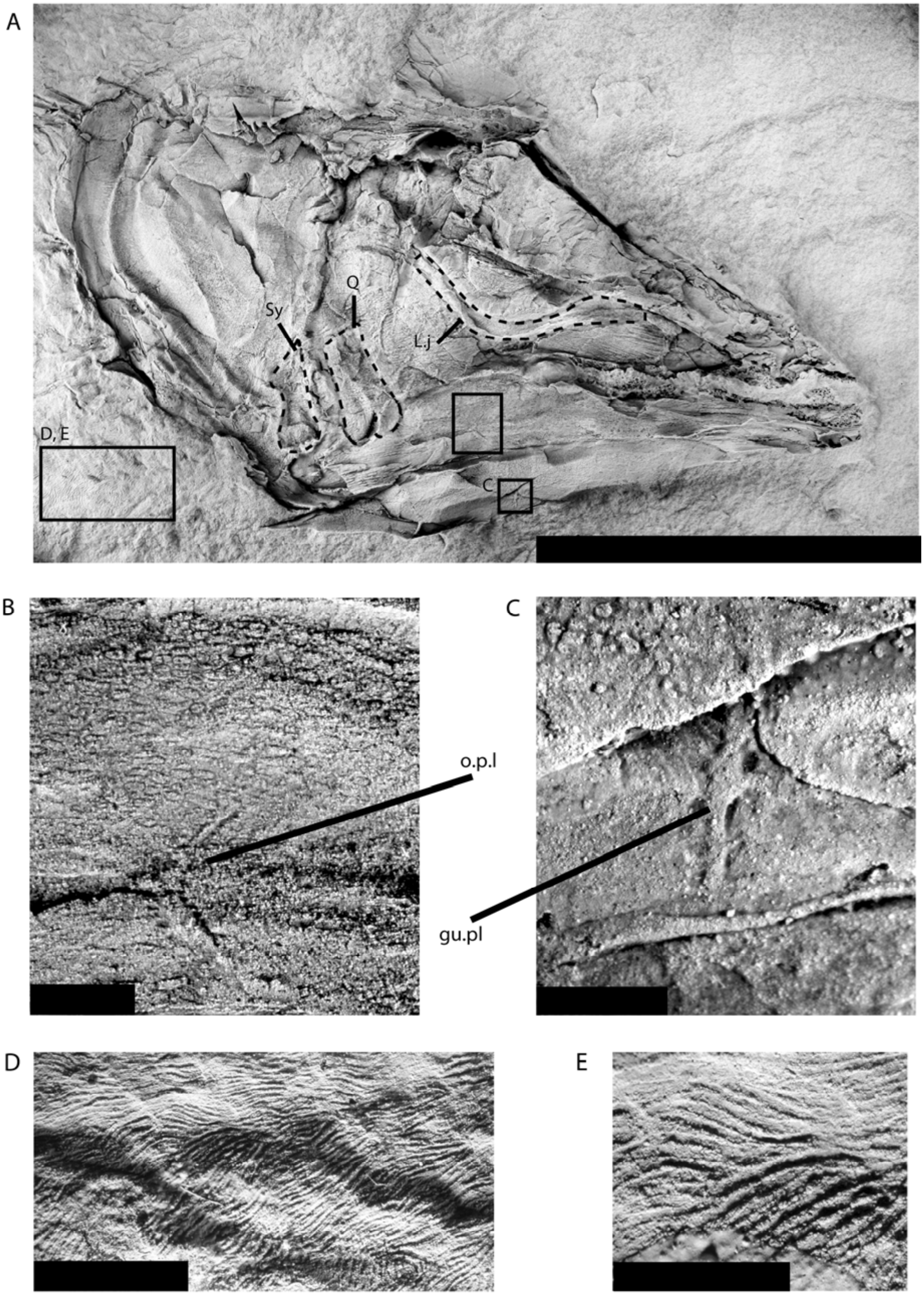

A
Sy
Q
L.j
D, E
C
B
o.p.l
C
gu.pl
D
E

FIGURE 3.4. Reconstructions of the skulls. **A**, reconstruction of *Whiteia lepta,* sp. nov.; **B,** reconstruction of *Whiteia durabilis,* sp. nov. **Abbreviations**: **Acl**, anocleithrum; **Ang**, angular; **Cl**, cleithrum; **Cla**, clavicle; **co.4**, fourth coronoid; **Dpl**, dermopalatine; **De**, dentary; **Ecl**, extracleithrum; **Ecpt**, ectopterygoid; **Gu**, gular plate; **L.j**, lachrymojugal; **L.r**, lateral rostral; **Na**, nasal; **Op**, operculum; **Pa**, parietal; **Part**, prearticular; **p.Co**, principal coronoid; **Pmx**, premaxilla; **Po**, postorbital; **Pop**, preoperculum; **Pp**, postparietal; **Q**, quadrate; **Rart**, retroarticular; **So**, supraorbital; **S.o**, sclerotic ossicles; **Sop**, suboperculum; **Spl**, splenial; **Sq**, squamosal; **Stt**, supratemporal; **Sy**, symplectic. Scale bar equals 10 cm (A, B). Dotted lines indicate incomplete or unknown bone boundaries.

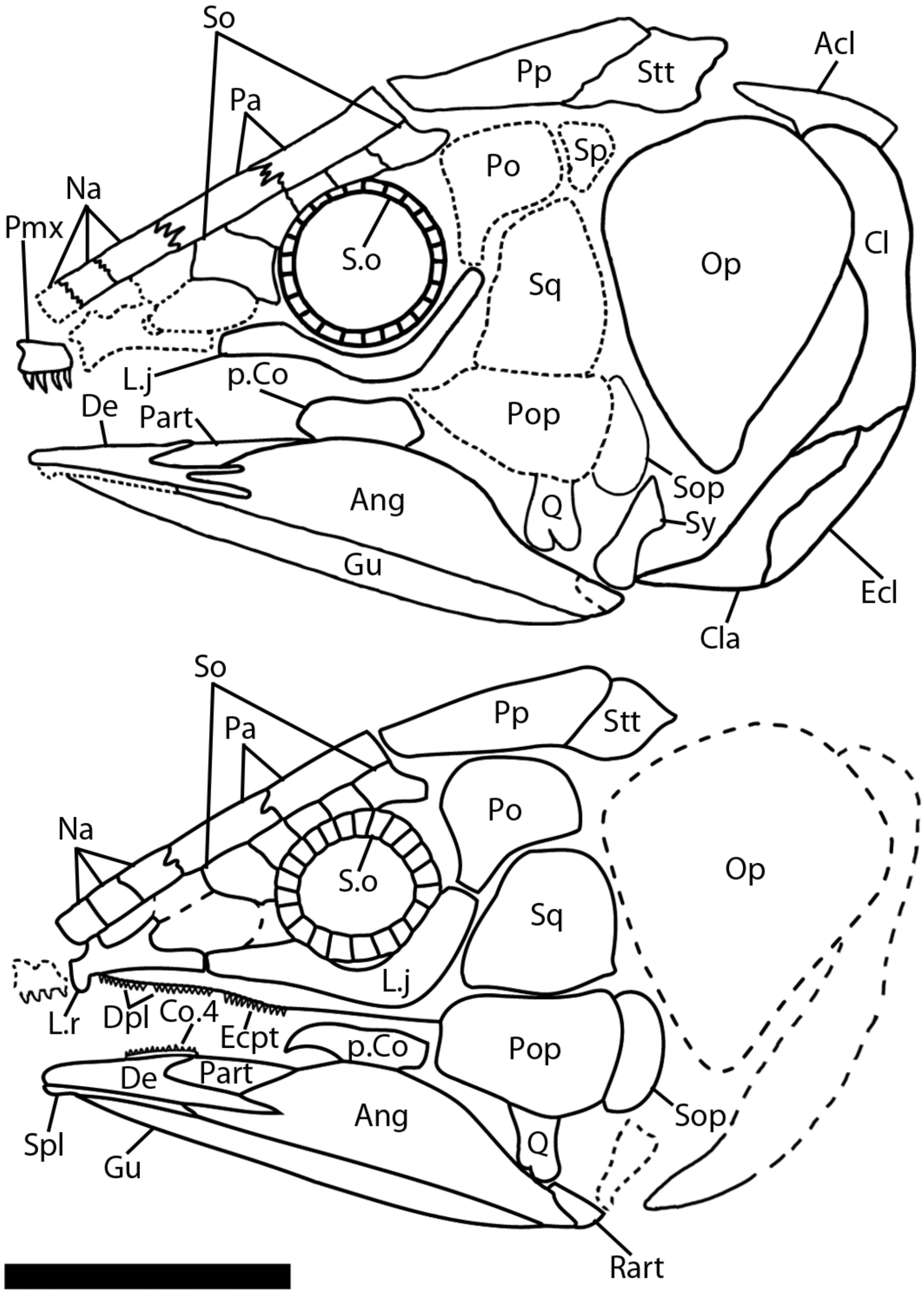

So
Pa
Na
Pmx
Pp
Stt
Acl
Po
Sp
S.o
Sq
Op
Cl
L.j
p.Co
De
Part
Pop
Ang
Q
Sop
Sy
Gu
Ecl
Cla
So
Pa
Pp
Stt
Na
Po
S.o
Op
Sq
L.j
L.r
Dpl
Co.4
Ecpt
p.Co
Pop
De
Part
Ang
Spl
Gu
Q
Sop
Rart

FIGURE 3.5. *Whiteia neilseni* Forey, 1998 (MGUH 2330) Lower Triassic of Greenland. **A**, skull in left lateral view; **B**, close up of ornamentation on preoperculum. **Abbreviations: L.j**, lachrymojugal; **Po**, postorbital; **Pop**, preoperculum; **Sop**, suboperculum; **Sp**, spiracular; **Sq**, squamosal. Scale bar equals 2 cm (A); 5 mm (B).

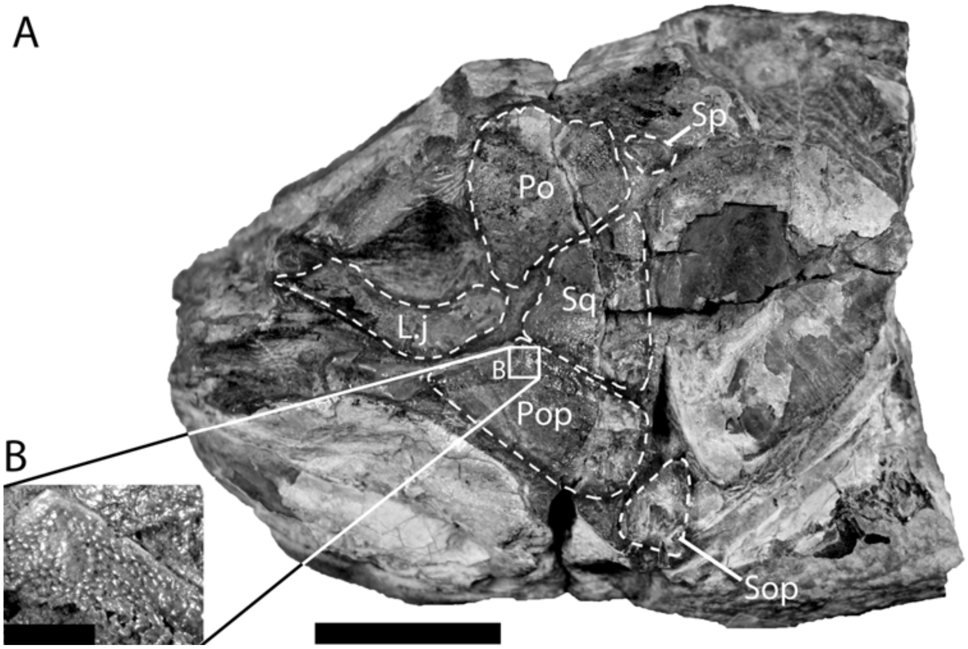

A
Po
Sp
Sq
Lj
B
Pop
Sop
B

FIGURE 3.6. *Whiteia lepta*, sp. nov. (Paratype AMNH 6249, A–D; TMP 1983.206.48, E). **A**, complete specimen in right lateral view; **B**, pelvic plate; **C**, posterior dorsal basal plate; **D**, anal basal plate; **E**, complete specimen in right lateral view. Scale bar equals 5 cm (A); 5 mm (B–D); 2 cm (E).

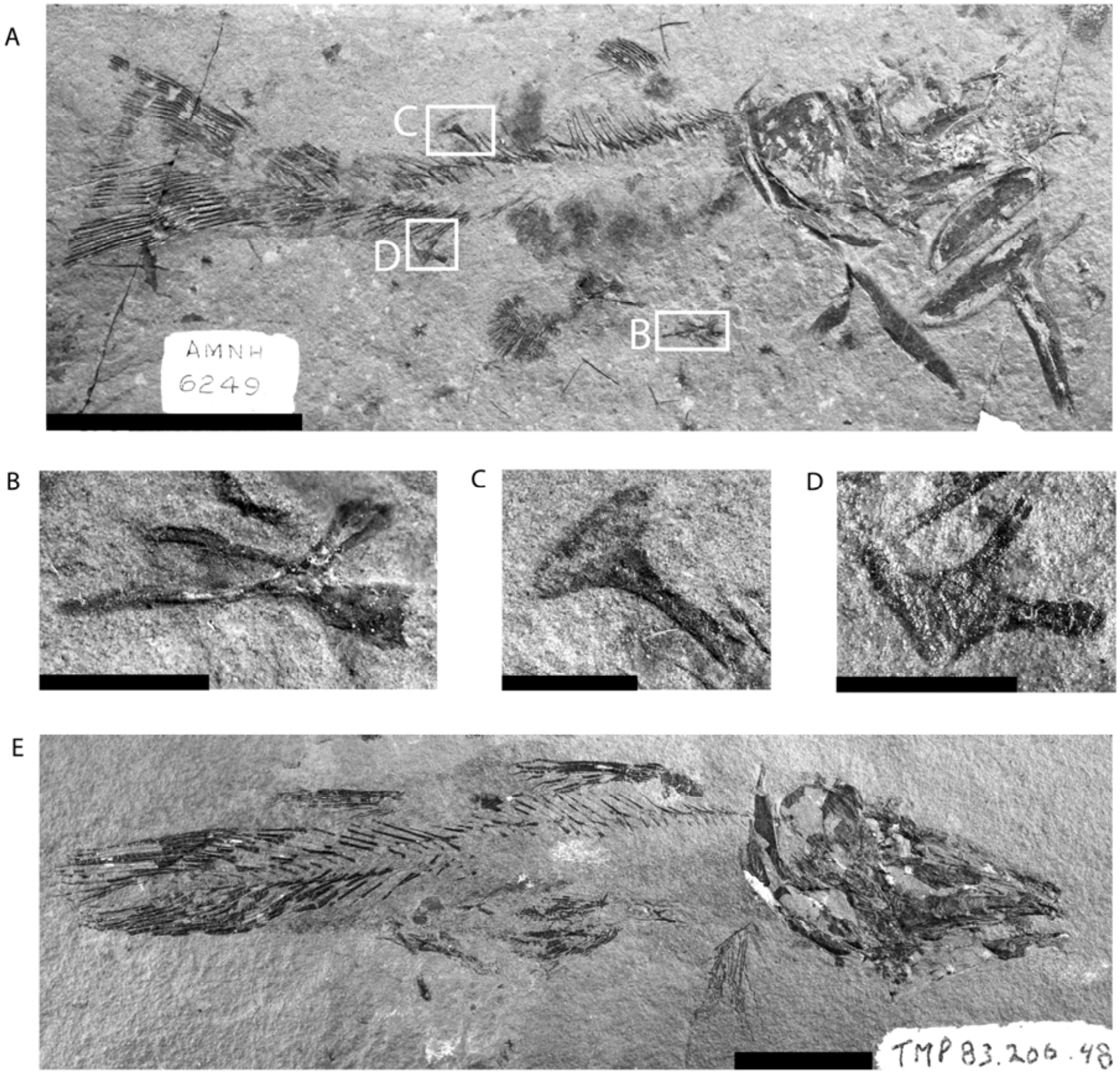

A
C
D
B
AMNH
6249
B
C
D
E
TMP 83.206.48

FIGURE 3.7. *Whiteia lepta*, sp. nov. (Paratype TMP 1984.131.28). **A**, caudal fin in left lateral view; **B**, outline drawing of caudal fin. Scale bar equals 5 cm (A, B).

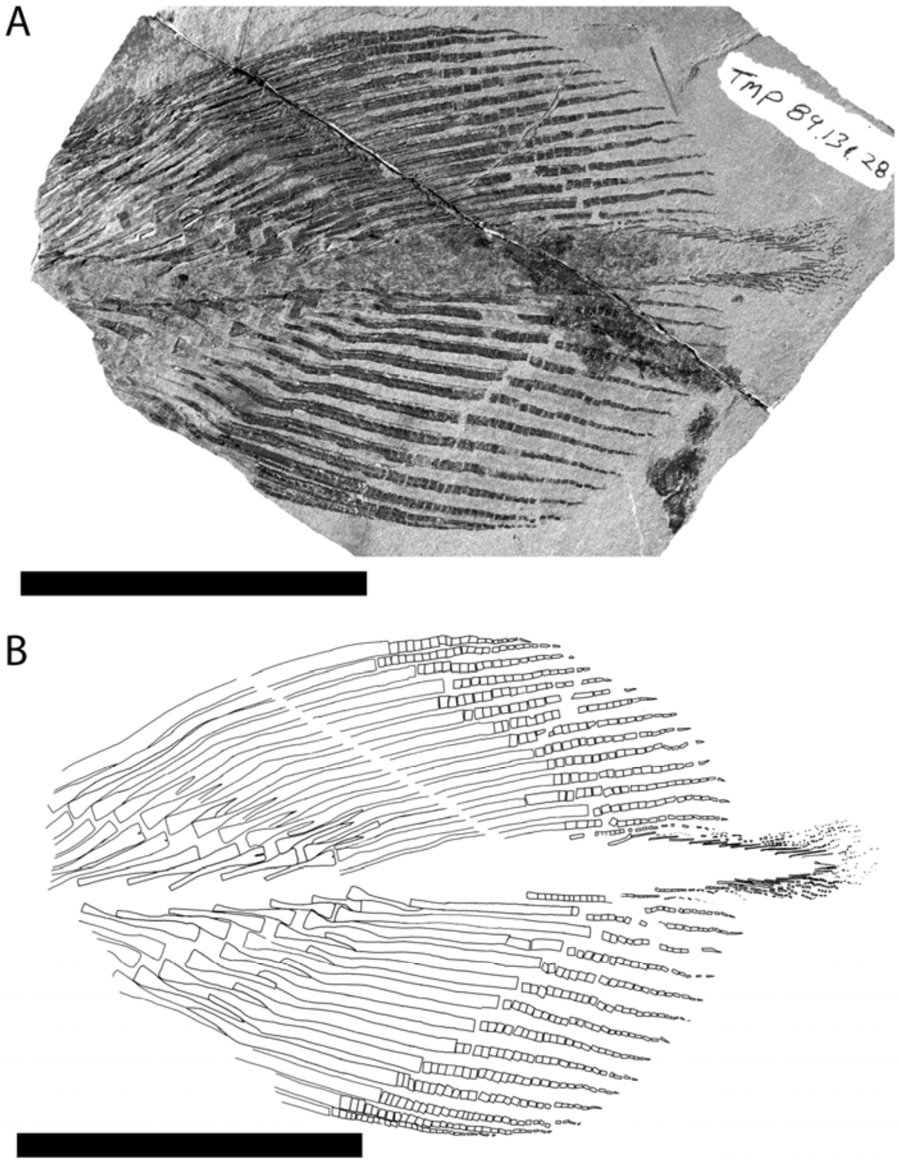

A
TMP 89.131.28
B

FIGURE 3.8. *Whiteia durabilis*, sp. nov. (Holotype TMP 1986.206.02), Lower Triassic, Sulphur Mountain Formation, British Columbia, Canada. **A**, right lateral skull; **B**, outline drawing of right lateral skull; **C**, left lateral skull; **D**, outline drawing of left lateral skull; **E**, skull roof; **F**, outline drawing of skull roof. **Abbreviations: Ang,** angular; **De**, dentary; **Gu**, gular; **i.j**, intracranial joint; **L.j**; lachrymojugal; **L.r**, lateral rostral; **l.Pg**, left pectoral girdle**; m.s.c**; mandibular sensory canal; **Nas**, nasals; **Op**, operculum; **Pa**, parietal; **Pa.r**, raised areas of parietals; **Part**; prearticular; **p.Co**, principal coronoid; **Po**, postorbital; **Pop**, preoperculum; **pop.sc**, preopercular sensory canal; **Pp**, postparietal; **Q**, quadrate; **Rart**, retroarticular; **S.o**, sclerotic ossicles; **So/Te**, supraorbital/tectal series; **Sp**, spiracular; **Spl**, splenial; **Sq**, squamosal; **Stt**, supratemporal. Scale bar equals 5 cm (A–F).

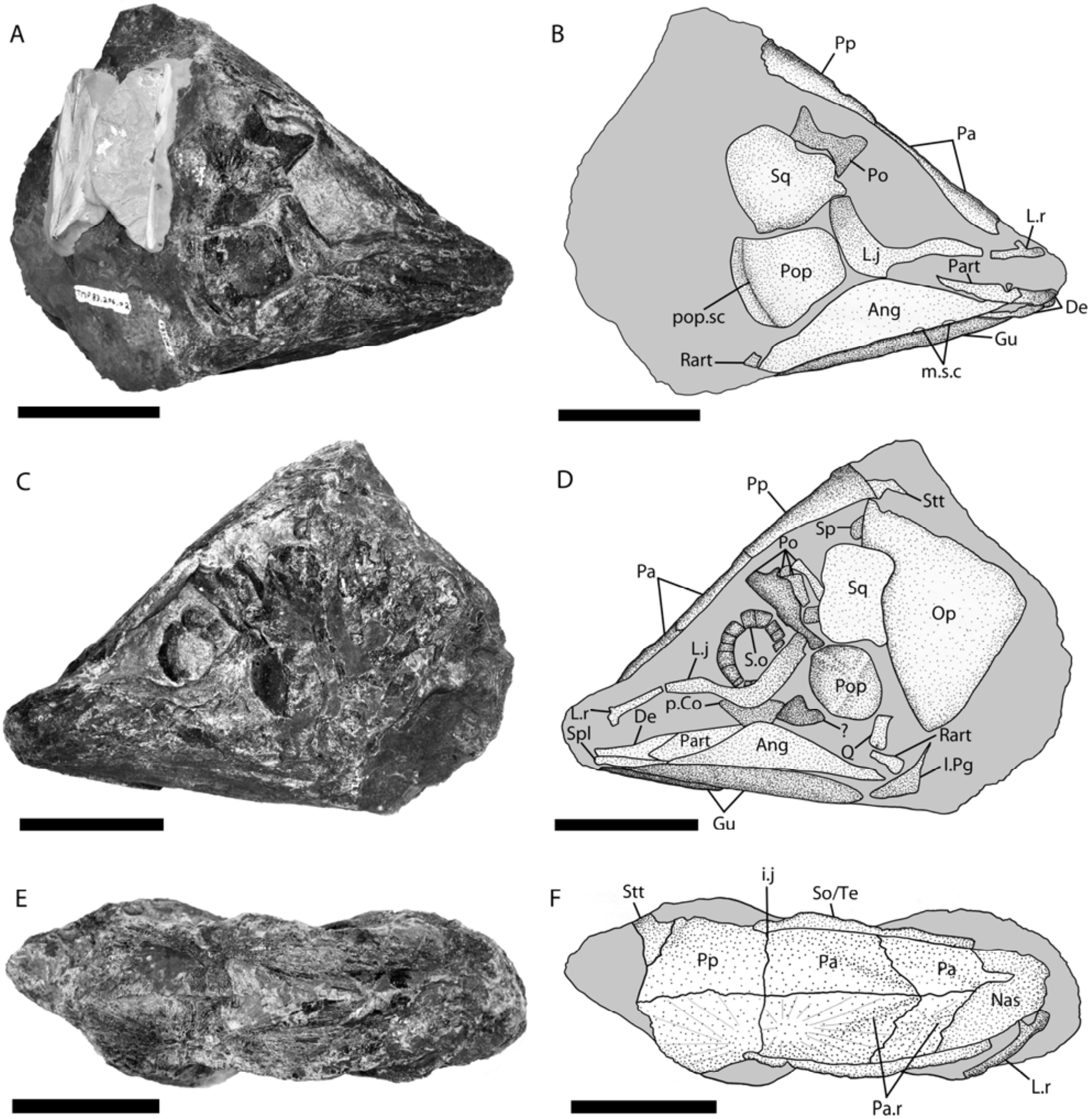

A
B
Pp
Pa
Sq
Po
L.r
Pop
L.j
Part
pop.sc
Ang
De
Gu
Rart
m.s.c
C
D
Pp
Stt
Sp
Po
Pa
Sq
Op
S.o
L.j
Pop
L.r
p.Co
?
De
Rart
Spl
Part
Ang
Q
I.Pg
Gu
E
F
Stt
i.j
So/Te
Pp
Pa
Pa
Nas
Pa.r
L.r

FIGURE 3.9. *Whiteia durabilis*, sp. nov. (Paratype TMP 1983.206.01). **A**, skull in right lateral view; B, ornamentation on angular; **C**, outline drawing of right lateral skull; **D**, skull in left lateral view; **E**, outline drawing of skull in left lateral view. **Abbreviations: Ang**, angular; **bucc.can,** buccal canal; **Aup**, autopalatine; **Co.4**, fourth coronoid; **De**, dentary; **Dpl**, dermopalatine; **Ecpt**; ectopterygoid; **Gu**, gular plate; **L.e**, lateral ethmoid; **L.j**, lachrymojugal; **Par**, parasphenoid; **Part**, prearticular; **p.Co**, principal coronoid; **Pmx**, premaxilla; **Pop**, preoperculum; **Pt**, pterygoid; **S.o**, sclerotic ossicles; **Spl**, splenial; **Sq**, squamosal; **S.r**, skull roof; **v.l.fo**, ventrolateral fossa. Scale bar equals 5 cm (A, C, D); 5 mm (B).

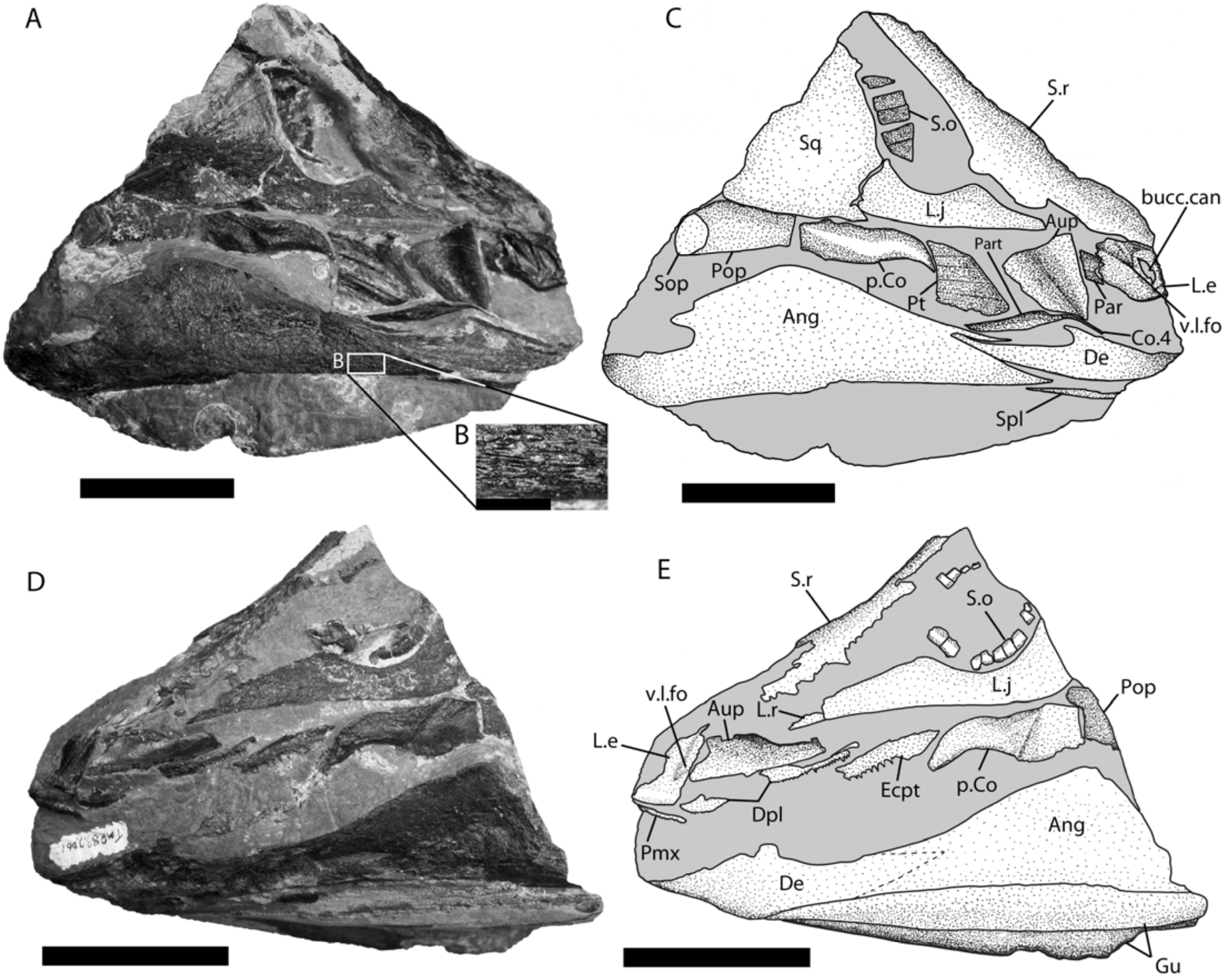

A
B
B
C
S.r
S.o
Sq
L.j
bucc.can
Aup
Part
Sop
Pop
p.Co
Pt
Par
L.e
v.l.fo
Ang
Co.4
De
Spl
D
E
S.r
S.o
L.j
Pop
v.l.fo
Aup
L.r
L.e
Ecpt
p.Co
Dpl
Pmx
Ang
De
Gu

FIGURE 3.10. *Whiteia durabilis*, sp. nov.2 (Paratype TMP 1983.207.02) Skull in right lateral view. **Abbreviations: Po**, postorbital; **Pop**, preoperculum; **So**, supraorbital; **Sop**, suboperculum; **Sq**, squamosal. Scale bar equals 2 cm.

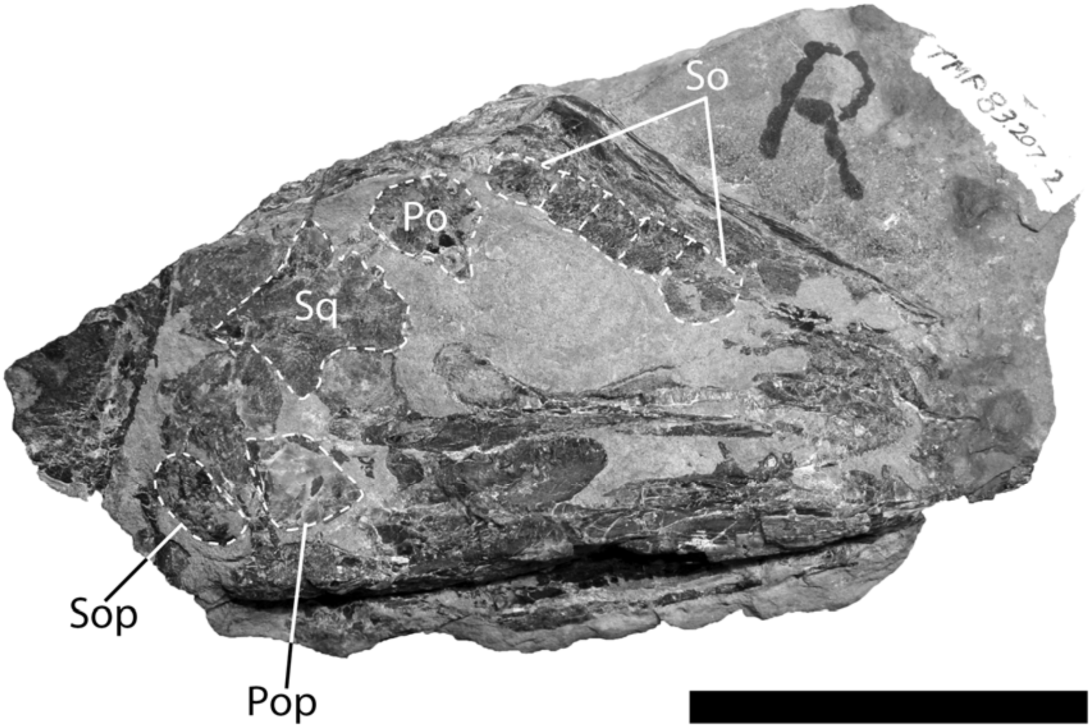
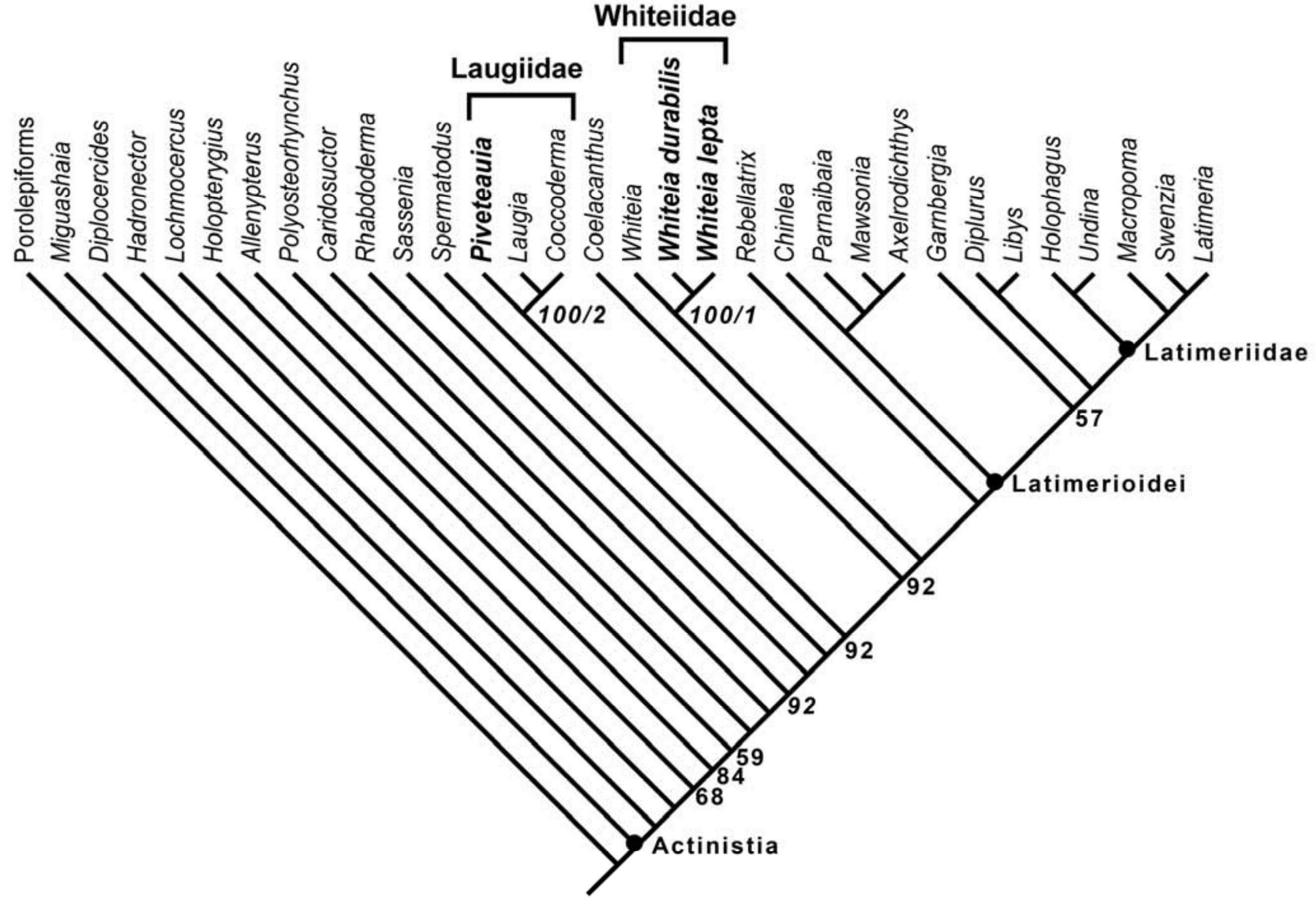

So
R
TMP 83.207.2
Po
Sq
Sop
Pop

FIGURE 3.11. 50% majority rule cladogram with the addition of *Whiteia lepta*, *Whiteia durabilis* and *Piveteauia madagascariensis* and exclusion of character 107 resulting from thirty-nine most-parsimonious trees (length = 249; CI = 0.454; HI = 0.546; RI = 0.702) resulting from a heuristic maximum-parsimony analysis using TBR and 100 random-addition-sequence replicates on an updated version of the character-taxon matrix of Forey (1998).


Whiteiidae
Laugiidae
Porolepiforms
Miguashaia
Diplocercides
Hadronector
Lochmocercus
Holopterygius
Allenypterus
Polyosteorhynchus
Caridosuctor
Rhabdoderma
Sassenia
Spermatodus
Piveteauia
Laugia
Coccoderma
Coelacanthus
Whiteia
Whiteia durabilis
Whiteia lepta
Rebellatrix
Chinlea
Parnaibaia
Mawsonia
Axelrodichthys
Garnbergia
Diplurus
Libys
Holophagus
Undina
Macropoma
Swenzia
Latimeria
100/2
100/1
Latimeriidae
57
Latimerioidei
92
92
92
59
84
68
Actinistia

APPENDIX III.

Character-taxon matrix used for phylogenetic analysis (modified from Forey, 1998) with 31 coelacanth taxa with the addition of *Whiteia lepta* gen. et sp. nov. *Whiteia durabilis* gen. et. sp. nov. and *Piveteauia madagascariensis*.

The first 108 characters are described in Forey (1998) and character 109 is discussed in Friedman and Coates (2006). Missing data = ‘?’; non-applicable states = ‘N’.

	10	20	30	40	50
Porolepiforms	00100N1??0	0000000000	00210?0001	1111NN0000	0000000010
Diplocercides	001???2101	0000000010	0021100001	1101000000	0000000010
Rhabdoderma	1000002001	1001001011	0000100001	1100000000	0000110010
Caridosuctor	1000002101	?0??001011	0000100001	11??000000	000??00010
Hadronector	00100021?1	?0??000010	0010100001	1100??0000	000?1?0?10
Polyosteorhynchus	00?0002101	???100?010	101???0001	11?0000000	000?1?0010
Allenypterus	0?????2001	?0??000010	000000001?	1100000000	01001??101
Lochmocercus	??????????	????????10	100???0001	11??000000	00?01000?0
Coelacanthus	00?11?2100	10010011?1	10?0?1101?	??00001??0	010?1?1?10
Spermatodus	1000002101	100110?111	?020?1001?	1101000000	00?????010
Whiteia	00?0002001	1001101111	1000100011	1100010000	0001110010
Laugia	11?0??1?01	1001001011	0000?10010	0000000000	0001001110
Sassenia	10????2?01	100100?01?	?020100011	1101000000	0000100010
Chinlea	00?01?2000	10??0011?1	10????2011	100?110000	100100?01?
Diplurus	00001?2110	1010102111	1000?11011	1000100000	0100111101
Holophagus	10?01?2110	101110?111	1?20?10010	1100100000	000?1??110
Undina	00?00?2110	101110211?	1?2???0110	1100??0000	000?101110
Coccoderma	10?011210?	1001001011	0020101010	0001001100	0001001100
Libys	0???1?????	10111??111	1?00?11010	000?1???01	000?1???01
Mawsonia	1?????2100	10100111?1	1020?12010	101?000120	101?000120
Macropoma	01?0?12110	1011102111	1120?10010	0001101110	0001101110
Latimeria	0011112110	1011102111	1100102111	0001111111	0001111111
Miguashaia	00?0001?0?	01??000000	002?00000?	000?000?10	000?000?10
Axelrodichthys	1000112100	101001111?	1020?12010	1011000120	1011000120
Garnbergia	??????21?0	?0?????1??	????????1?	000?????1?	000?????1?
Swenzia	01?0??2???	?011???1??	11?0101111	0001101110	0001101110
Holopterygius	?0?0??????	??????????	??0???????	??????????	??????????
Parnaibaia	0111??2000	?0??0011?1	??2??12011	001?????2?	001?????2?
Rebellatrix	??????????	??????????	??????????	??????????	????????1?
Piveteauia	1?????????	1011?0?1?1	?1?0??00?1	1??0000???	???01011?
Whiteia lepta	00?0??200?	1001??11?	???0??01??	?10?01????	????????1?
Whiteia durabilis	0??0??200?	?00????11?	???0??0111	1100010000	000?????1?

60	70	80	90	100	109
0100300070	0?00001001	01N000?101	000N0?0000	000000N000	000000000
0100300100	0000000001	1101001101	?010000??0	0010100000	??0000???
0101410000	1001001011	10110?0000	?000101101	0011100000	110000100
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CHAPTER FOUR

Two new deep-bodied coelacanths, *Everticauda pavoidea*, gen. et sp. nov., and *Wapitia robusta*, gen. et sp. nov., from the Lower Triassic Sulphur Mountain Formation of British Columbia, Canada

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INTRODUCTION

Lower Triassic coelacanths are currently known from Greenland, Madagascar, Spitsbergen, South Africa, China and Western Canada (Broom, 1905; Lambe, 1916; Stensiö, 1921, 1932; Moy-Thomas, 1935; Lehman, 1952; Liu, 1964; Gardiner, 1966; Forey, 1998; Tong et al., 2006; Geng et al., 2009). Coelacanths have been known from Western Canada for nearly one hundred years ever since Lambe (1916) described *Coelacanthus banffensis*, which has since been declared a nomen dubium (Chapter 3). Though several authors have discussed coelacanths from the Sulphur Mountain Formation (Wapiti Lake), no other specimens have been formally described. Schaeffer and Mangus (1976) attributed Wapiti Lake coelacanths exclusively to an undescribed species of *Whiteia* (Moy-Thomas, 1935) based on fin ray counts and the shape of the pelvic girdle. Thirty-five years since this assessment, there has been no formal description of the coelacanths present at this locality. More recently, Wendruff and Wilson (in review; Chapter 2) formally describe the first new coelacanth from this site. With the description of that coelacanth as well as those from Chapter 3, the number of species and known morphological diversity is increasing. *Everticauda pavoidea*, gen. et sp. nov., and *Wapitia robusta*, gen. et sp. nov., described in this chapter, continue to add to this diversity.

The description of *Everticauda*, gen. nov., not only adds a new body form to the coelacanth record but additionally augments information on the ontogenetic variation in fossil coelacanths. The unusual tail shape, massive anterior dorsal fin and truncated body make this one of the more functionally unusual body forms from the Lower Triassic. Conversely, *Wapitia*, gen. nov., has a *Latimeria*-like body form in that it is relatively deep bodied with a ‘typical’ coelacanth tail. However, it possesses a mixture of derived features, such as expanded neural arches, and primitive features, such as ten anterior dorsal fin rays and a low number of neural arches.

GEOLOGY

The Sulphur Mountain Formation from lowest to highest in stratigraphic succession comprises the Vega, Meosin, Phroso, Whistler and Llama Members (Gibson, 1975; Orchard and Zonneveld, 2009). The Sulphur Mountain Formation spans the Lower to Middle Triassic and sits on top of a Permian unconformity (McGugan and Rapson-McGugan, 1976; Neuman, 1992). Of the three main fossil beds that Neuman (1992) noted, the lowest stratigraphic bed produces the majority of the fossil fishes. This bed sits approximately 30–70 m above the Permian unconformity. Orchard and Zonneveld (2009) determined that the

Sulphur Mountain Formation extends from the Griesbachian to the Ladinian (Lower to Middle Triassic) based on conodonts and ammonoids.

Very few specimens have been collected in situ; rather, they are collected along scree slopes below the exposure in particular cirques (see cirque map in Mutter et al., 2009:fig. 1). As noted in Chapters 2 and 3, there are several problems associated with this material (i.e., fragmentary condition, fossil producing beds unknown, resulting in uncertain age). The majority of the specimens of *Everticauda*, gen. nov., were found within cirque C, in which the main fossil fish-producing bed is exposed (Neuman (1992). These specimens are from the Vega-Phroso Member (Meosin Member not present), and are preserved in a dark-grey to brownish-grey calcareous siltstone (Gibson, 1968; Neuman, 1992) (for detailed accounts of the geology see Neuman, 1992; Neuman and Mutter, 2005; Orchard and Zenneveld, 2009).

MATERIALS AND METHODS

UALVP 46608 was acid prepared by immersing the specimen in a dilute solution of hydrochloric acid (5% by volume) to dissolve the bones and create a negative mold. A silicone peel was then made by pouring Smooth-On Dragon Skin® on the negative mold. Once dried, the peel represents a positive cast that is detailed enough to examine under a microscope. The peel was dusted with ammonium chloride before photographing it to maximize contrast. The camera used was a Canon Rebel XS digital SLR (Figs. 1A, 2A, 3A, 4A, 5A, 6, 7A–B, 8A, 9A, 10, 11A, B). Close-ups were photographed using a Nikon DXM 1200C digital camera mounted on a Zeiss Discovery V8 stereo microscope (Figs. 2B–E, 5B–D). Outline drawings were prepared using Adobe Photoshop CS4. Outline drawings were then stippled by hand and scanned back into Photoshop. Phylogenetic analyses were performed using Phylogenetic Analysis Using Parsimony (PAUP*) version 4b10 (Swofford, 2002). MacClade was used to analyze the trees and Adobe Illustrator CS4 was used to re-create them.

Institutional Abbreviations—TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP**, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta, Canada; **PRPRC**, Peace Region Palaeontology Research Centre, Tumbler Ridge, British Columbia, Canada.

SYSTEMATIC PALEONTOLOGY

Class OSTEICHTHYES Huxley, 1880

Subclass SARCOPTERYGII Romer, 1955

Order ACTINISTIA Cope, 1871

EVERTICAUDA, gen. nov.

Type and Only Known Species—*Everticauda pavoidea*, sp. nov.

Diagnosis—As for the type and only species.

Etymology—From the Latin *evert*- meaning everted or inside-out and *cauda* from the Latin meaning tail, in reference to the highly unusual tail shape; gender feminine.

EVERTICAUDA PAVOIDEA, sp. nov.

(Figs. 4.1–4.7)

Holotype—TMP 1995.118.23, an articulated specimen, missing the skull and tips of the caudal fin, but otherwise nearly complete (Fig. 4.1), length 39 cm, collected in 1995 in Cirque C (see map in Mutter et al., 2009).

Paratypes—UALVP 46608, consisting of a complete juvenile specimen, caudal fin missing, skull slightly disarticulated (Fig. 4.2–4.3), length 21 cm, collected in Cirque C; UALVP 43698, consisting of a nearly complete caudal fin with supplementary lobe (Fig. 4.4), length 24 cm, collected in Cirque C, latitude 54° 30’N, longitude 120° 43’W; UALVP 19237, consisting of an articulated partial fish from pelvic girdle to anterior portion of caudal fin (Fig. 4.5), length 43 cm, collected in Cirque F (see map in Callaway and Brinkman, 1989; Mutter et al., 2009), latitude 54° 31’ 45”N, longitude 120° 55’ 45”W; TMP 1983.206.185, consisting of the posterior half of the skeleton, posterior dorsal and anal fins well preserved, caudal fin incomplete (Fig. 4.6), length 29.5 cm, collected in cirque C; PRPRC 2008.04.156, isolated posterior dorsal basal plate and scale; length 2.5 cm and 0.7 cm respectively (Fig. 4.7), collected within Wapiti Lake Provincial Park at latitude 54° 31’ 46”N, longitude 121° 15’ 46”W; PRPRC 2007.11.225, partial specimen missing the skull and caudal fin; length 23 cm, collected along the Hart Ranges at latitude 54° 56’ 8”N, longitude 122° 24’ 18”W.

Stratigraphic Horizon and Type Locality—Sulphur Mountain Formation, Vega-Phroso Siltstone Member, Lower Triassic, Cirque C, latitude 54° 30’N, longitude 120° 43’W.

Etymology—From the Latin *pavo* meaning peacock and the Latin *oidea* meaning resembling, in reference to the exceedingly large sail-like anterior dorsal fin.

Diagnosis—Deep-bodied coelacanth reaching estimated lengths of up to 50–60 cm. Apomorphies of taxon: wide parasphenoid with anteroposteriorly directed ridges and rounded anterior margin; shallow, short lower jaw; deepest part of angular in posterior half of the bone; simple dentary lacking hooked process; dentary nearly twice length of splenial; dentary pore at midpoint of dentary along dentary-splenial suture; anteroventrally curved splenial with anteriorly thickened tip; highly raised tubercles restricted to center of ossification of angular; splenial and dentary lacking ornamentation; elongate and compressed fourth coronoid with numerous small conical teeth; large retroarticular with posteroventral process; lingual surface of prearticular covered in small rounded ‘teeth’; y-shaped gular pit line; 52–53 neural arches; caudal fin with 16–17 dorsal and 15–16 ventral denticulated rays; caudal fin with dorsal and ventral lobes at least twice length of supplementary lobe; reduction of unsegmented fin rays in caudal fin; caudal fin rays longest towards supplementary lobe and three times length of shortest ones; clavicle of pectoral girdle with long, thin dorsal process that abuts against anterior border of cleithrum; large pectoral fin nearly two-thirds maximum body depth; pelvic girdle below pectoral girdle; 10–11 anterior dorsal fin rays with single row of denticles on each ray; elongate anterior dorsal fin that nearly touches posterior dorsal fin; posterior dorsal and anal fin tapering to point; ornamentation of scales as anteroposteriorly directed rows of tubercles.

DESCRIPTION AND COMPARISONS

Body Shape

Everticauda pavoidea was a large fish, unlike the majority of known Lower Triassic coelacanths, which do not exceed 15–20 cm in total length, though, smaller than *Whiteia lepta* (Chapter 3) and *Rebellatrix divaricerca* (Chapter 2), both of which are from the Wapiti Lake locality. The holotype is 35.5 cm long from the pectoral girdle to the tip of the caudal fin, with a caudal peduncle depth of 8 cm (Fig. 4.1). Based on the holotype and paratypes, *E. pavoidea* reached lengths of at least 50–60 cm. It is distinctly deep bodied and short relative to its depth, as if the post-cranium were foreshortened between the dorsal fins. It is superficially similar in body form to *Hadronector* Lund and Lund, 1984, and *Libys* Münster, 1842, both of which are short, deep-bodied coelacanths. A single ‘juvenile’ specimen UALVP 46608 (Fig. 4.2), with a standard length of 18.5 cm, is not as deep bodied (proportionally) as the larger holotype specimen. However, the depth of the ‘juvenile’ specimen is still two to three times the depth of similarly sized specimens of *Whiteia lepta* (Chapter 3) from the same locality.

Skull

Paratype UALVP 46608 is the only specimen that preserves a skull, though much of it is poorly preserved due to taphonomic crushing and a pyrite inclusion (Fig. 4.3A, B). The skull is 5.5 cm long and makes up nearly one-third of the standard length (measured from tip of skull to most posterior radial in caudal fin). The skull roof is present, but sutures and ornamentation are not preserved. The parietonasal shield is preserved as a single nasal and a long, narrow bone that likely represents the parietals; however, it is not possible to discern whether there is one or two pairs of parietals present. Lower Triassic coelacanths greatly vary in the number of parietals in the parietonasal shield;

Whiteia Moy-Thomas, 1935 and *Rhabdoderma* Reis, 1888, both have two pairs of parietals, whereas *Laugia* Stensiö, 1932, *Axelia* Stensiö, 1921, and *Wimania* Stensiö, 1921, all have a single pair of parietals (Forey, 1998). The intracranial margin is straight as judged by the posterior margin of the parietonasal shield. There is a slightly displaced nasal (Na) anterior to the parietal, with a v-shaped posterior margin (Fig. 4.3A, B). Paired premaxillae are preserved anterior to the nasal, though only the posterior portion of the premaxilla (Pmx) bears 5–6 conical teeth (Fig. 4.3B). Both premaxillae have broken outer margins. No pores are visible. A possible partial postparietal (Pp?) is preserved ventral to the displaced operculum (Fig. 4.3A, B). It is approximately half the length of the parietonasal shield, though both shields are likely missing a large portion of bone. No ornamentation is visible on either the parietonasal or postparietal shield.

No identifiable cheek bones are preserved on UALVP 46608. Both opercula (Op) are preserved on the paratype (Fig. 4.3A, B). The left operculum is in place, whereas the right operculum is flipped dorsally, a typical taphonomic occurrence in coelacanths of the Sulphur Mountain Formation (pers. obs.). The operculum is nearly as wide as it is deep and lacks ornamentation. A thickened ridge is present along the outer margin of the bone, but does not extend onto its posterior margin.

Parasphenoid—A complete parasphenoid is preserved in ventral view on paratype UALVP 46608 (Fig. 3A, B, Par). Its transverse width is nearly one-fourth the length of the entire parasphenoid. The parasphenoid is anteriorly expanded, with a rounded anterior margin. The posterior end is slightly flared laterally, with a straight posterior margin. The shape of the parasphenoid resembles that of *Wimania sinuosa* (Stensiö, 1921:fig. 23 and pl. 7, fig. 1). Both are robust and expand anteriorly, though there is a greater expansion proportionally in *W. sinuosa*. A triangular depressed area on the posterior end of the parasphenoid is present in both *E. pavoidea* and *W. sinuosa* (Stensiö, 1921:pl. 17, fig. 1), though this structure is absent from Stensiö's reconstruction of the same bone (Stensiö, 1921:fig 23). Similarly, the anterior end of *W. sinuosa* is reconstructed with a straight anterior margin, but the specimen shows a fragmentary, yet rounded anterior margin (Stensiö, 1921:pl. 7, fig. 1). Stensiö (1921) noted that the anterior half of the underside of the parasphenoid in *W. sinuosa* is covered in ridges of tiny teeth. *Everticauda pavoidea* has narrow textured ridges that extend from the midpoint of the bone to the anterior tip, but teeth do not appear to be present. A partial bone covered in crowded, rounded 'teeth' or tubercles abuts the dorsal side of the parasphenoid. This bone is part of the palate, most likely a partial ectopterygoid (Ecpt?) with crushing dentition (Fig. 4.3A, B).

Lower Jaw and Gular Plates—The lower jaw of *E. pavoidea* is remarkably well preserved compared to the rest of the skull on the paratype UALVP 46608 (Fig. 4.3A, B). Both lower jaws are preserved on this specimen, the right in place and the left displaced ventrally. The right jaw preserves the lingual side of the jaw, whereas the left one shows a labial view. The bones of the lower jaw preserved in this specimen consist of an angular, prearticular, splenial, dentary, fourth coronoid, retroarticular and gular plates, as well as a series of pores and pit lines on the jaw bones. Ornamentation consists of highly raised circular tubercles on the angular (Ang), which are restricted to the center of ossification (Figs. 4.2B, 4.3A, B); the dentary and splenial both lack ornamentation.

The angular is shallow and short (Figs. 4.2B, 4.3A, B) in comparison to that of most coelacanths, but is similar to that of *Whiteia* (Forey, 1998:figs. 5.9a-b, d). The deepest part of the angular, the center of ossification, is in the posterior half of the bone (Fig. 4.2B), as in *Coelacanthus granulatus* Agassiz, 1839 (Schaumberg, 1978:figs.11–13; Forey, 1998:fig. 5.4b). No oral pit line is preserved on the angular.

A large retroarticular (Rart) is situated along the posterior most portion of the angular (Fig. 4.3A, B). It has a posteriorly facing concave surface with a small posterior process. This area is the articular surface for the symplectic. The articular is not visible and therefore it is not known whether the retroarticular and articular are fused or separate from each other. Loss of fusion of these two bones is considered to be a trait of derived coelacanths (Forey, 1991, 1998).

The dentary (De) and splenial (Spl) are both shallow and curve ventrally. (Fig. 4.3A, B). The dentary is nearly twice the length of the splenial and half the depth of the deepest part of the splenial. The posterior end of the dentary reaches significantly farther back into the angular than does the splenial, as in *W. woodwardi* (Moy-Thomas, 1935; Forey, 1998:fig. 5.9a). No teeth are present on the dentary, though as Forey (1998) noted in *Whiteia*, the dentary teeth commonly disarticulate in coelacanths. A hooked posterodorsal process of the dentary is not present in *E. pavoidea*, a condition similar to that in *Laugia groenlandica* and *Coelacanthus granulatus* (Forey, 1998). The splenial is anteriorly thickened and resembles *Diplurus newarki* (Schaeffer, 1952:figs. 4, 7). Both the dentary and splenial are smooth and lack any form of ornamentation.

A shallow, elongate bone (Co.4) covered in numerous needle-like teeth is displaced anterior to the angular-dentary suture (Figs. 4.2B, 4.3B). It is nearly half the length of the dentary and is likely a modified fourth coronoid. It most closely resembles the fourth coronoid present in *W. woodwardi* (see Lehman, 1952:pl. 2, fig. d; Forey, 1998:fig.5.9a), *W. neilseni* (see Forey, 1998:fig. 5.9d) and *W. durabilis* (see Chapter 3:fig. 3.9A, C).

The prearticular, preserved in place, is exposed in lingual aspect (Fig. 4.3A, B, Part). The surface is covered in small, crowded, rounded ‘teeth’. This feature has been noted in *Laugia*, *Mawsonia*, *Axelrodichthys* (Forey, 1998:fig. 5.10b) and *Macropoma* (Forey, 1998:fig. 5.13c). The above-mentioned genera have been described as having “rounded teeth with fine striations radiating from the crown” on the prearticular (Forey, 1998). While the ‘teeth’ on the prearticular are rounded in *E. pavoidea*, no striations are preserved on the specimen.

Several important sensory structures are preserved on the ventrally displaced lower jaw. The mandibular sensory canal (m.s.c) runs across the ventral portion of the angular and splenial (Fig. 4.3B). There are five large, elongate pores on the angular. Anteriorly, three more pores are present on the splenial, though they are smaller. One of the pores on the splenial is distinctly ventral to the trajectory suggested by the other pores. A similar condition has been noted by Lehman (1952) and Forey (1998) in several specimens of *W. woodwardi*, though the significance of this feature is unknown (Lehman, 1952:fig. 10; Forey, 1998:fig. 5.9a). The dentary pore (d.p) is present in the center of the dentary along the ventral surface that abuts the splenial (Fig. 4.3A, B). It is located above the mandibular sensory canal and is significantly smaller than the mandibular sensory pores. Generally in most coelacanths, the dentary pore is larger than the mandibular sensory pores (Forey, 1998).

A depressed groove that surrounds the pores from the posterior end of the angular to the anterior tip of the splenial accommodated the external ramus of the facial nerve (Forey, 1998; Forey et al., 2000; Cavin et al., 2005).

Both gular plates (Gu) are preserved on paratype UAVLP 46608 (Fig. 4.3). The left displaced gular has a y-shaped pit line (Figs. 4.2C, 4.3B, gu.p.l), whereas most coelacanths have straight or curved pit lines (pers. obs.). Three slightly thickened ridges are also present along the outer margin of both gular plates. No other ornamentation is present.

Appendicular Skeleton

Pectoral Girdle and Fin—The left and right pectoral girdles, represented by two partial cleithra, are preserved on the holotype (TMP 1995.117.21) (Fig. 4.1). The cleithrum is wide, with an even broader rounded dorsal margin. Sparse, small, rounded tubercles are present across the girdle. Paratype UALVP 46608 preserves a complete left pectoral girdle consisting of a cleithrum, clavicle, extracleithrum and an anocleithrum (Figs. 4.2, 4.3A, B). The cleithrum is half the length of the pectoral girdle. In *E. pavoidea*, the clavicle has an unusual, thin dorsal process that runs along the anterior side of the cleithrum, whereas the extracleithrum is restricted to the posterior aspect of the girdle. The anocleithrum is partially obscured by the cleithrum. The anterior tip of the anocleithrum narrows dorsally into a small blade-like process, not forked as in *Coccoderma* Quenstedt, 1858, *Libys*, Munster, 1842, and *Macropoma* Agassiz, 1835.

The pectoral fin is preserved on the holotype TMP 1995.117.21 and on paratype UALVP 46608. The description is based on the former because it is better preserved. The left pectoral fin has 16–18 rays and is situated directly below the anterior dorsal basal plate (Fig. 4.1A, B). The fin has long fin rays, the longest being 6.3 cm. The position of the pectoral fin, although it is likely displaced, shows that the rays are half the body depth. The proximal half of each fin ray is thickened, whereas the distal half is slender and delicate in appearance

(Fig. 4.1). The outer margin of the pectoral fin does not exhibit the typical rounded, symmetrical appearance seen in most coelacanths (e.g., *Diplurus*, *Holophagus* and *Macropoma*); rather, the long rays create an extended asymmetrical outer margin.

Pelvic Girdle and Fin—The pelvic girdle (P.b) is present on the holotype, TMP 1995.117.21, and on paratypes UALVP46608 and 19237 (dorsal view), though it is best preserved in the former (Fig. 4.3A, B). The pelvic bones are unfused and each bone has two small posterior and two elongate anterior processes. The ventral posterior process is wide, with a rounded outer margin. It is approximately three times the width of the dorsal anterior process, which is small and rod-shaped. Both anterior processes are long, slender, and slightly curved inwards, though the distal process is nearly twice the length of the proximal process. A thin sheet of bone connecting the two anteriorly directed processes almost completely obscures the proximal process from view. Two rows of arched ridges cross this sheet between the anterior processes. The two pelvic bones articulate along this sheet of bone as well as at the smaller anterior processes. The pelvic girdle of *E. pavoidea* resembles the pelvic girdles of *W. woodwardi* (see Moy-Thomas, 1935:fig. 5) and *W. lepta* (see Wendruff and Wilson, in review; Chapter 3:fig. 3.6B) in that all three species have two anterior and two posterior processes as well as a connecting sheet of bone between the anterior processes.

The pelvic fins are preserved on the holotype (TMP 1995.118.23) and paratypes (UALVP 19237 and 46608). The fin is best preserved in the holotype, though the fin is slightly twisted (Fig. 4.1). Each pelvic fin has 20–22 fin rays, with the longest rays reaching lengths of 6.5 cm on the holotype. The pelvics are located abdominally, below the posterior dorsal basal plate, unlike the thoracic pelvic fins of the Lower Triassic coelacanth *Laugia* Stensiö, 1932, and *Piveteauia* Lehman, 1952. The posterior margin of the fin is straight, contrasting with the typical lobed fin shape in coelacanths, though the shape may have been distorted during preservation.

Anterior Dorsal Basal Plate and Fin

The anterior dorsal basal plate (D1.b) is preserved on the holotype and paratype (UALVP 46608) (Figs. 4.1, 4.2). It is situated nearly directly above the pectoral girdle, farther anteriorly than in most coelacanths. The basal plate is large and rounded, with a straight ventral margin that sits directly above the neural spines, but does not articulate with them unlike the condition in *Caridosuctor* Lund and Lund, 1984 (see Lund and Lund, 1985). A thickened median ridge is present that maintains a uniform thickness across the basal plate. Additionally, there is a small thickened ridge around the outer margin of the bone.

The anterior dorsal fin is only preserved in the holotype (TMP 1995.118.23) (Fig. 4.1) and paratype (PRPRC 2007.11.225, unfigured). The anterior dorsal fin has 10–11 long fin rays. The most distinctive feature of the anterior dorsal fin is its length, which extends from the pectoral girdle to the tip of the caudal fin, equivalent to one-third the post-cranial length in the holotype. The anterior dorsal fin rays are not all the same length, contrary to the condition in most coelacanths. The posterior three inserted fin rays are the longest on both specimens (TMP 1995.118.23 and PRPRC 2007.11.225). In the holotype, the longest ray measures 12.5 cm along its curve and nearly reaches the posterior dorsal fin (Fig.4.1).

The anterior dorsal fin in UALVP 46608 is shorter proportionally than in the holotype, making up only one-quarter of the length of the post-cranium as opposed to one-third in the holotype. However, UALVP 46608 may represent a juvenile specimen of *E. pavoidea* as it is significantly smaller than the holotype specimen at 17.5 cm long. The anterior dorsal fin rays all bear a single row of denticles. In contrast, the anterior dorsal fin rays in *W. woodwardi* and *W. neilseni* have a double row of saw-blade-like denticles (Forey, 1998).

Posterior Dorsal and Anal Fins

The posterior dorsal basal plate (D2.b) is known from a perfect isolated element (PRPRC 2008.04.156), and is preserved in the holotype (TMP 1995.118.23) and paratypes (TMP 1983.206.185 and UALVP 19237). Its distal end is a greatly expanded semi-circular process with a long, slender anterior process, which creates an overall forked appearance (Fig. 4.7). There is a long, rod-like proximal process that articulates with 1–2 neural spines. The ventral tip of the proximal process is slightly thickened. The basal plate is similar in shape to that in *Caridosuctor popusolum* (see Lund and Lund, 1984, 1985:fig. 19; Schultze, 1992:fig. e).

The anal basal plate (A.b) is preserved on the holotype (TMP 1995.118.23) and paratypes (UALVP 19237 and 46608). It is significantly smaller than the posterior dorsal basal plate, even though the fins are the same size. The distal end is semicircular and the proximal end is a small, anteroventrally curved process (Fig. 4.5D).

The posterior dorsal fin and the anal fin are best preserved in the holotype, TMP 1995.118.23 and paratypes UALVP 19237 and TMP 1983.206.185 (Figs. 4.1, 4.5 and 4.6 respectively). They are near mirror images of each other, although the anal fin is located slightly posterior to the dorsal fin (Figs. 4.5, 4.6). The posterior dorsal fin has 20–22 fin rays, whereas the anal fin has 18–19 fin rays. Both fins are very slender, and taper to a point. This is most apparent in paratype TMP 1983.206.185 (Fig. 4.6). *Rebellatrix* Wendruff and Wilson, in review (Chapter 3), describe a fork-tailed coelacanth with similar tapering posterior dorsal and anal fins. Typically, coelacanths have fins with rounded posterior margins. There is some intraspecific variation in the posterior dorsal and anal fin shapes in *E. pavoidea*. The holotype has tapering fins that have a straight posterior margin (best preserved in the anal fin) (Fig. 4.1), whereas the paratypes (TMP 1983.206.185 and UALVP 19237) both have significantly more slender fins with posterior concave margins (Figs. 4.5, 4.6).

Axial Skeleton and Caudal Fin

The axial skeleton comprises 52–53 neural arches in the holotype, TMP 1995.118.23, and 51–52 in the paratype, UALVP 46608 (Figs. 4.1, 4.2A). Forey (1991, 1998) noted that there is a tendency to increase the number of neural arches in more derived coelacanths. *Latimeria* Smith, 1939, the most derived coelacanth, has approximately 95 neural arches, whereas the plesiomorphic coelacanth *Hadronector* (Lund and Lund, 1984, 1985) had approximately 42–43 neural arches (Forey, 1998). The relatively low number of arches in *E. pavoidea* indicates that it has a primitive post-cranium. The neural arches and spines are the typical shape found in coelacanths. The anterior neural arches, termed the occipital neural arches, are not expanded. The neural arch bases are consistently the same thickness and the spines are the nearly the same height throughout the column. Neural spines are slightly shorter directly behind the pectoral girdle and longest, as well as thickest, anterior to the caudal fin.

There are 23–24 haemal arches. The anterior most arch is situated above the anal basal plate (Figs. 4.1, 4.2A). The haemal spines are long and strongly curve posteriorly. The caudal fin radials first appear opposite each other on the dorsal and ventral sides of the tail, producing a symmetrical caudal fin similar to that of *Whiteia* (see Lehman, 1952:pl. 5, fig. e) but dissimilar to that of *Laugia* (see Stensiö, 1921:fig. 21). No ossified ribs are present.

The caudal fin of *E. pavoidea* is among the most peculiar known in coelacanths apart from those of *Allenypterus* Melton, 1969, *Holopterygius* Jessen, 1973 (see Friedman and Coates, 2006), and *Rebellatrix* Wendruff and Wilson, in review (Chapter 2). In most coelacanths, the supplementary lobe extends behind the posterior margin of the caudal fin, whereas in *E. pavoidea*, the supplementary lobe is shorter than the posterior margin of the caudal fin. The dorsal and ventral (principal) lobes of the tail extend far beyond the tip of the supplementary lobe (Fig. 4.4). The only other coelacanth with a proportionally smaller supplementary lobe (though the supplementary lobe is not preserved on many fossil coelacanths) is *Rebellatrix divaricerca* Wendruff and Wilson, in review (Chapter 2); however, these two coelacanths drastically differ in caudal fin form because *R. divaricerca* has reduced segmented fin rays whereas *E. pavoidea* has lengthened them.

The caudal fin has 16–17 dorsal and 15–16 ventral fin rays based on the holotype TMP 1995.118.23 and UALVP 43698 (Figs. 4.1, 4.4 respectively). The posterior margin of the caudal fin on the holotype is incomplete posteriorly. The caudal fin (including the supplementary lobe) is best preserved on the isolated caudal fin of paratype UALVP 43698 (Fig. 4.4). The posterior tips of the caudal fin rays have been lost, yet the caudal fin of UALVP 43698 is 24 cm long. The fin rays are shortest along the dorsal and ventral margins of the caudal fin and are longest nearer the supplementary lobe. The shortest rays on UALVP 43698 are 7 cm long, whereas the longest rays, though incomplete, are nearly 24 cm long. Additionally, the caudal fin rays are highly segmented; the unsegmented fin rays make up nearly one-fifth of the entire caudal fin in UALVP 43698 (Fig. 4.4). This feature is the completely contrary to the condition in *R. divaricerca* Wendruff and Wilson, in review (Chapter 2), another unusual coelacanth from the Sulphur Mountain Formation, in which the segmented rays are reduced, and the unsegmented fin rays increased.

The supplementary lobe is preserved on the holotype TMP 1995.118.23, though it is best preserved on paratype UALVP 43698 (Fig. 4.4), on which it is 13 cm long, whereas the rest of the caudal fin is about twice that length. The supplementary lobe has a rounded posterior margin consisting of 22–25 small, segmented fin rays.

The depth of the notochord in fossil coelacanths can only be estimated when both the haemal and neural arches are preserved in place because the notochord is bounded by the arches. The notochord in *E. pavoidea* is very wide at the anal fin (Figs. 4.1, 4.5) and quickly tapers to the beginning of the caudal fin. The width remains constant between the most posterior radial and the supplementary lobe.

An ossified 'swim bladder' (sb) is preserved behind the pectoral girdle of the holotype (TMP 1995.118.23) and paratype (UALVP 19237) (Figs. 4.1, 4.5). It is deep and extends posteriorly to the point where the pelvic fins originate. In UALVP 19237, the posterior tip of the 'swim bladder' narrows quickly (Fig. 4.5).

Its surface is heavily pitted in UALVP 19237, but smooth in the holotype; this may be due to preservational differences.

Scales

There are 54–55 scales from the pectoral girdle to the base of the supplementary lobe. In comparison, the long and slender *Whiteia lepta* (Chapter 3) has 67–70 scales. The ornamentation of the scales of *E. pavoidea* is best preserved on the holotype TMP 1995.118.23 as well as on a scale preserved with an isolated posterior dorsal basal plate (PRPRC 2008.04.156) (Figs 4.1, 4.7B respectively). The ornamentation consists of anteroposteriorly oriented short rows of tubercles (Fig. 4.7B). The scale ornament is most similar to those of *Chauhuichthys majiashanensis* (see Tong et al., 2006:fig. 15), although the rows of tubercles on *Everticauda* are not radial. Tubercle-bearing and ridged scales are plesiomorphic amongst coelacanths (Forey, 1991, 1998). The most derived coelacanths have scales characterized by sparse denticles such as those found in *Latimeria chalumnae* (see Forey, 1998;fig. 11.9b) and several species of *Macropoma* (Forey, 1998:fig. 11.12a–d).

The holotype (TMP 1995.118.23) and paratype (UALVP 19237) of *E. pavoidea* preserve an intricate lateral line system (Fig. 4.2A). A series of bony tubes runs from the pectoral girdle to the tip of the supplementary lobe. Each opens into a single pore in the anterior portion of a scale. A similar lateral line system is described in *R. divaricerca* (see Wendruff and Wilson, in review; Chapter 2).

WAPITIA, gen. nov.

Type and Only Known Species—*Wapitia robusta*, sp. nov.

Diagnosis—As for the type and only species.

Etymology—*Wapitia*, in reference to Wapiti Lake Provincial Park where this specimen was found; gender feminine.

WAPITIA ROBUSTA, sp. nov.

(Figs. 4.8–4.11)

Holotype—UALVP 24228, length 47.5 cm, collected along Ganoid Ridge within the vicinity of Fossil Fish Lake in Wapiti Provincial Park (Fig. 4.8–4.9).

Paratypes—PRPRC 2008.04.110, consisting of an isolated posterior dorsal basal plate (Fig. 4.10), length 2.5 cm, collected within Wapiti Lake Provincial Park at latitude 54° 31’ 27”N, longitude 121° 15’ 54”W; UALVP

43604, isolated scale (Fig. 4.11A), 1.8 cm wide, collected in cirque F along the Ganoid Range (see map in Callaway and Brinkman, 1989; Orchard and Zonneveld, 2009), latitude 54° 31’ 45”N, longitude 120° 44’ 45”W; UALVP 43605, isolated complete scale (Fig. 4.11B), 2.2 cm wide, collected in cirque F along the Ganoid Range, latitude 54° 31’ 45”N, longitude 120° 44’ 45”W.

Stratigraphic Horizon and Type Locality—Sulphur Mountain Formation, Vega-Phroso Siltstone Member, Lower Triassic, latitude 54° 32’N, longitude 120° 45’ 24”W.

Etymology—From the Latin *robusta* in reference to the deep body.

Diagnosis—Deep-bodied coelacanth reaching estimated lengths of more than approximately 45 cm. Apomorphies of taxon: skull nearly as deep as it is long; two pairs of parietals of same size; skull roof covered in rows of closely spaced elongated tubercles; preoperculum with anterodorsal curved excavation for lachrymojugal; low angular with near consistent depth; low-crowned tubercles confined to posterior half of angular; long, narrow splenial with thickened anterior tip; 47–48 neural arches; 3–4 expanded occipital neural arches; posterior neural spines four times length of anterior-most neural spines; symmetrical caudal fin; 15–16 dorsal and 14–15 ventral caudal fin rays; anteriorly situated pelvic plates; 10 anterior dorsal fin rays lacking denticles; posterior dorsal basal plate with semi-circular distal process.

DESCRIPTION AND COMPARISON

Body Shape

Wapitia robusta is a relatively deep-bodied coelacanth and of the coelacanths found in the Sulphur Mountain Formation, only *Everticauda pavoidea* has a deeper body than *W. robusta.* The holotype has a maximum body depth of 10.5 cm and a total length of 45.5 cm (standard length 40 cm). In comparison, a specimen of *W. lepta* of similar length has a maximum body depth of only 6 cm. The holotype of *Everticauda pavoidea*, which has a similar length (from pectoral girdle to most posterior radial) as the type of *W. robusta*, has a maximum body depth of 12.3 cm; thus, *E. pavoidea* is 20% deeper than *W. robusta*. The outline of the body on the holotype specimen was highlighted for display at the Earth Sciences Museum at the University of Alberta; actual shapes of the posterior dorsal, anal and pelvic fins are slightly shorter and less ‘squared-off’ than they appear in the photograph (Fig. 4.8A).

Skull

Although the skull bones are poorly preserved, the outline of the skull is still informative. The skull is relatively large, making up one-third the standard length. Additionally, the skull is nearly as deep as it is long, and resembles the skull of another deep bodied coelacanth, *Libys* Munster, 1842 (see Forey, 1998).

Skull Roof—Both the parietonasal and postparietal shields are preserved on the holotype UALVP 24228 (Fig. 4.9A, B). The intracranial joint has a straight margin. Ornamentation of the skull roof is characterized by crowded rows of tubercles that are oriental anteroposteriorly (Fig. 4.9C). The tubercles are more elongate along the lateral margins of the postparietals. Additionally, the rows of tubercles curve along the lateral edges of the bone. Neither sensory lines nor pit lines are preserved on the skull roof.

Elements of the parietonasal shield that are preserved are two pairs of parietals, a single nasal and three supraorbitals. Anterior to the nasal, a number of unidentifiable broken elements outline the anterior margin of the skull (Fig. 4.9B, outline dotted). Both pairs of parietals (Pa) are the approximately same length and width (Fig. 4.9A, B). The center of ossification of each parietal is situated at the posterior half of the bone. The sutures between the two pairs of parietals and nasals are nearly straight. The nasal bone (Na) represents one-half of the first pair of nasals (Fig. 4.9A, B). The total number of nasals cannot be estimated because coelacanths vary in the total number of paired nasals (Forey, 1998). The nasal bone preserved in *W. robusta* is two-thirds the length of the parietals. Three supraorbitals (So) flank the parietonasal shield (Fig. 4.9A, B), though the total number of supraorbitals cannot be estimated as this feature is highly variable amongst coelacanths (Forey, 1991, 1998). The posterior two supraorbitals of *W.*

robusta laterally abut against the posterior parietal, whereas the anterior-most supraorbital is against the posterior portion of the anterior parietal. No tectals are preserved anterior to the supraorbitals.

The postparietal shield consists of two pairs of postparietals that are approximately one and a half times the length of a single pair of parietals. Comparisons between the two shields, a common comparison in coelacanths, cannot be made because the parietonasal shield is incomplete. The postparietal shield of *W. robusta* is longer than it is wide, as in *Rhabdoderma* Reis, 1888 (see also Woodward, 1910; Moy-Thomas, 1939; Forey, 1981, 1998), but unlike the condition in other Lower Triassic coelacanths such as *Whiteia*, *Axelia* and *Wimania*, in which the postparietal shields are wider than long (Stensiö, 1921; Moy-Thomas, 1935; Lehman, 1952; Forey, 1998). The right postparietal is wider than the left one, though this may be an artifact or preservation or individual variation. Only the right supratemporal is preserved and is relatively small, comprising less than one-fifth the length of the entire shield. Supratemporal size is greatly variable in coelacanths.

Cheek and Sclerotic Ossicles—None of the cheek bones is preserved in place. The left preoperculum (Pop) is displaced ventral to the pectoral girdle (Fig. 4.9A, B). The preoperculum is a large bone most similar in shape to those found in *Whiteia woodwardi* (Moy-Thomas, 1935; Lehman, 1952:pl. 2, fig. a; Forey, 1998:fig. 4.14). In *W. robusta*, the depth of the preoperculum is nearly two-thirds the length. The preopercular canal (pop.sc) runs along the straight posterior margin (Fig. 4.9B). The preoperculum has a short, straight dorsal margin that likely abuts the squamosal. The sinuous ventral margin is longest. The anterior margin is straight ventrally, but angled (embayed) posterodorsally. A similar shape, though more exaggerated, is also present in *W. woodwardi* (see Lehman, 1952:pl. 2, fig. a; Forey, 1998:fig. 4.14). In *W. woodwardi*, this preopercular margin is embayed so that the ventral curved portion of the lachrymojugal fits against it. It is likely that this was also the case in *W. robusta*. No cheek pit line is present. Since the preoperculum is the only cheek bone that is preserved, it is not possible at this time to determine whether the cheek bones were separate from one another as in *Whiteia* (Moy-Thomas, 1935; Lehman, 1952), or sutured to each other as in *Rhabdoderma* (Forey, 1981, 1998).

Several sclerotic ossicles (Fig. 9A, B, S.o) present below the supraorbitals are relatively thick compared to those of other Lower Triassic coelacanths, with the exception of *Whiteia durabilis* (Chapter 3). Based on their size and shape, it can be estimated that there were approximately 20–24 sclerotic ossicles in the complete bony ring.

Operculum—Both opercula (Op) are preserved on the holotype (Fig. 4.9-A, B). The left operculum is in place, whereas the right operculum has flipped to expose the underside, which is a typical taphonomic feature in coelacanths from the Sulphur Mountain Formation (pers. obs.). The operculum is deeper than it is wide, with a pronounced narrowing of the ventral margin as well as a rounded posterior margin, a shape most similar to that of *Diplurus newarki* (Schaeffer, 1952:fig. 4b, pl. 9, fig. 1, pl. 10, fig. 1). The outer margin of the operculum has a thickened ridge, though it is not developed along the dorsal margin. A pronounced anterodorsal, squared off projection resembles that figured for *Axelrodichthys* (Maisey, 1986:figs. 22a, 26a, 1991; Forey, 1998). No ornamentation is observed on the operculum of *W. robusta*.

Palate and Symplectic—The palate is well preserved on the holotype and consists of the pterygoid (Pt), quadrate (Q) and metapterygoid (Mpt) (Fig. 4.9A, B). None of the typical toothed elements, such as the dermopalatines or ectopterygoid, are exposed because the ventral margin of the pterygoid is obscured by the angular. The pterygoid has the typical triangular shape found in coelacanths (Cloutier, 1991; Forey, 1998). Two large, thickened ridges extend from the quadrate to the metapterygoid along the posterior margin of the palate. Between these two ridges is a very deep groove. A similar feature is noted in *Rhabdoderma elegans* (Newberry, 1856; Forey, 1998:fig. 7.1e). The quadrate is a tall, thin bone. Its articular surface is obscured, although there is no reason to doubt that it formed part of a double condyle as in all other coelacanths. The quadrate is approximately half the height of the pterygoid. The metapterygoid is rectangular with a straight but slightly anteriorly angled dorsal articular surface. No ornamentation is present on the palate.

A complete symplectic (Sy) is in place in the holotype (Fig. 4.9A, B). It is one of two bones that form the usual double articulation (along with the quadrate) of the lower jaw in coelacanths (Smith, 1939; Eaton, 1945; Millot and Anthony, 1958; Alexander, 1973; Forey, 1998). The symplectic in *W. robusta* is long and slender, similar to that in *Latimeria* (Smith, 1939; Eaton, 1945:fig. 1). The ventral half is nearly fifty percent thinner than the dorsal half of the bone. The articular surface is rounded and the dorsal margin is straight.

Lower Jaw and Gular—The lower jaw consists of an angular (Ang), retroarticular (Rart) and splenial (Spl) as preserved in the holotype (UAVLP 24228) (Fig. 4.9A, B). The very shallow angular thickens only slightly at its center, much as in the lower jaws of *Undina pencillata* Münster, 1834, and *Holophagus gulo* Egerton, 1861, both Upper Jurassic coelacanths (Forey, 1998:fig. 5.12a–c). The angular has small, low-crowned tubercles that are restricted to the posterior portion of the bone. No other ornamentation is present on the lower jaw. The splenial is long and narrow with a slightly anteriorly thickened tip. The dentary is likely preserved in the broken bone above the splenial, though neither teeth nor identifiable markers could be discerned. The retroarticular is square and situated along the posterior half of the articular surface for the quadrate. The articular, the other half of the articular surface of the quadrate, is not preserved on the holotype.

Four large, depressed, oval mandibular sensory canals (m.s.c) are preserved on the angular (Fig. 4.9B). None are visible on the splenial, though this is likely due to preservation rather than the pores being absent. As noted with *Everticauda*, *Laugia* and *Latimeria*, the size, shape and number of these pores changed through ontogeny.

The left gular (Gu) is well preserved and in place (Fig. 4.9). There are elongate tubercles along the outer margin of the gular (Fig. 4.9D). The posterior and anterior ends of the gular plate both taper to a point. A small, straight pit line (gu.p.l) is present on the gular, located posteriorly off-center (Fig. 4.9B).

Appendicular Skeleton

Pectoral Girdle and Fin—The pectoral girdle of coelacanths consists of a cleithrum (Cl), clavicle (Cla), extracleithrum (Ecl) and an anocleithrum (Acl); all of these elements are preserved on the left pectoral girdle in the holotype specimen (Fig. 4.9A, B). The posterior margin of the extracleithrum is broken. The cleithrum makes up nearly 50% of the girdle as it does in *Whiteia woodwardi* Moy-Thomas, 1935, and *Holophagus gulo* Egerton, 1861 (see also Moy-Thomas, 1935; Lehman, 1952; Forey, 1991, 1998). The dorsal margin of the cleithrum is rounded and slightly expanded. The extracleithrum and clavicle are nearly the same size. This is reminiscent of the condition in *H. gulo* (Egerton, 1861) but distinct from that in some coelacanths such as *Diplurus newarki* Bryant, 1934 (see also Schaeffer, 1952, in which the extracleithrum is reduced to a tiny sliver (Forey, 1998). The cleithrum is straight, whereas the extracleithrum and clavicle curve around the ventral margin of the operculum. The anocleithrum is a short, stout, rectangular bone with rounded margins and a small anterior process that is obscured by the right operculum. The anocleithrum is simple, not forked. There is no ornamentation present on the entire girdle.

The pectoral fin is well preserved on the holotype and consists of 20–21 fin rays (Fig. 4.8A, B). It is large, approaching nearly two-thirds the maximum body depth. The longest fin ray is 7 cm and nearly reaches the posterior dorsal basal plate. The pectoral fin is asymmetrical and most similar in shape to that of *Latimeria chalumnae* (Smith, 1939; Fricke and Hissman, 1992:fig. 1; Forey, 1998:fig. 8.1). Most fossil coelacanths such as *Macropoma* Agassiz, 1835, and *Holophagus* Egerton, 1861, have a nearly symmetrical pectoral fin with a rounded outer margin.

Pelvic Girdle and Fin—The pelvic girdle is directly ventral to the pectoral fin and anterior dorsal basal plate as in *Laugia groenlandica* (Stensiö, 1921; Forey, 1998:fig. 11.10), though it does not contact the pectoral girdle (Fig. 4.8A, B). Both the left and right pelvic bones that comprise the pelvic girdle are preserved, though the lateral portion of the left one is incomplete. They are preserved in dorsal view and are unfused at the midpoint. The pelvic bone of *Wapitia robusta* has two anterior processes and two posterior processes. The dorsal anterior process is long, slender, and curved, whereas the ventral anterior process is half the length of the dorsal, and nearly twice its width. The dorsal posterior process is wide, with a rounded posterior margin, whereas the ventral process is thinner, with a straight posterior margin. A thin sheet of bone spans the anterior processes. This feature is present in both *Coelac-anthus* and *Whiteia*

(Moy-Thomas, 1935; Moy-Thomas and Westoll, 1935; Lehman, 1952; Forey, 1998). The pelvic plate of *W. robusta* most closely resembles that of *Coelacanthus granulatus* (Agassiz, 1839; Moy-Thomas and Westoll, 1935:fig. 9; Schultze, 1992) in shape and size of the anterior and posterior processes, as well as in the presence of a thin sheet of bone that spans the anterior processes.

The pelvic fin (P.f), situated below the level of the posterior dorsal basal plate, has 15–16 fin rays (Fig. 4.8A, B). The longest fin ray is nearly 8.5 cm long. The fin rays are significantly longer along the outer margin of the fin and quickly shorten towards the body. The fin rays are not expanded, unlike the condition in *Laugia* and *Coccoderma* (Quenstedt, 1858; Lambers, 1991; Forey, 1998).

Anterior Dorsal Fin

The only remnant of the poorly preserved dorsal basal plate is a small triangular impression. Judging by its small size and unusual shape, it is doubtful that it is complete. The anterior dorsal fin is better preserved than the basal plate. A break in the holotype specimen goes through the rays and was repaired slightly offset. Similar to *E. pavoidea*, *W. robusta* has an anterior dorsal fin that is situated farther anteriorly than most coelacanths (Fig. 4.8). There are 10 rays in the anterior dorsal fin. Most Triassic coelacanths such as *Whiteia* (known in 5 of the 6 species), *Laugia*, and *Piveteauia* (Moy-Thomas, 1935; Lehman, 1952; Clément, 1999 and Forey, 1998) have fewer than 10 fin rays. Three of the four coelacanths from the Sulphur Mountain Formation known from post-crania (*E. pavoidea*, *W. lepta* and *W. robusta*) have 10 or more anterior dorsal fin rays. The fin rays are long, though not as proportionally long as in *E. pavoidea*. The longest anterior dorsal fin ray is 8.7 cm and extends to the posterior margin of the second dorsal basal plate.

Posterior Dorsal and Anal Fins

The posterior dorsal basal plate is preserved in the holotype UALVP 24228 and paratype PRPRC 2008.04.110 (Figs. 4.8, 4.10 respectively). It is strongly forked with a straight posterior end. It is most similar in shape to those of *Rhabdoderma elegans* (see Forey, 1981:fig. 9) and *Coelacanthus granulatus* (Moy-Thomas and Westoll, 1935; Schultze, 1992:fig. 6i), though the forked portion is more slender than in *C. granulatus* and the thin forked processes are longer proportionally than in *R. elegans*. The anal basal plate is not preserved on the holotype or paratypes.

The posterior dorsal and anal fins are opposite each other, though the anal fin is situated slightly posterior to the dorsal fin. The posterior dorsal fin has 19–21 rays, whereas the anal fin has 17–18 fin rays. The posterior margin of both fins is slightly lobe-shaped, though less so than in coelacanths such as *Coelacanthus granulatus* Agassiz, 1839, *Laugia groenlandica* Stensiö, 1932, and *Latimeria chalumnae* Smith, 1939.

Axial Skeleton and Caudal Fin

The well preserved axial skeleton in the holotype displays 47–48 neural arches (Fig. 4.8). The first 3–4 neural arches, known as the occipital neural arches, are expanded; this feature is found in the most derived coelacanths (Forey, 1991, 1998) as well as *Rebellatrix* (in review; Chapter 2). Additionally, the neural spines are short and stout on the occipital neural arches (Fig. 4.8A, B). The neural arches maintain a consistent distance apart along the body until the caudal fin, where the neural arches nearly abut. The neural spines directly anterior to the caudal fin are longest, reaching a maximum length of 5 cm; this is four times the length of the shortest occipital neural spine, which is the largest disproportion in neural spine length of all fossil coelacanths. There is no known functional significance of these elongate spines. The haemal arches first insert at the posterior margin of the pelvic fin, with a total of 19 haemal arches (Fig. 4.8A, B). The haemal spines curve slightly posteriorly, a feature also noted in *Everticauda pavoidea*. Both the haemal and neural spine lengths decrease quickly once they articulate with the radials of the caudal fin. No ossified ribs are preserved, though several Triassic coelacanths such as *Diplurus newarki* Bryant, 1934, and *Chinlea sorenseni* Schaeffer, 1967, do preserve them.

The caudal fin on the holotype is symmetrical, with the dorsal and ventral radials inserting approximately opposite each other (Fig. 4.8). There are 15–16 dorsal and 14–15 ventral fin rays in the caudal fin. In coelacanths, it is common for the dorsal lobe to have 1–3 more fin rays than the ventral lobe. The posterior margin of the caudal fin is rounded; this is the typical caudal fin shape in coelacanths, unlike that in *E. pavoidea* or *R. divaricerca*. The caudal fin in *Wapitia robusta* makes up approximately one-third of the entire body length (skull to tip of caudal fin). The supplementary lobe is only partially preserved, but based on what is seen, it did not extend much past the posterior margin of the caudal fin.

The notochord (measured from neural to haemal arch) is 1.5 cm thick at the anterior end of the haemal arch series and 0.7 cm thick at the caudal fin. The depth of the notochord anterior to the haemal spines is unknown, though if it were similar to that of *Latimeria*, it would maintain the diameter attained at the anterior end of the haemal arch series.

A poorly preserved ossified ‘swim bladder’ (sb) is present in the holotype (Fig. 4.8A, B). It is relatively small, and extends only to the posterior margin of the pectoral fin. Very little structural detail can be made out.

Scales

The scales are best preserved on the holotype directly below the pectoral fin where they had begun to disarticulate (Fig. 4.9E). Additionally, two large isolated scales (UALVP 43604 and 43605) have been designated as paratypes.

The scales are covered in crowded ridges, which is a plesiomorphic feature (Forey, 1991; 1998). The scales on the holotype have nearly 40 ridges. The ridged portion of the scale is 1.2 cm wide. Paratype UALVP 43604 has an exposed area that is 1.8 cm wide and has approximately 24-25 ridges (Fig. 4.11A). The largest scale, paratype UALVP 43605, measures 2.2 cm and has 20–22 ridges (Fig. 4.11B). There is a reduction in the number of ridges as the scales increase in size. It appears that some of the ridges have fused into wider ridges on this largest scale. These scales, particularly those on the holotype (Fig. 4.9E), are nearly identical to scales described from the Upper Triassic Pardonet Formation in British Columbia, Canada (Yabumoto and Neuman, 2004:figs. 1, 2). The Pardonet scales were attributed to a possible new occurrence of the European coelacanth *Garnbergia* (Martin and Wenz, 1984), but it is possible that they represent a second occurrence of *W. robusta.*

PHYLOGENETIC ANALYSIS

Analytical Methods

The taxon-character matrix from Wendruff and Wilson (in review; Chapter 2) and Wendruff and Wilson (Chapter 3) was ultimately based on Forey's (1998) taxon-character matrix. Forey (1998) used 24 ingroup and 2 outgroup taxa and 108 characters. Friedman and Coates (2006) added character 109 (presence or absence of ventral keel scales). Wendruff and Wilson (in review; Chapter 2) added the new taxon *Rebellatrix* and included *Holopterygius* (Friedman and Coates, 2006), *Swenzia* (Clément, 2005, 2006) and *Panaibaia* (Yabumoto, 2008). Wendruff and Wilson (Chapter 3) also added two new species of *Whiteia*, *W. lepta* and *W. durabilis,* to Forey's (1998) original matrix. *Piveteauia* was re-evaluated in Chapter 3 based on Lehman (1952) and Clément (1999) as there were numerous miscodings in Geng et al. (2009). Additionally, character 107, presence or absence of an ossified 'swim bladder' is excluded for reasons noted in Chapter 3.

The two new taxa described above, *Everticauda pavoidea* and *Wapitia robusta* are added to this modified taxon-character matrix (Appendix IV). The final data set includes 33 taxa and 109 characters. Cladograms were produced using PAUP version 4.0 b10 (Swofford, 2002) employing heuristic search with TBR and 100 random-addition-sequence replicates to yield a maximum-parsimony solution. Characters were unweighted and unordered. Character state changes were examined using Acctran character state optimization in MacClade (Maddison and Maddison, 2005).

Results

Maximum-parsimony analysis yielded 30 most-parsimonious trees of 251 steps (CI = 0.450, RI = 0.701, HI = 0.550). The 50% majority rule tree has a polytomy among *Wapitia, Rebellatrix*, and the Latimerioidei. Additionally, better resolution is achieved within the Latimerioidei in comparison with results of Clément (2005), although *Diplurus*, *Libys*, and *Garnbergia* were resolved as successive sister taxa to the Latimeriidae. Forey (1998) resolved *Libys* and *Garnbergia* within the Mawsoniidae; however, he noted that this was likely due to convergence and missing information. Clément (2005) noted that both *Garnbergia* and *Libys* had an indeterminate position within the Latimerioidei.

Additionally, the utility of some characters within the original character-taxon matrix of Forey (1998) was tested (continuation from Chapter 3). The deletion of two additional post-cranial characters (character 98, presence or absence of denticles on the anterior dorsal fin, and character 105, single or multiple pores in lateral line canals), yields 26 trees and a length of 245 (CI = 0.453, RI = 0.700 and HI = 0.547) (Fig. 4.12). Character 98, while useful in diagnosing a species, appears to be highly homoplastic among coelacanths likely due to preservational bias. The denticles are not discernable on coelacanths from the Sulphur Mountain Formation unless the specimens have been acid prepared. It is possible that incomplete information about specimens from localities with similar preservation will bias the character states of this feature. Character 105 is only coded for 13 out of 33 coelacanths in the character-taxon matrix and in our current state of knowledge is not phylogenetically useful.

Eleven synapomorphies support the clade consisting of (*Everticauda* + (Whiteiidae + (*Wapitia* + *Rebellatrix* + Latimerioidei))): characters 1, 8, 36, 53, 59, 71, 76–78, 82 and 86. Of these 11 characters, only character one is coded in *Everticauda* (intracranial joint margin straight) (Forey, 1998). The synapomorphy that excludes *Everticauda* from the clade (Whiteiidae + (*Wapitia* + *Rebellatrix* + Latimerioidei))) is character 57: simple [0], or hooked dentary [1] (Forey, 1998).

Wapitia robusta forms a polytomy with *R. divaricerca* and the Latimerioidei; this polytomy is held together by 9 synapomorphies: characters 5, 6, 10, 13, 32, 35, 48, 51 and 91. *Wapitia* is only coded for character 91: occipital neural arches expanded (Forey, 1998). This synapomorphy supports this clade in all most-parsimonious topologies. *Wapitia robusta* is excluded from the Latimerioidei based on a single character: ten or more anterior dorsal fin rays (character 96) (Forey, 1998).

Discussion

In Wendruff and Wilson (in review; Chapter 2; Chapter 3), a phylogenetic analysis produced a polytomy within the Latimerioidei among (*Chinlea* (*Parnaibaia* (*Mawsonia* + *Axelrodichthys*))), (*Diplurus* + *Lybis* (Latimeriidae)) and *Garnbergia*. In this new analysis, the 50% majority rule consensus resolves the interrelationships of latimerioid taxa. The Latimerioidei consist of (*Chinlea* (*Parnaibaia* (*Mawsonia* + *Axelrodichthys*))) + (Garnbergia + (*Diplurus* + *Lybis* (Latimeriidae))).

Of the nine synapomorphies that support the polytomy among *Wapitia*, *Rebellatrix* and the Latimerioidei, a single character, presence of expanded neural arches (character 91) is preserved on the specimens of *W. robusta*. Forey (1998) discussed that this feature is only found in the most derived coelacanths (Latimerioidei). Prior to the addition of *W. robusta* and *R. divaricerca*, only the Latimerioidei, the Laugiidae and *Polyosteorhynchus* had expanded neural arches; however, the presence of this feature in the distantly related *Polyosteorhynchus* and Laugiidae may render this feature homoplastic.

A single synapomorphy supports the Latimerioidei: 8–9 fin rays in the anterior dorsal fin (character 96). The Latimeriidae, comprising the most derived coelacanths such as *Macropoma*, *Swenzia* and *Latimeria* (Berg, 1940; Forey, 1998; Clément, 2005), have a reduction in its anterior dorsal fin rays further to fewer than eight (Forey, 1998). In more basal coelacanths, the number of fin rays in the anterior dorsal fin (character 96); the most plesiomorphic coelacanths, such as *Miguashaia* and *Allenypterus*, have at least 18 fin rays (Melton, 1969; Schultze, 1973; Lund and Lund, 1984, 1985; Forey, 1998). *Laugia* and the Whiteiidae possess unusually high and low fin ray counts, respectively, compared to the general trend of reduction in the number of anterior dorsal fin rays. It was noted in Chapter 3 that there are miscodings within the Whiteiidae that need to be resolved as both *W. woodwardi* and *W. lepta* have 7–8 rays (coding of 1 or 2) and *W. neilseni* has nine anterior dorsal fin rays (coding of 1). Further complicating this issue is the fact that Forey (1998) used the genus *Whiteia* as a terminal taxon and did not account for intraspecific variation in this feature, which is now apparent.

Everticauda pavoidea was resolved within the clade (*Everticauda* + (Whiteiidae [as defined in Chapter 3) + (*Wapitia* + *Rebellatrix* + Latimerioidei))). Eleven synapomorphies support this clade, although only character 1 (straight intracranial margin) can be coded for *E. pavoidea.* Forey (1998) noted that a straight intracranial margin is likely the plesiomorphic condition with respect to porolepiforms. The intracranial joint is straight in most coelacanths, undergoing reversals in *Sassenia*, *Rhabdoderma* and *Caridosuctor*, *Spermatodus*, *Mawsonia* and *Axelrodichthys* and *Holophagus* (though straight in *Latimeria*). No functional significance is known for these changes in the intracranial joint. *Everticauda* is excluded from (Whiteiidae + (*Wapitia* + *Rebellatrix* + Latimerioidei) by a single character: a simple dentary lacking a posterior hooked process (character 57). The presence of a posterodorsal hook on the dentary has been noted by numerous authors (Martin and Wenz, 1984; Cloutier, 19991; Forey, 1991, 1998) as a derived feature of coelacanths. It is first found in the Lower Triassic Whiteiidae (*W. africana*, *W. durabilis*, *W. lepta*, *W. neilseni*, *W. tuberculata* and *W. woodwardi)* and continues through to the extant *Latimeria*. A single reversal in this feature, to a simple unhooked dentary, has been noted in *Diplurus* (Forey, 1991, 1998).

DISCUSSION

Forey (1998) diagnosed the Coelacanthiformes based on several neurocranial characteristics, none of which are preserved on *Everticauda pavoidea* and *Wapitia robusta*. The more derived Latimerioidei are characterized by a postparietal shield that is shorter than the parietonasal shield, by denticles on the anterior dorsal and caudal fins, and by an unfused retroarticular and articular (Forey, 1998). *Everticauda pavoidea* has denticles on anterior dorsal and caudal fins and *W. robusta* has a postparietal shield that is shorter than the parietonasal shield (though this feature is also present within the Whiteiidae); none of the other characteristic features is present on any of the specimens. Both *E. pavoidea* and *W. robusta* exhibit a reversal in the number of anterior dorsal fin rays, possessing 10 or more fin rays. All taxa within the Latimerioidei have 8–9, whereas other members of the Latimeriidae possess fewer than eight anterior dorsal fin rays (Forey, 1991, 1998). As the Latimerioidei are also characterized by a reduction in these fin rays, both new taxa are clearly excluded from this suborder.

Everticauda pavoidea and *W. robusta* are both relatively deep-bodied coelacanths, especially in contrast to *W. lepta* (Chapter 3) and *R. divaricerca* (Wendruff and Wilson, in review; Chapter 2), both from the Sulphur Mountain Formation, which are very slender. A number of similarities between *E. pavoidea* and *W. robusta* are apparent, though as the skulls of both are poorly preserved, no skull features are comparable. As such, comparisons were limited to post-cranial features. Both new coelacanths have 10 or more anterior dorsal fin rays. Such high counts are traditionally thought of as a plesiomorphic feature because it is present in the earliest coelacanths such as *Miguashaia, Allenypterus, Caridosuctor, Hadronector* and *Lochmocercus* and *Gavinia* (Melton, 1969; Schultze, 1973; Lund and Lund, 1984, 1985; Long, 1999; Forey, 1998). The fin positions of *E. pavoidea* and *W. robusta* are nearly identical to each other: anterior dorsal fins are located directly posterior to the pectoral girdle; posterior dorsal and anal fins are opposite each other with the anal fin set slightly more posteriorly; pectoral fins are directly below the anterior dorsal basal plates; pelvic fins are ventral to the posterior dorsal basal plate.

The skulls of the coelacanths from the Sulphur Mountain Formation are rarely preserved undistorted and uncrushed. Commonly, the cheek bones are not preserved, but the less informative palate is usually preserved. Additionally, few sensory pores, pit lines and canals are preserved on these specimens. Even though the skulls of these two new species have better than average skull preservation for the formation, extensive comparisons between the two new taxa is not possible at this time; however, *E. pavoidea* and *W. robusta* differ in a vast number of morphological post-cranial features: occipital neural arches, pelvic girdle shape and position, posterior dorsal basal plate. Additionally, they differ greatly in the shape and form of the anterior dorsal and caudal fins.

The occipital neural arches are anteroposteriorly expanded in *W. robusta*, but not in *E. pavoidea*. This expansion of these elements was considered by Forey (1991, 1998) as a derived feature because previously it was only found in the Latimerioidei. The position of the pelvic girdle in *E. pavoidea* is farther anterior than in *W. robusta*, and most similar in the position to that in smaller specimens of *Laugia* (before the pelvic girdle articulates/fuses with the pectoral girdle) (Stensiö, 1932; Forey, 1998). While both *W. robusta* and *E. pavoidea* have pectoral girdles with two anterior and two posterior processes, the overall morphological features differ between them.

The posterior dorsal basal plates vary from species to species (pers. obs). The posterior dorsal basal plate of *E. pavoidea* has a semi-circular distal end, whereas that of *W. robusta* has a squared-off distal end. A small process extends anteriorly from the semi-circle, whereas a larger rod-like process is found on *W. robusta*. The varying shapes in the basal plate among species of coelacanths likely indicate changes in function, though at this time these are unknown.

While the fin positions are very similar between *E. pavoidea* and *W. robusta*, the body shapes are very different. *Everticauda pavoidea* (holotype) has a truncated body that is 20% deeper than that of *W. robusta* (holotype). The anterior dorsal and caudal fins display the greatest disparity of morphological form between the two species. Both coelacanths have long anterior dorsal fins that are situated farther anteriorly than in most coelacanths; however, *E. pavoidea* has a significantly larger fin proportionally to its body. On the holotype of *E.*

pavoidea, the anterior dorsal fin nearly touches the posterior dorsal fin, whereas on *W. robusta* it only extends back to the posterior margin of the posterior dorsal basal plate. The overall shape of the caudal fin of *W. robusta* is what can be considered the ‘typical’ coelacanth tail form. Conversely, the caudal fin of *E. pavoidea* is extraordinarily unusual, marking the second novel form of coelacanth tail from the Sulphur Mountain Formation, the first being a high-aspect-ratio forked tail (Wendruff and Wilson, in review; Chapter 2). The caudal fin of coelacanths consists of a dorsal and ventral (principal) lobe, and between those two lobes, a flag-like fin called the supplementary lobe. In *E. pavoidea,* the principal lobes extend farther posteriorly than the supplementary lobe, at least twice the length of the supplementary lobe. Additionally, the unsegmented caudal rays are reduced yielding a tail comprised mostly of highly segmented fin rays. Though a complete adult specimen is currently unknown, it is possible that the caudal fin comprised nearly half the body length. This configuration may have created a highly flexible caudal fin analogous to that of the modern male Paradisefish, *Macropodus opercularis* (Linneaus, 1758).

Ontogenetic Features

Ontogenetic variation in fossil coelacanths is poorly known, but it is poorly known in *Latimeria* as well (Balon et al, 1988; Forey, 1990). Comparisons were made between the ‘juvenile’ paratype of *E. pavoidea* and the larger ‘adult’ holotype specimen. The holotype of *E. pavoidea* has a length of 28 cm from the pectoral girdle to the base of the supplementary lobe, whereas paratype UALVP 46608 has a length of 12.5 cm. There are no specimens intermediate in size between these two, meaning no growth series is known. There is an obvious increase in body depth from the ‘juvenile’ to ‘adult’. The holotype (‘adult’) is 13 cm deep from the anterior dorsal fin to the midpoint of the pelvic girdle, whereas paratype UALVP 46608 (‘juvenile’) is 4.5 cm deep (measured from the anterior dorsal fin to the pelvic fin). Comparing the depth to the length of the fish, the holotype is half as deep as it is long (50%), whereas the juvenile is slightly over one-third as deep as it is long (36%). This denotes a major increase in the depth of the fish through development. The extended anterior dorsal fin is another unique feature of *Everticauda pavoidea*, most noticeable in the holotype specimen (Fig. 4.1). The fin is 12.5 cm long in the holotype and 3.8 cm long in the juvenile paratype. Both body depth and anterior dorsal fin ray length are positively allometric through ontogenetic development. In life, the anterior dorsal fin likely would have been a huge sail-like fin similar to that of *Latimeria chalumnae* (Smith, 1939, Fricke et al., 1987; Uyeno, 1991; Fricke and Hissmann, 1992). Whether this feature of *E. pavoidea* is strictly ontogenetic or perhaps sexually dimorphic (sexual display) cannot be determined until a greater sample size of material is found.

Ontogenetic variation has been noted by numerous authors in relation to supplementary lobe length of the Pennsylvanian coelacanth *Rhabdoderma elegans*

Newberry, 1956 (see also Eastman, 1902; Schultze, 1972, 1980; Cloutier, 2010). Scultze (1972, 1980) and Cloutier (2010) argued that a long supplementary lobe was present on specimens deemed ‘embryonic’ and ‘juvenile’, though it was proportionally smaller on larger specimens (negatively allometric). This is one of the few recorded ontogenetic variations in fossil coelacanths. Unfortunately, no comparisons could be made with the caudal fin of *E. pavoidea*, as the ‘juvenile’ specimen has an incomplete caudal fin.

Forey (1998) demonstrated ontogenetic variation in the angular of *Laugia groenlandica* (Stensiö, 1921; Forey, 1998). He noted an inverse relationship in size of pores and a direct relationship in the number of pores through development. The angular of the smallest specimen of *Laugia groenlandica* has 8–9 large pores, whereas the largest specimen has 31 small pores across the angular (Forey, 1998:fig. 5.6a–e). Millot and Anthony (1952, 1965) showed this same trend in juvenile and adult specimens of *Latimeria chalumnae*. Additionally, the shape of the pores changes in the specimens of *Laugia groenlandica* from an elongated oval in the smallest specimens to rounded pores in the largest specimens (presumably adults) (Forey, 1998:fig. 5.6a–e). The lower jaw of *E. pavoidea* as preserved on paratype UALVP 46608 has 7–8 large, elongated mandibular sensory pores (Figs. 4.2B, 4.3). If the lower jaw of *E. pavoidea* follows the same pattern noted in *Latimeria chalumnae* and *Laugia groenlandica*, then these features indicate that paratype UALVP 46608 is a juvenile.

CONCLUSION

Everticauda pavoidea and *Wapitia robusta* represent two distinctly different deep-bodied coelacanths from the Sulphur Mountain Formation (Wapiti Lake). Though, similarities are apparent ion body-depth, fin ray counts and paired fin positions, numerous differences were discussed particularly in reference to the anterior dorsal and caudal fins. Additionally, ontogenetic variations present between ‘juvenile’ and ‘adult’ specimens of *E. pavoidea* are related to body depth and length as well as the mandibular sensory canal in the lower jaw. These two new genera add to both the species and morphological diversity of the Sulphur Mountain Formation as well as to the diversity of coelacanths globally in the Lower Triassic.

LITERATURE CITED

Agassiz, L. 1835. Recherches sur les Poissons Fossiles. Vol. II. 4th Livraison. Feuilleton, pp. 35–64. Neuchâtel.

Agassiz, L. 1839. Recherches sur les Poissons Fossiles. Vol. 2. Neuchâtel.

Alexander, R. McN. 1973. Jaw mechanisms of the coelacanth *Latimeria chalumnae*. Copeia 1973:156–158.

Berg, L. 1940. Classification of fishes, both recent and fossil. Trudy Zoologicheskogo Instituta, Akademiya Nauk SSSR 5:1–141.

Bryant, W. L. 1934. New fishes from the Triassic of Pennsylvania. Proceedings of the American Philosophical Society, Philadelphia 73:319–326.

Cavin, L., P. L. Forey, E. Buffetaut and H. Tong. 2005. Latest European coelacanth shows Gondwanan affinities. Biology Letters 1:176–177.

Clément, G. 1999. The Actinistian (Sarcopterygii) *Piveteauia madagascariensis* Lehman from the Lower Triassic of Northwestern Madagascar: A redescription on the basis of new material. Journal of Vertebrate Paleontology 19(2):234–242.

Clément, G. 2005. A new coelacanth (Actinistia, Sarcopterygii) from the Jurassic of France and the question of the closest relative fossil [sic] to *Latimeria*. Journal of Vertebrate Paleontology 25(3):481–491.

Clément, G. 2006. *Swenzia*, n. nov., a replacement name for the preoccupied coelacanth genus *Wenzia* Clément, 2005. Journal of Vertebrate Paleontology 26:461.

Cloutier, R. 1991. Patterns, trends and rates of evolution within the Actinistia. Environmental Biology of Fishes 32:23–58.

Eaton, T. H., Jr. 1945. The symplectic in coelacanthids and actinopteri. Copeia 1945:22–25.

Egerton, P. 1861. *Holophagus gulo*. In Huxley, T. H., Preliminary essay upon the systematic arrangement of the fishes of the Devonian epoch. Memoirs of the Geological survey of the United Kingdom 10:1–40.

Forey, P. L. 1981. The coelacanth *Rhabdoderma* in the Carboniferous of the British Isles. Palaeontology 24:203–229.

Forey, P. L. 1991. *Latimeria chalumnae* and its pedigree. Environmental Biology of Fishes 32:75–97.

Forey, P. L. 1998. History of the coelacanth fishes. Chapman and Hall, London, 419 pp.

Forey, P. L., P. E. Ahlberg, E. Luksevics and I. Zupins. A new coelacanth from the Middle Devonian of Latvia. Journal of Vertebrate Paleontology 20(2):243–252.

Fricke, H., O. Reinicke, H. Hofer and W. Nachtigall. 1987. Locomotion of the coelacanth *Latimeria chalumnae* in its natural environment. Nature 329:331–333.

Fricke, H. and K. Hissmann. 1992. Locomotion, fin coordination and body form of the living coelacanth *Latimeria chalumnae*. Environmental Biology of Fishes 34:329–356.

Friedman, M., and M. I. Coates. 2006. A newly recognized fossil coelacanth highlights the early morphological diversification of the clade. Proceedings of the Royal Society B 273:245–250.

Geng, B.-H., M. Zhu and J. Fan. 2009. A revision and phylogenetic analysis of *Guizhoucoelacanthus* (Sarcopterygii, Actinistia) from the Triassic of China. Vertebrata Palasiatica 47:165–177.

Jessen. H. 1973. Weitere Fischreste aus dem Oberen Plattenkalk der Bergische-Gladbach-Paffrather Mulde (Oberdevon, Rheinisches Schiefergebirge). Palaeontographica A 143:159-187.

Lambers, P. H. 1991. The identity of the type specimen of *Coelacanthus harlemensis* Winkler (Pisces, Actinistia) from the lithographic limestone of Solnhofen (Tithonian), Bavaria. Paläontologische Zeitschrift 65:173–189.

Lehman, J. P. 1952. Etude complémentaire des poissons de l’Eotrias du Nord-Ouest de Madagascar. Kungliga Svenska Vetenskapsakademiens Handlingar 2:1–201.

Linnaeus, C. 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tenth ed. Vol. 1. Laurentii Salvii, Stockholm, 824 pp.

Liu, H. –T. 1964. A new coelacanth from the marine Lower Triassic of N. W. Kwangsi, China. Vertebrata Palasiatica 8:211–214.

Lund, R. and W. L. Lund. 1984. New genera and species of coelacanths from the Bear Gulch Limestone (Lower Carboniferous) of Montana (USA). Geobios 17:237–244.

Lund, R. and W. L. Lund. 1985. Coelacanths from Bear Gulch limestone (Namurian) of Montana and the evolution of Coelacanthiformes. Bulletin of the Carnegie Museum of Natural History 25:1–74.

Maddison, W. P. and D. R. Maddison. 2005. MacClade: Analysis of Phylogeny and Character Evolution, version 4.08. Sunderland, Massachusetts.

Maisey, J. G. 1986. Coelacanths from the Lower Cretaceous of Brazil. American Museum Novitiates 2866:1–30.

Mantell, G. 1822. The Fossils of the South Downs; or Illustrations of the Geology of Sussex. 327 pp., London: Lupton Relfe.

Martin, M. and S. Wenz. 1984. Découverte d’un nouveau Coelacanthidé, *Garnbergia ommata* n. gen., n. sp., dans le Muschelkalk supérieur du Baden-Württemberg. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) 105:1–17.

Melton, W. G. 1969. A new dorypterid fish from central Montana. Northwest Science, Cheney 43:196–206.

Millot, J and T. Anthony. 1958. Anatomie de *Latimeria chalumnae*. 1. Squellette et muscles. 122 pp., Paris: C.N.R.S.

Millot, J. and T. Anthony. 1965. Anatomie de *Latimeria chalumnae.* II Systèm. Nerveux et Organes des Sens. 131 pp., Paris: C.N.R.S.

Moy-Thomas J. A. 1935. The coelacanth fishes from Madagascar. Geology Magazine 72:213–227.

Moy-Thomas, J. A. and T. S. Westoll. 1935. On the Permian coelacanth, *Coelacanthus granulatus*, Ag. Geological Magazine 72:446–457.

Münster, G. von. 1834. Mitteilungen an Professor Bronn gerichtet. Neues Jahrbuch für Mineralogie Geognosie. Geologie und Petrefakten-Kunde, Stuttgart 1834:538–542.

Münster, G. von. 1842. Beitrag zur Kenntniss einiger neuen seltenen Versteinerungen aus den lithographischen Schiefern in Baiern. Neues Jahrbuch für Mineralogie Geognosie. Geologie und Petrefakten-Kunde, Stuttgart 1842:35-46.

Newberry, J. S. 1856. Descriptions of several genera and species of fossil fish from Carboniferous strata of Ohio. Proceedings of the Academy of Natural Sciences Philadelphia 8:96–100.

Quenstedt, F. A. 1858. Der Jura. Tubingen. 823 pp.

Reis, O. M. 1888. Die Coelacanthinen, mit besonderer Berücksichtigung de rim Weissen Jura Bayerns vorkommednde Gattungen. Palaeontographica, Stuttgart 35(1):1–96.

Schaeffer, B. 1952. Rates of evolution in the coelacanth and dipnoan fishes. Evolution 6:101–111.

Schaeffer, B. 1967. Late Triassic fishes from the western United States. Bulletin of the American Museum of Natural History 135:285–342.

Schaumberg, G. 1978. Neubeschreiburg von *Coelacanthus granulates* Agassiz (Actinistia, Pisces) aus dem Kupferschiefer can Richelsdorf (Perm, W.–Deutschland). Paläontologische Zeitschrift, Stuttgart 52:169–197.

Schultze, H.-P. 1973. Crossopterygier mit heterozerker Schwanzflose aus dem Oberdevon Kanadas, Nebst einer Beschreibung von Onychodontida-Resten aus dem Mittledevon Spaniens und dem Karbon der USA. Palaeontographica 143A:188208.

Schultze, H.-P. 1993. Osteichthyes: Sarcopyerygii; pp. 657–663 in M. J. Benton (ed), The Fossil Record 2. Chapman and Halls, London.

Smith, J. L. B. 1939. A living fish of Mesozoic type. Nature 143:455–456.

Stensiö, E. 1921. Triassic fishes from Spitzbergen. Part. 1. Xxviii + 307 pp., Vienna: Adolf Holzhausen.

Stensiö, E. 1932. Triassic fishes from East Greenland collected by the Danish expedition 1929-1931. Meddelelser om Grønland 83(3):1–305.

Swofford, D. L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Tong, J., X. Zhou, D. H. Erwin, J. Zuo and L. Zhao. 2006. Fossil fishes from the Lower Triassic of Majiashan, Chaohu, Anhui Province, China. Journal of Paleontology 80(1):146–161.

Uyeno, T., 1991. Observations on locomotion and feeding of released coelacanths, *Latimeria chalumnae*. Environmental Biology of Fishes 32:267–273.

Woodward, A. S. 1910. On some Permo-Carboniferous fishes from Madagascar. Annals and Magazine of Natural History, London 5(8):1–6.

Yabumoto, Y. 2008. A new Mesozoic coelacanth from Brazil (Sarcopterygii, Actinistia). Paleontological Research 12:329–342.

Yabumoto Y. and A. Neuman. 2004. A coelacanth scale from the Upper Triassic Pardonet Formation, British Columbia, Canada. Paleontological Research 8(4):337–340.

FIGURE 4.1. *Everticauda pavoidea*, gen. et sp. nov. (holotype TMP 1983.206.185). **A**, specimen in left lateral view; **B**, outline drawing. **Abbreviations**: **A.b**, anal basal plate; **Cl**, cleithrum; **D1.b**, anterior dorsal basal plate; **D2.b**, posterior dorsal basal plate; **P.b**, pelvic bone; **sb**, swim bladder. Scale bar equals 10 cm (A–B).

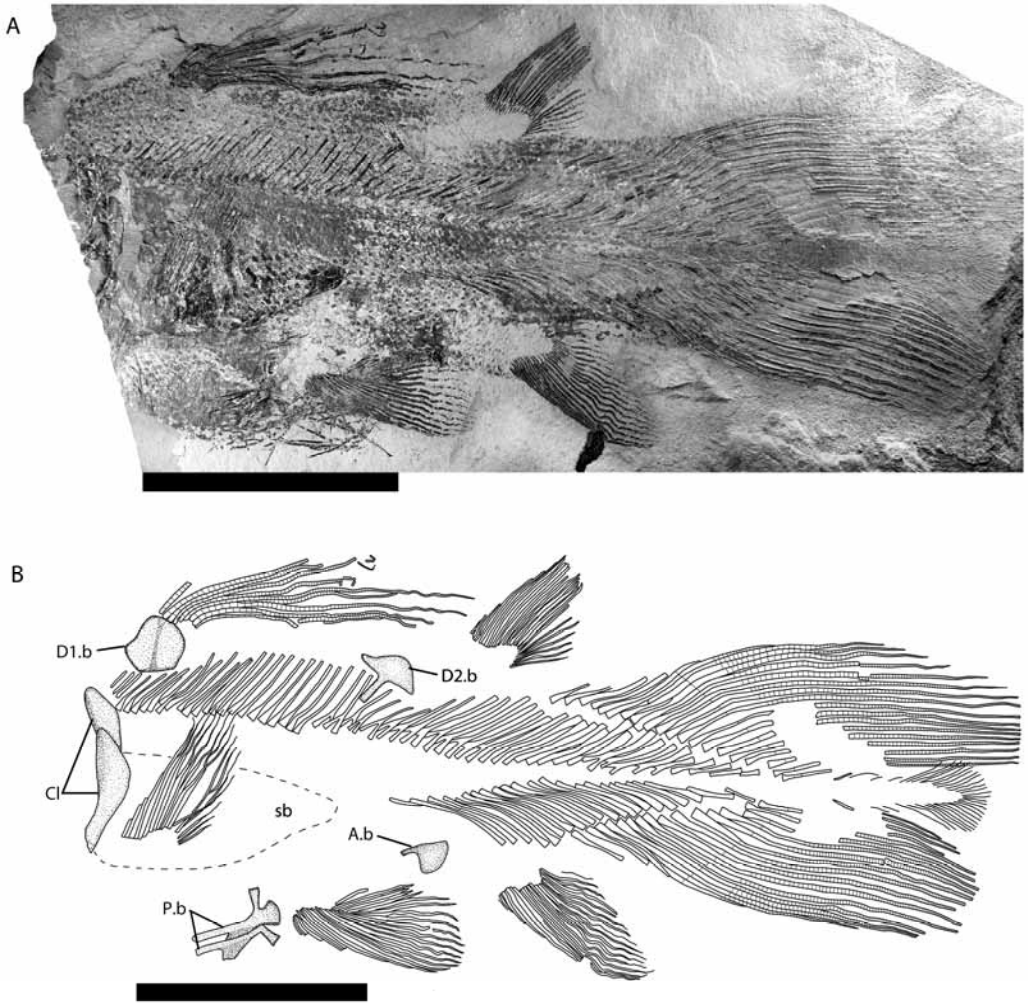
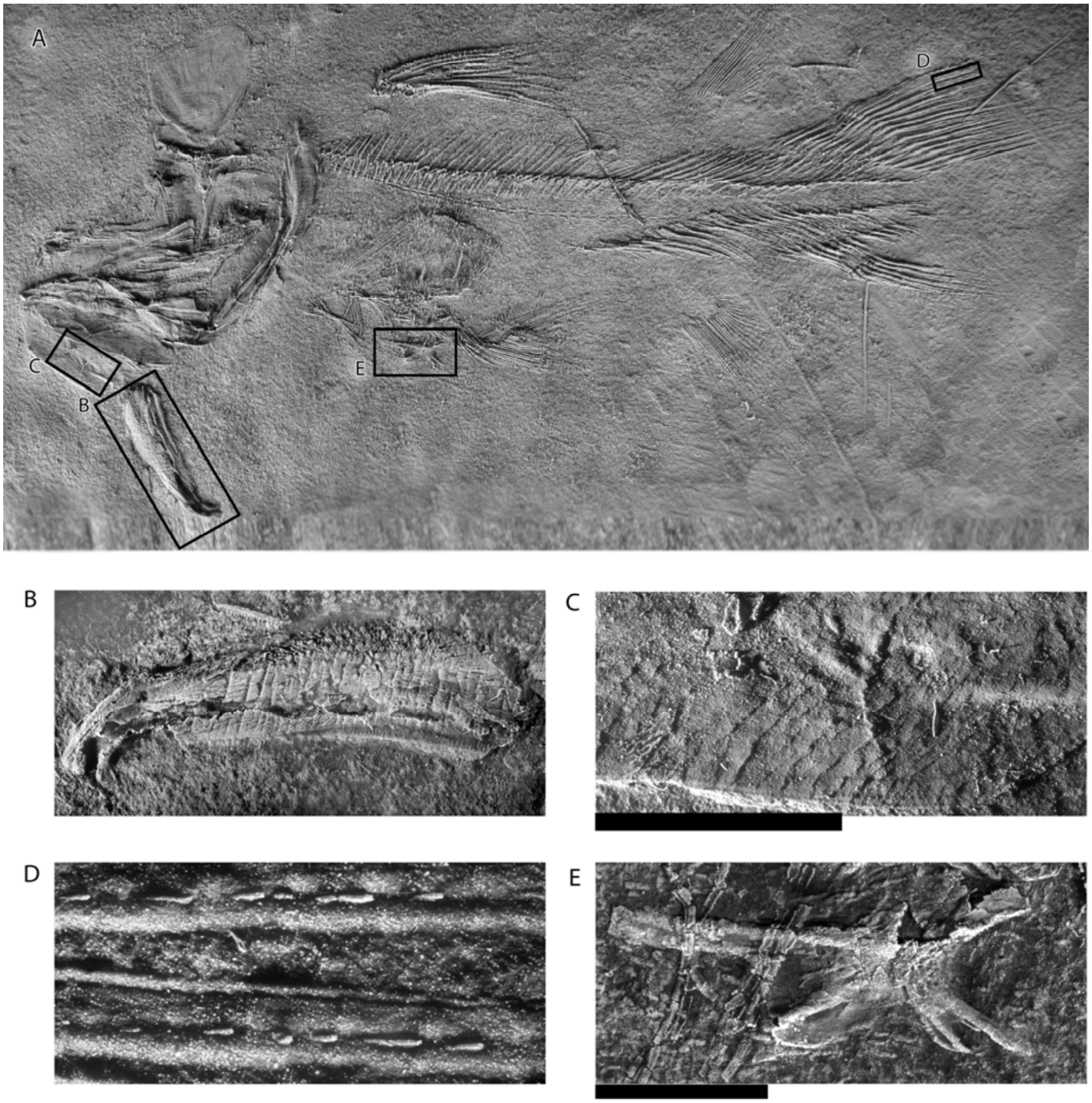

A
B
D1.b
D2.b
Cl
sb
A.b
P.b

FIGURE 4.2. *Everticauda pavoidea*, gen. et sp. nov. (paratype UALVP 46608). **A**, ammonium chloride dusted peel of complete specimen; **B**, displaced left lower jaw; **C**, close up of gular pit line on the gular plate; **D**, denticles on caudal fin rays; **E**, close up of left pelvic bone. Scale bar equals 5 cm (A); 3 cm (B); 5 mm (C–E).


A
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B
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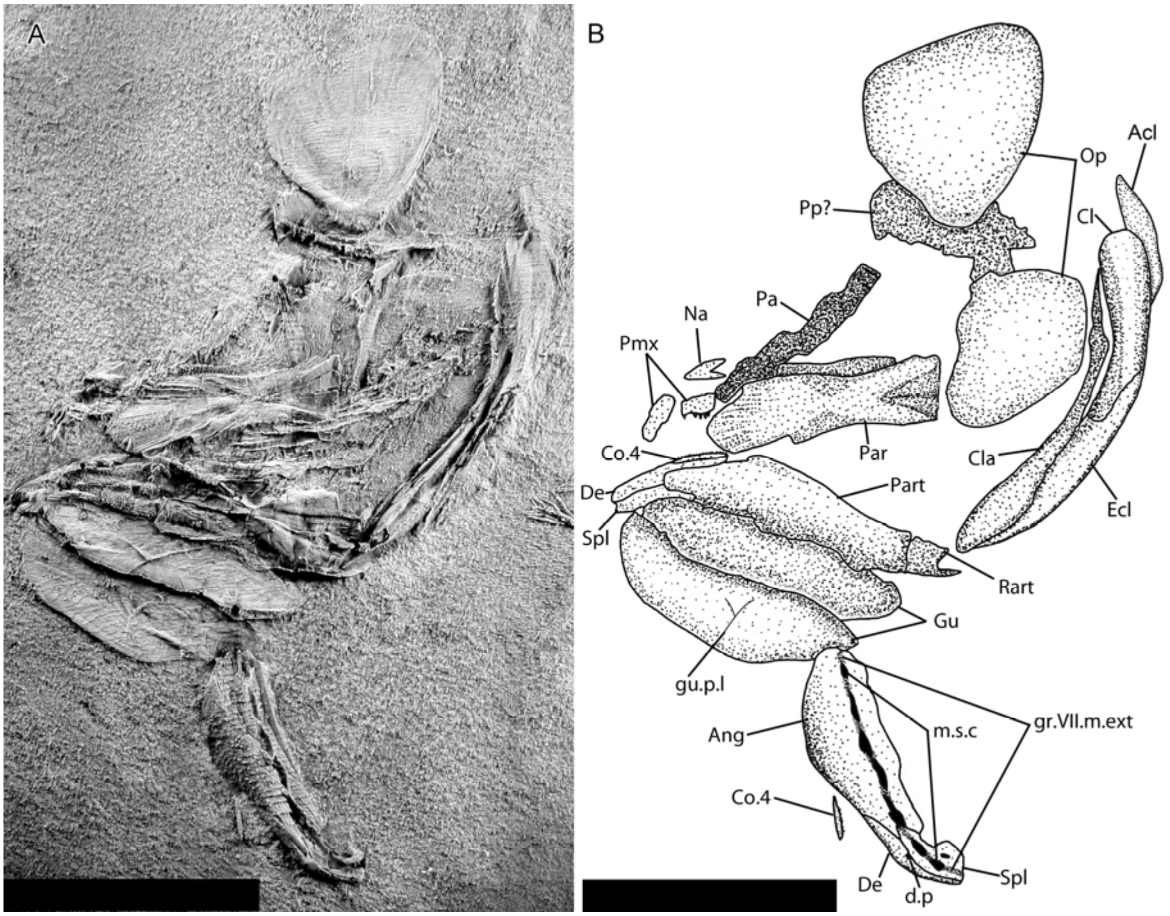
E

FIGURE 4.3. *Everticauda pavoidea*, gen. et sp. nov. (paratype UALVP 46608). **A**, close up of skull peel dusted with ammonium chloride; **B**, outline drawing of skull. **Abbreviations**: Acl, anocleithrum; **Ang**, angular; **Cl**, cleithrum; **Cla**, clavicle; **Co.4**, fourth coronoid; **De**, dentary; **d.p**, dentary pore; **Ecl**, extracleithrum; **Gu**, gular; **gu.p.l**, gular pit line; **gr.VII.m.ext**, groove for the external mandibular ramus of the facial nerve; **m.s.c**, mandibular sensory canal; **Na**, nasal; **Op**, operculum; **Pa**, parietal; **Par**, parasphenoid; **Part**, prearticular; **Pmx**, premaxilla; **Pp**, postparietal; **Rart**, retroarticular; **spl**, splenial. Scale bar equals 3 cm (A–B).


A
B
Op
Acl
Pp?
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Pmx
Co.4
Par
Cla
De
Part
Spl
Ecl
Rart
Gu
gu.p.l
m.s.c
gr.VII.m.ext
Ang
Co.4
De
d.p
Spl

FIGURE 4.4. *Everticauda pavoidea*, gen. et sp. nov. (paratype 43698). **A**, caudal fin in left lateral view; **B**, outline drawing of caudal fin. Scale bar equals 5 cm (A–B).

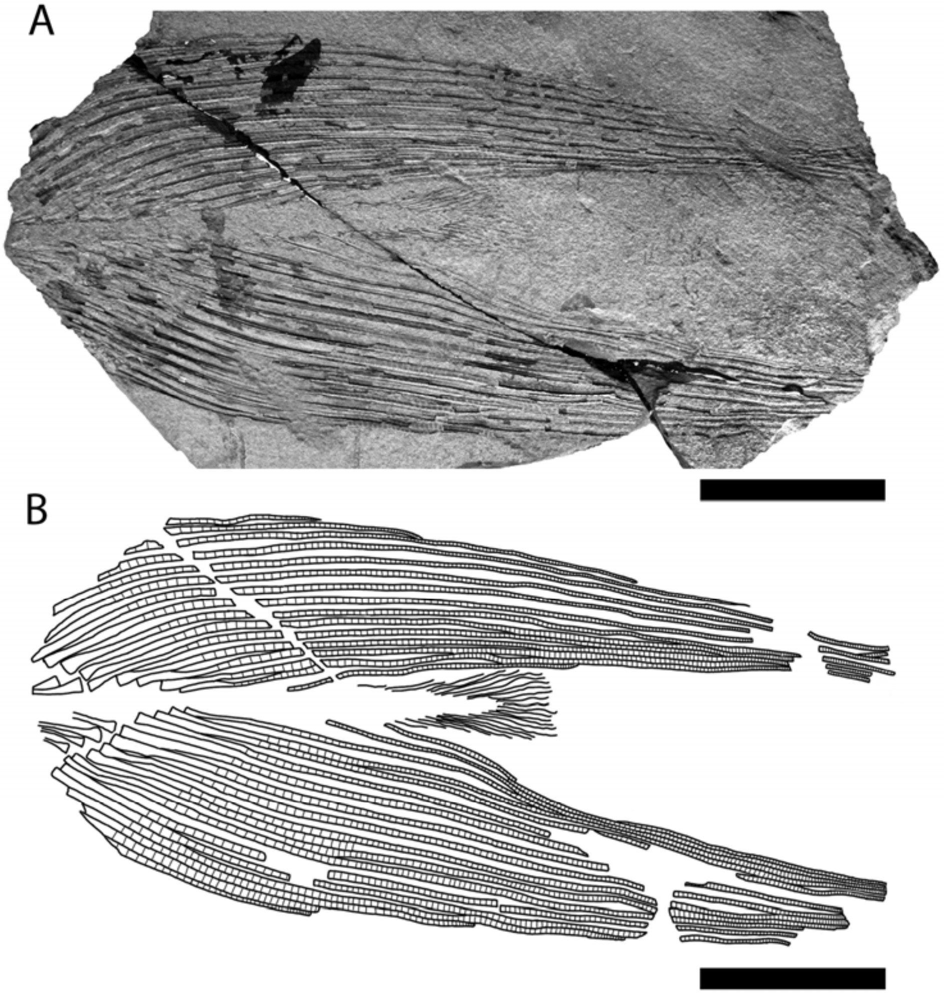

A
B

FIGURE 4.5. *Everitucada pavoidea*, gen. et sp. nov. (paratype UALVP 19237). **A**, partial specimen in left lateral view; **B**, pelvic girdle; **C**, posterior dorsal basal plate; **D**, anal basal plate. Scale bars equals 5 cm (A); 2 cm (B–D).

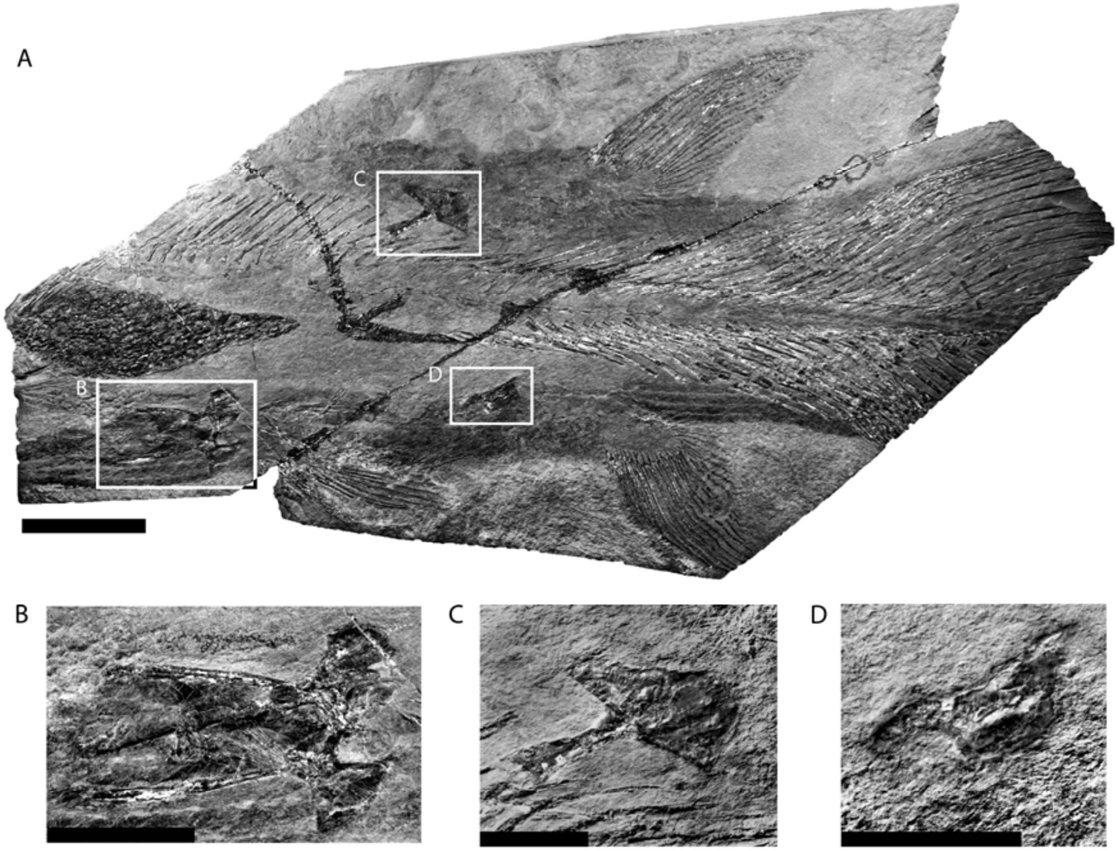

A
B
C
D
B
C
D

FIGURE 4.6. *Everticauda pavoidea*, gen. et sp. nov. (paratype TMP 1983.206.185), partial specimen in left lateral view with well preserved tapered posterior dorsal and anal fins. Scale bar equals 5 cm.

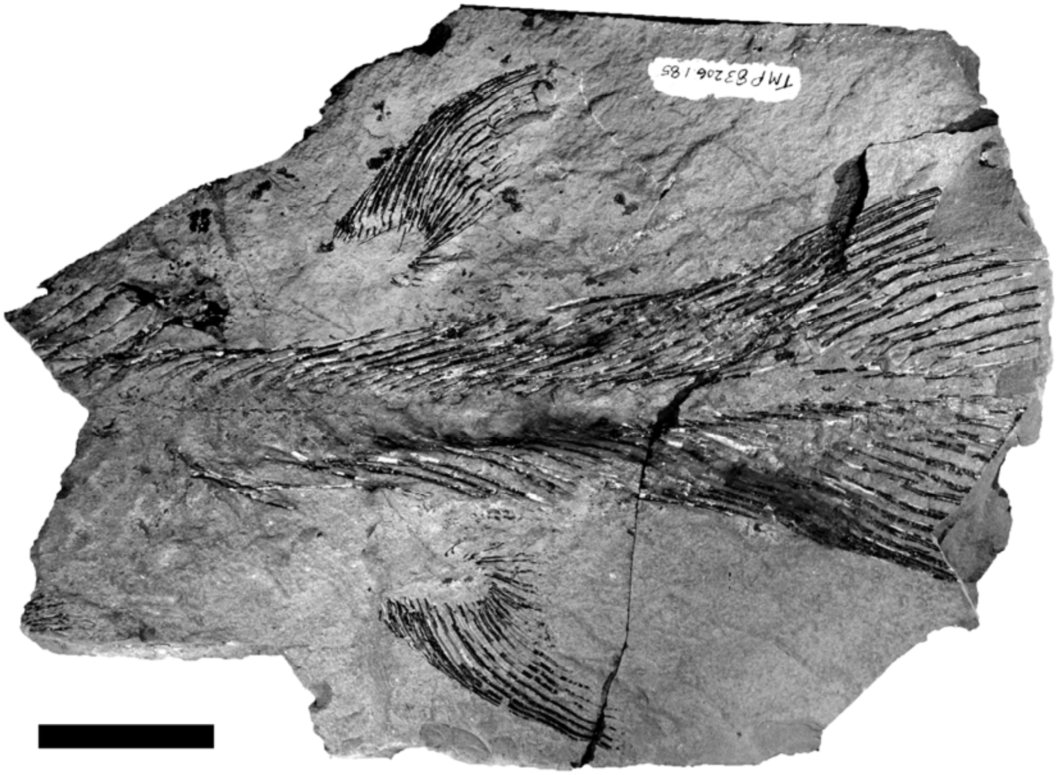

TMP 83.206.185

FIGURE 4.7. *Everticauda pavoidea*, gen. et sp. nov. (paratype PRPRC 2008.04.156). **A**, posterior dorsal basal plate; **B**, isolated scale on same specimen. Scale bar equals 2 cm (A); 5 mm (B).

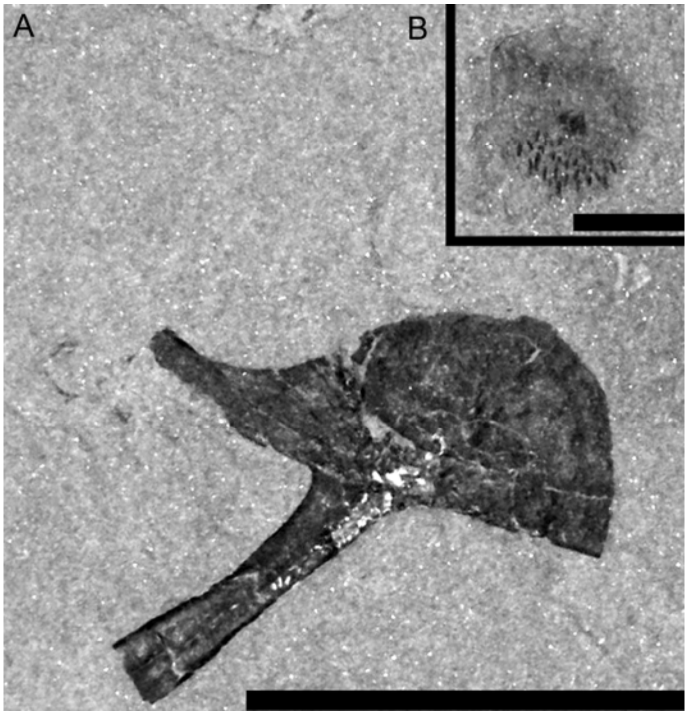

A
B

FIGURE 4.8. *Wapitia robusta*, gen. et sp. nov. (holotype UALVP 24228). **A**, complete specimen in left lateral view; **B**, outline drawing of complete specimen. **Abbreviations**: **D1.b**, anterior dorsal basal plate; **D2.b**, posterior dorsal basal plate; **P.b**, pelvic bone; **sb**, ‘swim bladder’. Scale bar equals 5 cm (A–B).

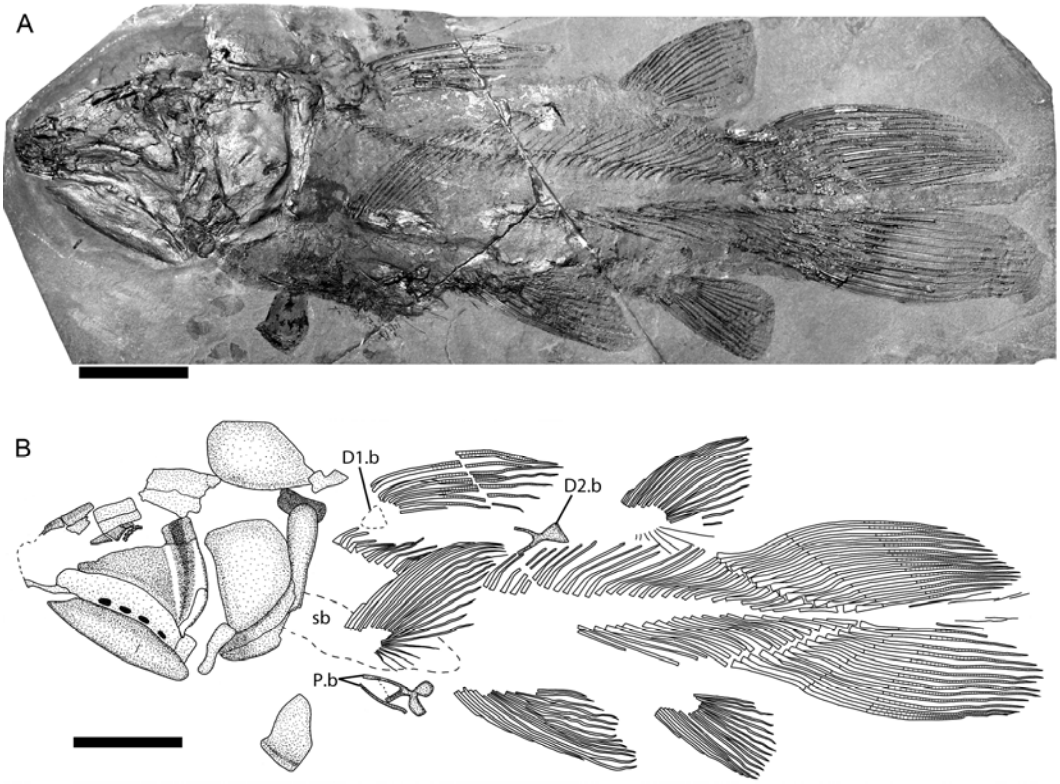

A
B
D1.b
D2.b
sb
P.b

FIGURE 4.9. *Wapitia robusta*, gen. et sp. nov. (holotype UALVP 24228). **A**, close up of skull; **B**, outline drawing of skull; **C**, close up of ammonium chloride dusted postparietals; **D**, close up of ammonium chloride dusted gular plate; **E**, close up of ammonium chloride dusted isolated scale (image rotated). **Abbreviations**: **Acl**, anocleithrum; **Ang,** angular; **Cl**, cleithrum; **Cla**, clavicle; **Ecl**, extracleithrum; **Gu**, gular; **gu.p.l**, gular pit line; **Mpt**, metapterygoid; **m.s.c**, mandibular sensory canal; **Na**, nasal; **Op**, operculum; **Pa**, parietal; **Pop**, preoperculum; **pop.s.c**, preopercular sensory canal; **Pp**, postparietal; **Pt**, pterygoid; **Q**, quadrate; **Rart**, retroarticular; **So**, supraorbital; **S.o**, sclerotic ossicles; **Spl**, splenial; **Sy**, symplectic; **?**, unknown. Scale bar equals 5 cm (A–B); 1 cm (C–E).

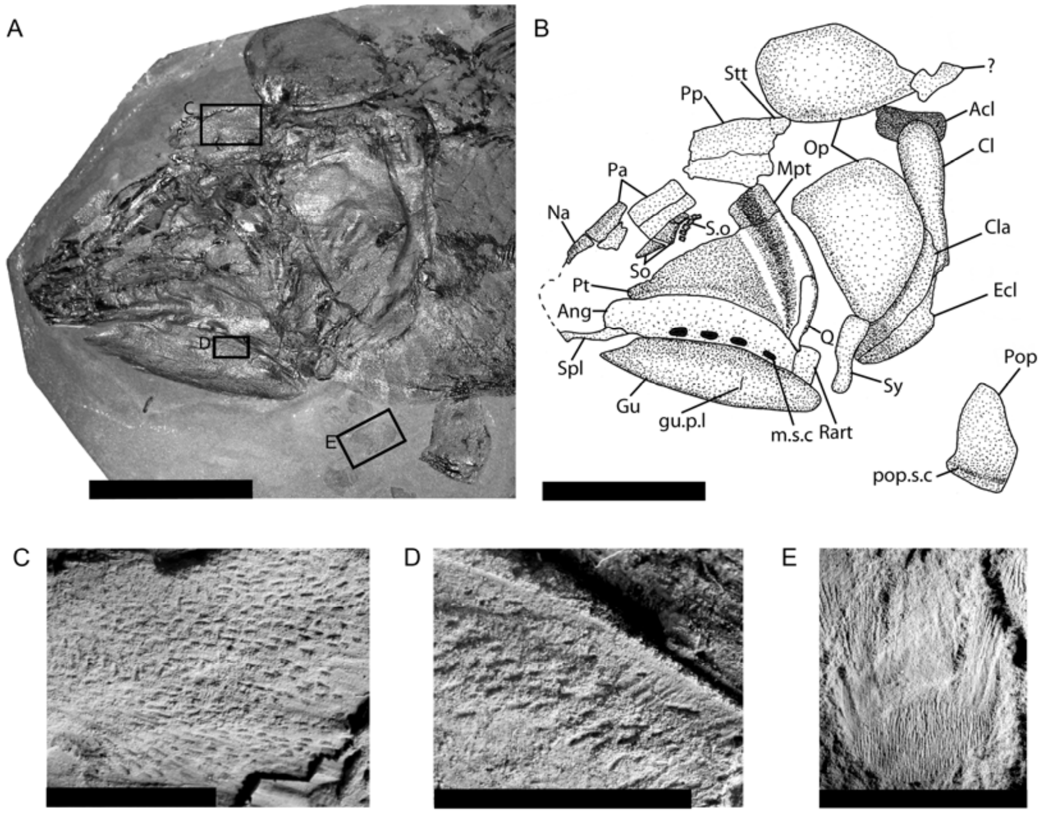

A
C
D
E
B
Stt
Pp
?
Acl
Cl
Op
Mpt
Pa
Na
S.o
So
Cla
Pt
Ang
Ecl
Q
Spl
Sy
Pop
Gu
gu.p.l
m.s.c
Rart
pop.s.c
C
D
E

FIGURE 4.10. *Wapitia robusta*, gen. et sp. nov. (paratype PRPRC 2008.04.110), isolated posterior dorsal basal plate. Scale bar equals 2 cm.

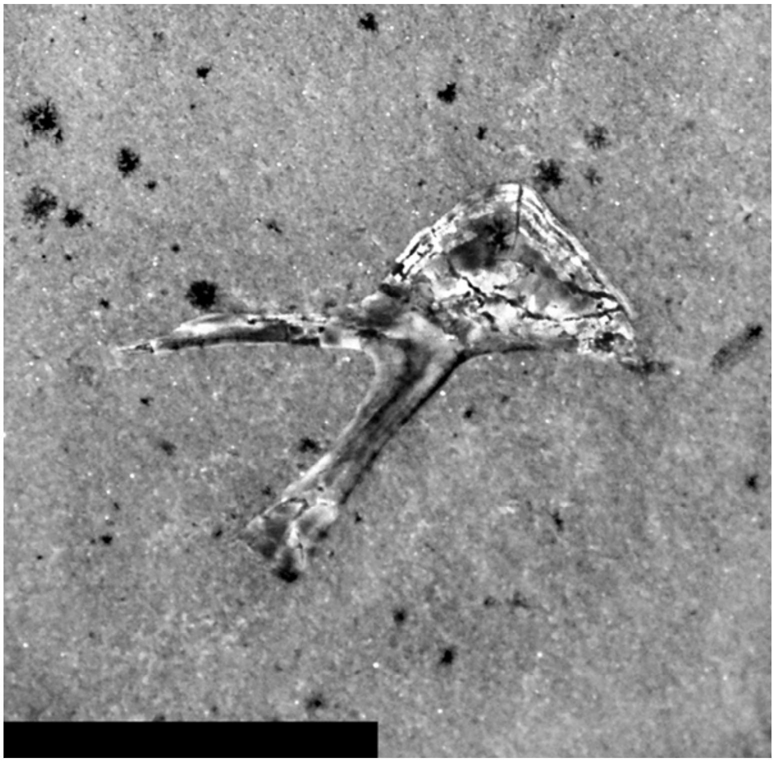


FIGURE 4.11. *Wapitia robusta*, gen. et sp. nov. scales. **A**, ammonium chloride coated isolated scale (UALVP 43604); **B**, ammonium chloride coated isolated scale (UALVP 43605). Scale bar equals 2 cm.

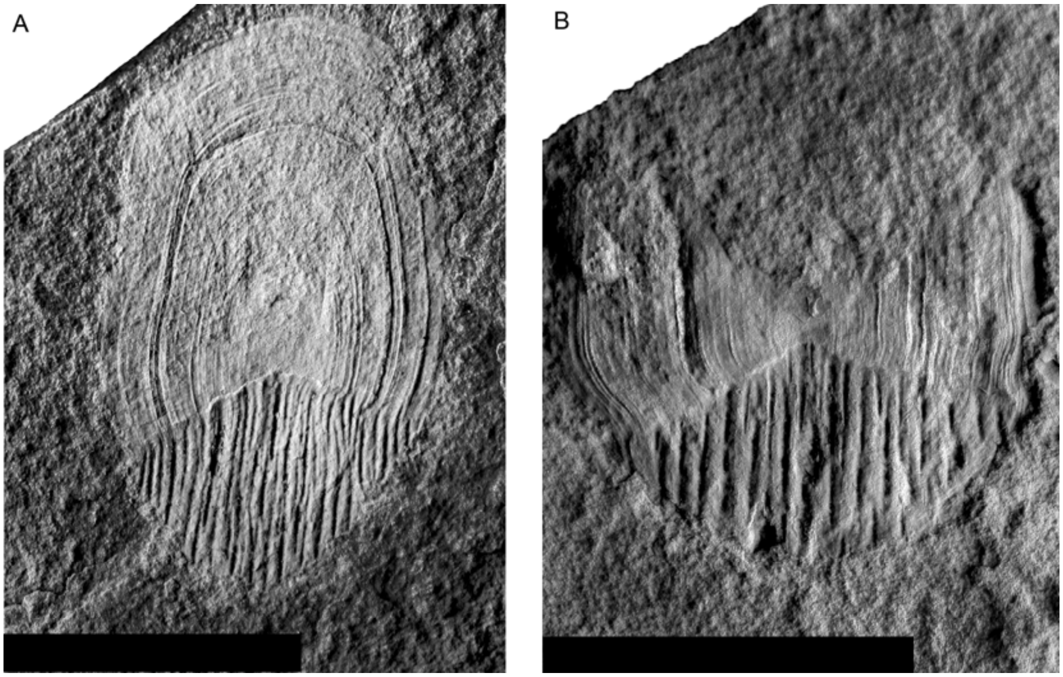
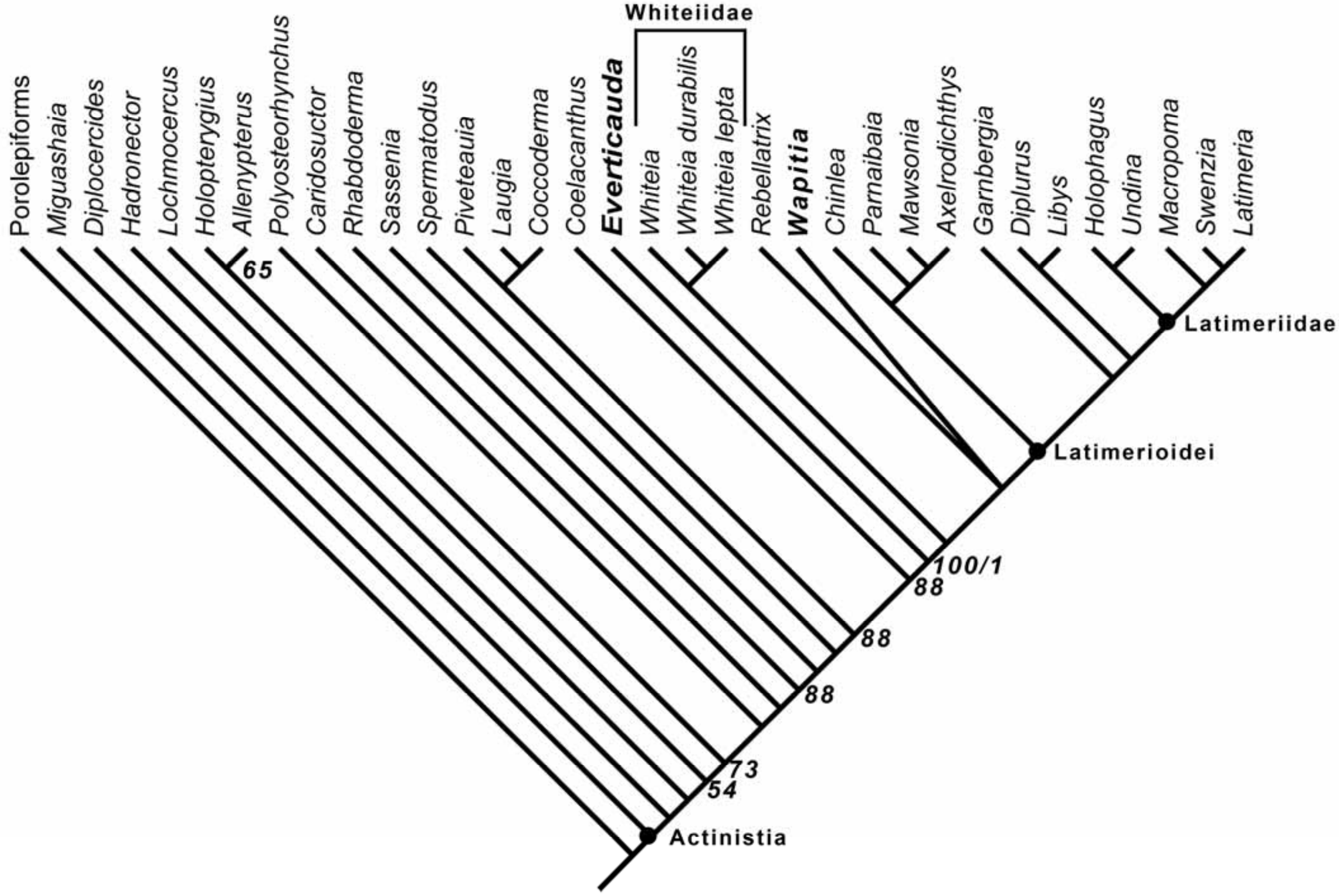

A
B

FIGURE 4.12. 50% majority rule cladogram of 26 most parsimonious tree (length = 245; CI = 0.453; HI = 0.547; RI = 0.700) resulting from a heuristic maximum-parimony analysis using TBR and 100 random-addition-sequence replicates on an updated version of the character taxon matrix of Forey (1998).


Whiteiidae
Porolepiforms
Miguashaia
Diplocercides
Hadronector
Lochmocercus
Holopterygius
Allenypterus
Polyosteorhynchus
Caridosuctor
Rhabdoderma
Sassenia
Spermatodus
Piveteauia
Laugia
Coccoderma
Coelacanthus
Everticauda
Whiteia
Whiteia durabilis
Whiteia lepta
Rebellatrix
Wapitia
Chinlea
Parnaibaia
Mawsonia
Axelrodichthys
Garnbergia
Diplurus
Libys
Holophagus
Undina
Macropoma
Swenzia
Latimeria
65
Latimeriidae
Latimerioidei
100/1
88
88
88
73
54
Actinistia

APPENDIX IV.

Character-taxon matrix used for phylogenetic analysis (modified from Forey, 1998) with 33 coelacanth taxa with the addition of *Everticauda pavoidea* gen et sp. nov. and *Wapitia robusta*, gen. et sp. nov.

The first 108 characters are described in Forey (1998) and character 109 is discussed in Friedman and Coates (2006). Missing data = ‘?’; non-applicable states = ‘N’.

	10	20	30	40	50
Porolepiforms	00100N1??0	0000000000	00210?0001	1111NN0000	0000000010
Diplocercides	001???2101	0000000010	0021100001	1101000000	0000000010
Rhabdoderma	1000002001	1001001011	0000100001	1100000000	0000110010
Caridosuctor	1000002101	?0??001011	0000100001	11??000000	000??00010
Hadronector	00100021?1	?0??000010	0010100001	1100??0000	000?1?0?10
Polyosteorhynchus	00?0002101	???100?010	101???0001	11?0000000	000?1?0010
Allenypterus	0?????2001	?0??000010	000000001?	1100000000	01001??101
Lochmocercus	??????????	????????10	100???0001	11??000000	00?01000?0
Coelacanthus	00?11?2100	10010011?1	10?0?1101?	??00001??0	010?1?1?10
Spermatodus	1000002101	100110?111	?020?1001?	1101000000	00?????010
Whiteia	00?0002001	1001101111	1000100011	1100010000	0001110010
Laugia	11?0??1?01	1001001011	0000?10010	0000000000	0001001110
Sassenia	10????2?01	100100?01?	?020100011	1101000000	0000100010
Chinlea	00?01?2000	10??0011?1	10????2011	100?110000	100100?01?
Diplurus	00001?2110	1010102111	1000?11011	1000100000	0100111101
Holophagus	10?01?2110	101110?111	1?20?10010	1100100000	000?1??110
Undina	00?00?2110	101110211?	1?2???0110	1100??0000	000?101110
Coccoderma	10?011210?	1001001011	0020101010	0001001100	0001001100
Libys	0???1?????	10111??111	1?00?11010	000?1???01	000?1???01
Mawsonia	1?????2100	10100111?1	1020?12010	101?000120	101?000120
Macropoma	01?0?12110	1011102111	1120?10010	0001101110	0001101110
Latimeria	0011112110	1011102111	1100102111	0001111111	0001111111
Miguashaia	00?0001?0?	01??000000	002?00000?	000?000?10	000?000?10
Axelrodichthys	1000112100	101001111?	1020?12010	1011000120	1011000120
Garnbergia	??????21?0	?0?????1??	????????1?	000?????1?	000?????1?
Swenzia	01?0??2???	?011???1??	11?0101111	0001101110	0001101110
Holopterygius	?0?0??????	??????????	??0???????	??????????	??????????
Parnaibaia	0111??2000	?0??0011?1	??2??12011	001?????2?	001?????2?
Rebellatrix	??????????	??????????	??????????	??????????	????????1?
Piveteauia	1?????????	1011?0?1?1	?1?0??00?1	1??0000???	???01011?
Whiteia lepta	00?0??200?	1001???11?	???0??01??	?10?01????	????????1?
Whiteia durabilis	0??0??200?	?00????11?	???0??0111	1100010000	000?????1?
Everticauda	00?0??????	????1?????	??????????	??????????	??????????
Lithocoelacanthus	0?????20??	???????11?	??20?1001?	1??????00?	?????????0

60	70	80	90	100	109
01003000?0	0?00001001	01N000?101	000N0?0000	000000N000	000000000
0100300100	0000000001	1101001101	?010000??0	0010100000	??0000???
0101410000	1001001011	10110?0000	?000101101	0011100000	110000100
0101410000	1010001???	??????????	???????101	?011101000	1100?0100
010???0010	000000????	??????????	???????101	?011100000	010??0100
0101?00010	10??000???	??????????	???????1?1	10111?1000	1000?0000
0101?00010	001000????	??????????	???????101	0010101000	000000001
01?0?00??0	00??000???	??????????	???????101	??10100000	100??0?00
0101410??0	1?110000??	??????????	???????101	0011101000	0100?0100
010141?000	?1???01110	101??0110?	?00?101???	??????????	???0?0???
011141101?	1111000010	00111??00?	11011111?1	0011120100	010010000
0101400000	1111000011	101110110?	?000101101	1011111011	0100?0110
01?1?10??0	111100??01	1011001?01	?0011011??	??????????	???0?0??0
10???11???	1?11001???	??????????	???????1?1	?11111?000	?101?1?00
101??00000	1?11000010	001?11?00?	??0?111101	1111110100	0101?0000
101??11001	1110001???	????11????	?1??1??1?1	101111?110	0110?0100
101??1101?	1100001010	001011?01?	?1??111101	?011110100	010010100
01?1410000	1111000???	??????????	???????111	1011100011	010011110
?1?1411001	1?110001??	??????????	???????111	1011110110	011010100
0011??1??0	1?111101??	??????????	?????????1	??111?0100	0101?1?0?
10114?1011	1111000010	001011?01?	110?111111	1011120100	010110100
1011411011	1N11001010	0010110010	1100111101	1011120100	010010000
?1?0??001?	?0??0000??	??????????	???????1?0	??0000?000	??0000??0
1011401??0	1?11110110	001111?0??	110?1111?1	1111110100	0101?1100
10????????	??????????	??????????	??????????	?????1?0??	0100?0??0
?0?1??101?	1N110??0??	????????1?	?????????1	?011??0??0	01?0?01?0
??00??0???	??????00??	???????00?	???????10?	?111110100	?00???0?1
101??01???	11111?00??	??????????	???????1?1	1011100000	0?01?0100
??1?????1?	??????????	??????????	???????101	1011100000	010000?0?
?111??0???	1???00?0??	???????11?	???????1??	10??111001	0100?01?0
011???101?	?111000???	????????0?	???????101	0011120000	010010100
0111?11???	?1110000??	??????????	????1?????	??????????	?????????
???1?10??0	11110?????	??????????	???????1?1	0011100100	0100?0100
?1???????0	?1?0??????	??????????	???????101	1011100000	?100?0100

CHAPTER FIVE

New coelacanth *Belemnocerca prolata*, gen. et sp. nov. (Actinistia: Laugiidae), from the Lower Triassic near Wapiti Lake, British Columbia, Canada

INTRODUCTION

The coelacanths of the Sulphur Mountain Formation exposed near Wapiti Lake, British Columbia, currently represent the most morphologically diverse assemblage of coelacanths, particularly in respect to the caudal fin. In chapters 2–4, five new coelacanths were described with three different caudal morphotypes; two not previously observed in coelacanths.

Though represented by a single specimen, the coelacanth described here clearly represents a distinctly different caudal fin morphotype from the previous species described from Wapiti Lake (Chapters 2–4). While none of the synapomorphies previously recognized as diagnostic for the Laugiidae (see Chapter 3) are preserved on this specimen, several unusual features link the new form with *Laugia* Stensiö, 1932, and the Laugiidae Berg, 1940, a family with a temporal range from the Early Triassic to the Late Jurassic (Forey, 1998). The Laugiidae include two Lower Triassic coelacanths, *Laugia* from Greenland (Stensiö, 1932; Forey, 1998) and *Piveteauia* Lehman, 1952 (see also Clément, 1999) from Madagascar, along with one Upper Jurassic coelacanth, *Coccoderma* Quenstedt, 1858 (see also Lambers, 1991) from Germany. The new coelacanth< *Belemnocerca prolata*, gen. et sp. nov., from British Columbia suggests new diagnostic features for laugiids, adds to the morphological and taxonomic diversity of coelacanths from the Lower Triassic, and extends the geographic range of the family westward.

GEOLOGY

The geology of the Sulphur Mountain Formation has been described in detail in Neuman (1992) and Orchard and Zonneveld (2009); the reader is also referred to the geology sections within Chapters 2–4. The only known specimen, UALVP 43606, was collected from the most prolific fossil-bearing cirque known as cirque C along the Ganoid Ridge (see maps in Callaway and Brinkman, 1989; Orchard and Zonneveld, 2009). This cirque exposes the lowest and most diverse fossil fish-producing bed within the Sulphur Mountain Formation according to Neuman (1992) and has also produced the greatest number of coelacanths of any cirque within Wapiti Lake Provincial Park (pers. ob.).

MATERIALS AND METHODS

UALVP 43606 was photographed with a Rebel EOS XS digital SLR (Fig. 5.1A). Scales were coated in ammonium chloride for better contrast and photographed using a Nikon DXM 1200C digital camera mounted on a Zeiss Discovery V8 stereo microscope (Fig. 5.2A, B). Adobe CS4 Photoshop was used to edit images and create line drawings. Images of the specimens of *Laugia groenlandica* (MGUH VP.2011 and VP.3262) were provided by the MGUH (Fig. 5.3–5.4).

Institutional Abbreviations—MGUH, Geological Museum at the University of Copenhagen, Denmark; **UALVP**, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta, Canada.

SYSTEMATIC PALEONTOLOGY

Class OSTEICHTHYES Huxley, 1880

Subclass SARCOPTERYGII Romer, 1955

Order ACTINISTIA Cope, 1871

Family LAUGIIDAE Berg, 1940

BELEMNOCERCA, gen. nov.

Type and Only Known Species—*Belemnocerca prolata*, sp. nov.

Diagnosis—As for the type and only species

Etymology—From the Greek noun *belemnon* meaning arrow or spear and the Greek noun *kerkos,* tail, Latinized in feminine form as *cerca.*

BELEMNOCERCA PROLATA, sp. nov.

(Figs. 5.1–5.2)

Holotype—UALVP 43606 (Fig. 5.1–5.2), consisting of a nearly complete caudal peduncle and fin with supplementary lobe and anal fin, length 31.5 cm.

Stratigraphic Horizon and Locality—Sulphur Mountain Formation, Vega-Phroso Siltstone Member, Lower Triassic; collected in cirque C (see maps in Callaway and Brinkman, 1989; Orchard and Zonneveld, 2009), latitude 54° 32’N, longitude 120° 45’ 24”W.

Etymology—The specific epithet is from the Latin adjective *prolata*, meaning elongated, in reference to the long tail and supplementary lobe.

Diagnosis—Apomorphies of taxon: posteriorly situated anal fin; caudal fin long, slender; deepest part of caudal fin is just over one-third length of principal lobes; tail asymmetrical; 21–22 dorsal and 17–18 ventral caudal fin rays; 3–4 fin rays closest to the notochord are distanced farther posteriorly than the other fin rays; posterior margin of caudal fin tapered; supplementary lobe extending well past posterior margin of caudal fin; supplementary lobe robust, half depth of principal lobes; 29 or more fin rays in supplementary lobe; single-pore lateral line openings; scales characterized by crowded tubercles that curve along lateral edges.

DESCRIPTION AND COMPARISONS

Anal Fin

The anal fin of *Belemnocerca prolata* is situated anterior to the first ventral radial of the caudal fin, yet posterior to the two most anterior dorsal radials (Fig. 5.1). This posterior position of the anal fin is not known in any other coelacanth. Eighteen highly segmented rays form the lobed anal fin, a count that is most similar to that of *Laugia groenlandica* (Stensiö, 1932; Forey, 1998:fig. 11.10), *Caridosuctor populosum* (Lund and Lund 1984, 1985), *Holophagus gulo* (Egerton, 1861) and *Latimeria chalumnae* (Smith, 1939; Forey, 1998), though such counts are highly variable amongst coelacanth species. The anal basal plate is missing because the specimen is broken between the fin and the basal plate.

Caudal Fin

The caudal fin of *B. prolata* is elongate, though incomplete, and has a robust supplementary lobe that extends well past the posterior margin of the caudal fin (Fig. 5.1A, B). The outline of the posterior margin of the caudal fin is distinctly tapered. The tail has a maximum depth of 9 cm and, although incomplete, is elongate, with a preserved length of 31.5 cm.

The caudal fin is incomplete because the anterior edge of the dorsal lobe is missing. Approximately 17 dorsal and 17–18 ventral fin rays lacking ornamentation are preserved in the tail of *B. prolata*. The proximal tips of 5 additional dorsal radials are visible along the fracture edge of the dorsal lobe (Fig. 5.1B, 5 black arrows at the left side of the figure point to fractured radials). Assuming that the anterior-most radial is truly the first radial, it would not have articulated with a fin ray because the first radial present in coelacanths does not carry a fin ray (Forey, 1998). It is possible that there were originally several additional radials anterior to first preserved dorsal radial, but additional material would be necessary to confirm this. While the dorsal lobe is incomplete, the ventral lobe is well preserved and complete. As preserved, there at least 21–22 dorsal and 17–18 ventral fin rays present. Coelacanths differ in the number of rays in their dorsal lobe, though the typical range is between 16–24; *L. groenlandica* and *Coccoderma suevicum*, both members of the Laugiidae, have 17–18 and 21 fin rays in their dorsal caudal lobes, respectively (Lambers, 1991; Forey, 1998). *Laugia groenlandica* has 13–14 rays in the ventral lobe of its caudal fin; therefore, both *B. prolata* and *L. groelandica* have a difference of 4–5 rays between the dorsal and ventral principal lobes of the tail. Additionally, both coelacanths have asymmetrical caudal fins (*Piveteauia* also has an asymmetrical tail but the fin ray count in unknown) because the dorsal radials insert anterior to the ventral radials (Stensiö, 1932; Forey, 1998). A 3 cm distance is recorded in *B. prolata* between the anterior-most dorsal and ventral radials. In contrast, most coelacanths, such as *Coccoderma suevicum* (Lambers, 1991; Forey, 1998), have symmetrical tails in which the dorsal radials insert directly opposite of the ventral radials.

The caudal fin has an overall tapering outline characterized by two features: 1) the rays closest to the supplementary lobe extend farther than the rays along the outer margin of the tail 2) the dorsal and ventral lobes (principal lobes) of the tail are continuous with the supplementary lobe.

The posterior margin of the caudal fin in *Belemnocerca prolata* tapers gradually (Fig. 5.1) in a way most similar to that of *Laugia groenlandica* (see Forey, 1998:fig. 11.10; Fig. 5.4). The posterior margin of the principal lobes in both species shallows at an angle approximately 40^{o} from the notochord, though the fin rays are longer as they get closer to the notochord in *B. prolata.* While the fin rays of the caudal fin appear to get longer towards the supplementary lobe, they actually are spaced farther and farther apart, creating this tapered effect (Fig. 5.1B, 3 grey arrows on the right side of the figure).

In most coelacanths, there is a clear division between where the principal lobes of the caudal fin end and the supplementary lobe begins. However, in *B. prolata* the fin rays at the base of the supplementary lobe form the posterior margin of the caudal fin outline closest to the notochord. These rays continue posteriorly to form a robust (though incomplete in the specimen) supplementary lobe. The supplementary lobe extends far posterior to the posterior margin of the principal lobes (Fig. 5.1). *Diplurus longicaudatus* (Schaeffer, 1948:fig. 1a) and *Laugia groenlandica* (Figs. 5.3, 5.4) have been described as possessing supplementary lobes that extend well beyond the principal lobes as well (Forey, 1998). However, the supplementary lobe of *B. prolata* is significantly broader (Fig. 5.1) than that of either *D. longicaudatus* or *L. groenlandica* (Fig. 5.4). The supplementary lobe in *B. prolata*, UALVP 43606, is just over half the width of the caudal fin (4.8 cm). *Coccoderma suevicum* (Lambers, 1991:fig. 1) has a similarly broad supplementary lobe, though it does not extend much past the posterior margin of the principal lobes. The supplementary lobe, though incomplete, has a length of at least 7 cm, with 29 fin rays preserved; however, there were likely many more as the posterior tip of the lobe is incomplete.

Scales and Lateral Line

The scales of *B. prolata* are unique amongst the coelacanths of the Sulphur Mountain Formation. The ornamentation consists of closely packed, elongate tubercles in rows, which are longer and curved close to and parallel to the dorsal and ventral margins of the scale (Fig. 5.2B). The lateral line is preserved as a positive infilling of the pore system. Each lateral-line scale bears a large unbranched tubule that opens into a single pore within each scale (Fig. 5.2A, l.l), a feature that is consistent with that of *L. groenlandica* (Forey, 1998). However, most coelacanths, other than four genera in the Latimerioidei (*Undina*, *Libys*, *Macropoma* and *Latimeria*) as well as *Coccoderma* (member of Laugiidae) and *Whiteia*, have a single lateral-line scale pore (Forey, 1991, 1998).

DISCUSSION

The family Laugiidae Berg, 1940, is composed of *Piveteauia* Lehman, 1952, *Laugia* Stensiö, 1932, and *Coccoderma* Quenstedt, 1858 (see also Forey, 1998, Clément, 1999, and Lambers, 1991, respectively). One of the most diagnostic features that support this family is the anterior placement of the pelvic girdle, though such a feature cannot be observed on the specimen considered here due to its fragmentary nature. While *Belemnocerca prolata* is distinct from members of the Laugiidae in the posterior placement of the anal fin and in scale ornamentation, its shares four caudal features that appear to relate it to members of the Laugiidae, particularly *Laugia*: 1) asymmetry of caudal fin (longer dorsal lobe) (also shared with *Piveteauia*, though not *Coccoderma*); 2) dorsal lobe of caudal fin with 4–5 more fin rays than ventral lobe; 3) gradually tapering caudal fin; 4) long supplementary lobe extending well beyond posterior margin of caudal fin.

Most coelacanths have a symmetrical caudal fin in which the dorsal radials are directly opposite to the ventral radials. However, coelacanths with an asymmetrical tail have dorsal radials that are begin farther anteriorly than the ventral radials (‘longer’ dorsal lobe). *Caridosuctor* Lund and Lund, 1984 (see also Lund and Lund, 1985), *Polyosteorhynchus* Lund and Lund, 1984 (see also Lund and Lund, 1985), *Allenypterus* Melton, 1969 (see also Lund and Lund 1984, 1985), *Coelacanthus* Agassiz, 1839 (see also Schaumberg, 1978), *Laugia* Stensiö, 1932, and *Piveteauia* Lehman, 1952 (see also Clément, 1999) all have asymmetrical tails. In many of these coelacanths, not only does the dorsal lobe begin anterior to the ventral lobe, but it also has significantly more fin rays (most coelacanths have a dorsal lobe with only 1–2 rays more than the ventral lobe). *Allenypterus* is the most dramatic example of disproportion of fin rays in the caudal fin, with 72 dorsal and 15 ventral fin rays (Melton, 1969; Lund and Lund, 1984, 1985; Forey, 1998). Of coelacanths with a more 'traditional' body form, *Laugia groenlandica* (Stensiö, 1932) has the next greatest disparity in caudal fin rays with 17–18 dorsal and 13–14 (Fig. 5.3), a difference of 4–5 rays. Similarly, *B. prolata* has a dorsal lobe with 4–5 more fin rays than the ventral lobe.

The overall caudal-fin shape of *B. prolata* is most similar to that in *L. groenlandica*. Both have gradually tapering fins in which the fin rays extend farther posteriorly closer to the supplementary lobe. This shape contrasts greatly with the square-cut tails present in coelacanths such as *Hadronector* (Lund and Lund, 1984, 1985) and *Coccoderma* (Quenstedt, 1858; Lambers, 1991) or tails with rounded posterior caudal margins found in coelacanths such as *Rhabdoderma elegans* Newberry, 1856 (see also Forey, 1981), *Diplurus newarki* Bryant, 1934 (see also Schaeffer, 1952) and *Coelacanthus granulatus* Agassiz, 1839 (see also Schaumberg, 1978). Additionally, Forey's (1998) emended diagnosis of *L. groenlandica* noted that the supplementary lobe extends well past the posterior margin of the dorsal and ventral lobes. Contrarily, many coelacanths, such as *Latimeria* Smith, 1939 (see also Forey, 1998:fig. 8.1), and *Macropomoides* Woodward, 1942 (Woodward, 1942:fig. 4), have reduced supplementary lobes that barely extend beyond the posterior margin of the dorsal and ventral lobes. Additionally, the supplementary lobe, though incomplete on the only known specimen of *B. prolata*, is significantly larger proportionally than those known from previously described coelacanths from the Sulphur Mountain Formation.

CONCLUSION

Belemnocerca prolata is placed within the family Laugiidae and likely closely related to *Laugia groenlandica* based on the disparate number of rays between the principal lobes, high number of caudal fin rays, the high degree of asymmetry in the tail, the tapering posterior caudal outline, and the supplementary lobe that extends well beyond the principal lobes of the tail. Currently, no other coelacanth has all of these features, including other members of the Laugiidae. *Belemnocerca prolata* has a robust supplementary lobe, unlike that of *Laugia groenlandica*, but very similar to that of *Coccoderma suevicum* (Quenstedt, 1858; Lambers, 1991:fig. 1), another member of the Laugiidae. Two features present in *B. prolata* that are not found in any other member of the Laugiidae are the posteriorly situated anal fin and the distinct scale ornamentation. Pending the discovery of more complete material, *B. prolata* is classified in the new genus *Belemnocerca* and placed within the Laugiidae.

LITERATURE CITED

Agassiz, L. 1839. Recherches sur les Poissons Fossiles. Vol. 2. Neuchâtel.

Berg, L. 1940. Classification of fishes, both recent and fossil Trudy Zoologicheskogo Instituta, Akademiya Nauk SSSR, Leningrad 5:1–141.

Bryant, W. L. 1934. New fishes from the Triassic of Pennsylvania. Proceedings of the American Philosophical Society, Philadelphia 73:319–326.

Callaway, J. M., and D. B. Brinkman. 1989. Ichthyosaurs (Reptilia, Ichthyosauria) from the Lower and Middle Triassic Sulphur Mountain Formation, Wapiti Lake area, British Columbia, Canada. Canadian Journal of Earth Sciences 26:1491–1500.

Clément, G. 1999. The Actinistian (Sarcopterygii) *Piveteauia madagascariensis* Lehman from the Lower Triassic of Northwestern Madagascar: A redescription on the basis of new material. Journal of Vertebrate Paleontology 19(2):234–242.

Cope, E. D. 1871. Contribution to the ichthyology of the Lesser Antilles. Transactions of the American Philosophical Society 14:445–483.

Egerton, P. 1861. *Holophagus gulo*. In Huxley, T. H., Preliminary essay upon the systematic arrangement of the fishes of the Devonian epoch. Memoirs of the Geological survey of the United Kingdom, London, Dec. 10:1–40.

Forey, P. L. 1981. The coelacanth *Rhabdoderma* in the Carboniferous of the British Isles. Palaeontology 24:203–229.

Forey, P. L. 1991. *Latimeria chalumnae* and its pedigree. Environmental Biology of Fishes 32:75–97.

Forey, P. L. 1998. History of the coelacanth fishes. Chapman and Hall, London, 419 pp.

Huxley, T. H. 1880. On the applications of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. Proceedings of the Zoological Society 1880:649–662.

Lambers, P. H. 1991. The identity of the type specimen of *Coelacanthus harlemensis* Winkler (Pisces, Actinistia) from the lithographic limestone of Solnhofen (Tithonian), Bavaria. Paläontologische Zeitschrift 65:173–189.

Lehman, J. P. 1952. Étude complémentaire des poisons de l'Éotrias du Nord-Ouest de Madagascar. Kungliga Svenska Vetenskapsakademiens Handlingar 2:1–201.

Lund, R. and W. L. Lund. 1984. New genera and species of coelacanths from the Bear Gulch Limestone (Lower Carboniferous) of Montana (USA). Geobios 17:237–244.

Lund, R. and W. L. Lund. 1985. Coelacanths from Bear Gulch limestone (Namurian) of Montana and the evolution of Coelacanthiformes. Bulletin of the Carnegie Museum of Natural History 25:1–74.

Melton, W. G. 1969. A new dorypterid fish from central Montana. Northwest Science 43:196–206.

Neuman, A. G. 1992. Lower and Middle Triassic Sulphur Mountain Formation, Wapiti Lake, British Columbia: Summary of Geology and Fauna. Contributions to Natural Science, Royal British Columbia Museum 16:1–12.

Newberry, J. S. 1856. Descriptions of several genera and species of fossil fish from Carboniferous strata of Ohio. Proceedings of the Academy of Natural Sciences Philadelphia 8:96–100.

Newberry, J. S. 1878. Descriptions of new fossil fishes from the Trias. Annals of the New York Academy of Sciences. 1:127–128.

Orchard, M. J., and J.-P. Zonneveld. 2009. The Lower Triassic Sulphur Mountain Formation in the Wapiti Lake area: Lithostratigraphy, conodont biostratigraphy, and a new biozonation for the lower Olenekian (Smithian). Canadian Journal of Earth Sciences 46:757–790.

Quenstedt, F. A. 1858. Der Jura. Tubingen. 823 pp.

Reis, O. M. 1888. Die Coelacanthinen, mit besonderer Berücksichtigung de rim Weissen Jura Bayerns vorkommednde Gattungen. Palaeontographica 35(1):1–96.

Romer, A. S. 1955. Herpetichthyes, Amphibioidei, Choanichthyes or Sarcopterygii? Nature 176:126.

Schaeffer, B. 1948. A study of *Diplurus longicaudatus* with notes on the body form and locomotion of the Coelacanthini. American Museum Novitates 1378:l–32.

Schaeffer, B. 1952. The Triassic coelacanth *Diplurus*, with observations on the evolution of the coelacanthini. American Museum Novitates 1378:1–32.

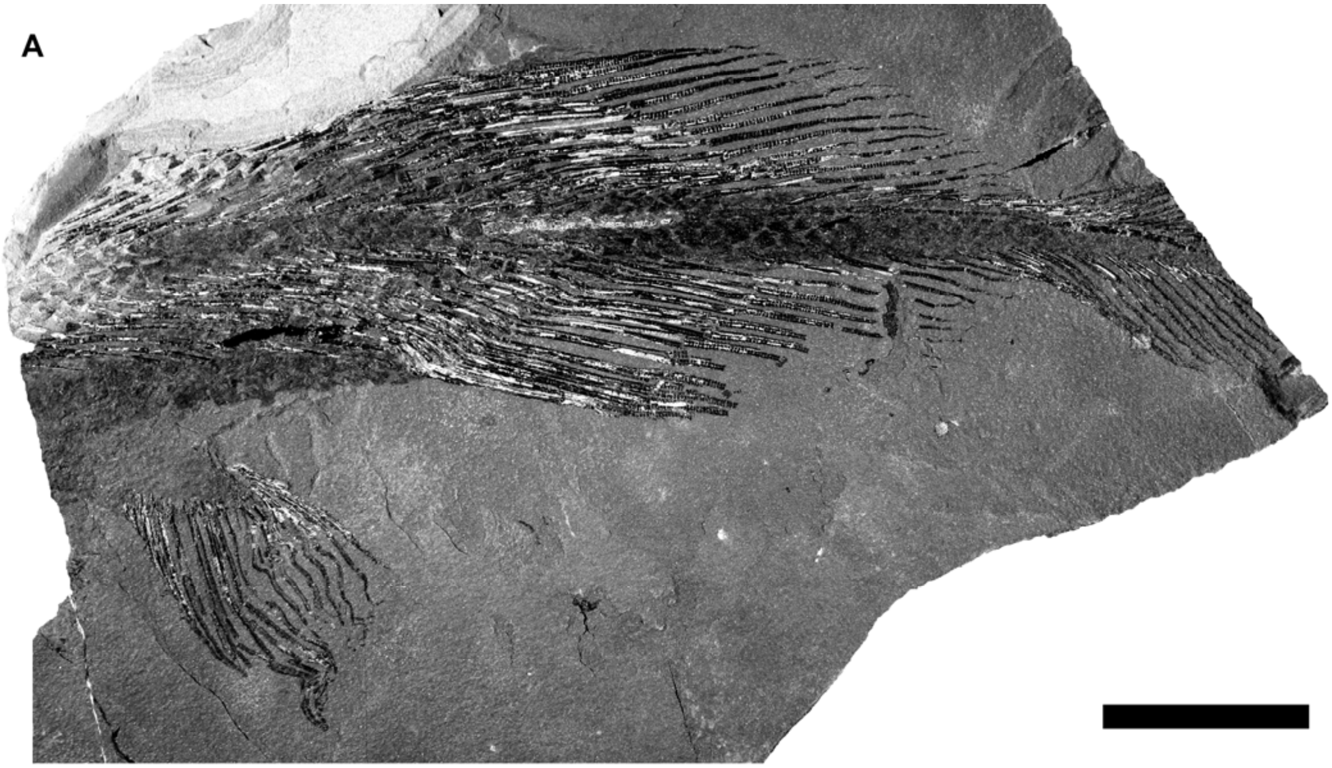
Schaumberg, G. 1978. Neubeschreiburg von *Coelacanthus granulatus* Agassiz (Actinistia, Pisces) aus dem Kupferschiefer can Richelsdorf (Perm, W.–Deutschland). Paläontologische Zeitschrift 52:169–197.

Smith, J. L. B. 1939. A living fish of Mesozoic type. Nature 143:455–456.

Stensiö, E. A. 1932. Triassic fishes from East Greenland. Meddelelser Grønland 83(3):l–305.

Woodward, A. S. 1942. Some new and little known Upper Cretaceous fishes from Mount Lebanon. Annals and Magazine of Natural History 9(11):537–568.

FIGURE 5.1. *Belemnocerca prolata*, gen. et sp. nov. (holotype UALVP 43606), Lower Triassic, Sulphur Mountain Formation, British Columbia, Canada. **A**, anal and caudal fin in left lateral view; **B**, outline drawing (black arrows point to fragmented radials; grey arrows point to widely spaced rays that create tapered appearance of the principal lobes). Scale bar equals 5 cm (A–B).


A

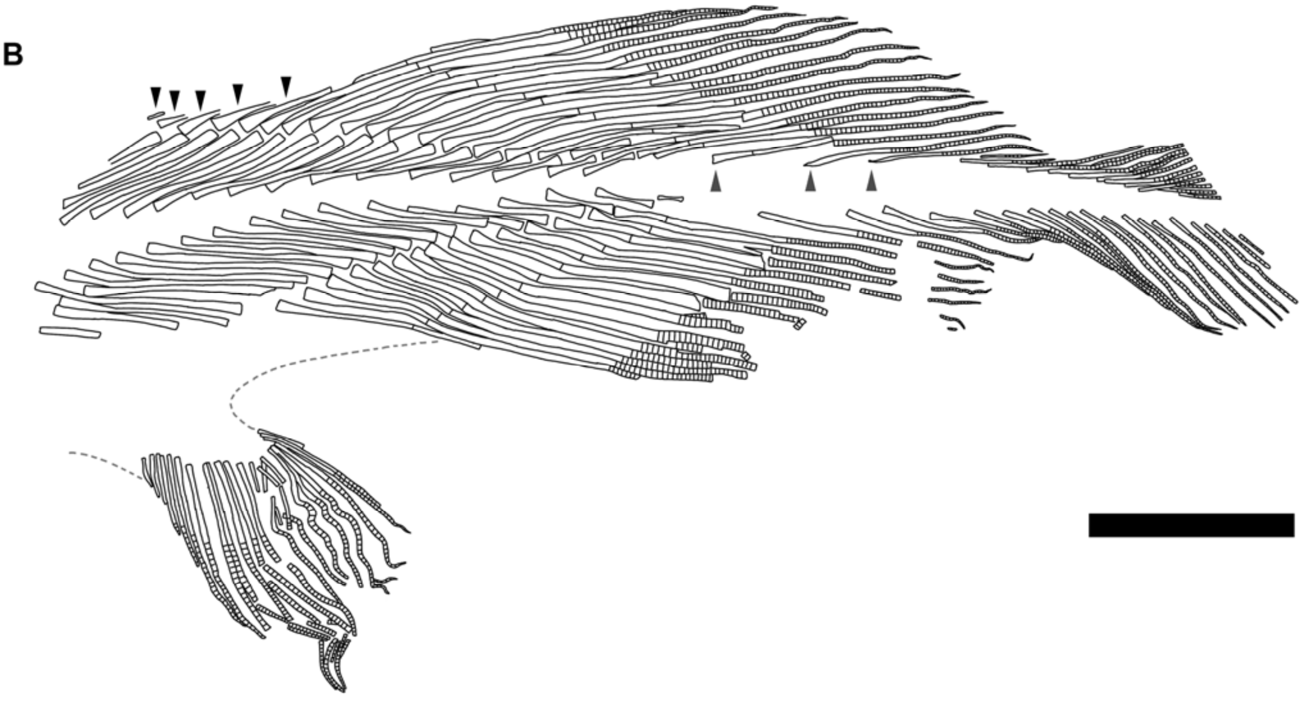

B

FIGURE 5.2. *Belemnocerca prolata*, gen. et sp. nov. (holotype UALVP 43606). **A**, close up of lateral line scales; **B**, close up of single scale. Abbreviations: **l.l**, lateral line. Scale bar equals 5 mm (A–B).

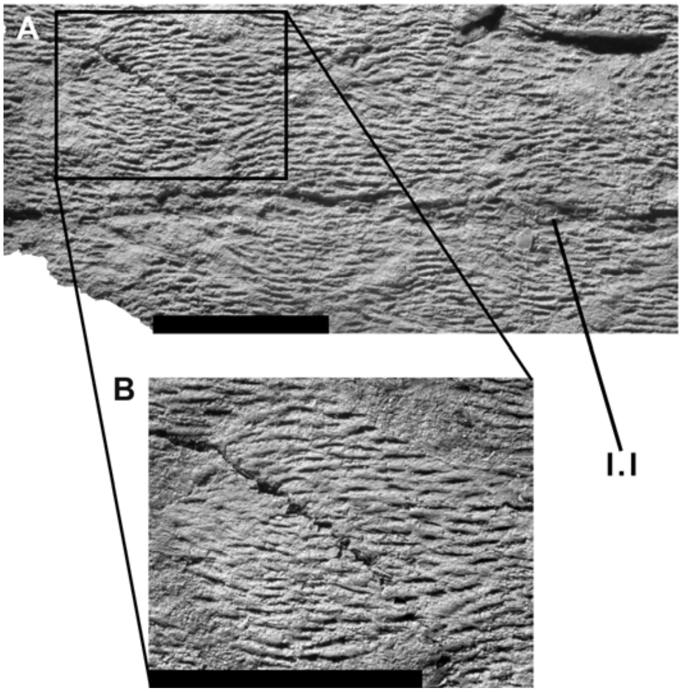

A
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FIGURE 5.3. *Laugia groenlandica* Stensiö, 1932 (MGUH VP.2011), posterior half of skeleton in right lateral view (arrows indicate fins rays, though most are incomplete). Scale bar equals 5 cm. Photo provided by the MGUH and used with permission.

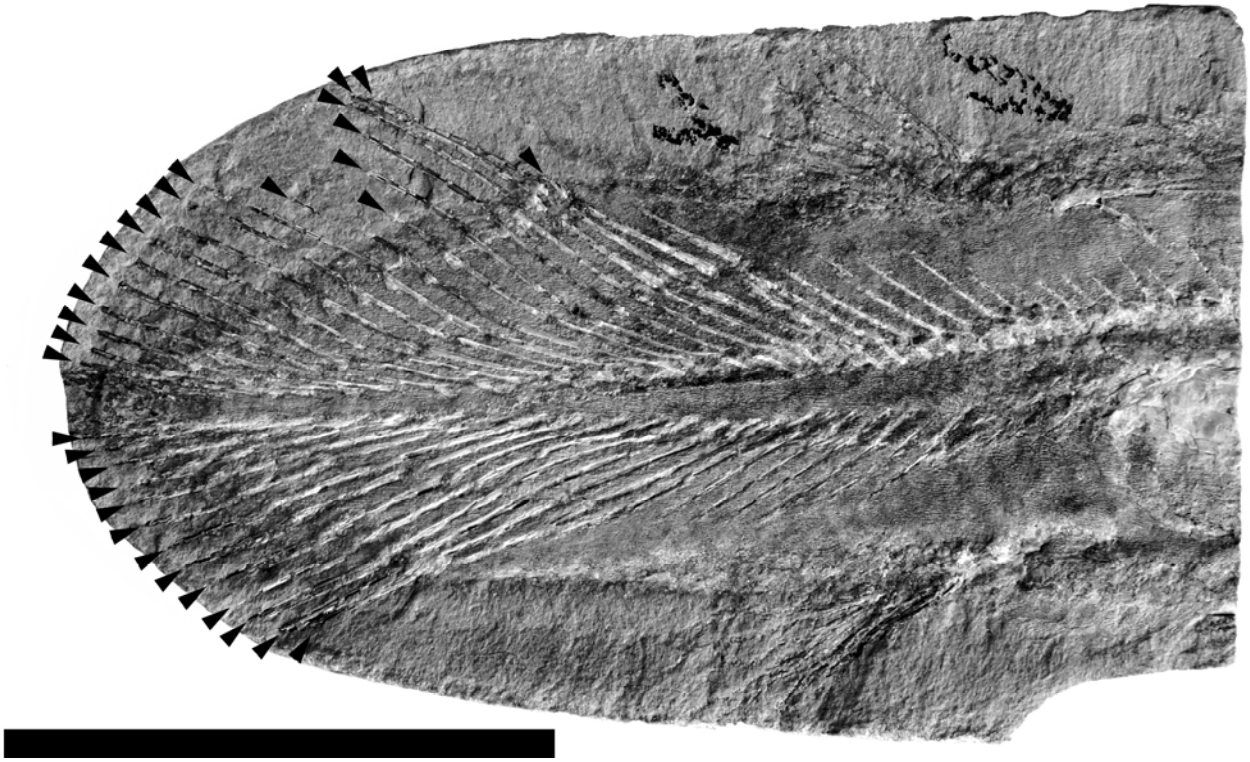
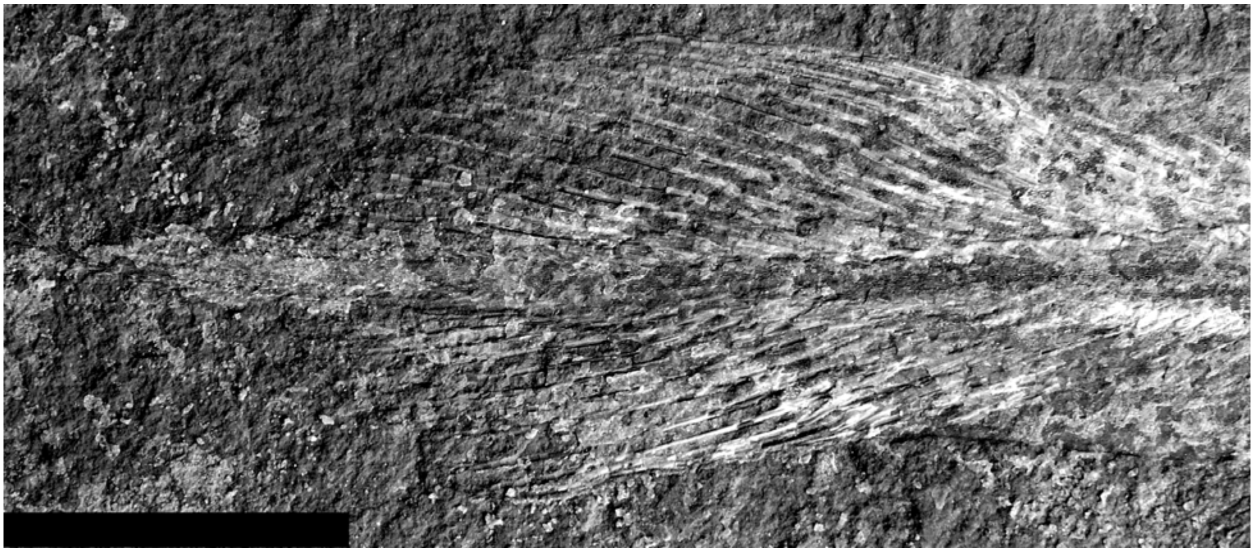


FIGURE 5.4. *Laugia groenlandica* Stensiö, 1932 (MGUH VP.3262), caudal fin in right lateral view. Scale bar equals 5 cm. Photo provided by the MGUH and used with permission.



CHAPTER SIX

Morphological diversity in the caudal fin of Lower Triassic coelacanths from British Columbia, Canada

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INTRODUCTION

Coelacanths are extraordinary vertebrates that have a long temporal range of approximately 409 million years (Johanson et al., 2006), extending from the Devonian to the present day. Only one genus, *Latimeria* Smith, 1939, is extant. The earliest coelacanths from the Early Devonian through the end of the Mississippian display a wide array of caudal fin forms (Schultze, 1973; Lund and Lund, 1984, 1985; Forey, 1998; Long, 1999; Friedman and Coates, 2006), indicating that early in their history, coelacanths underwent periods of rapid morphological change (Schaeffer, 1952). Following the Mississippian, they were formerly thought to have deviated little from a *Latimeria*-like body plan (Huxley, 1861; Moy-Thomas and Miles; 1971; Jarvik, 1980; Forey, 1984; Lund and Lund, 1985; Schultze, 1986; Balon et al., 1988; Cloutier, 1991; Schultze, 2004). However, Forey (1998) argued that coelacanths reached a peak in both species and morphological diversity slightly later, during the Early Triassic. The coelacanths described in Chapters 2 and 4 support Forey's (1998) idea.

Among the most distinctive parts of the coelacanth is the caudal fin, which has broad, rounded dorsal and ventral lobes (principal lobes). Between these lobes is one of the most peculiar features, a small terminal fin, known as a supplementary lobe, extending to or well beyond the posterior margin of the principal lobes. In the more than one hundred species of Paleozoic and Mesozoic coelacanths known from the fossil record, the caudal fin scarcely changes in form (notable exceptions are *Miguashaia*, *Gavinia*, *Holopterygius*, *Allenypterus*, *Rebellatrix* and *Everticauda*). Indeed, had the caudal fin changed drastically in the 70 million years between the youngest fossil and the living coelacanth, J. L. B. Smith might not have recognized the significance of Ms. Latimer's find (Smith, 1956). Considering that most fossil coelacanths appear similar in body form to *Latimeria*, it is reasonable to assert that their locomotion was also similar. Based on direct observations of modern coelacanths, it is known that *Latimeria chalumnae* is a slow moving fish whose primary mode of locomotion is achieved via sculling motions of the posterior dorsal and anal fins, while the paired fins move alternately, resembling the alternating motion of the legs of a tetrapod walking (Frick et al., 1987). *Latimeria* rarely uses its caudal fin other than for short bursts of rapid acceleration (lunging) to catch prey (Fricke et al., 1987; Fricke and Hissmann, 1992).

Coelacanths of the Sulphur Mountain Formation

Following the Permo-Triassic extinction, morphological diversity of coelacanths arguably peaked in the Early Triassic (Wendruff and Wilson, in review; Chapters 2–5), coincident with the peak in their taxonomic diversity suggested by Forey (1998).

Coelacanths are common in the diverse Early Triassic fossil assemblage of the Sulphur Mountain Formation, British Columbia, Canada. Four distinct caudal morphologies have been identified (Fig. 6.1): 1) a *Latimeria*-like tail (*Whiteia lepta*, Fig. 6.1A), 2) a high-span (high aspect ratio) forked tail with a reduced supplementary lobe (*Rebellatrix divaricera,* Fig. 6.1B), 3) an everted tail

(*Everticauda pavoidea*, Fig. 6.1C) with a supplementary lobe much shorter than the main lobes, and 4) a slender, elongate, tapered tail with an extended supplementary lobe (*Belemnocerca prolata*, Fig. 6.1D). These disparate forms are taxonomically as well as functionally significant.

Caudal Fin Shape and Lifestyles

The shape of the caudal fin has a significant impact on swimming performance in fishes and can be used to draw conclusions about lifestyle (Nursall, 1958). While considering the correlation strictly between tail shape and locomotion (without considering musculature), Nursall (1958) viewed the tail as a hydrofoil structure, which provides forward thrust. He used aspect ratios (vertical height or span of caudal fin divided by surface area) to quantify the efficiency and ability of a fish to produce thrust for locomotion. Fishes at the lowest end of the aspect-ratio spectrum (AR ≈ 0–1) typically swim using large-amplitude body movements (Fig. 6.2). This is an adaptation for quick acceleration over short distances (lunging) that has been observed in bowfins. Moreover, low-aspect-ratio tails are highly flexible and make up a large area of the body. Such tails produce considerable propulsive forces during acceleration from rest (lunging); however, they produce considerable drag at higher speeds and the fishes do not sustain higher speeds for more than a few seconds (Walters, 1962; Webb, 1982). Tails with high aspect ratios are typical of fishes with high cruising speeds, where propulsion is provided by high-frequency, lower-amplitude undulations of the caudal fin, such as those seen in tunas and marlins (Fig. 6.2). Fishes with high-aspect-ratio tails, although slow starters or weak accelerators from rest, are able to minimize high-speed drag to sustain fast swimming over long distances and extended times (Walters, 1962; Webb, 1982). High-aspect-ratio tails, which represent a much smaller percentage of the total body surface, are characterized by a narrow caudal peduncle supporting a forked tail with narrow and usually pointed dorsal and ventral lobes, and are stiffened to maintain their shape during high-frequency swimming motions (Nursall, 1958).

As noted previously, coelacanths are usually categorized as lunging predators, being slow swimmers or positioning themselves at rest, then using their broad, low-aspect-ratio tail to accelerate suddenly at prey (Fricke et al., 1987; Fricke and Hissmann, 1992). Webb (1982) noted five ‘requirements’ for a non-cruising lifestyle (slow swimmers), three of which can be adapted for studies of fossil fish: 1) low-aspect-ratio caudal fin, 2) deep caudal peduncle, and 3) flexible body. *Latimeria* is an example of a non-cruising fish that uses its caudal fin in large-amplitude motions (Webb, 1982).

It seemed unlikely that the typical coelacanth body form could have evolved to accommodate a cruise-swimming lifestyle (Forey, 2009). The change from a slow-moving fish to a cruise swimmer requires streamlining of the body to reduce drag (friction) associated with increased speed. Three ‘requirements’ (adapted for fossils from Webb, 1982) for cruise swimming are: 1) high-aspect-ratio caudal fin, 2) narrow caudal peduncle, and 3) stiffened body. These features minimize the drag (friction) on a fish, while increasing the ability of the tail to produce greater forward thrust (Webb, 1982). The narrowing of the caudal peduncle reduces drag created by the turbulence generated during high-frequency tail motion (Walters, 1962; Webb, 1982). Additionally, a stiffened body reduces the portions of the body that are flexing and creating unwanted drag (Webb, 1982).

Webb (1982) suggested that cruising body forms developed multiple times in the evolutionary history of actinopterygians due to their role in “predator evasion and food capture.” There is no reason why this would not apply to sarcopterygians as well. The fork-tailed high-aspect-ratio form has developed three times in Sarcopterygii: 1) the Tristichopteridae (*Tristichopterus* Egerton, 1861 and *Eusthenopteron* Whiteaves, 1881), 2) the Onychodontiforms (*Strunius* Jessen, 1966) and 3) the coelacanth Rebellatricidae (*Rebellatrix* Wendruff and Wilson, in review). However, only in *Rebellatrix* are the segmented fin rays of the tail reduced (stiffened by loss of fin-ray segmentation), suggesting that *Rebellatrix* was using its caudal fin in a distinctly different fashion even from that of the other ‘fork-tailed’ sarcopterygians.

Fishes with similar caudal fin shapes tend to converge on similar body plans owing to hydrodynamic constraints (Webb and Weihs, 1986; Webb, 1988). Often this will lead to these fishes occupying similar niches. It is hypothesized here that the different coelacanth tail forms examined herein represent disparate locomotory patterns and associated lifestyles that are analogous to those of modern fishes having similar tail shapes.

MATERIALS AND METHODS

Specimens were photographed with a Rebel XS digital SLR and outline drawings were created using Adobe CS4 Photoshop. Caudal fin areas were calculated with the image processing software ImageJ (Abramoff et al., 2004). Images of the specimens were loaded into the program and the scale of the image was correlated to a scale included in the photo. The outline of the caudal fin was selected and the ‘analyze particles’ function was applied to calculate the area of the selected region. The image being analyzed must have been taken from directly above the specimen. If the image were taken from an angle, the calculated measurements would not reflect the true area of the specimen. Aspect ratio (AR) is calculated as: $AR = S^2/A$ where S is the span of the caudal fin, and A is the surface area of the caudal fin. Comparisons to extant fishes (*Latimeria*) and their corresponding aspect ratios are taken from Nursall (1958).

One possible source of error is the flexibility of the caudal fins. The fin rays could be at full span (erect) or collapsed. This would affect the span and surface area variables of the calculated aspect ratio. A larger sample size may be more informative yielding more reliable results; however, if the cause of the distortion is taphonomic, this may apply to all specimens found at the locality.

RESULTS

Latimeria-like Tail (*Whiteia lepta*)

This morphotype (Fig. 6.1A) is characterized by a broadly rounded tail similar to that of *Latimeria*. The principal lobes are symmetrical, in that the dorsal and ventral radials first insert opposite each other; though, as with most fossil and extant coelacanths, there are an additional 1–2 fin rays on the dorsal lobe of the caudal fin. Approximately half of the caudal fin is composed of segmented fin rays, which would have made the tail flexible. The aspect ratio of this form approaches 1, similar to that of a bowfin (Fig. 6.2). Based on the shape of the tail and comparison of body form to those of extant fishes, this fossil fish was likely a lunging predator capable of short bursts of acceleration, but unable to sustain long periods of rapid swimming.

Forked Tail (*Rebellatrix divaricerca*)

This morphotype, as the species epithetic suggests, has a bifurcated caudal fin (Fig. 6.1B). The tail has a wide span, three times the depth of the caudal peduncle, and a reduced supplementary lobe. The caudal fin shape resembles that of more derived teleosts such as perch or smallmouth bass with an aspect ratio slightly above 3 (fig. 6.2). In contrast to the *Latimeria*-like tail, unsegmented fin rays predominate. Lack of segmentation, in combination with fusion of these fin rays to the radials, would significantly stiffen the fin. A similar structure is seen in tunas and jacks, in which higher aspect ratios permit prolonged high-speed swimming (Nursall, 1958). The combination of a high-aspect-ratio tail and unsegmented, thickened fin rays in the forked-tailed morph suggests fast swimming and an active lifestyle, unique among known fossil and extant coelacanths.

Everted Tail (*Everticauda pavoidea*)

This caudal fin is characterized by two exceedingly long principal lobes (Fig. 6.1C), and a supplementary lobe that is at least half the length of the principal lobes. The unsegmented fin rays are reduced in number, and highly segmented rays comprise nearly 75% of caudal fin length. The aspect ratio of this form was calculated to be 0.62, slightly lower than that of the *Latimeria*-like caudal fin. With such large, highly flexible principal lobes, this everted tail may have moved in high-amplitude movements analogous to those of the extant male Paradise fish (*Macropodus opercularis*). These massive caudal lobes in extant fish are generally considered for display rather than locomotion; *Everticauda*'s unusual tail may have primarily used for (sexual) display.

Extended Tail (*Belemnocerca prolata*)

The extended-tail coelacanth is characterized by tapering principal lobes and a robust supplementary lobe, which is just over half the height of the caudal fin, and extends far posterior to the principal lobes (Fig. 6.1D).The fin rays are continuous and appear to blend the principal and supplementary lobes together, making it difficult to discern where one begins and the other ends. Unlike the ‘typical’ coelacanth tail form, segmented fin rays of the dorsal and ventral lobes nearer the notochord extend farthest posterior to the principal lobes. These features give an overall tapered appearance and a very low aspect ratio (0.40), comparable to that of modern lungfish (e.g. *Neoceratodus*). Like its modern analogs, it was likely an ambush predator capable of quick bursts of speed. Thrust was likely produced via high-amplitude undulations of the body, rather than by high-frequency undulations of the tail.

DISCUSSION

As described above, a wide array of caudal morphological forms is present among the coelacanths from the Sulphur Mountain Formation. Such diversity is approached only in the coelacanths preserved in the Mississippian Bear Gulch Limestone of Montana. Three types of caudal fin forms have been recorded from the Bear Gulch (see Melton, 1969; Lund and Lund, 1984, 1985: 1) a *Latimeria*-like tail (*Caridosuctor*, *Polyosteorhynchus* and *Lochmocercus*), 2) a deep tail (*Hadronector*), and 3) a dacriform (teardrop-shaped) tail (*Allenypterus*). Although the first two are similar, presumably the deeper caudal fin could generate greater thrust for quicker lunges.

The caudal fins of *Whiteia lepta* (Chapter 3), *Everticauda pavoidea* (Chapter 4) and *Belemnocerca prolata* (Chapter 5) all fall within the low range of aspect ratios (0–1), which suggests that they were capable of quick acceleration from rest but not sustained high speeds. Caudal fins of both *B. prolata* and *E.*

pavoidea have a lower aspect ratio than that of *W. lepta*, and have very long principal caudal lobes with relatively deep caudal peduncles. Conversely, *W. lepta* has a shorter, broadly rounded tail. The greater surface area of its caudal fin likely allowed for quicker lunges than did the tails of *E. pavoidea* and *B. prolata*. Nevertheless, all three fishes were likely lunging predators exhibiting comparable swimming characteristics.

In contrast, *Rebellatrix divaricerca* has an aspect ratio approximately three times that of any other coelacanth from the Sulphur Mountain Formation. The high-span tail (nearly lunate) and low surface area yields the highest-aspect-ratio caudal fin known in coelacanths. The caudal peduncle is also narrow, whereas in most coelacanths the caudal peduncle is only slightly less than the span of the caudal fin. Additionally, more complete specimens of *R. divaricerca* indicate that the body is slender and streamlined (Chapter 2:fig. 2.1A, D). The caudal aspect ratio in *R. divaricerca* is comparable to that of the yellow perch, suggesting similar locomotor characteristics, although the preponderance of thickened, unsegmented fin rays and a more lunate caudal fin as well as an anteriorly thickened notochord (to reduce lateral flexibility in the body) indicates that it may have been a faster swimmer than the aspect ratio alone signifies.

CONCLUSION

The diversity seen in the coelacanths of the Sulphur Mountain Formation represents several departures from the conservative caudal fin form. To the extent that caudal morphology is correlated with swimming characteristics and capacity, these differences in form imply that diverse lifestyles had evolved, and that distinct niches were occupied by these coelacanths. This demonstrates that coelacanths were still evolving new body forms following the Paleozoic. The most unusual coelacanth, *Rebellatrix divaricerca*, is interpreted as being a relatively active, fast predator, while the other three morphotypes, *Whiteia lepta*, *Everticauda pavoidea* and *Belemnocerca prolata*, suggest a variety of ambush-predator lifestyles. The fin rays of the forked-tailed coelacanth *Rebellatrix divaricerca* are mostly unsegmented, a feature that likely stiffened the tail. The wide span of the fin and the unsegmented fin rays suggest a stiff, high-aspect-ratio tail adapted for rapid swimming, which has not previously been attributed to coelacanths. In the other three morphologies, the aspect ratio is much lower. These tails have segmented fin rays as in the majority of coelacanths. The segmented fin rays create a more flexible tail that allows for greater acceleration from rest. Nevertheless these three coelacanths exhibit significant differences in caudal-fin form that likely reflected differences in their feeding and locomotion. These differences in caudal fin morphology suggest a more diverse locomotory repertoire than was previously recorded in coelacanths.

LITERATURE CITED

Abramoff, M.D., P. J. Magelhaes and S. J. Ram. 2004. Image Processing with ImageJ. Biophotonics International 11(7):36–42.

Balon, E. K., M. N. Bruton and H. Fricke. 1988. A fiftieth anniversary reflection on the living coelacanth, *Latimeria chalumnae*: some new interpretations of its natural history and conservation status. Environmental Biology of Fishes 32:241–280.

Cloutier, R. 1991. Patterns, trends and rates of evolution within the Actinistia. Environmental Biology of Fishes 32:23–58.

Egerton, P. de M. G. 1861. *Tristichopterus alatus*. *Memoirs of the Geological Survey of the U.K., Figures and Descriptions Illustrative of British Organic Remains* 10:51–55.

Forey, P. L. 1984. The coelacanth as a living fossil. pp. 166–169. In: N. Eldredge and S. M. Stanley (eds.), Living Fossils. Springer, New York.

Forey, P. L. 1998. History of the Coelacanth Fishes. Chapman and Hall, London, U.K., pp. 248-260.

Forey, P. L. 2009. Coelacanth: Portrait of a Living Fossil. Forrest Text, U.K., 209 pp.

Friedman M. and M. I. Coates. 2006. A newly recognized fossil coelacanth highlights the early morphological diversification of the clade. Proceedings of the Royal Society: B 273:245-250.

Fricke, H., O. Reinicke, H. Hofer and W. Nachtigall. 1987. Locomotion of the coelacanth *Latimeria chalumnae* in its natural environment. Nature 329:331–333.

Fricke, H. and K. Hissmann. 1992. Locomotion, fin coordination and body form of the living coelacanth *Latimeria chalumnae*. Environmental Biology of Fishes 34:329–356.

Huxley, T. H. 1861. Preliminary essay upon the systematic arrangement of the fishes of the Devonian epoch. Memoirs of the Geological Survey of the United Kingdom 10:1–40.

Jarvik, E. 1980. Basic structure and evolution of vertebrates. Volume I. 575 pp., London: Academic Press.

Jessen, H. 1966. Die Crossopterygier des Oberen Plattenkalkes (Devon) der Bergisch-Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge) unter Berücksichtigung von americkanischem und europäischem *Onychodus*-material. Arkiv för Zoologi 18:305–389.

Johanson, Z., J. A. Long, J. A. Talent, P. Janvier and J. W. Warren. 2006. Oldest coelacanth, from the Early Devonian of Australia. Biology Letters 2:443–446.

Long, J. A. 1999. A new genus of fossil coelacanth (Osteichthyes: Coelacanthiformes) from the Middle Devonian of southeastern Australia. Records of the Western Australian Museum 57:37–53.

Lund, R. and W. Lund. 1984. New Genera and Species of Coelacanths from the Bear Gulch Limestone (Lower Carboniferous) of Montana (U.S.A.). Geobios 17:237-244.

Lund, R. and W. L. Lund. 1985. Coelacanths from Bear Gulch limestone (Namurian) of Montana and the evolution of Coelacanthiformes. Bulletin of the Carnegie Museum of Natural History 25:1–74.

Moy-Thomas, J. A. and R. S. Miles. 1971. Palaeozoic Fishes. Chapman and Hall, 259 pp.

Nursall, J. R. 1958. The Caudal Fin as a Hydrofoil. Evolution 12:116-120.

Schaeffer, B. 1952. The Triassic coelacanth fish *Diplurus*, with observations on the evolution of the Coelacanthini. Bulletin of the American Museum of Natural History 99(2):25–78.

Schultze, H.-P. 1973. Crossopterygier mit heterozerker Schwanzflose aus dem Oberdevon Kanadas, Nebst einer Beschreibung von Onychodontida-Resten aus dem Mittledevon Spaniens und dem Karbon der USA. Palaeontographica 143A:188208.

Schultze, H.-P. 1986. Dipnoans as sarcopterygians. Journal of Morphology Supplement 1:39–74.

Schultze, H.-P., 2004. Mesozoic sarcopterygians; pp. 463–492 in Arratia, G., Tintori, A. (eds.), Mesozoic Fishes 3—Systematics, Paleoenvironments and Biodiversity. Verlag Dr.Friedrich Pfeil, München.

Smith, J. L. B. 1939. A living fish of Mesozoic type. Nature 143:455-456.

Smith, J. L. B. 1956. Old Four Legs: the story of the Coelacanth. London: Longman Green, 260 pp.

Walters, V. 1962. Body form and swimming performance in the scombroid fishes. American Zoologist 2:143–149.

Webb, P. W. 1982. Locomotor Patterns in the Evolution of Actinopterygian Fishes. American Zoologist 22:329–342.

Webb, P. W. 1988. Simple Physical Principles and Vertebrate Aquatic Locomotion. American Zoologist 28:709-725.

Webb, P. W. and D. Weihs. 1986. Functional Locomotor Morphology of Early Life History Stages of Fishes. Transactions of the American Fisheries Society 115:115-127.

Whiteaves, J. F. 1881. On some remarkable fossil fishes from the Devonian rocks of Scaumenac Bay, Province of Quebec. American Journal of Science and Arts 21(3):494–496.

FIGURE 6.1. Caudal fin forms from the Sulphur Mountain Formation of British Columbia, Canada. **A**, *Latimeria*-like tail, *Whiteia lepta* (TMP 1989.131.28; **B**, forked tail, *Rebellatrix divaricerca* (TMP TMP 1989.138.33); **C**, everted tail, *Everticauda pavoidea* (UALVP 43698); **D**, extended tail, *Belemnocerca prolata* (UALVP 43606). Images not to scale.

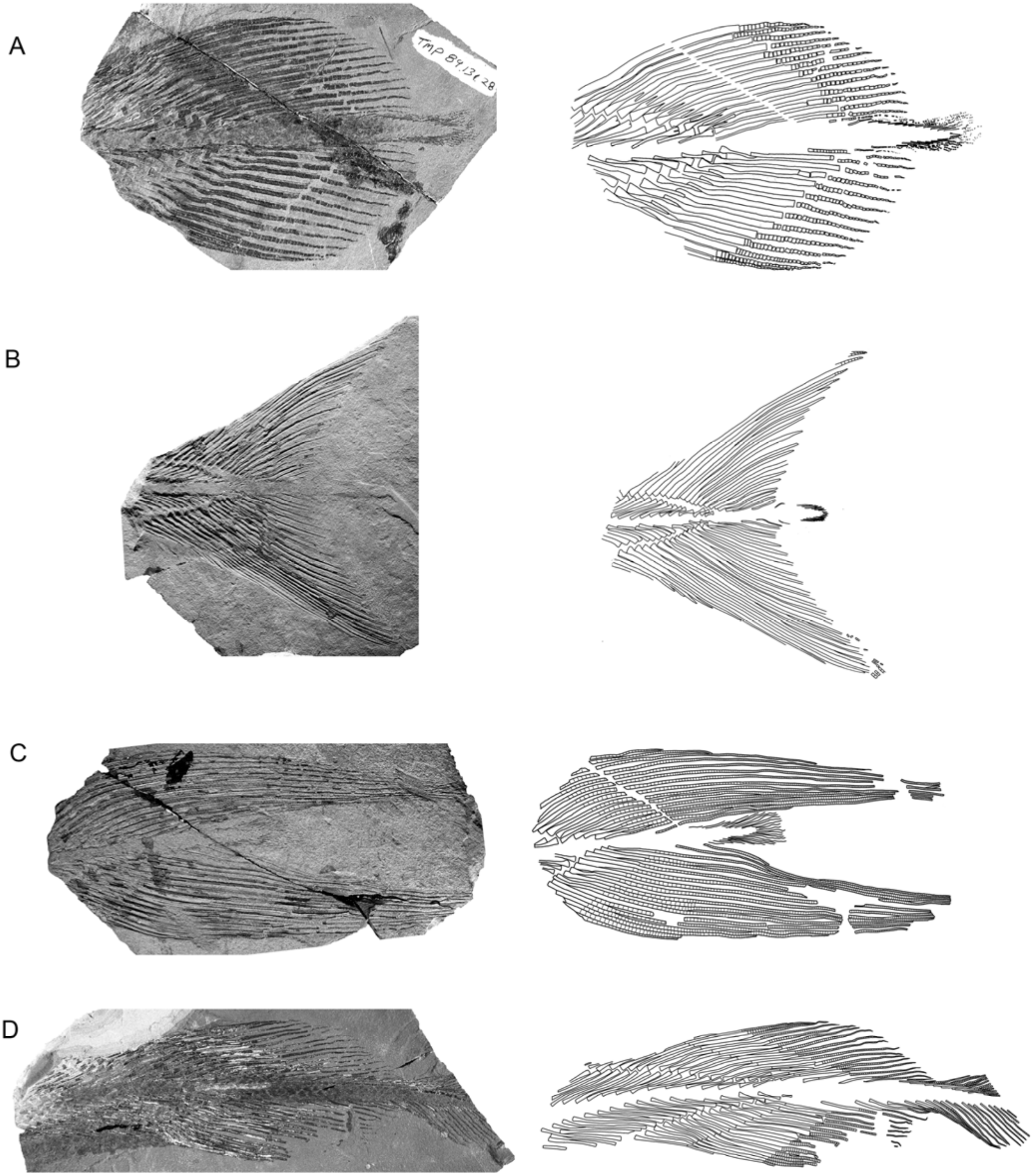
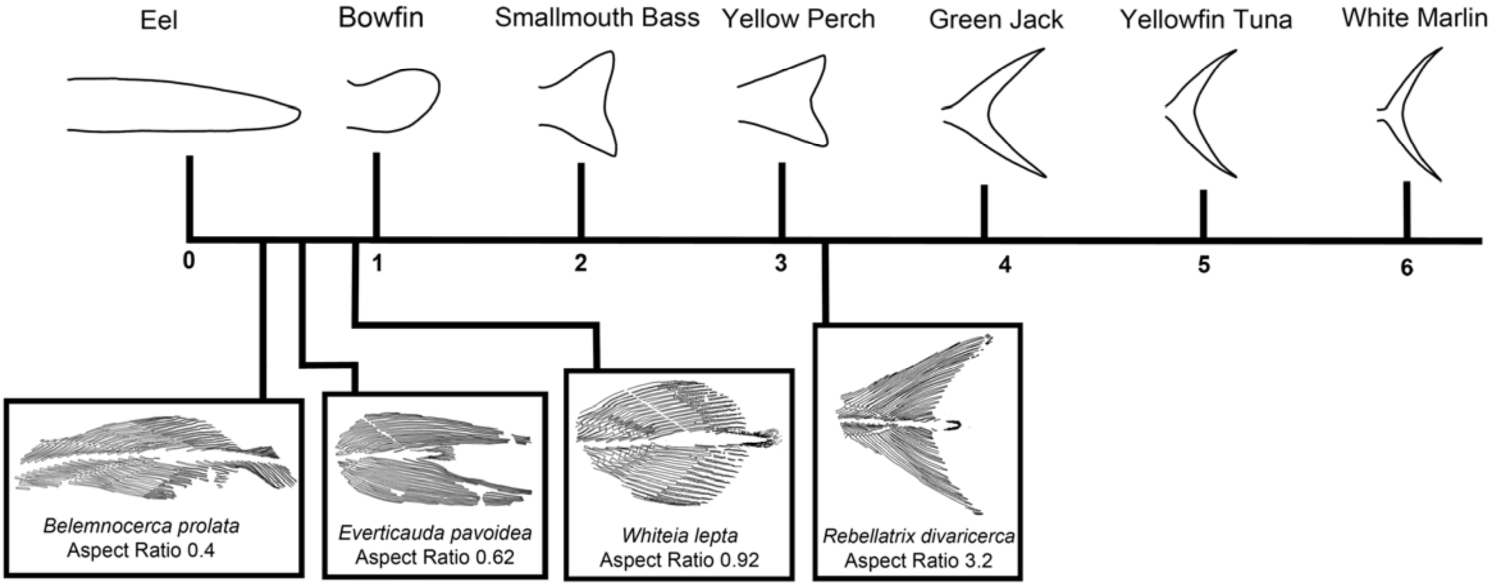

A
TMP 84.131.28
B
C
D

FIGURE 6.2. Aspect Ratio Comparison Chart (based on Nursall, 1958). Aspect ratio values of extant forms based on Nursall (1958). Extant tail outlines based on comparative material. Images not to scale.


Eel
Bowfin
Smallmouth Bass
Yellow Perch
Green Jack
Yellowfin Tuna
White Marlin
0
1
2
3
4
5
6
Belemnocerca prolata
Aspect Ratio 0.4
Everticauda pavoidea
Aspect Ratio 0.62
Whiteia lepta
Aspect Ratio 0.92
Rebellatrix divaricerca
Aspect Ratio 3.2

CHAPTER SEVEN

GENERAL CONCLUSION

In this thesis, the description and comparisons of the coelacanths from the Lower Triassic Sulphur Mountain Formation (near Wapiti Lake) were undertaken. More than 500 specimens (collected in the last 75 years) from Wapiti Lake were examined from the UALVP, TMP, AMNH, PRPRC and CMN collections, including the holotype of *Coelacanthus banffensis* Lambe, 1916, the only formally described coelacanth from the Sulphur Mountain Formation. Lower Triassic coelacanths are known from Madagascar, Spitsbergen, China, South Africa and Greenland. The ichthyofauna at Wapiti Lake is most closely related to that of Madagascar and Greenland, based on examination of comparative material from the MGUH and BMNH.

Previous works on the coelacanths of the Wapiti Lake localities always attributed them to an undescribed species of the genus *Whiteia* (Gardiner, 1966; Schaeffer and Mangus, 1976; Neuman, 1992; Forey, 1998). Upon review of this material, six new and distinct species were recognized (Fig. 7.1), only two of which belong within *Whiteia* (Moy-Thomas, 1935): *W. lepta* and *W. durabilis*, both described in Chapter 3. Both new species of *Whiteia* are significantly larger than all other described species. *Rebellatrix divaricerca*, described in Chapter 2, is a member of the new family Rebellatricidae, which is characterized by a forked and stiffened caudal fin. *Everticauda pavoidea* and *Wapitia robusta*, described in Chapter 4, represent two new deep-bodied coelacanths that differ from each other particularly in the anterior dorsal and caudal fins. Finally, a new member of the unusual family Laugiidae Berg, 1940, is described in Chapter 5 based on a single specimen, consisting of an isolated caudal fin, which is distinct from that of other previously described laugiids.

The large amount of material yielded several additional important findings. As previous authors have noted (Schaeffer, 1952; Cloutier, 1991; Forey, 1998), the species diversity of coelacanths peaked in the Early Triassic. New species described in Chapters 2–5 bring the total number of described Early Triassic coelacanth species to nearly two dozen (Forey, 1998; Tong et al., 2006; Geng et al. 2009; Wendruff and Wilson, in review). While Forey (1998) argued that coelacanth species diversity and morphological diversity should peak concurrently, Schaeffer (1952) and Cloutier (1991) argued that peak morphological diversity occurred during their first radiation in the Devonian through the Mississippian. The descriptions of *Rebellatrix divaricerca* (Chapter 2) and *Everticauda pavoidea* (Chapter 4) document the first major deviations in their body form in 70 million years (since the Mississippian). These highly unusual forms suggest that peaks in both species and morphological diversity did coincide during the Early Triassic and that coelacanths underwent significant anatomical evolution, contrary to the view that they were morphologically stagnant (Schaeffer, 1948, 1952; Moy-Thomas and Miles, 1971; Lund and Lund, 1985; Schultze, 1986; Cloutier, 1991; Schultze, 2004).

Finally, the morphological changes within the post-cranium were examined for possible functional significance. The four caudal forms indicate differences in locomotory habits and drastically different lifestyles. The lungfish-like *Belemnocerca prolata* (Chapter 5) was likely a lunging predator that used large transverse waves to generate forward thrust, whereas *Rebellatrix divaricerca* (Chapter 2) likely was an active predator using high-frequency oscillations of its stiffened, forked caudal fin to minimize drag and sustain higher speeds (Walters, 1962; Webb, 1982, 1988). This is the first functional analysis of coelacanth tail forms. The coelacanths of the Sulphur Mountain Formation not only represent the most diverse coelacanth assemblage of all Lower Triassic localities, but also the most morphologically diverse of all post-Mississippian coelacanth assemblages.

LITERATURE CITED

Berg, L. 1940. Classification of fishes, both recent and fossil Trudy Zoologicheskogo Instituta, Akademiya Nauk SSSR, Leningrad 5:1–141.

Broom, R. 1909. The fossil fishes of the Upper Karoo Beds of South Africa. Annals of the South African Museum, East London 7:251–269.

Cloutier, R. 1991. Patterns, trends and rates of evolution within the Actinistia. Environmental Biology of Fishes 32:23–58.

Forey, P. L. 1998. History of the Coelacanth Fishes. Chapman and Hall, London, U.K., pp. 248-260.

Gardiner, B. G. 1966. Catalogue of Canadian fossil fishes. Contribution to Life Sciences at the Royal Ontario Museum, Toronto 61:1–153.

Geng, B.-H., M. Zhu and J. Fan. 2009. A revision and phylogenetic analysis of *Guizhoucoelacanthus* (Sarcopterygii, Actinistia) from the Triassic of China. Vertebrata Palasiatica 47:165–177.

Lambe, L. M. 1916. Ganoid fishes from near Banff. Transactions of the Royal Society of Canada 10:35–44.

Lehman, J. P. 1952. Etude complémentaire des poisons de l'Eotrias du Nord-Ouest de Madagascar. Kungliga Svenska Vetenskapsakademiens Handlingar 2:1–201.

Lund, R. and W. L. Lund. 1985. Coelacanths from Bear Gulch limestone (Namurian) of Montana and the evolution of Coelacanthiformes. Bulletin of the Carnegie Museum of Natural History 25:1–74.

Moy-Thomas, J. A. 1935. Coelacanth Fishes from Madagascar. Geological Magazine 72:213–227.

Moy-Thomas, J. A. and R.S. Miles. 1971. Palaeozoic Fishes. 2nd ed. Chapman and Hall, London. 259 pp.

Neuman, A. G. 1992. Lower and Middle Triassic Sulphur Mountain Formation, Wapiti Lake, British Columbia: summary of geology and fauna. Contributions to Natural Science, Royal British Columbia Museum 16:1–12.

Schaeffer, B. 1948. A study of *Diplurus longicaudatus* with notes on the body form and locomotion of the Coelacanthini. American Museum Noviates 1378: l–32.

Schaeffer, B. 1952. The Triassic coelacanth fish *Diplurus,* with observations on the evolution of the Coelacanthini. Bulletin of the American Museum of Natural History 99(2):25–78.

Schaeffer, B., and M. Mangus. 1976. An early Triassic fish assemblage from British Columbia. Bulletin of the American Museum of Natural History 156:515–564.

Schultze, H.-P. 1986. Dipnoans as sarcopterygians. Journal of Morphology Supplement 1:39–74.

Schultze, H.-P., 2004. Mesozoic sarcopterygians; pp. 463–492 in Arratia, G., Tintori, A. (eds.), Mesozoic Fishes 3—Systematics, Paleoenvironments and Biodiversity. Verlag Dr. Friedrich Pfeil, München.

Stensiö, E. 1921. Triassic Fishes from Spitzbergen. Part. 1. Adolf Holzhausen, Vienna, Xxviii + 307 pp.

Stensiö, E. 1932. Triassic fishes from East Greenland collected by the Danish expedition 1929-1931. Meddelelser om Grønland 83(3):1–305.

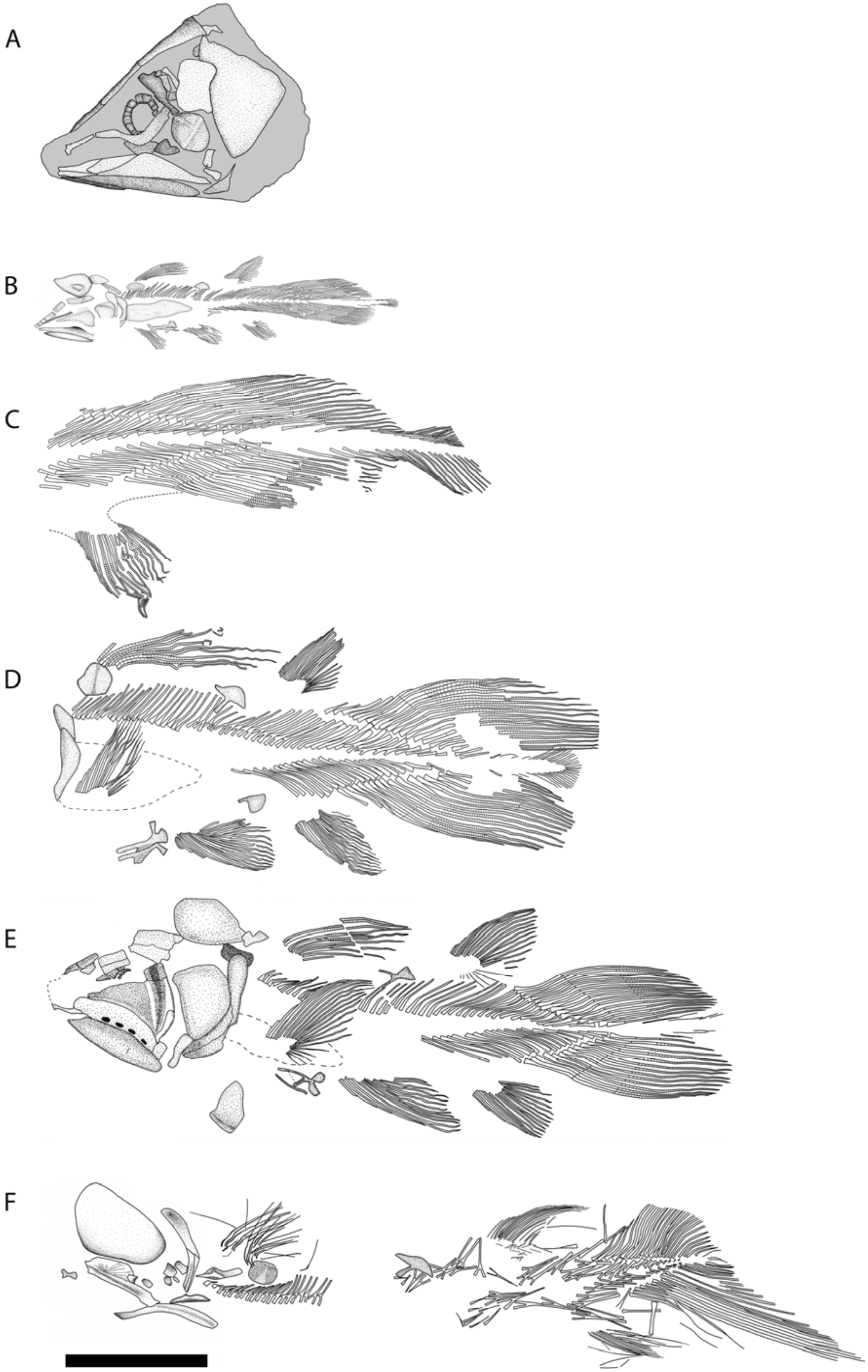
Tong, J., X. Zhou, D. H. Erwin, J. Zuo and L. Zhao. 2006. Fossil fishes from the Lower Triassic of Majiashan, Chaohu, Anhui Province, China. Journal of Paleontology 80(1):146–161.

Walters, V. 1962. Body form and swimming performance in the scombroid fishes. American Zoologist 2:143–149.

Webb, P. W. 1982. Locomotor Patterns in the Evolution of Actinopterygian Fishes. American Zoologist 22:329–342.

Webb, P. W. 1988. Simple Physical Principles and Vertebrate Aquatic Locomotion. American Zoologist 28:709-725.

FIGURE 7.1. Comparison of the six holotype specimens described in chapters 2–5. **A**, *Whiteia durabilis* (TMP 1986.206.02); **B**, *Whiteia lepta* (Holotype RBCM.EH 1986.001.0022); **C**, *Belemnocerca prolata* (UALVP 43606); **D**, *Everticauda pavoidea* (TMP 1995.118.23); **E**, *Wapitia robusta* (UALVP 24228); **F**, *Rebellatrix divaricerca* (PRPRC 2006.10.001). Scale bar is 10 cm; all specimens to scale.


A
B
C
D
E
F