UNRAVELING THE SYSTEMATICS OF PALAEONISCOID FISHES—LOWER ACTINOPTERYGIANS IN NEED OF A COMPLETE PHYLOGENETIC REVISION

by

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ABSTRACT

Actinopterygian fishes are the most diverse and speciose vertebrates on the planet. Lower actinopterygians, or fishes basal to teleosts, are critical to our understanding of the early evolution of this group, but extant lower actinopterygians are only represented by a few species. A larger diversity is preserved in the fossil record, but these fishes are poorly understood. This dissertation focuses on a subset of the extinct diversity; palaeoniscoid actinopterygians. The term "palaeoniscoid" has been used to refer to a large paraphyletic grouping of fossil fishes ranging from the Devonian to the Cretaceous. Our poor understanding of the diversity and relationships of palaeoniscoids reflects the many taxa of palaeoniscoids that remain to be described and included in phylogenetic analyses, as well as our understanding of morphological characters amongst lower actinopterygians. The main goal of this dissertation is to dismantle the paraphyletic grouping of palaeoniscoid fishes by concentrating on reassessments of morphological characters, descriptions of new taxa, and phylogenetic analyses of a vast number of taxa from the Devonian to the recent using both parsimony and Bayesian methodologies. Chapter One gives a taxonomic review of lower actinopterygians and discusses obstacles that must be overcome in order to form stronger hypotheses of relationships for palaeoniscoids. These obstacles are then addressed in the subsequent chapters. Chapters Two and Three are investigations into morphological characters. Chapter Two examines the preoperculum, a cheek bone considered important in the evolution of actinopterygians. Chapter Three presents problems with how the bones in the snout of lower actinopterygian fishes have been identified and proposes a new identification and nomenclature scheme for the bones of the snout. Chapters Four and Five are descriptions of new taxa from the Carboniferous of Utah and New Brunswick, Canada. Lastly, Chapter 6 presents results of phylogenetic analyses of lower actinopterygians.

The data matrix analyzed incorporates the findings from the previous chapters with the addition of new characters, character states, and taxa. This matrix represents the largest analysis to date of lower actinopterygian fishes, and the first time Bayesian methodology is used to investigate the relationships of palaeoniscoid fishes. Results of both methodologies are compared to each other and previously published hypotheses. Most importantly, analysis of this matrix has resulted in the recovery of a monophyletic Paleonisciformes. The results of this chapter suggest that palaeoniscoid actinopterygians represent a natural grouping.

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INTRODUCTION

Despite the fact that actinopterygian fishes are the most speciose and diverse vertebrates on the planet, their early evolution is poorly understood largely because we do not have a strong understanding of lower actinopterygians—i.e., fishes basal to teleosts. Lower actinopterygians are critical to our understanding of the success of actinopterygians in general, but extant lower actinopterygians make up a miniscule portion of the actinopterygian diversity we see today. Although extant lower actinopterygians are known from only four groups—the bichirs, bowfins, gars, and sturgeons—a large extinct diversity is recorded in the fossil record. Unfortunately, fossil lower actinopterygians have the distinction of being "among the least studied of all fossil vertebrates" (Hurley, et. al., 2006). To understand the early evolutionary history of actinopterygians as a whole, it is necessary to examine these understudied extinct forms. This study focuses on a subset of the extinct diversity, the palaeoniscoid lower actinopterygians.

Why Concentrate on Palaeoniscoids?—More than 250 genera of extinct lower actinopterygians compose an assemblage of fishes collectively and informally termed palaeoniscoids. The body plan of extant fishes is thought to have been derived from that of an ancestor within this grouping (Gardiner, 1984; Zhu and Schultze, 2001) and there is evidence that some of the fishes belonging to this grouping are closely related to neopterygians (Cloutier and Arratia, 2004; Hurley et al., 2006). The apparent evolutionary relevance of the fishes lumped into the palaeoniscoid grouping is diminished by controversy engendered by their systematic relationships. We are unable to identify the probable evolutionary lineage because the systematics and relationships of palaeoniscoids are poorly understood. A brief history of the systematic placement of lower actinopterygians reveals this fact.

Systematic and taxonomic history—Early actinopterygian fishes from the Devonian to the Cretaceous have been lumped together with extant chondrosteans (sturgeons and paddlefish). This tradition stems from Agassiz's (1833–1843) placement of Paleozoic actinopterygians, sturgeons, gars—and even lungfish and acanthodians, into his concept of the Ganoidei. Early on, it was recognized that Ganoidei had no diagnostic characters and was in need of revision (Müller, 1845). Müller (1845) tackled this problem by removing lungfish and further breaking down the Ganoidei into two orders, the Chondrostei and the Holostei. This said, Müller did continue to use the term Ganoidei to refer to the subclass that contained the Chondrostei and Holostei as a way to honor Agassiz's work (p. 522-523, 1845). Müller also erected a new subclass, the Teleostei, to contain the teleostean fishes originally included by Agassiz in his concept of the Ganoidei (1845; Patterson, 1982). Müller was the first to use the three main divisions—the Chondrostei, Holostei, and Teleostei in a classification of bony fishes.

In 1871, Cope coined the term Actinopteri and included in it the divisions previously described by Müller, minus *Polypterus. Polypterus* was included in a separate subclass, Huxley's (1861) Crossopterygii (Cope, 1871). In 1877, Cope revised his classification and ranked Crossopterygia, Chondrostei, and Actinopteri as subgroups. It should be noted that the Paleozoic actinopterygians were not placed within the subgroup Chondrostei, rather they remained in Actinopteri (Cope, 1877). In 1887, Cope changed the name from Actinopteri to Actinoptergyia but did not change the make up of the group (Patterson, 1982).

Actinopterygii was used by Woodward in 1891 in his *Catalogue of fossil fishes in the British Museum (Natural History)*. It referred to Cope's original 1871 description of Actinopteri and included the Chondrostei, Holostei, and Teleostei. Paleozoic actinopterygians were placed within the Chondrostei (Woodward, 1891).

Goodrich (1909) placed polypterids in their own division, Polypterini. Polypterini was not a part of the Actinopterygii (ibid.). Actinopterygii was divided into two subdivisions—one that held the Order Chondrostei and its suborders Palaeoniscoidei and Acipenseroidei, and the other the Holostei. The subdivision Holostei was broken down further into three orders—the Amioidei, Lepisosteoidei, and the Teleostei (ibid.).

In his study on *Lepisosteus*, Regan (1923) recognized the Holostei and Teleostei as one group and proposed to use the name Neopterygii to describe Holostei + Teleostei. Regan also suggested that the ‘palaeoniscoids’, Chondrostei, and the Belonorhynchii be described as the Palaeopterygii (ibid.). Polypterids were placed within their own group, Cladistia (ibid.). The Palaeopterygii, Neopterygii, and Cladistia were recognized as subclasses of Pisces. The Neopterygii was composed of numerous orders, including the Protospondyli with amiids and fossil relatives, the Ginglymodi with the Lepisosteidae, and the Halecostomi with the fossil Pholidophoridae and Oligopleuridae (ibid.).

There were researchers that recognized problems with the divisions of Chondrostei, Holostei, and Teleostei. In 1932, Stensiö noted that there were no clear boundaries between these divisions because the Chondrostei contained forms transitional to the Holostei, and the Holostei to the Teleostei. Though he recognized this problem, Stensiö felt that the three divisions should be maintained. One problem that was addressed dealt with the Chondrostei itself. Stensiö recognized that the diversity of the Chondrostei was higher than previously described and accepted. To deal with this diversity, Stensiö divided the families within the Chondrostei into six different groups, groups A–F, that he believed to represent distinct lines of evolution. Paleozoic actinopterygians, those typically considered to be ‘palaeoniscoids’ were placed within Group A in the Family Palaeoniscidae (Stensiö, 1932).

Agreeing with Stensiö, Berg (1940) recognized the separations between the Chondrostei and Holostei and the Holostei and Teleostei were not distinct. Berg went a step further and rejected these groupings and divided the subclass Actinopterygii into 57 orders. Thirteen of these orders included fishes typically considered to belong to the Chondrostei whereas the remaining 44 contained neopterygians. Important to note is the order Palaeonisciformes, which was further divided into two suborders—the Palaeoniscoidei and the Platysomoidei. The Palaeoniscoidei contains fusiform fishes from seven families whereas the Platysomoidei contains deep bodied fishes from the single family Platysomidae (ibid.).

Aldinger (1937) had a very different classification of lower actinopterygian fishes. In this classification there are three orders—Cheirolepidomorpha, Sturiomorpha, and Elonichthyomorpha. Cheirolepidomorpha contains *Cheirolepis* and *Tarrasius*. Sturiomorpha is divided into two suborders—the Chondrosteiformes, which is divided into four families—the Birgeriidae, Polyodontidae, Chondrosteidae, and Acipenseridae; and the Saurichthyiformes which is divided into three families of Mesozoic fishes. The last order, Elonichthyomorpha, is divided into three suborders—the Platysomiformes, Eugnathiformes, and Elonichthyiformes. The Platysomiformes contain families of deep-bodied Paleozoic and Mesozoic fishes. The Eugnathiformes contains Mesozoic fossil fishes considered by other researchers to belong to the Holostei, as well as "remaining Holostei and Teleosti" families (Aldinger, 1937, p. 378). Here, the Holostei and Teleostei are condensed into one suborder. The last suborder, Elonichthyiformes, is interesting in that it contains the families of Paleozoic 'palaeoniscoids' as well as the Brachiopterygii—*Polypterus* and *Erpetoichthys* (Aldinger, 1937). Here, polypterids are placed within the Actinopterygii and aligned with the 'palaeoniscoids.'

Lehman (1966) did not use the divisions of Chondrostei, Holostei, and Teleostei in his classification of the Actinopterygii. Lehman divided fossils within the Actinopterygii into a series of 26 orders (plus unnamed "other orders of Teleostean fishes", p.71). One order, the Paleonisciformes was divided into two suborders—the Palaeoniscoidei and the Platysomoidei. Again, the Palaeoniscoidei contained families of Paleozoic fusiform fishes whereas Platysomoidei contained deep-bodied fishes (ibid.). Other orders include Chondrosteiformes, Acipenseriformes, Amiiformes, and Lepisosteiformes. In the Chondrosteiformes Lehman (1966) included the Mesozoic fossil fish, *Chondrosteus*, but excluded paddlefish, sturgeons, and the fossil *Birgeria* that have been included in the Chondrosteiformes (or equivalents) by other authors (see Aldinger, 1937). The Order Acipenseriformes contained the families Acipenseridae (sturgeons) and Polyodontidae (paddlefish) and the Order Palaeonisciformes contained *Birgeria* (Lehman, 1966). Polypterids were not included in the Actinopterygii, rather they were placed within the Brachiopterygii (ibid.).

Not all accepted the dismantling of the Chondrostei. Gardiner (1967a) retained the Chondrostei, but divided it into 18 different orders. One of the orders, Palaeonisciformes, was composed of 39 families of Paleozoic lower actinopterygians. Moy-Thomas and Miles (1971) also placed the Paleozoic fossil actinopterygian fishes within the Chondrostei, but within the Order Palaeoniscida. The Palaeoniscida was further divided into two suborders—the Palaeoniscoidei, which contain the fusiform fishes, and the Platysomoidei made up of dorsoventrally deepened and laterally compressed fishes (Moy-Thomas and Miles, 1971).

Berg, Kazantseva, and Obruchev limited which fishes were considered to be chondrosteans with the erection of the superorders Chondrostei and Palaeonisci (1964). The superorder Chondrostei was limited to a subset of Mesozoic fishes, sturgeons, and paddlefish. Many families of fishes once lumped into the Chondrostei were placed within the Palaeonisci. The Palaeonisci was further broken down into eight orders—one of which, the Palaeoniscida, has 21 different families of fishes that range from the Devonian to the Cretaceous (ibid.).

Patterson (1973) hypothesized that *Amia* was more closely related to teleosts than to *Lepisosteus*. This meant that the Holostei was a paraphyletic group that needed revision. Patterson (1973) dismantled the Holostei and replaced this category with a new classification of neopterygian fishes based on monophyletic groups. The Halecomorphi was erected to contain amiids and their fossil relatives. The Halecomorphi + Teleostei were placed within the Halecostomi. The Ginglymodi, not a part of the Halecostomi, was erected for the gars. The Ginglymodi + Halecostomi formed the Neopterygii (Patterson, 1973).

Rosen et al. (1981) defined Actinopterygii to include all actinopterygian fishes and resurrected Cope's 1871 Actinopteri for all actinopterygian fishes minus the Cladistia. Actinopterygii was defined as Cladistia + Chondrostei + Neopterygii (ibid.). The Chondrostei contained sturgeons, paddlefish, and their fossil relatives whereas the Cladistia contained polypterids. Patterson (1982) attempted to test the monophyly of and characterize the Actinopterygii and Actinopteri of Rosen et al. (1981). The monophyly of the three main groups—the Neopterygii, Chondrostei, and Cladistia, were all supported, as was the monophyly of the Teleostei, Halecomorphi, Halecostomi, and Ginglymodi (Patterson , 1982). The Palaeonisciformes were found to be paraphyletic (Patterson, 1982). Gardiner (1984) presented a classification that supported both Rosen et al. 1981 and Patterson (1982) with the Actinopterygii defined as Actinopteri + Cladistia and the Actinopteri as the Chondrostei + Neopterygii.

Like Rosen et al., (1981) Lauder and Liem (1983) also recognized the Actinopterygii and Actinopteri. Lauder and Liem (1983) defined the Actinopterygii as including fossil Paleozoic fishes, such as *Cheirolepis* and *Moythomasia,* + Cladistia + Chondrostei + Mesozoic fossil fishes, such as Redfieldiids and Perleids, + Neopterygii. The Actinopteri includes all these groups minus the Paleozoic fossil fish and the Cladistia (ibid). Again, here the Cladistia is considered to be a basal actinopterygian (ibid). Lauder and Liem (1983) recognized that the traditional definition of the Chondrostei did not describe a natural grouping and so used Chondrostei sensu Patterson (1982) to refer to Acipenseridae + Polyodontidae + closely related fossil groups. The Neopterygii included the Halecostomi, Halecomorphi, and Teleostei of Patterson, 1982.

Kazantseva-Selezneva (1982) divided the subclass Actinopterygii into categories on the basis of morphofunctional analysis of the respiratory system of lower actinopterygians. In regards to the palaeoniscoids, the superorder Palaeonisci was formed and divided into three orders—Cheirolepiformes, Palaeonisciformes, and Elonichthyiformes. Cheirolepiformes, and its eight families, was defined by the presence of an epipreoperculum between the operculum and cheek areas (the so called border zone). The Elonichthyiformes, with its four suborders and 26 families, was defined by the presence of a dermohyal in this border zone. The “true” palaeoniscoids, those in Palaeonisciformes, were divided into 13 families that shared the characteristic of an absence of bones in this border area (Kazantseva-Selezneva, 1982).

Carroll (1988) divided Actinopterygii into the Chondrostei and the Neopterygii. One of the orders of the Chondrostei was the Palaeonisciformes, which contains the suborders Palaeoniscoidea and Platysomoidei (ibid.). Other orders within the Chondrostei include the Polypteriformes with modern day polypterids and the Acipenseriformes, which contain extant sturgeons and paddlefish (ibid.). This differs from Rosen et al. (1981), Patterson (1982) and Gardiner (1984) who put polypterids in a separate grouping that was sister to all other actinopterygians. Because the Polypteriformes are placed within the Chondrostei, there is no distinction between Actinopterygii and Actinopteri in this classification. The Neopterygii contains orders of Mesozoic fossil fish, the Amiiformes, and Lepisosteiformes and the Division Teleostei (Carroll, 1988).

Gardiner and Schaeffer (1989) attempted the first computer aided phylogenetic analyses on lower actinopterygian fishes. The authors state that they were not satisfied with the previous classification schemes and attempted to identify monophyletic groups of genera. Not included in the list of monophyletic groups were the ‘palaeoniscoid’ fishes which were found to be paraphyletic (ibid.). Janvier (1996) discussed Gardiner and Schaeffer’s (1989) hypothesis, and presents their phylogeny.

Lund et al. (1995) recovered a clade composed of Paleozoic lower actinopterygians, the Palaeoniscimorpha. The Palaeoniscimorpha was recovered as the sister group to the Neopterygii (Lund et al., 1995).

Nelson (2006) has the class Actinopterygii divided into three subclasses—Cladistia, Chondrostei, and Neopterygii, and so supported the scheme of Patterson (1982). Cladistia contains the polypterids in the order Polypteriformes whereas the Chondrostei is made up of numerous orders and suborders of Paleozoic fossil fish, some Mesozoic fossil fish, and the Acipenseriformes (paddlefish and sturgeons). One order, the Paleonisciformes, is broken down into the suborders Palaeoniscoidei (Paleozoic fishes), Redfieldioidei (Mesozoic fishes) Platysomoidei (deep bodied fishes), and Dorypteroidei (Mesozoic fishes). The Neopterygii contains Mesozoic fossil fish, gars, bowfins and the teleosts.

All of the information above shows that, to date, there is not a stable classification of lower actinopterygians. Specifically important to this work is the uncertainty regarding the Paleozoic lower actinopterygians, those typically referred to as palaeoniscoids. With all of this confusion, what does the term palaeoniscoid refer to? Here, the term palaeoniscoid is used in the common vernacular to refer to the fishes that have been included in Berg's (1940) Palaeoniscoidei, Gardiner's (1967a) Paleonisciformes, Berg, Kazantseva, and Obruchev's (1964) Palaeoniscida, Moy-Thomas and Miles' (1971) Palaeoniscoidei, Lund et al.'s (1995) Palaeoniscimorpha, and Nelson's (2006) Palaeoniscoidei. The term palaeoniscoid refers to lower actinopterygians ranging from the Late Silurian to the Cretaceous that share a similar arrangement of cranial bones (Janvier, 1996; Poplin and Lund, 2002). Palaeoniscoids are generally characterized by a fusiform or elongate fusiform body shape, single triangular dorsal and anal fin, heterocercal caudal fin, immobile maxilla-palato-preopercular complex, and rhombic scales with peg and socket articulation and a histological make-up of an outer layer of ganoine, a middle layer of dentine, and a basal layer of bone (isopedine) (Moy-Thomas and Miles, 1971; Schultze, 1977; Janvier, 1996; Fig. 1). Though recovered as paraphyletic in numerous investigations discussed above and in Chapter 6, palaeoniscoids is recovered as a monophyletic group in this work. Because of these results presented in Chapter 6, the term palaeoniscoid is used here without the use of shutter quotes.

Despite the taxonomic confusion, palaeoniscoids have been described as the primitive or basic actinopterygian that all later forms are traced back to (Moy-Thomas and Miles, 1971). Though considered to be representatives of the ancestral actinopterygian condition, palaeoniscoid fishes are neglected and understudied (Moy-Thomas and Miles, 1971; Carroll, 1988; Janvier, 1996). Many palaeoniscoids remain to be studied and described; thus, little is understood about the diversity and relationships of these fishes.

Why use Fossil Taxa?—There is disagreement on the value of including fossil taxa in phylogenetic analyses. Very damaging is the "Patterson Rule," (so named by Grande, 2000), that states that examples of fossils overturning hypotheses of relationships based on recent organisms are rare or non-existant (Patterson, 1981). There is also the fear that the addition of fossil taxa; which do not preserve information regarding soft anatomical structures, physiology, molecules, behavior, etc., and may be represented by incomplete and poorly preserved specimens; may actually add unknown or missing data and increase the number of possible trees (Gauthier et al., 1988). These concerns can lead researchers to opt for excluding extinct taxa from analyses and to rather fit the fossil taxa to the tree post analysis (Gauthier et al. 1988).

While there is the concern that fossil taxa and their missing data may be harmful or at least not helpful in the formation of hypotheses of relationships, there are many examples in the literature that do not support this statement. Simulation work has shown that the addition of fossil taxa can lead to better phylogenetic resolution (Huelsenbeck, 1991; Wiens, 2005). Recent simulations studies designed to investigate the effects of fossils on the number of most parsimonious trees and measures of homoplasy in parsimony analyses performed by Cobbett et al. (2007) suggest that these metrics did not change with the addition of fossil taxa.

The inclusion of fossils may lead to better phylogenetic resolution in cases in which the extant group in question is old and represented by a few highly modified taxa (Gauthier et al., 1988; Huelsenbeck, 1991; Wiens, 2005). This could occur because fossil taxa show combinations of character states that are not seen in the extant taxa, and so help bridge problematic morphological gaps (Cobbett et al., 2007). The use of fossil taxa is necessary to investigate the relationships of extinct forms, but it is also important in clarifying the relationships of the extant. Three examples with actinopterygians illustrate this point.

Example one: Holostei—The Holostei, a clade that includes bowfins + gars, was resurrected by a study that included fossilized forms in morphological and phylogenetic analyses (Grande, 2010). As explained previously, in 1973, Patterson dismantled the Holostei and erected the Ginglymodi, the Halecomorphi, and the Halecostomi. Since 1973, these groupings were recovered by other researchers (Wiley, 1976; Lauder and Liem, 1983; Gardiner et al., 1996) and widely accepted and used. But, there was morphological (Olsen and McCune, 1991) and molecular evidence (Normark et al., 1991; Kikugawaa et al., 2004; Hurley et al., 2006; Chenhong et al., 2008) that did not support a monophyletic Halecostomi, but rather a monophyletic Holostei. In 2010, Grande resurrected the Holostei based on morphological studies of extant and fossil amiid and gar specimens, as well as a reevaluation of other neopterygians. One of the most important findings was the discovery of an interoperculum in a newly described genus of fossil gar that eliminated a supposed synapomorphy of the Halecomorphi. Overall, Grande's reassessment eliminated five of the seven purported Halecomorphi synapomorphies and found the remaining two to be unclear (2010). Morphological evidence supported a monophyletic Holostei. Grande (2010) concluded that if only extant fishes are included, important morphological details are missed and a monophyletic Holostei is not recovered. Only with the addition of the fossilized forms was the relationship between gars and bowfins recovered by morphological analysis (ibid.).

Example two: *Polypterus*—Conflicting hypotheses regarding the phylogenetic position of the extant lower actinopterygian *Polypterus* illustrate how with such a long evolutionary history, extinct lower actinopterygians may be critical to understanding the relationships among extant actinopterygians. From the above review of the systematics of actinopterygians, it is clear that the position of polypterids has been very controversial. Polypterids have been placed within the Sarcopterygii or Crossopterygii (Huxley, 1861; Cope, 1871), the Actinoptergyii (Romer, 1945; Gardiner, 1967a), the Actinopterygii but not the Actinopteri (Rosen et al., 1981; Patterson, 1982), and in their own grouping separate from the Actinopterygii and Sarcopterygii (Goodrich, 1909; Lehman, 1966; Jessen, 1973). While it is now widely accepted that polypterids are actinopterygians, their relationships to other actinopterygians remain controversial. In phylogenetic analyses, polypterids have been recovered in two different positions—either as the basal-most actinopterygian, or well embedded in the actinopterygian tree.

The first scenario, polypterids as the basal-most actinopterygian, seems to be recovered when the extant *Polypterus* is included in analyses with high numbers of advanced or recent actinopterygians and little to no Devonian and Carboniferous forms, regardless of whether they are morphological studies (Nelson, 1969; Bemis et al., 1997) or molecular investigations (Lê et al., 1993; Venkatesh et al., 2001; Inoue et al., 2003). This said, there are other morphological analyses that do contain numerous Paleozoic taxa that result in a basal placement of the polypterids (Gardiner, 1984; Gardiner, and Schaeffer, 1989; Coates, 1998, 1999).

Fossil-based divergence estimates for polypterids date from the Mid-Devonian, or 392 million years ago (Hurley et al., 2006). This is somewhat problematic because the fossil record of polypterids does not support these estimates. Overall, the fossil record of polypterids is poor, both in terms of number and preservation of specimens and localities (Greenwood, 1984). Ten fossil genera are known—two that have been described on the basis of isolated bones and scales, six on the basis of the articular heads of pinnules, one on an articulated skeleton missing the head (Dutheil, 1999) and one, a fossil species within *Polypterus*, is known from an articulated complete specimen (Ortero et al., 2006). The majority of fossil polypterids are recovered from Africa, which is where extant polypterids are confined to, though two genera of fossil polypterids have been recovered from South America (Greenwood, 1984; Otero et al., 2006). The earliest evidence of a polypterid comes from the Cenomanian (Cretaceous) of Africa (Gayet et al., 2002).

If this divergence rate is correct, then polypterids are a prime example of a ghost lineage that extends from the Cretaceous to the Devonian.

Also, while numerous authors find that *Polypterus* is a basal actinopterygians, there is evidence of polypterids having a higher phylogenetic position. Paleohistological work regarding the scales of *Polypterus* has shown that polypterid scales are more similar to those of the Triassic *Scanilepis* than those of the basal actinopterygian *Dialipina* and other Devonian actinopterygians (Aldinger, 1937; Schultze, 1968). A close relationship between *Polypterus* and the Triassic scanilepiform *Evenkia* has also been hypothesized based on shared characteristics of the scales, dorsal fin, lobed pectoral fin, caudal fin, and cranial bones (Sytchevskaya, 1999). It should then not be surprising that polypterids are not always recovered as the basal-most actinopterygian in phylogenetic analyses.

When the ingroup includes high proportions of early actinopterygians from the Devonian and Carboniferous, there is support for a higher phylogenetic position of the Polypteriformes. In Lund's (2000) analysis of *Polypterus* and 12 Paleozoic actinopterygians, *Polypterus* is not recovered as a basal taxon. *Polypterus* is well embedded in the topology of the tree and is the sister taxon to the advanced Paleozoic order Guildayichthyiformes (Lund, 2000). Cloutier and Arratia's (2004) analysis of lower actinopterygians also includes a high proportion of Devonian and Carboniferous forms. Here, *Polypterus* groups with other advanced lower actinopterygians (*Amia calva, Leptolepis coryphaenoides, Lepisosteus,* and *Acipenser*) and together they are recovered as sister to the Guildayichthyidae and Tarrasiidae (Cloutier and Arratia, 2004). Mickle et al. (2009) also recovered *Polypterus* as sister to the Guildayichthyidae and *Polypterus* + Guildayichthyidae is recovered as sister to neopterygians. It should be noted that a member of the Guildayichthyidae, *Discoserra pectinodon*, has recently been hypothesized to be a stem neopterygian (Hurley, et al., 2006). In these analyses, polypterids are recovered as sister to the Guildayichthyidae, or within a clade that is sister to the Guildayichthyidae, and are well embedded within the actinopterygian tree (Lund, 2000; Cloutier and Arratia, 2004; Mickle et al., 2009).

The position of *Polypterus* within actinopterygians as a whole appears to depend on the inclusion or exclusion of early fossilized forms. Extinct lower actinopterygians are critical to understanding the relationships of extant lower actinopterygians, and may also be important in the understanding of the diversification and success of actinopterygians in general.

Example three: neopterygians—There is a discrepancy between the ages of neopterygian fishes recovered by morphological and molecular analyses. Morphological data, based on the first fossil occurrences of neopterygian fishes, support the hypothesis that the diversity of fishes today is a product of radiations that took place at the end of the Paleozoic and in the Mesozoic (Hurley et al., 2006). In contrast, molecular data suggest that today's diversity is a product of radiations that occurred early in the Paleozoic (Hurley et al., 2006). Hurley et al. (2006) provided morphological evidence to support the molecular results with an actinopterygian from the Carboniferous Bear Gulch Limestone (MT, USA), *Discoserra pectinodon* (Lund, 2000). *Discoserra* was recovered as an advanced stem-group neopterygian (Hurley et al., 2006). As such, Hurley et al. (2006) concluded that *Discoserra,* which possesses neopterygian apomorphies, supports the assertion that neopterygian characters evolved by the end of the Early Carboniferous and are not a product of the Mesozoic.

Why the discrepancy between ages based on morphological and molecular data? Hurley et al. (2006) suggested that it may be because lower actinopterygians are "among the least studied of all fossil vertebrates" and that neopterygians have not yet been identified from the Paleozoic.

More work must be done to describe and investigate fossil lower actinopterygians and phylogenetic analysis with more fossil forms is needed to test this hypothesis (Hurley et al., 2006).

Review of phylogenetic hypotheses of relationships—Given the paucity of available data, it is no surprise that the phylogenetic investigations of palaeoniscoids have produced incongruent hypotheses of relationships (reviewed by Cloutier and Arratia, 2004; Friedman and Blom, 2006). Currently, the majority of recent phylogenetic analyses (reviewed by Cloutier and Arratia, 2004) have resulted in the recovery of paraphyletic groupings of Paleozoic palaeoniscoids. Familial level relationships are typically not tackled; instead, analyses typically focus on the level of genera. The majority of previously published investigations into the relationships of lower actinopterygians have recovered palaeoniscoids as a paraphyletic grouping of more than 250 extinct genera with a similar arrangement of cranial bones (Janvier, 1996; Poplin and Lund, 2002). In general these analyses recovered a comb of palaeoniscoid genera. Devonian forms typically are separated from Permocarboniferous forms and some of the later Paleozoic forms appear to be closely related to Mesozoic and extant fishes (Cloutier and Arratia, 2004; Mickle et al., 2009; Fig. 2, above).

To date, neither a stable classification system nor hypothesis of relationship for these fishes exists. This is attributed to several causes, but according to Cloutier and Arratia (2004), among the most important is the need for:

1. **More well-preserved Paleozoic fishes to be described and/or redescribed**
2. **A better understanding of characters among lower actinopterygians, and**
3. **More Paleozoic forms to be included in phylogenetic analyses.**

This study seeks to investigate the interrelationships of lower actinopterygian fishes, specifically those lumped into the palaeoniscoid grouping in a comprehensive phylogenetic study. The ultimate goal of this study is to **dismantle the paraphyletic groupings of palaeoniscoids by identifying the characters that support monophyletic groups of these fishes**. Potentially important **phylogenetic characters will be studied in depth for a variety of actinopterygian fishes—extinct and extant.** This study also seeks to answer the questions: **What are the relationships between the extinct fishes and extant lower actinopterygians? Is there morphological evidence to support the existence of stem-group neopterygians in the Paleozoic?** To answer these questions, phylogenetic analysis must be performed on a large pool of lower actinopterygian fishes from the Devonian to the Recent. To increase taxon sampling, more Carboniferous palaeoniscoids, especially Early Carboniferous forms to bridge between the Devonian to the Carboniferous, will be described. This will increase our understanding of the diversity of the fishes that are the roots of the extant forms. A suite of morphological characters that traditionally has been considered important to our understanding of the evolution of actinopterygians, but never truly studied in a phylogenetic context, will be investigated for extinct and extant actinopterygians. The goals of the following chapters are described below.

Chapter 2: Reevaluation of the snout in lower actinopterygians—The snout of lower actinopterygians presents a great amount of morphological diversity. A review of the literature shows that there is no standardized nomenclatural scheme used by the community to identify individual bones in the snout. This makes comparing taxa from different localities and building character matrices for phylogenetic analyses much more difficult than it needs to be and potential sources of error. In Chapter 2, reasons for multiple nomenclatural schemes for the identification of the bones of the snout in lower actinopterygians are discussed. A new nomenclature scheme that proposes new definitions of snout bones in lower actinopterygians is proposed. This nomenclature scheme proposes that bones should be identified on the basis of certain morphological characters. Previously described Devonian and Carboniferous fishes are reinterpreted using the newly proposed criteria and morphological patterns are revealed.

Chapter 3: Character study of the preoperculum and associated bones—One specific character that has previously received much attention is the preoperculum. It has been proposed that changes in the configuration of the preopercular bones and the underlying suspensorium have gradually occurred across "primitive" Paleozoic palaeoniscods, "more advanced" subholosteans, and holosteans (Gregory, 1932; Brough, 1939; Schaeffer, 1956; Schaeffer and Rosen, 1961; Gardiner, 1967b). A fundamental problem with this hypothesis is that it never has been investigated in a phylogenetic context, nor has it been examined in a systematic fashion. Past publications dealing with the importance of the preopercular bone (Schaeffer, 1956; Schaeffer and Rosen, 1961; Gardiner, 1967b) provide few examples of the preopercular condition of Paleozoic, Mesozoic, and Recent fishes. These papers do not take into account or investigate, the great diversity the preoperculum shows in these fishes.

Chapter 3 seeks to test the strength of this hypothesis by examining the preopercular condition of a broad array of fishes. This study has shown that the preopercular bone is characterized by a staggering diversity of shapes, inclinations, number of individual elements, and associations with other bones. The conventional wisdom that there is a gradual and progressive change from the primitive palaeoniscoid to a more advanced condition in holostean and teleostean fishes is a gross oversimplification. This diversity is examined for a large subset of Paleozoic, Mesozoic, and Recent fishes in a phylogenetic light for the first time.

Chapters 4–5: Descriptions of Paleozoic fishes—Carboniferous fishes are described in Chapters 4–5. The concentration on Carboniferous fishes is deliberate—though the earliest articulated actinopterygian is known from the Early Devonian (*Dialipina,* Schultze and Cumbaa, 2001), whole actinopterygians from this period remain rare (with the exception of *Cheirolepis* and the remarkable actinopterygians from the Gogo Formation of Australia (Gardiner, 1984; Long, 1988a)). It is not until the Carboniferous that actinopterygians are abundant and diverse, suggesting that a radiation of these fishes took place at the end of the Devonian/beginning of the Carboniferous (Janvier, 1996). It is the Carboniferous actinopterygians that show relationships to more advanced and extant forms. Fishes from two North American Carboniferous sites—the Upper Mississippian/Lower Pennsylvanian Manning Canyon Formation of Utah and the Mississippian Albert Formation of New Brunswick, Canada will be described in Chapters 4–5, respectively. The Early Mississippian Albert Formation fishes are especially important because if a radiation of these fishes occurred at the end of the Devonian/beginning of the Carboniferous, these fishes are products of the first actinopterygian radiation.

Chapter 6: Phylogenetic analyses— Most recent phylogenetic analyses (reviewed by Cloutier and Arratia, 2004) have recovered paraphyletic groupings of palaeoniscoids. Analyses differ drastically between the number of taxa included—from 5 to 50 (Zhu and Schultze, 2001; Dietze, 2000); number of characters, and outgroup choice—chondrichthyan, placoderm and acanthodians (Zhu and Schultze, 2001); sarcopterygians (Schultze and Cumbaa, 2001); and basal actinopterygians (Gardiner and Schaeffer, 1989; Coates, 1998; Cloutier and Arratia, 2004).

Many analyses are performed with different end goals in mind. Some analyses concentrate solely on the relationships of Devonian forms and only include fishes from this period (i.e., Friedman and Blom, 2006; Long et al*.*, 2008). Other analyses are concerned with investigating the relationships of specific groups (*e.g.*, the Tarrasiiformes, Taverne, 1996, 1997; Lund and Poplin, 2002), whereas others are designed to investigate relationships of basal osteichthyans as a whole (Zhu and Schultze, 2001). Emphasis on certain taxa or time periods undoubtedly affects resulting hypotheses of relationship and makes comparing the different results difficult.

The goal of this chapter is to include as many actinopterygian fishes as possible from the Devonian to the Recent in phylogenetic analyses, especially forms that have not been represented in previous analyses. It is hoped that as more species and characters are discovered, described, and included in phylogenetic analyses, the interrelationships of these fishes will become clearer. A matrix that is a compilation of previously published matrices, with the addition of new taxa and characters, is employed. For the first time, Bayesian methodologies are used to investigate the relationships of lower actinopterygians. Results from Parsimony and Bayesian analyses are compared.

SUMMARY OF GOALS

The main goal of this study is to show the importance of fossil palaeoniscoid fishes for the systematic and phylogenetic understanding of the interrelationships of actinopterygians below teleosts. To accomplish this, the following objectives must be met: (1) increase taxon and character sampling for phylogenetic analyses of lower actinopterygians; (2) perform phylogenetic analyses to investigate the relationships of lower actinopterygians; (3) investigate the relationships of extinct and extant lower actinopterygians; (4) increase the understanding of palaeoniscoid diversity by describing more Carboniferous forms from a variety of North American sites; (5) present a new standardized nomenclatural scheme for identifying the bones in the snout of lower actinopterygians; (6) reinterpret the snouts of previously described Devonian and Carboniferous lower actinopterygian in an attempt to reveal morphological patterns in Devonian and Carboniferous forms; and (7) test hypotheses regarding the importance of the preopercular bone in the evolution of actinopterygians. It is hoped that lower actinopterygians, and specifically palaeoniscoids will no longer have the distinction of being one of the "least studied" and understood fossil vertebrates (Hurley et al., 2006).

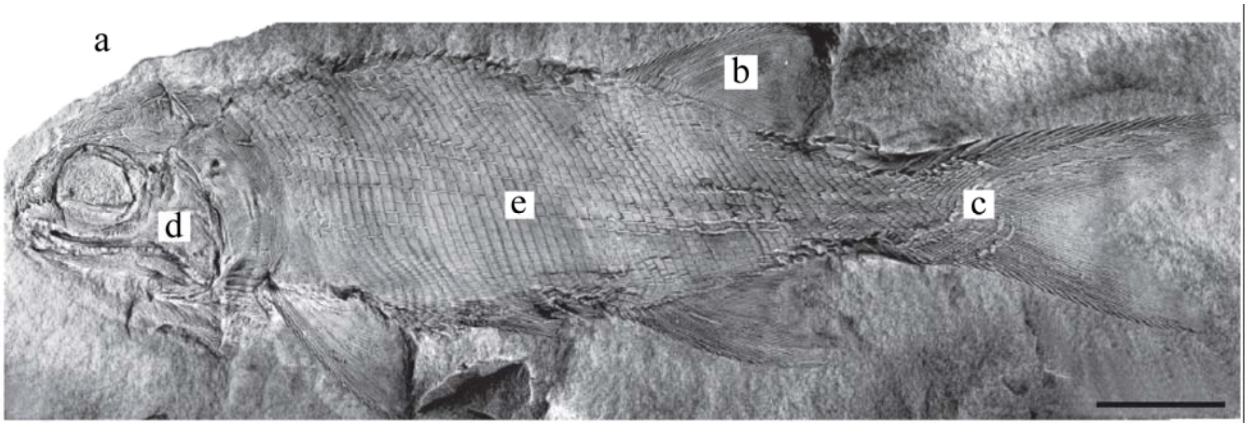


Figure 1—Common palaeoniscoid characteristics. Labels represent: **a.** elongated fusiform body shape **b.** single triangular dorsal fin, **c.** heterocercal caudal fin, **d.** immobile maxilla-palato-preopercular complex, **e.** rhombic scales. Specimen from the Bear Gulch Limestone, MT, CM35349 (Mickle et al., 2009).

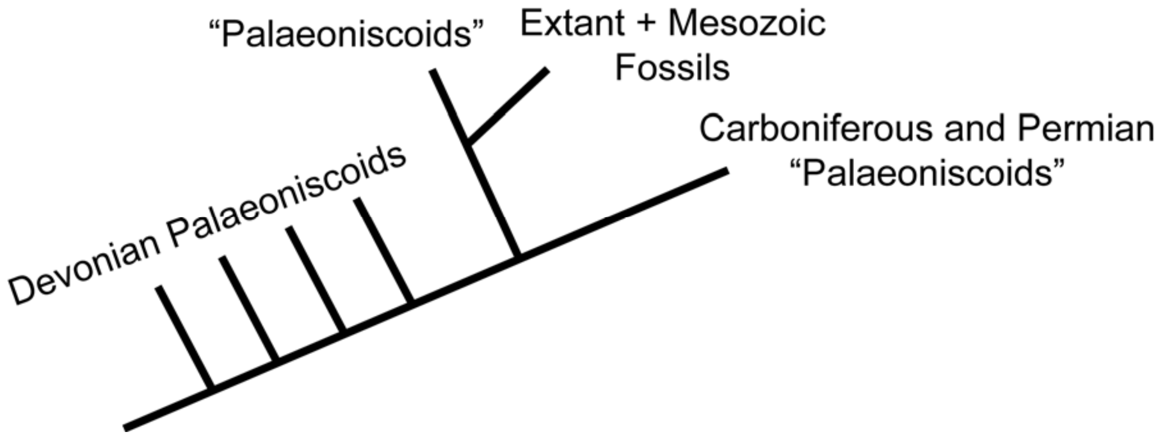


Figure 2—Generalized tree of relationships for palaeoniscoid fishes. Based on trees from Cloutier and Arratia, 2004 and Mickle et al. (2009).

CHAPTER TWO—IDENTIFICATION OF THE BONES OF THE SNOUT IN LOWER ACTINOPTERYGIANS—A NEW NOMENCLATURE SCHEME BASED ON CHARACTERS

ABSTRACT

Currently, there is no standardized nomenclatural scheme for identifying and naming the bones of the snout in lower actinopterygian fishes. This creates a situation where the same bone names are used to identify very different bones. This is problematic because it makes comparing taxa described by different scientists difficult and presents potential pitfalls for building character matrices for phylogenetic analyses. Because of the problems the absence of a standardized nomenclature scheme presents, a new set of rules for the identification of the bones of the snout of lower actinopterygians is proposed here. The new definitions are based on the presence of characters that are commonly preserved such as the presence or absence of sensory canal lines, location of bones in relation to other bones, and whether or not the bones contribute to the formation of the nasal openings. When numerous characters are present in a single bone, this bone is considered to be a complex bone and the name reflects this. The snout bones of various Devonian and Carboniferous actinopterygians are re-identified using this new nomenclature scheme. This has led to the identification of patterns regarding the makeup of the snout in Devonian and Carboniferous fishes and has implications for future phylogenetic studies.

INTRODUCTION

The snout region of lower actinopterygians is characterized by a great deal of diversity, specifically in regard to the number of individual bones present. Though this diversity has been the subject of much investigation (Nielsen, 1942; Westoll, 1944; Gardiner, 1963, 1984; Poplin and Lund, 1995, 1997; Arratia and Cloutier, 1996; Schultze, 2008) a consensus regarding the identities of the snout bones or what the primitive make-up of the actinopterygian snout is, has not been reached. Instead, investigations have led to multiple hypotheses on the evolution of the snout in actinopterygians and conflicting nomenclatural schemes.

The different hypotheses regarding the evolution of the actinopterygian snout can be divided into two categories—those supporting a primitive macromeric pattern of snout bones (e.g. Gardiner, 1963, 1984) and those supporting a mesomeric pattern (e.g. Poplin and Lund, 1995). A primitive macromeric snout would have a few large bones (e.g., *Dialipina*). In different lineages, these bones would be fragmented into smaller bones. A primitive mesomeric snout would be composed of numerous bones (e.g., *Cheirolepis*). These bones would fuse or be lost in different lineages to produce the diversity seen in actinopterygians. Some of the classical macromeric and mesomeric hypotheses are discussed below. It is suggested in this paper that a standardized nomenclatural scheme where bones are identified on the basis of physical characteristics such as the presence of sensory canals and nasal openings or the location of the bone in relation to surrounding bones should be utilized. Such identifications are attempts at identifying homologous structures across different taxa following Remane's (1952, 1956) criteria of similarity in position and detail. Such a nomenclatural scheme is proposed and employed to redescribe the pattern of snout bones in a variety of Devonian and Carboniferous lower actinopterygians.

Macromeric Snout Hypotheses (Gardiner, 1963, 1984)

Postrostral, Nasals, and Rostro-premaxillo-antorbitals--Gardiner (1963) identified the primitive actinopterygian snout as being composed of three bones—the postrostral, rostro-premaxillo-antorbitals, and nasals. Gardiner defined the postrostral as a median anamestic bone, laterally bordered by the nasal bones that may or may not contribute to the formation of the border of the medial nasal opening. The nasal bones are paired, bear the supraorbital canal, and are notched along the medial and anterio-lateral margins of the bone to form the lateral border of the medial nasal opening, and the anterior-medial border of the lateral nasal opening, respectively (ibid.). The third and final bone is the paired rostro-premaxillo-antorbital (Gardiner, 1963). This bone is primitively toothed and bears a tripartite canal formed by the ethmoid commissure, the supraorbital, and infraorbital (ibid.).

Gardiner (1963) contended that all diversity in the actinopterygian snout can be accounted for by the fragmentation of some or all of these three bones. Three different bone patterns could results from such fragmentations. The first and most common pattern is the rostro-premaxillo-antorbital (antorbital is also known as the lachrymal) fragmenting into a rostro-premaxilla and an antorbital (lachrymal). The rostro-premaxilla bears the ethmoid commissure and is toothed, whereas the antorbital (lachrymal) bears the junction of the infraorbital and supraorbital canals (ibid.). This would result in four bones in the snout—nasals, postrostral, rostro-premaxilla, and antorbitals. Further diversity includes whether or not the antorbital (lachrymal) bone is part of the oral margin and toothed, or whether it is edentulous and not a part of the upper jaw margin (ibid.).

The snout with separate antorbital (lachrymal), premaxillary, rostral, postrostral, and nasal bones is the result of another fragmentation. The rostro-premaxilla can fragment into separate rostral and premaxillary bones. The premaxilla is typically toothed and is anamestic, whereas the rostral bone bears the ethmoid commissure.

Gardiner (1963) explained all of the diversity in the actinopterygian snout as being a result of various fragmentations of this primitive three boned snout. Further diversity could be described via a loss of bones or a fusion of bones (ibid).

Rostral, Nasal, Premaxillary Bones—In 1984, Gardiner reversed and revised his hypothesis about the actinopterygian snout. Instead of a primitive three bone pattern of a median anamestic postrostral, paired nasals, and paired rostro-premaxillo-antorbital, Gardiner (1984) redescribed the primitive actinopterygian snout as having a median rostral, paired premaxillary, and paired nasal bones, all of which bear sensory canals. The ethmoid commissure transverses the rostral bone, the nasals bear the supraorbital canal, and the premaxillae bear the junction of the ethmoid, supraorbital, and infraorbital canals (ibid.). This hypothesis explains the make up of the snouts of the Devonian *Mimipiscis* (Choo, 2011; *Mimia* of Gardiner and Bartram, 1977) and *Moythomasia* described by Gardiner in the same work and supported by the presence of similar bones in the sarcopterygian *Holoptychius* (ibid.). Though not discussed by Gardiner, it can be assumed that a fragmentation of these bones have led to the diversity seen in later actinopterygians.

Mesomeric Snout Hypothesis (Poplin and Lund, 1995, 1997)

Rostral, Postrostral, Nasals, Premaxillary, and Antorbital (Lachrymal) Bones—Poplin and Lund (1995; 1997) discuss how the rostral, postrostral, premaxillary, and antorbital bones can be separate, fused, or lost in different lineages. This diversity is explained as being a product of a primitively micromeric or mesomeric snout and subsequent fusions or losses of the premaxillary bone (ibid.). Poplin and Lund (1995, 1997) support the claims of a mesomeric pattern with evidence from larval polypterids, which have separate ossifications that fuse later in development. The general condition of the snout of sarcopterygians is also used by Poplin and

Lund (1995, 1997) as further evidence. Overall, Poplin and Lund (1995, 1997) claimed that the primitive pattern of bones in the snout of actinopterygians consists of separate rostral, postrostral, premaxillary, antorbital, and nasal bones. For the premaxillary bones specifically, Poplin and Lund (1997) claimed that the premaxillae are separate and distinct bones in basal actinopterygian larvae. These separate premaxillae can fuse to surrounding bones later in development, remain separate bones in adults via neoteny, or can be lost completely (ibid.).

Poplin and Lund (1995) discussed another pattern regarding the rostral and postrostral bones. Often, there is a large median bone in the snout that bears the ethmoid commissure near its ventral margin. Poplin and Lund (1995) mentioned that this bone has been referred to as a rostral, a shield-like rostral, or a postrostral. Poplin and Lund (1995) named this bone a rostro-postrostral and consider it to be the result of a fusion of the canal bearing rostral to the anamestic median postrostral.

A NEW STANDARDIZED NOMENCLATURAL SCHEME

The need

The various hypotheses regarding the primitive condition of the actinopterygian snout have led to snout bones being identified differently by different workers. The assignment of names to the bones in the snout varies throughout the literature, creating much confusion. To illustrate—the bone name ‘rostral’ has been used to describe a median bone that is notched on its lateral borders and contribute to the formation of the medial nasal opening (e.g. *Mimipiscis* and *Moythomasia,* Gardiner, 1984) and paired bones that are not notched (e.g. *Canobius*, *Rhadinichthys canobiensis,* Moy-Thomas and Bradley Dyne, 1938; *Kentuckia deani* Rayner, 1951); a bone that bears the ethmoid commissure (e.g. *Mimipiscis* and *Moythomasia,* Gardiner, 1984) and bones that bear the tripartite canal (e.g. *Canobius*, *Rhadinichthys canobiensis,* Moy-

Thomas and Bradley Dyne, 1938; *Kentuckia deani* Rayner, 1951); a median bone that comes in contact with the frontal/parietal bones (e.g. *Mimipiscis* and *Moythomasia,* Gardiner, 1984), or where another bone, the 'postrostral', is intercalated (e.g. *Canobius*, *Rhadinichthys canobiensis,* Moy-Thomas and Bradley Dyne, 1938; *Kentuckia deani* Rayner, 1951).

The term 'postrostral' has been used to refer to small, variable bones (e.g. *Cheirolepis canadensis* Arratia and Cloutier, 1996; *Gogosardinia coatesi* Choo et al., 2009) as well as large median bones notched to form the nasal openings (e.g. *Cheirolepis trailli* Pearson and Westoll, 1979; *Canobius, Rhadinichthys* Moy-Thomas and Bradley Dyne, 1938; *Kentuckia,* Rayner, 1951; *Kalops* Poplin and Lund, 2002). 'Postrostral' bones have been described as anamestic (e.g. *Cheirolepis canadensis* Arratia and Cloutier, 1996; *Gogosardinia coatesi* Choo et al., 2009) or bearing sensory canals (e.g. *Canobius* Moy-Thomas and Bradley Dyne, 1938).

The name 'premaxilla' has been used to describe anamestic toothed bones anterior to the maxilla (e.g. *Kalops* Poplin and Lund, 2002; *Beagiascus* Mickle et al., 2009), as well as bones that bear sensory canals (e.g. *Cheirolepis trailli* Pearson and Westoll, 1979; *Mimipiscis* and *Moythomasia* Gardiner, 1984). Bones contributing to the anteroventral corner of the orbit (e.g. *Howqualepis rostridens* Long, 1988b; *Mimipiscis* and *Moythomasia* Gardiner, 1984) or excluded from the orbit (*Beagiascus* Mickle et al., 2009) have both been termed the 'premaxillae.'

The term 'lachrymal' has been used to describe a bone in the anteroventral corner of the orbit that bears the tripartite canal as well as the rectangular bone ventral to the orbit that bears only the infraorbital canal (e.g. *Mansfieldiscus sweeti,* Long, 1988b). The bone in the anteroventral corner of the orbit bearing the tripartite canal has also been termed an 'antorbital' (*Cyranorhis* and *Wendyichthys,* Lund and Poplin, 1997*; Beagiascus* and *Lineagruan* Mickle et al., 2009).

These discrepancies cause confusion when comparing fishes described by different scientists and poses potential problems for coding characters for phylogenetic analyses. The continued use of the same terms for bones that differ in terms of placement, association with other bones, and presence or absence of sensory canal lines, should not continue.

Newly proposed nomenclatural scheme

While it may seem that conflicting nomenclature schemes could be remedied by a strong hypothesis regarding the primitive condition of the actinopterygian snout, such a hypothesis does not exist. Evidence from larval polypterids has been used to support a mesomeric snout hypothesis, but it should be remembered that the fossil record of polypterids only extends back to the Cretaceous and that our understanding of the identities and homologies of the cranial bones in *Polypterus* is poor (Greenwood, 1984; Gayet et al., 2002; Cloutier and Arratia, 2004). The fact that there are separate premaxillary bones in larval polypterids that fuse to surrounding bones later in development does not necessarily mean that the same occurred in Paleozoic larval fishes.

Evidence from sarcopterygians, specifically dipnoans which have numerous bones in the snout region, has also been used as support for a mesomeric pattern, but other sarcopterygians present a different pattern. Primitive sarcopterygians like *Meemania, Psarolepis,* and *Youngolepis,* have a few large bones that form a snout that is similar to that of primitive actinopterygians (Schultze, 2008). *Psarolepis* (Yu, 1998) and *Diabolepis* (Chang and Yu, 1984) have a single median rostral bone flanked by canal bearing premaxillary bones. Schultze (2008) pointed out that this suggests that lower actinopterygians present the basal osteichthyan condition. The sarcopterygians with multiple small bones in the snout may be derived and not the best comparison to determine if the primitive actinopterygian snout was macromeric or mesomeric.

Though, it should be noted that *Cheirolepis* is also characterized by the presence of many small, and variable, bones in the snout. In fact, the snout of *Cheirolepis,* with its multiple rostral bones, is more similar to some sarcopterygians fishes rather than actinopterygian fishes (Arratia and Cloutier, 1996). Early actinopterygians show patterns similar to sarcopterygians with large snout bones as well as sarcopterygians with a mesomeric pattern. Because of this, there is not enough evidence to describe the actinopterygian primitive condition using similarities with sarcopterygians.

In the absence of developmental evidence, it is most parsimonious to follow the suggestion of Schultze (2008) and to consider the snout being made up of a complex of bones. Such a complex has characters (i.e. presence of canals, teeth, placement in regard to other bones, etc) that are separated into distinct bones in more advanced actinopterygians. For example—the premaxillae are not separate anamestic bones in Devonian actinopterygians. Instead, Schultze (2008) proposes that the premaxilla is part of a complex of bones in which individual bones are not visible. An example of this complex would be the 'premaxilla' described in *Mimipiscis*, *Moythomasia*, *Howqualepis*, and *Gogosardinia* (Gardiner, 1984; Long, 1988b; Choo et al., 2009). This bone fills the space of the premaxillary and lachrymal bones and contains characters that define all of these bones (teeth, position anterior to the maxilla, forming anteroventral margin of orbit, bearing the tripartite canal). Consequently, this bone should be termed a premaxillo-lachrymal.

As proposed by Nielsen (1942), Gardiner (1963), and Poplin and Lund (1995, 1997) compound bone names should be used for these complex bones. It must be stressed that here, the use of such names is not done to support a certain hypothesis regarding the primitive state of the actinopterygian snout. Calling a bone a premaxillo-lachrymal because it takes the place of those bones and presents characters that are found in separate bones in some actinopterygians is not done with an underlying idea of how these have formed. The compound bone name just presents information on the characters and placement of the bones, as well as the lack of sutures to distinguish them as separate bones. Another thing that should be noted when trying to determine what is the primitive condition of the actinopterygian snout is that it may be more prudent to treat the snout as separate modalities rather than a cohesive whole. There is no reason to support one common pattern for all the bones in the snout region of actinopterygians.

Snout bone definitions

Definitions of individual bones and the characters that define these bones are listed below, with examples of taxa that possess these bones. Definitions of complex bones are also explained.

Premaxilla—The premaxilla is an anamestic paired bone that is toothed and contributes to the anterior oral rim of the upper jaw. A separate and distinct premaxillary bone is seen in *Kalops* (Poplin and Lund, 2002; here Figure 4C), *Beagiscus* (Mickle et al., 2009; here Figure 7C) and others listed in Table 1. This bone is commonly part of a bone complex in Devonian and Carboniferous forms (Table 1, Figures 2A, 5AC).

Rostral—The rostral bone bears the ethmoid commissure and is notched to form the medial margins of the medial nasal opening (though these characters can be separated into two different bones; see below). A single rostral bone is seen in *Dialipina* (Schultze, 1992; Schultze and Cumbaa, 2001; here Figure 1), *Gogosardinia* (Choo et al., 2009; here Figure 4AB) and others listed in Table 1.

Dorsal and Ventral Rostrals—The characters that define the rostral bone—the presence of the ethmoid commissure and the notches that form the medial margins of the medial nasal opening, can be separated into two different bones. These bones are termed the dorsal and ventral rostral bones. The ventral rostral bone bears the ethmoid commissure, whereas the dorsal rostral bone is notched on its lateral margins. Dorsal and ventral rostral bones are present in *Kalops* (Poplin and Lund, 2002; here Figure 4C,D) and others listed in Table 1. Ventral rostral bones can be part of larger complex bones, as described below.

Postrostral—The postrostral(s) is/are an anamestic bone(s) that come(s) in contact with the anterior margins of the frontal/parietal bones, often separating the paired skull roofing bones anteriorly. Postrostral bones are seen in *Dialipina* (Schultze, 1992; Schultze and Cumbaa, 2001; here Figure 1), *Cheirolepis* (Pearson and Westoll, 1979; Arratia and Cloutier, 1996; here Figure 2), *Gogosardinia* (Choo et al., 2009; here Figure 4A, B) and other listed in Table 1. Postrostrals do not carry the ethmoid commissure, nor are they notched to contribute to the formation of nasal openings. This definition is different from that of Nielsen (1942) and Poplin and Lund (1995), among others.

Lachrymal—A bone that bears a tripartite canal formed by the fusion of the infraorbital and supraorbital canals and the continuation of the infraorbital canal as the ethmoid commissure into the rostral bone. The lachrymal usually contributes to the anteroventral corner of the orbit. Lachrymal bones are present as separate and distinct bones in *Lineagruan, Beagiscus,* (Mickle, et al., 2009; here Figure 7A–D) and others listed in Table 1. The lachrymal bone is part of a bone complex in many Devonian and Carboniferous fishes (Table 1; Figures 4A,B; 5A–F).

Nasal—The nasal bone is paired, flanks the rostral and/or postrostral bones, and bears the supraorbital canal. Nasal bones are typically notched laterally to form the lateral margin of the medial nasal opening and the medial margin of the lateral nasal opening. There can be more than one nasal bone as in *Cheirolepis trailli* (Pearson and Westoll, 1979, here Figure 2C) and *Paratarrasius hibbardi* (Lund and Melton, 1982; here Figure 3E, F). Nasal bones are present in all lower actinopterygians and the identification of this bone is practically unproblematic (See Table 1).

Infraorbital 2—The lachrymal is considered to be the first infraorbital bone. The second infraorbital is a rectangular bone bearing the infraorbital canal ventral to the orbit (Table 1). Paleozoic actinopterygians usually have one infraorbital bone ventral to the orbit—this is fragmented in *Amia* to form two infraorbital bones (Grande and Bemis, 1998).

Infraorbital 3/Jugal—In palaeoniscoids the infraorbital bearing bone in the posteroventral corner of the orbit is typically the third infraorbital bone (see Figures 4, 5 for examples). This bone is typically crescent shaped and homologous to the jugal of sarcopterygians (Schultze, 2008).

Complex bones

Complex bones are named based on the placement of the bones as well as the presence of characters that define the individual bones above. Complex bones should be thought of in the manner of "this single bone takes the place of" the individual bones listed as a complex bone. Complex bones include:

Ventral rostro-lachrymal—A ventral rostro-lachrymal bone bears the tripartite canal and the complete ethmoid commissure. The ventral rostro-lachrymal bone is separate from a distinct anamestic premaxilla. A ventral rostro-lachrymal is reinterpreted as being present in *Mansfieldiscus sweeti* (Long, 1988b; here Figure 8B). This bone is ventral to a dorsal rostral bone that contributes to the formation of the medial nasal opening. The use of the term ventral rostro-lachrymal implies that there is an additional rostral bone.

Ventral rostro-premaxillo-lachrymal—A ventral rostro-premaxillo-lachrymal is a complex bone that takes the place of the ventral rostral, premaxilla, and lachrymal bones. This bone is toothed, contributes to the oral margin of the upper jaw, and bears the infraorbital and supraorbital canals and the entire extent of the ethmoid commissure. This bone does not contribute to the formation of the nasal openings; a separate dorsal rostral bone does. A ventral rostro-premaxillo-lachrymal bone is seen in *Kentuckia deani* (Rayner, 1951; here Figure 9A) and others listed in Table 1.

Premaxillo-lachrymal—Following the terminology of Gardiner (1963) but not his macromeric hypothesis, a premaxillo-lachrymal is defined by the presence of the tripartite canal in a bone that forms the anteroventral margin of the orbit and extends anterior to the maxilla. The premaxillo-lachrymal is separate from another bone bearing the ethmoid commissure. *Mimipiscis, Moythomasia* (Gardiner, 1984; here Figure 5C, E) and others listed in Table 1 have been reinterpreted as having premaxillo-lachrymal bones.

Ventral rostro-premaxillo—This bone is defined by its placement anterior to the maxilla and the presence of the ethmoid commissure and teeth. This bone contributes to the oral rim of the upper jaw and is separate from a lachrymal bearing the tripartite canal and a dorsal rostral bone that is notched for the medial margin of the medial nasal opening. *Gonatodus punctatus* (Gardiner, 1967a; here Figure 8D) is an example of a fish with ventral rostro-premaxillo bones.

REINTERPRETATIONS OF SNOUT BONES IN DEVONIAN AND CARBONIFEROUS FISHES

The bones in the snouts of various Devonian and Carboniferous actinopterygian fishes are detailed below to discuss the diversity of snout patterns in Paleozoic actinopterygians. Bones are identified using the new nomenclature scheme detailed above, with changes from the original descriptions noted. The descriptions presented below are primarily a product of a literature review and so the original descriptions and illustrations are relied upon for accuracy. Figures are labeled with the newly proposed bone names in bold and the old bone names that have been changed in italics and parentheses. Bone names that are in Roman typeset represent original names that have not been changed.

Abbreviations

AnB, anamestic bones; **APr**, anterior postrostral; **AnPr**, anamestic postrostral; **Ao,** antorbital; **DR**, dorsal rostral bone; **ec**, ethmoid commissure; **F/P,** frontal/parietal bone; **IO2,** second infraorbital bone; **IO3**, third infraorbital bone; **ioc**, infraorbital canal; **La**, lachrymal; **lno,** lateral nasal opening; **LPr,** lateral postrostral; **LR**, lateral rostral; **M,** maxilla; **mno,** median nasal opening; **MPr**, median middle postrostral; **MR**, median rostral; **N**, nasal bone; **N1, N2, N3,** first, second, and third nasal bone; **Nd,** dorsal nasal bone; **nar,** notch for the anterior rectus muscle; **Nv**, ventral nasal bone; **Nv2,** second ventral nasal bone; **Pmx**, premaxilla; **Pmx-La**, premaxillo-lachrymal bone; **P/Pp,** parietal/post parietal bone; **PPr**, posterior postrostral; **Pr**, postrostral; **Pre,** preorbital; **R**, rostral; **Rn**, rostral notch; **rom,** rostral membrane; **R-Pmx,** rostro-premaxillo bone; **Rpr**, rostro-postrostral; **soc**, supraorbital canal; **Sup,** supraorbital; **Spi,** spiracular opening; **VR**, ventral rostral bone, **VR-La,** ventral rostro-lachrymal bone; **VR-Pmx-La,** ventral rostro-premaxillo-lachrymal bone.

Rostral and postrostral bones

***Dialipinia* (Fig. 1)—**Separate rostral and postrostral bones have been described in numerous Devonian fishes. The number of individual bones can vary from taxon to taxon, and within taxa. The Early Devonian *Dialipinia,* considered to be the oldest articulated actinopterygian, has a single median bone identified as the rostral and a single median postrostral bone (Schultze and Cumbaa, 2001, postrostral identified as a pineal plate in *D. markae* Schultze, 1992). The rostral bone of *D. salgueiroensis* (Fig. 1) is notched on its lateral margins and is widest posterior to these notches (Schultze and Cumbaa, 2001). These notches contribute to the formation of the medial nasal openings. The bone identified as the postrostral does not bear any sensory canals, is triangular in shape, is not notched, and separates the left and right frontal/parietal bones anteriorly (ibid.). In *Dialipinia salgueiroensis,* the rostral bone does not contribute to the oral rim of the upper jaw. Instead, there are paired toothed premaxillary bones. Schultze's (1992) and Schultze and Cumbaa's (2001) original identification of the rostral, postrostral, and premaxillary bones are upheld here (Fig. 1)

***Cheirolepis* (Fig. 2, 3)—**The Devonian genus *Cheirolepis* has a rather complicated snout with many bones that can be variable in number from specimen to specimen (Pearson and Westoll, 1979; Arratia and Cloutier, 1996). Understanding the snout in this fish is complicated by the poor preservation of this region in many of the specimens that results in areas of ambiguity. What is clear is that there are rostral and postrostral bones. In *Cheirolepis canadensis* (Fig. 2A-B), there is a series of anamestic posterior postrostral bones inserted between the left and right frontal/parietal bones, preventing these bones from contacting each other anteriorly (Arratia and Cloutier, 1996). One to three posterior postrostral bones can be present between the left and right frontal/parietal bones (ibid.).

Anterior to the maxilla is a large bone identified by Arratia and Cloutier (1996) as a 'premaxilla.' This bone is toothed, contributes to the oral rim of the upper jaw, and bears canal lines on its internal surface (Arratia and Cloutier, 1996). The infraorbital canal is seen in the 'premaxilla,' and the ethmoidal part of this canal is described as exiting one 'premaxilla' to connect to the ethmoidal portion of the infraorbital canal in the 'premaxilla' from the other side of the head (ibid.). In other words, the bones identified as 'premaxillae' bear the ethmoid commissure. Based on the placement of this bone, the presence of teeth, the infraorbital canal, and the ethmoid commissure, this bone is reinterpreted here as a ventral rostro-premaxillo-lachrymal bone. It is considered a ventral rostro-premaxillo-lachrymal bone because it is not notched for the formation of the medial nasal opening and the presence of dorsally placed rostral bones, and in comparison to *Cheirolepis trailli* (Fig. 2C–D) which has a more completely preserved snout.

Posterior to the ventral rostro-premaxillo-lachrymal bone is a rhombic bone identified as the 'lachrymal' (Arratia and Cloutier, 1996). This bone is ventral to the orbit and bears only the infraorbital canal. This bone is reinterpreted here as the second infraorbital bone (Fig. 2A). The large crescent shaped bone in the posteroventral corner of the orbit is the third infraorbital, or jugal (Fig. 2A). Dorsal to the second infraorbital bone and contributing to the formation of the anterior margin of the orbit is a preorbital bone (Fig. 2A). The posterior margin of the preorbital bone is notched—not for the formation of the lateral nasal opening but for a notch for the protrusion of the anterior rectus muscle (Pearson and Westoll, 1979). Dorsal to the preorbital bone is a rhombic supraorbital bone (ibid.).

Anterior to the preorbital bone and dorsal to the ventral rostro-premaxillo-lachrymal bone is an area of ambiguity. Dorsal to this area is a series of bones. Anterior to the supraorbital bone is a nasal bone bearing the supraorbital canal (Arratia and Cloutier, 1996). No notches are seen on the nasal bone for the formation of the nasal openings, but there is the area of ambiguity ventral to this bone that could have been filled with a continuation of the nasal bone, or a separate ventral nasal bone, as seen in *Cheirolepis trailli* (discussed below).

Anterior to the nasal bones is a series of bones that make up the anterior-most portion of the snout. There is a median bone, identified as a median middle postrostral, flanked laterally by lateral rostral bones (Arratia and Cloutier, 1996). These identifications are kept here, but are considered tentative because the ventral margins of these bones are unclear. It cannot be determined if the bones identified as lateral rostrals are notched to form the medial margin of the medial nasal opening, or where the placement of the medial and lateral nasal openings are (ibid.).

The snout of *Cheirolepis trailli* (Figs. 2C–D) is more complete than that of *C. canadensis,* though information regarding the extent of some of the canal lines is lacking. As in *C. canadensis, C. trailli* has an anamestic postrostral bone that separates the left and right frontal/parietal bones from meeting in midline anteriorly (Pearson and Westoll, 1979). This bone was referred to as a posterior postrostral by Pearson and Westoll (1979) but is considered to be just a postrostral here. Pearson and Westoll (1979) identified a large median bone that is notched on its lateral margins and contribute to the formation of the medial margins of the medial nasal openings as an ‘anterior postrostral’ bone. Based on the presence of the notches, this bone is reidentified as being a dorsal rostral bone (Fig. 2C-D).

Lateral to the dorsal rostral bone are two nasal bones bearing the supraorbital canal (Pearson and Westoll, 1979). The dorsal most nasal bone is notched on its anteriomedial and posteriolateral margins for the formation of the medial and lateral nasal opening. The dorsal-most nasal bone is larger than the rhombic ventral nasal bone (ibid).

The nasal bones do not form the anterior margin of the orbit. Instead, like in *Cheirolepis canadensis,* there is a supraorbital and a preorbital bone (Pearson and Westoll, 1979). Both of these bones are anamestic, and the preorbital bone is notched on its posterior border to allow for the protrusion of the anterior rectus muscle (ibid.). Ventral to the orbit is a rectangular bone bearing the infraorbital canal (ibid.). This bone is identified as a ‘lachrymal’ (ibid.), but reinterpreted here as the second infraorbital bone.

Pearson and Westoll's (1979) reconstruction of *Cheirolepis trailli* (Fig. 2C-D) includes paired 'premaxillae' that are toothed and form the anterior margin of the upper jaw (ibid.). This bone also bears the infraorbital canal, and the ethmoid extension off the infraorbital canal. Though not preserved, it is plausible that the supraorbital canal was also present in this bone to form a tripartite canal. The supraorbital canal would extend into the dorsally placed nasal bone from this bone in question as shown in Figure 3B. Pearson and Westoll (1979) hypothesized the trajectory of the sensory canals in the snout of *Cheirolepis trailli* based on what was preserved in the specimens they examined. These hypotheses are presented in Figure 3. Based on the trajectory of the supraorbital canal and the ethmoid commissure in other lower actinopterygians, and its trajectory in *C. canadensis,* it is most likely that Figure 3B presents the most plausible trajectory for the ethmoid commissure and supraorbital canals. If the ethmoid commissure meets in midline in the bones originally described by Pearson and Westoll (1979) as 'premaxillae', these bones need to be reinterpreted. These bones are reinterpreted here as ventral rostro-premaxillo-lachrymals on the basis of the presence of canals, plausible trajectory of these canals, and teeth. Accordingly, the median bone identified as an 'anterior postrostral' by Pearson and Westoll (1979) is more accurately described as a dorsal rostral bone.

Separating the dorsal margin of the ventral rostral-premaxillo-lachrymal bone from the ventral margin of the dorsal rostral bone is a series of anamestic bones. These bones were identified as 'anamestic postrostrals' by Pearson and Westoll (1979). Here, the terminology of Arratia and Cloutier (1996) is used and these bones are simply named anamestic bones because they lack any of the characters that identify rostral and postrostral bones.

***Gogosardinia coatesi* (Fig. 4A–B)—**The Late Devonian *Gogosardinia coatesi* (Fig. 4A–B) has a median rostral bone that is notched to form the medial borders of the medial nasal openings

(Choo et al., 2009). The rostral bears the ethmoid commissure ventrally (canal visible when the internal surface of the rostral bone is viewed, Choo et al., 2009). This bone is anterior to a series of smaller postrostral bones—two lateral postrostrals, a median postrostral, and a posterior postrostral. These four bones are inserted between the left and right frontal/parietal bones and separate them from meeting anteriorly (ibid.). A large 'premaxilla' is described by Choo et al. (2009), but this bone is reinterpreted here as being a premaxillo-lachrymal. The premaxillo-lachrymal is a tall bone that extends up to about mid orbit and contributes to the anteroventral margin of the orbit and the anterior-most portion of the oral rim of the upper jaw. Sensory canals are apparent when the internal surface of the premaxillo-lachrymal is viewed (Choo et al., 2009). The infraorbital canal is present, as well as the supraorbital canal. The ethmoid commissure branches off and extends into the rostral.

Kalops **(Fig. 4C–D)**—At first glance, the Carboniferous *Kalops monophrys* (Fig. 4C–D) and *K. diophrys* (Poplin and Lund, 2002) seem to be examples of Carboniferous actinopterygians with separate rostral and postrostral bones. A 'rostral' bone bearing the ethmoid commissure and a median anamestic 'postrostral' were identified in the Carboniferous *Kalops monophrys* (Fig. 3A-B) and *K. diophrys* (Poplin and Lund, 2002), but these bones need to be reinterpreted. The bone identified by Poplin and Lund (2002) as being a 'postrostral' is notched on the lateral margins to form the medial margins of the medial nasal openings. This bone is reinterpreted here as a dorsal rostral bone (Fig. 4C–D). The bone bearing the ethmoid commissure, originally identified as a 'rostral' (ibid.) is reinterpreted as a ventral rostral bone (Fig. 4C–D). The ventral rostral is excluded from the oral rim of the upper jaw by a pair of small rhombic anamestic premaxillary bones (ibid.). Posterior to the premaxilla and ventral to the nasal bone is a single bone that forms the anteroventral margin of the orbit. This bone, identified as an 'antorbital' by Poplin and Lund

(2002), bears the tripartite canal formed from the junction of the ethmoid commissure, supraorbital and infraorbital canals. This 'antorbital' is reinterpreted here as a lachrymal bone (Fig. 4C).

***Paratarrasius hibbardi* (Fig. 4E–F)**—Another Carboniferous fish described as having separate 'rostral' and 'postrostral' bones must be reinterpreted. *Paratarrasius hibbardi* (Lund and Melton, 1982) has been described as having a 'rostral' bone bearing the ethmoid commissure and an anamestic 'postrostral' bone (ibid.). The anamestic 'postrostral' is notched and contributes to the formation of the medial nasal opening and must be reinterpreted as a dorsal rostral bone (Fig. 4E–F). The bone original described as a 'rostral' (ibid.) must be reinterpreted as a ventral rostral bone. Lund and Melton (1982) have described two nasal bones in this genus, whereas Lund and Poplin (2002) describe three separate nasal bones. *Paratarrasius* possesses premaxillary bones that are toothed and contribute to the oral margin of the upper jaw (Lund and Melton, 1982). The bone bearing the tripartite canal and forming the anteroventral margin of the orbit was identified as an 'antorbital' by Lund and Melton (1982) but is reinterpreted here as a lachrymal bone. There is a single infraorbital ventral to the orbit, and a single infraorbital bone in the posteroventral corner of the orbit. These bones are interpreted here as the second infraorbital and third infraorbital 3 (Fig. 4E).

With the reinterpretations of the rostral and postrostral bones in *Kalops* and *Paratarrasius,* there are no known Carboniferous fishes with separate rostral and postrostral bones. The presence of both rostral and postrostral bones seems to be limited to Devonian forms.

Single median rostral bone bearing the ethmoid commissure

Various Devonian fishes possess a single median bone that bears the ethmoid commissure and is laterally notched to form the medial margin of the medial nasal opening. This is seen in *Donnrosenia schaefferi* (Fig. 5A–B; Long et al., 2008), *Mimipiscis toombsi* (Fig. 5C–D; Gardiner, 1984), *Moythomasia durgaringa* (Figs. 5E–F; Gardiner, 1984), and *Howqualepis rostridens* (Figs. 6A–B; Long, 1988b). A single laterally notched bone is present in Devonian *Limnomis delaneyi* and *Stegotrachelus finlayi* but the presence of an ethmoid commissure in these bones is questionable because of the preservation, and so these fish will not be considered in detail here (Daeschler, 2000; Swartz, 2009).

***Donnrosenia schaefferi* (Fig. 5A–B)**—The Middle Devonian *Donnrosenia schaefferi* has a single median rostral bone and a nasal bone bearing the supraorbital canal (Long et al., 2008). The rostral bone is notched laterally for the medial margin of the medial nasal opening. The rostral bone does not reach between the left and right frontal/parietal bones—these paired bones meet in midline. Instead, the rostral bone has a convex posterior margin that is situated within the concave anterior margin of the frontal/parietal bones (ibid.). The ventral-most portion of the rostral bone is not preserved, so the presence of an ethmoid commissure in this bone cannot be determined. The bone identified by Long et al. (2008) as a 'premaxilla' forms the anteroventral margin of the orbit and bears the infraorbital canal. Long et al. (2008) described that the sensory canal in the 'premaxilla' branches and presumable extends into the rostral and nasal bones. This bone is reinterpreted here as a premaxillo-lachrymal because of the canal lines and its placement in relation to the orbit.

***Mimipiscis toombsi* (Fig. 5C–D)—**The Late Devonian *Mimipiscis toombsi* (Fig. 5C-D) has a median rostral bone that bears the ethmoid commissure and is notched laterally to form the medial margin of the medial nasal opening (Gardiner, 1984). The rostral bone is prevented from contributing to the oral margin of the upper jaw by the presence of bones that are identified by Gardiner (1984) as 'premaxillae'. These 'premaxillary' bones form the anterior-most extent of the oral rim of the upper jaw, are toothed, bear the tripartite canal, and form the anteroventral margin of the orbit (ibid.). This bone is reinterpreted here as a premaxillo-lachrymal because of the presence of characters that define both premaxillary and lachrymal bones. Ventral to the orbit and dorsal to the maxilla is a rectangular bone bearing the infraorbital canal. This bone was identified as the 'lachrymal' (ibid.), but is now identified as the second infraorbital. The bone in the posteroventral corner of the orbit bearing the infraorbital canal is the third infraorbital.

***Moythomasia durgaringa* (Fig. 5 E–F)**—The snout of *Moythomasia durgaringa* (Fig. 5E-F) is similar to *Mimipiscis toombsi.* Like *Mimipiscis,* the bone identified as the 'premaxilla' by Gardiner (1984) is reinterpreted as a premaxillo-lachrymal. Unlike *Mimipiscis toombsi,* which has premaxillo-lachrymals that meet in midline and prevent the rostral bones from contributing to the oral rim of the upper jaw, *Moythomasia* has a median rostral bone that is toothed, contributes to the upper jaw margin, and separates the premaxillo-lachrymal bones from meeting in midline (Gardiner, 1984). As with *Mimipiscis,* the bone originally identified as the 'lachrymal' (Gardiner, 1984) is reinterpreted as the second infraorbital.

Howqualepis rostridens* (Fig. 6A–B)—Howqualepis rostridens* (Fig. 6A–B) has been described as having a large median rostral that is toothed, contributes to the oral margin of the upper jaw, and contacts the anterior margin of the frontal/parietal bones (Long, 1988b). The rostral bone is notched laterally to contribute to the formation of the medial nasal opening (ibid.). The rostral bone is inserted between two bones, preventing them from meeting in midline (ibid.). The paired bones are identified as 'premaxillae' by Long (1988). The 'premaxillary' bones themselves contribute to the anteroventral margin of the orbit, bear the infraorbital and supraorbital canals, are toothed, and form the anterior most margin of the upper jaw (ibid.). Because of these characters, the bone originally identified as being a 'premaxilla' is reinterpreted as a premaxillo-lachrymal (Fig. 4A). The rectangular bone ventral to the orbit bearing the infraorbital canal is originally described as a 'lachrymal' (Long, 1988b) but is reinterpreted here as the second infraorbital (Fig. 6A). The crescent shaped bone in the posteroventral corner of the orbit is identified here as the third infraorbital (Fig. 6A).

***Woodichthys bearsdeni* (Fig. 6C)—**The Carboniferous *Woodichthys bearsdeni* (Fig. 6C) has a median bone flanked laterally by nasal bones (Coates, 1998). The median bone, identified as a rostral bone, bears the median section of the ethmoid commissure and is notched laterally to contribute to the formation of the medial nasal openings (Coates, 1998). The rostral bone is excluded from the oral margin of the upper jaw (ibid.). There are paired toothed bones, identified as 'premaxillaries', which bear the tripartite canal (ibid.). These 'premaxillaries' are reinterpreted here as being premaxillo-lachrymal bones (Fig. 6C).

***Cyranorhis, Wendyichthys, Lineagruan,* and *Beagiscus* (Figs. 6D–E, 7A–D)—**A single median bone bearing the ethmoid commissure has also been identified in the Carboniferous Bear Gulch fishes *Cyranorhis bergeraci* (Fig. 6D), *Wendyichthys dicksoni* (Fig. 6E), and *W. lautreci* (Lund and Poplin, 1997), and *Lineagruan judithi* (Fig. 7A–B), *L. snowyi,* and *Beagiscus pulcherrimus* (Fig. 7C–D, Mickle et al., 2009). These Carboniferous fishes differ from the above mentioned Devonian and Carboniferous fish in that they possess a separate bone bearing the tripartite canal in the anteroventral margin of the orbit. This bone has been identified as an 'antorbital' in these fishes (Lund and Poplin, 1997; Mickle, 2009), but are reinterpreted here as a lachrymal bone (Figs. 6D-E, 7A, C). In the original descriptions, the median bone bearing the ethmoid commissure has been identified as a 'rostro-postrostral' and considered to be the result of a fusion of the rostral and postrostral bones (Lund and Poplin, 1997; Mickle, 2009). The median bone that bears the ethmoid commissure and is notched to form the medial of the margin of the medial nasal openings is considered to be a 'rostral' bone. The term 'rostro-postrostral' is rejected here because there is no definitive evidence of a fusion of separate rostral and postrostral bones in these fishes. The median bone identified as a 'rostro-postrostral' has all the characters that define a rostral bone and so, it is reinterpreted as such (Figs. 4D–E, 5A, 5C). Postrostral bones are absent in these fishes.

Lineagruan judithi, L. snowyi, and *Beagiscus pulcherrimus* have paired anamestic bones anterior to the maxilla, as well. These bones are identified as premaxillary bones (Mickle et al., 2009). Such bones are considered absent in *Wendyichthys dicksoni, W. lautreci,* and *Cyranorhis bergeraci,* with their absence forming a rostral notch (Lund and Poplin, 1997).

***Aesopichthys erinaceus* (Fig. 7E)**—The Carboniferous *Aesopichthys erinaceus* (Poplin and Lund, 2000) also has a median rostral bone. Originally identified as a 'rostro-postrostral' by Poplin and Lund (2000), the median bone that bears the ethmoid commissure and is notched laterally is reinterpreted here as a rostral bone. Postrostral bones are considered to be absent. A separate and distinct bone bears the tripartite canal. Originally identified as an 'antorbital' (ibid.), this bone is renamed a lachrymal. Ventral to the lachrymal is a toothed anamestic premaxilla (ibid.). Ventral to the orbit, and continuing posteroventral to the orbit, is a large infraorbital bone that was considered the 'first infraorbital' by Poplin and Lund (2000) but is considered to be the second infraorbital in this work. Dorsal to this second infraorbital is a small infraorbital named by Poplin and Lund (2000) the 'second infraorbital,' but it is re-termed the third infraorbital after its position in the posteroventral corner of the orbit.

***Canobius* (Figs. 7F, 8A)—**The Carboniferous genus *Canobius* deserves some attention. Moy-Thomas and Bradley Dyne (1938) described *Canobius ramsayi* (Fig. 7F) as having an anamestic premaxilla, a bone in the anteroventral corner of the orbit with the tripartite canal, and a median bone bearing a short branch of a sensory canal (Fig. 5F). This large median bone is notched laterally and in contact with the frontal/parietal bones dorsally. This pattern is similar to the above mentioned Carboniferous fishes, but how Moy-Thomas and Bradley Dyne (1938) identified these bones in *Canobius* is problematic. The large median bone was considered to be a ‘postrostral’ and the bone bearing the tripartite canal the ‘rostral’ (ibid.). It seems that the short stretch of the sensory canal on the ‘postrostral’ could be the beginning of the ethmoid commissure. This, as well as the presence of notches to form the medial margins of the medial nasal openings, would mean that the ‘postrostral’ is best interpreted as a rostral bone. The bone bearing the tripartite canal in the anteroventral corner of the orbit is best considered a lachrymal, and the anamestic bone anterior to the maxilla a premaxilla (Fig. 5F). After reinterpreting the bones of the snout, *Canobius ramsayi* is another example of a Carboniferous fish with a median rostral bone and separate premaxillary and lachrymal bones. This pattern is similar to what is seen in *Lineagruan, Beagiscus,* and *Aesopichthys* and not as different from other Carboniferous fishes as the original bone identifications would seem to indicate.

Canobius elegantulus (Fig. 8A) is described as having a single median bone flanked by nasal bones that is in contact dorsally with the frontal/parietal bones (Moy-Thomas and Bradley Dyne, 1938.). Ventral to this median bone is a single bone bearing a sensory canal. This single bone forms the anteroventral margin of the orbit and extends anterior to the anterior tip of the maxilla (ibid.). The small portion that is anterior to the maxilla bears teeth. Again, the original identities of these bones are problematic. The median bone, which does bear a small branch of a sensory canal, is identified as a ‘postrostral’, whereas the large bone ventral to this ‘postrostral’ is identified as the ‘rostral’ bone (Moy-Thomas and Bradley Dyne, 1938). The median bone is reidentified here as a rostral bone. It is notched and it seems that the ethmoid commissure enters this median bone (Fig. 6A). The bone identified by Moy-Thomas and Bradley Dyne (1938) as a 'rostral' bone should be considered a premaxillo-lachrymal because of how it contributes to the oral rim of the upper jaw, is toothed, and bears the tripartite canal. It should be noted that the original specimens of *Canobius elegantulus* should be reexamined to check the positions of the sensory canals, specifically whether the ethmoid commissure extends into the bone identified here as the rostral, or if it is found solely in the bone identified as the premaxillo-lachrymal. If the canal is in the premaxillo-lachrymal, this bone would have to be reinterpreted as the ventral rostro-premaxillo-lachrymal and the rostral would then be the dorsal rostral bone. Regardless, the pattern of snout bones in *Canobius elegantulus* differs from that of *Canobius ramsayi* (Figs. 7F, 8A).

The presence of a single median rostral bone and no postrostral bones is common in both Devonian and Carboniferous fishes (Table 1). A difference seen between Devonian fishes with a single median rostral bone and Carboniferous fishes with the same bone is whether the premaxilla and lachrymal bones are present as complex or individual bones. Devonian fishes with single median rostral bones have complex bones, whereas Carboniferous fishes can have individual premaxillary and lachrymal bones (Table 1).

Two rostral bones

Above were examples of fishes with a single median rostral bone with the ethmoid commissure and notches that form the medial wall of the medial nasal openings. There are examples of fishes where the characters that define a rostral bone are separated into two different bones. The Carboniferous fishes *Kalops monophrys*, *K. diophrys*, and *Paratarrasius hibbardi* are three examples of fishes that must be reinterpreted as having dorsal and ventral rostral bones.

These fishes have been discussed above, explaining why they do not have rostral and postrostral bones as originally described. Additional fishes with two rostral bones are described below.

***Mansfieldiscus sweeti* (Fig. 8B)—**The Carboniferous *Mansfieldiscus sweeti* (Fig. 8B) is described as having a single median 'rostral' bone that is laterally notched (Long, 1988b). It is dorsal to paired 'antorbitals' which bear the tripartite canal and the entire ethmoid commissure (ibid.). These 'antorbital' bones are reinterpreted here as being complex bones—ventral rostro-lachrymals because of the presence of the tripartite canal, the entire extent of the ethmoid commissure, and the placement of the bone so that it contributes to the formation of the anteroventral corner of the orbit. Accordingly, the bone originally identified as the 'rostral' must be considered the dorsal rostral bone. The newly named dorsal rostral bone is anamestic, but is notched to contribute to the formation of the medial nasal openings (ibid.). There are toothed premaxillary bones that form the anterior most margin of the upper jaw (ibid.). The bone bearing the infraorbital canal ventral to the orbit identified as the 'lachrymal' (ibid.), is reinterpreted here as the second infraorbital. The crescent shaped bone bearing the infraorbital canal in the posteroventral corner of the orbit is the third infraorbital. This set up of two rostral bones—one bearing the ethmoid commissure and the other bearing the lateral notches is similar to the condition seen in the Carboniferous genera *Kalops* and *Paratarrasius* (Figs. 4C–F) with the difference of *Kalops* and *Paratarrasius* having separate lachrymal and rostral bones.

***Rhadinichthys canobiensis* (Fig. 8C)—**There are three bones present in the snout of the Carboniferous *Rhadinichthys canobiensis* (Fig. 8C)—paired nasal bones bearing the supraorbital canal, a median 'anamestic' bone that contacts the nasals laterally and the frontals/parietals dorsally, and a bone in the anteroventral corner of the orbit that is toothed, extends past the anterior tip of the maxilla, and bears the tripartite canal (Moy-Thomas and Bradley Dyne, 1938).

The notched median bone is identified by Moy-Thomas and Bradley Dyne as a ‘postrostral’ bone. The bone in the anteroventral corner of the orbit bearing the tripartite canal is identified as the ‘rostral.’ In the original descriptions, the branch of the tripartite canal that contributes to the ethmoid commissure is described as running very close to, but not crossing, the anteroventral margin of the ‘postrostral’ bone. If this canal does not extend into the median bone, the bone bearing the tripartite canal is best considered a ventral rostro-premaxillo-lachrymal and the dorsally placed median bone a dorsal rostral bone. Specimens of *Rhadinichthys canobiensis* should be reexamined to better understand the trajectory of the canal lines in the snout. If the ethmoid commissure does in fact enter the median bone, this bone must be reinterpreted as a rostral bone, and the bone bearing the tripartite canal would be a premaxillo-lachrymal.

***Gonatodus punctatus* (Fig. 8D)—**After the bones of *Gonatodus punctatus* are reinterpreted, this fish is another example of a Carboniferous fish with two rostral bones. This fish also shows a different compound bone not yet described—a ventral rostro-premaxilla. This bone bears the ethmoid commissure, is toothed, and is positioned anterior to the maxilla. It is ventral to a bone that is notched on its lateral margin to contribute to the formation of the medial nasal opening. This notched bone was identified as a ‘postrostral’ bone by Gardiner (1967) but is reinterpreted here as a dorsal rostral bone. Accordingly, the ventrally placed bone identified by Gardiner (1967) as a ‘rostro-premaxilla’ is redescribed as a ventral rostro-premaxilla. Posterior to the ventral rostro-premaxillo bone is a separate bone forming the anteroventral corner of the orbit and bearing the tripartite canal. This bone, identified by Gardiner (1967) as an ‘antorbital,’ is renamed a lachrymal bone here.

***Kentuckia deani* (Fig. 9A)—**The Devonian *Kentuckia deani* (Fig. 9A) has a large median bone that is flanked by nasal bones and in contact with the anterior margins of the frontal/parietal bones (Rayner, 1951). Ventral to this median bone is a roughly rectangular bone that forms the anteroventral corner of the orbit and has a toothed ventral margin that contributes to the oral rim of the upper jaw (ibid.). This bone is figured by Rayner (1951) as bearing the tripartite canal and entirely enclosing the ethmoid commissure. The ethmoid commissure is not reconstructed on the median bone (ibid.). The median bone was identified as a 'postrostral' bone, whereas the bone bearing teeth and sensory canals was identified as a 'rostral' (ibid.). Rayner (1951) noted that she followed the terminology of Moy-Thomas and Bradley Dyne (1938), but that the 'rostral' bone identified in *Kentuckia* could be considered a 'premaxilla' (Westoll, 1944), or a 'rostro-antorbito-premaxilla' (Nielsen, 1942). Based on the placement of the canals and the notches that form the medial margin of the medial nasal opening, the median bone is best considered a dorsal rostral bone and the toothed and canal bearing bone a ventral rostro-premaxillo-lachrymal (Fig. 9A, Table 1).

There are examples of Carboniferous fishes that have two rostral bones—a dorsal and a ventral rostral bone. These rostral bones can be separate and distinct as in *Kalops* (Fig. 4C–D; Poplin and Lund, 2002) and *Paratarassius* (Fig. 4E–F; Lund and Melton, 1982), or can be part of a bone complex such as a ventral rostro-lachrymal (e.g. Fig. 8B, *Mansfieldiscus sweeti* Long, 1988b), a ventral rostro-premaxilla (e.g. Fig. 8D *Gonatodus punctatus* Gardiner, 1967a), or a ventral rostro-premaxillo-lachrymal (e.g. Fig. 9A, *Kentuckia deani* Rayner, 1951). No Devonian fishes are known to have clear, unmistakable multiple rostral bones (see below for a possible exception).

Problematic taxa

***Tegeolepis clarki* (Figs. 9B, 10)—**The snout of lower actinopterygians is not always well preserved and some fishes are difficult to interpret. One such fish is the Devonian *Tegeolepis.*

With its prominent rostrum, *Tegeolepis clarki* (Fig. 9B, 10) is different than the majority of Paleozoic fishes. The lack of information on the sensory canals and placement of the nasal openings makes the identification of the rostral and postrostral bones difficult (Fig. 10). What can easily be determined is the presence of a single nasal bone bearing the supraorbital canal (Dunkle and Schaeffer, 1973). Notches that contribute to the margins of the medial and lateral nasal openings are not apparent on the nasal bone. Because the nasal bone is identifiable, the medial nasal openings can be hypothesized as being present between the nasal bone and the anteriorly placed large median bone. This bone, identified as a 'postrostral' by Dunkle and Schaeffer (1973) is reinterpreted here as a rostral bone because of the hypothesized placement of the medial nasal opening.

Ventral to the nasal bone is a triangular bone that forms the anteroventral margin of the orbit and bears a tripartite canal (Figs. 9B, 10A). This bone was originally identified as an 'antorbital bone,' but is reidentified as a lachrymal here. Ventral to the lachrymal bone is a tooth bearing bone identified by Dunkle and Schaeffer (1973) as a 'rostro-premaxilla.' The 'rostro-premaxilla' from the left and right side meet in midline and prevent the lachrymal bones from doing the same. Overhanging these bones is a large median bone reidentified here as a rostral bone. The trajectory of the ethmoid commissure is not detailed. It is unclear whether the ethmoid commissure extends into the bone identified as the 'rostro-premaxilla,' therefore supporting this identification, or if it extends into the median rostral bone. If the ethmoid commissure extends into the median bone, the toothed bone in question is a premaxilla, not a 'rostro-premaxilla.' If the ethmoid commissure is enclosed in the toothed paired bones, Dunkle and Schaeffer's (1973) identification of a rostro-premaxilla is correct, with the clarification of it being a ventral rostro-premaxilla and the median bone being a dorsal rostral. The two hypotheses regarding the identities of the bones in the snout of *Tegeolepis* based on hypotheses of the trajectory of the canal lines are provided in Figure 10. If the trajectory of the ethmoid commissure resembles that of Figure 10C, *Tegeolepis* is unique among Devonian fish for having dorsal and ventral rostral bones. Regardless of the trajectory of the ethmoid commissure, *Tegeolepis* is unique among Devonian fish for the presence of a separate lachrymal bone. Described briefly by Dunkle and Schaeffer (1973), *Tegeolepis clarki* seems to be an important Devonian fish deserving of further attention.

***Platysomus* (Fig. 11)—**The canal lines in deep bodied fishes from the Carboniferous genus *Platysomus* are difficult to interpret, but it is clear that there is at least one rostral bone and no postrostral bones in *Platysomus superbus* (Fig. 11A), *P. schultzei* (Fig. 11B), and *P. swaffordae* (Fig. 11C). In *Platysomus superbus* and *P. schultzei*, there is a median bone that is notched on its lateral margins to contribute to the formation of the medial nasal opening (Moy-Thomas and Bradley Dyne, 1938; Zidek, 1992). A similarly placed bone is present in *P. swaffordae* but a notch is not apparent (Mickle and Bader, 2009). This bone has been identified as a 'postrostral' in *P. superbus* (Moy-Thomas and Bradley Dyne, 1938) and *P. swaffordae* (Mickle and Bader, 2009) and as a rostral in *P. schultzei* (Zidek, 1992). Here, Zidek's identification of a rostral bone is upheld and extended to the other *Platysomus* species (Fig. 11).

In all three *Platysomus* species, a nasal bone that is notched for the formation of the medial and lateral nasal openings is lateral to the rostral bone. In *Platysomus swaffordae*, a portion of the supraorbital canal is seen in this bone (Mickle and Bader, 2009). Ventral to the median rostral and nasal bones is a large bone. A canal that extends into the nasal bone is seen in this bone in *P. superbus* and *P. schultzei.* Identified as a 'rostral' in *P. superbus* (Zidek, 1992) and an 'antorbital' in *P. schultzei* (Moy-Thomas and Bradley Dyne, 1938) and *P. swaffordae*

(Mickle and Bader, 2009), the bone is probably best interpreted as a lachrymal because of the presence of the infraorbital canal and how the supraorbital canal exits this bone to enter the nasal. Though a tripartite canal is not seen, the supraorbital canal must branch off the infraorbital canal in this bone in order for the supraorbital canal to enter the dorsally placed nasal bone. An ethmoid commissure is not apparent in any of the bones of the three species. It cannot be ruled out that this large bone did not house the ethmoid commissure—if it did, it would be a ventral-rostro-lachrymal and the dorsally placed median rostral would then be a dorsal rostral bone.

The large bone bearing the infraorbital canal identified as an infraorbital by Moy-Thomas and Bradley Dyne (1938) in *P. superbus* is reinterpreted here as the second infraorbital. In *P. schultzei,* the bone in a similar position is identified as a 'lachrymal' by Zidek (1992). This bone is also reinterpreted as the second infraorbital. Rather than a single bone, there are two bones posterior to the lachrymal in *P. swaffordae*. These were originally identified by Mickle and Bader (2009) as the 'first' and 'second' infraorbital, but in comparison with the other *Platysomus* species, these bones are re-termed the second infraorbital bones.

Platysomus schultzei (Fig. 11B) and *P. swaffordae* (Fig. 11C) have anamestic premaxillae (Zidek, 1992; Mickle and Bader, 2009). Though this bone does not bear teeth, it is still interpreted as a premaxilla because the upper and lower jaws in these species are edentulous (Zidek, 1992; Mickle and Bader, 2009). As described by Moy-Thomas and Bradley Dyne (1938) premaxillae are absent in *Platysomus superbus* (11A).

Overall, the three species of *Platysomus* dealt with here have a median rostral bone and no postrostral bones. There is a large lachrymal bone that, if it does bear the ethmoid commissure, should be reinterpreted as a ventral rostro-lachrymal. Though these deep bodied fish have drastically different morphologies than Carboniferous fusiform fishes, the bones that make up the snout region of these fishes are not that different.

CONCLUSIONS

In summary, different hypotheses regarding the primitive condition of the actinopterygian snout have contributed to different nomenclatural schemes for the bones of the snout. A review of the literature shows that there are no standardized nomenclatural rules regarding how snout bones should be identified in lower actinopterygians. Such confusion impedes the construction of character matrices for phylogenetic analyses, comparing taxa from different localities, and the understanding of the diversity of snouts in actinopterygians. The identification of the bones in the snout should be based on the presence or the absence of particular characters that define the individual bones, and the location of bones in relation to other bones. This is an attempt at identifying homologous structures in different taxa using Remane's (1952, 1956) criteria of similarity in position and detail. When characters from numerous bones are present in one bone, that bone must be considered a bone complex and the names should reflect this.

When this new nomenclature scheme is used to re-identify the bones in the snouts of previously described Devonian and Carboniferous fishes, certain patterns stand out. Devonian fishes can have separate rostral and postrostral bones, whereas postrostral bones are never found in Carboniferous actinopterygians. Devonian and Carboniferous fishes can have a single median rostral bone and no postrostrals, but a difference between fishes from these two periods is that Carboniferous fishes can have separate and distinct lachrymal and premaxillary bones, whereas these bones are almost always part of complex bones in Devonian fishes. The one exception to this seems to be the Devonian *Tegeolepis clarki* which does have a separate lachrymal bone. Carboniferous fishes can have the characters that define the rostral bone separated into two bones—the dorsal and ventral rostrals. Further diversity is seen in whether the ventral rostral bone is separate or part of a bone complex.

This new nomenclature scheme is used in the descriptions of new taxa in Chapters 4 and 5. Most importantly, it is used in Chapter 6 in the character matrix. Characters and character states have been updated using this terminology. Taxa were coded following the reidentifications presented here.

Table 1 (Following page)—Original identifications and the current identifications based on the nomenclature scheme presented here. Headings in the first row are the original identifications in the cited descriptions. Names in the columns are the current names based on the new nomenclatural scheme. A '—' signifies that the bone name in the heading was not identified in the original descriptions. Abbreviations follow those in the above figures and: **C,** Carboniferous; **D**, Devonian. **X,** no information.

Taxon	Source	Age	R	Pr(s)	Pmx	Ao	N	RPR	La	R-Pmx	AnPr
Dialipina salgueiroensis	Schultze & Cumbaa, 2001	D	R	Pr	Pmx	—	X	—	—	—	—
Cheirolepis canadensis	Arratia & Cloutier, 1996	D	R (LR, DR)	Prs	R-Pmx-La	—	N	—	IO2	—	—
Cheirolepis trailli	Pearson & Westoll, 1979	D	—	Pr, DR	VR-Pmx-la	—	N	—	IO2	—	AnB
Gogosardinia coatesi	Choo et al., 2009	D	R	Prs	Pmx-La	—	N	—	IO2	—	—
Kalops monophrys	Poplin & Lund, 2002	C	VR	DR	Pmx	La	N	—	—	—	—
Kalops diophrys	Poplin & Lund, 2002	C	VR	DR	Pmx	La	N	—	—	—	—
Paratarrasius hibbardi	Lund & Melton, 1982	C	VR	DR	Pmx	La	N	—	—	—	—
Donnrosenia schaefferi	Long et al. 2008	D	R	—	Pmx-La	—	N	—	—	—	—
Mimipiscis toombsi	Gardiner, 1984	D	R	—	Pmx-La	—	N	—	IO2	—	—
Moythomasia durgaringa	Gardiner, 1984	D	R	—	Pmx-La	—	N	—	IO2	—	—
Howqualepis rostridens	Long, 1988b	D	R	—	Pmx-La	—	N	—	IO2	—	—
Woodichthys bearsdeni	Coates, 1998	C	R	—	Pmx-La	—	N	—	—	—	—
Cyranorhis bergeraci	Lund & Poplin, 1997	C	—	—	—	La	N	R	—	—	—
Wendyichthys dicksoni	Lund & Poplin, 1997	C	—	—	—	La	N	R	—	—	—
Wendyichthys lautreci	Lund & Poplin, 1997	C	—	—	—	La	N	R	—	—	—
Lineagruan judithi	Mickle et al., 2009	C	—	—	Pmx	La	N	R	—	—	—
Lineagruan snowyi	Mickle et al., 2009	C	—	—	Pmx	La	N	R	—	—	—
Beagiscus pulcherrimus	Mickle et al., 2009	C	—	—	Pmx	La	N	R	—	—	—
Aesopichthys erinaceus	Poplin & Lund, 2000	C	—	—	Pmx	La	N	R	—	—	—
Canobius ramsayi	Moy-Thomas & Bradley Dyne, 1938	C	La	R	Pmx	—	N	—	—	—	—
Canobius elegantulus	Moy-Thomas & Bradley Dyne, 1938	C	Pmx-La	R	—	—	N	—	—	—	—
Mansfieldiscus sweeti	Long, 1988b	C	DR	—	Pmx	VR-La	N	—	IO2	—	—
Rhadinichthys canobienesis	Moy-Thomas & Bradley Dyne, 1938	C	Pmx-La	DR	—	—	N	—	—	—	—
Gonatodus punctatus	Gardiner, 1967a	C	—	DR	—	La	N	—	—	VR-Pmx	—
Kentuckia deani	Rayner, 1951	D	VR-Pmx-La	DR	—	—	N	—	—	—	—
Tegeolepis clarki	Dunkle & Schaeffer, 1973	D	—	Pr or R	—	La	N	—	—	R-Pmx or Pmx	—
Platysomus superbus	Moy-Thomas & Bradley Dyne, 1938	C	La	R	—	—	N	—	—	—	—
Platysomus schultzei	Zidek, 1992	C	R	—	Pmx	La	N	—	IO2	—	—
Platysomus swaffordae	Mickle & Bader, 2009	C	—	R	Pmx	La	N	—	—	—	—

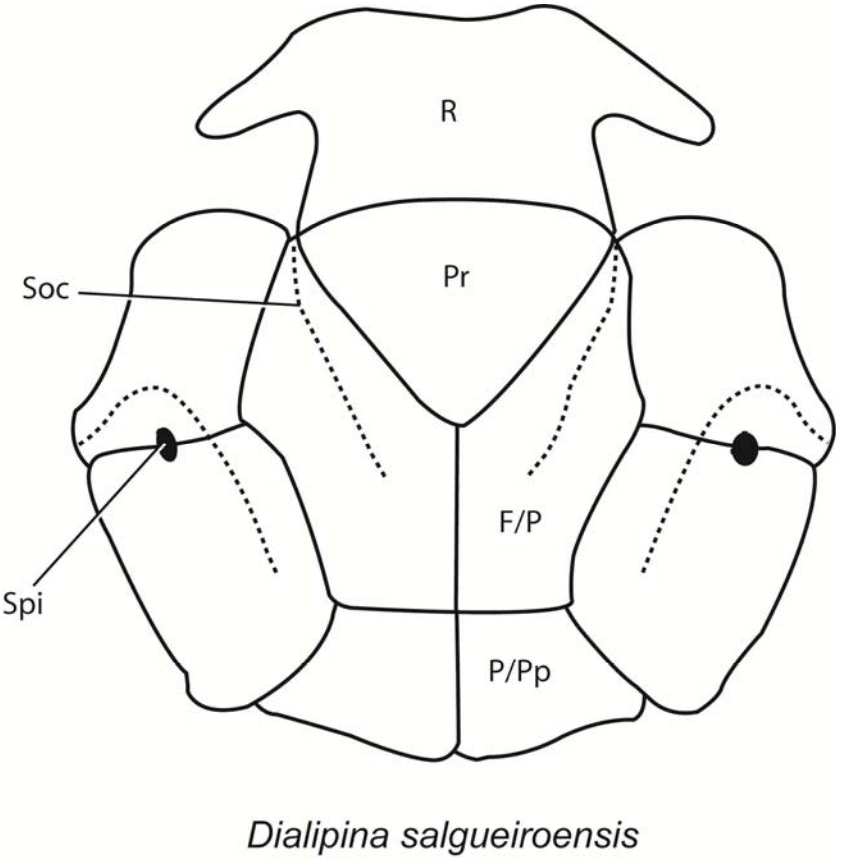


Figure 1—Dorsal view of the skull roof and snout region of *Dialipina salgueironensis* depicting a snout pattern of rostral and postrostral bones*.* Illustration modified from Schultze and Cumbaa, 2001. **Abbreviations: F/P**, frontal/parietal bone; **P/Pp**, parietal/post parietal bone; **Pr**, postrostral bone; soc, supraorbital canal; **R,** rostral bone; **soc,** supraorbital canal; **Spi**, spiracular opening. Bone identifications the same as original identifications by Schultze and Cumbaa (2001).

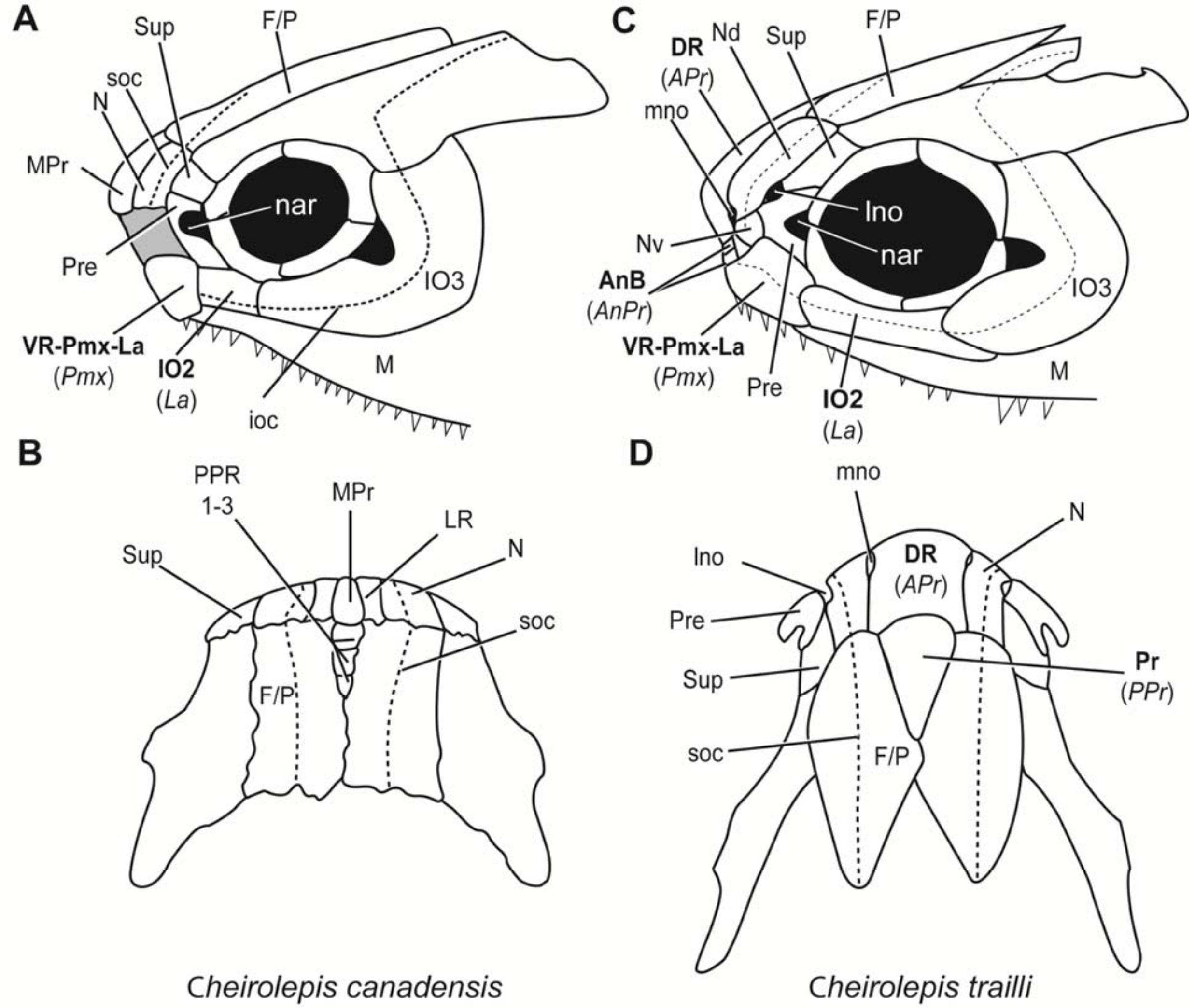


Figure 2—Lateral and dorsal views of the snout region of *Cheirolepis* depicting a snout pattern of rostral and postrostral bones. **A**, lateral and **B**, dorsal views of *Cheirolepis canadensis;* **C**, lateral and **D**, dorsal views of *Cheirolepis trailli.* Illustrations and bone identifications are modified from Arratia and Cloutier, 1996 (**A, B**); Pearson and Westoll, 1979 (**C, D**). Bone names in bold are reinterpretations, bone names in parentheses and italics are original names that have been changed in this paper, bone names in roman type set are unchanged from the original descriptions. **Abbreviations:** see previous figure and **AnB**, anamestic bones; **AnPr**, anamestic postrostral bones; **APr**, anterior postrostral bone; **DR,** dorsal rostral bone; **IO2**, second infraorbital bone, **IO3**, third infraorbital bone; **La,** lachrymal bone; **lno,** lateral nasal opening; **LR,** lateral rostral bone; **M,** maxilla; **mno,** medial nasal opening; **MPr,** median middle postrostral bone; **N,** nasal bone; **Nd**, dorsal nasal bone; **Nv,** ventral nasal bone; **nar**, notch for the protrusion of the anterior rectus muscle; **Pmx,** premaxilla; **PPr**, posterior postrostral bone; **Pre**, preorbital bone; **Sup**, supraorbital bone; **VR-Pmx-La,** ventral rostro-premaxillo-lachrymal.

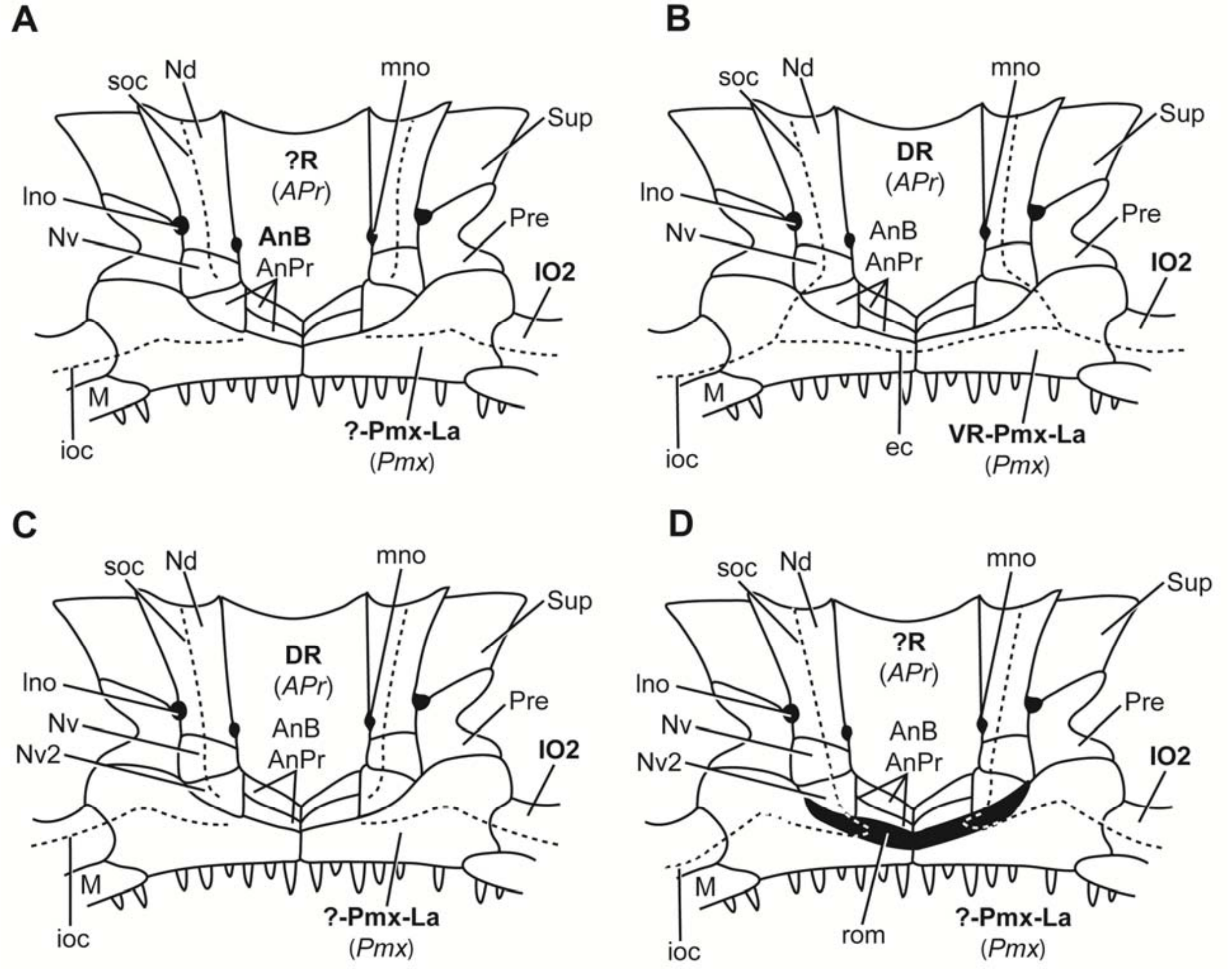
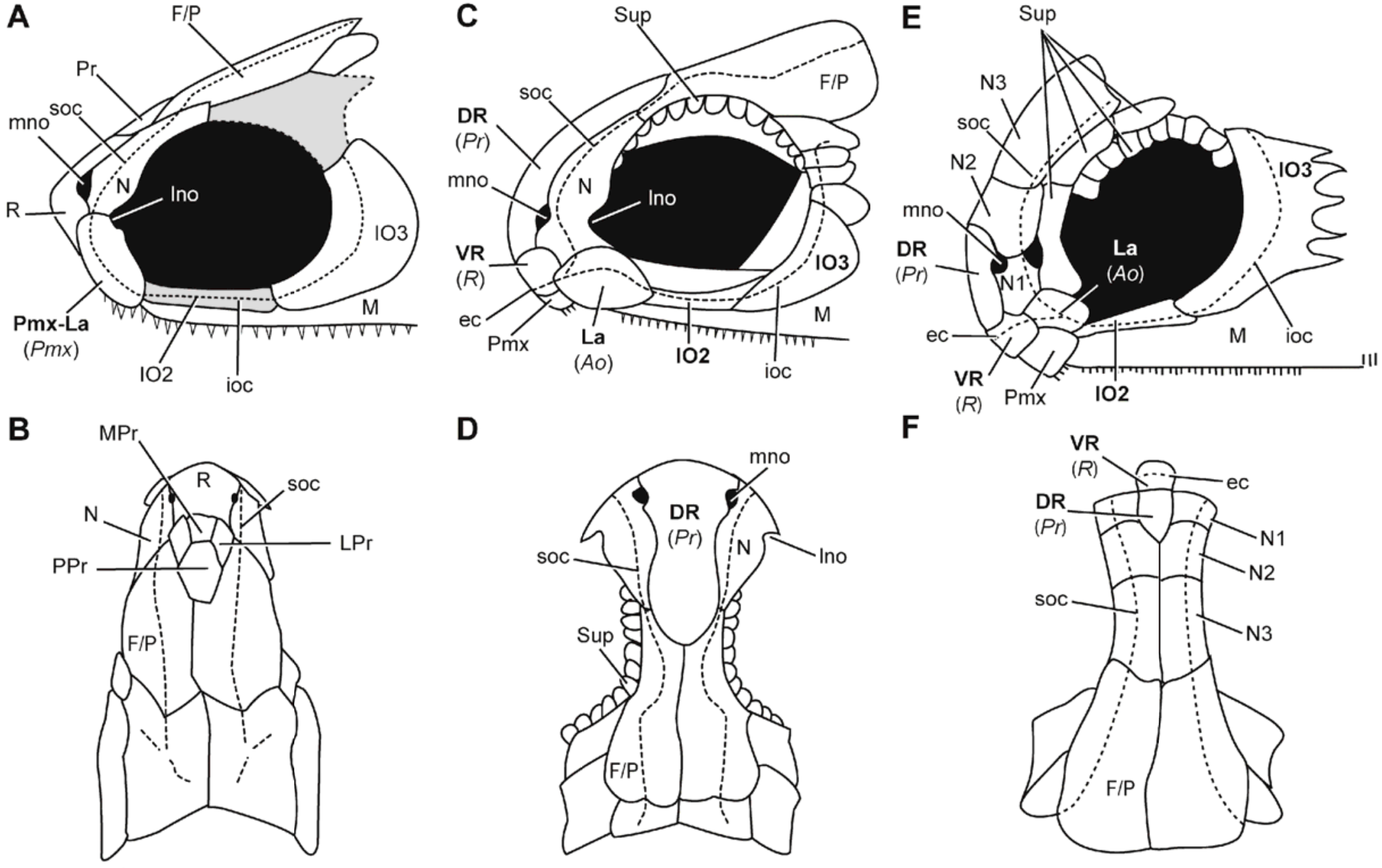


Figure 3—Hypotheses regarding the trajectory of canal lines in *Cheirolepis trailli* and subsequent bone identifications. **A**, known paths of the sensory canals of the snout; **B,** hypothesized trajectory of the sensory canals, with the ethmoid commissure fully enclosed in the ventral rostral-premaxillo-lachrymal bone; **C,** hypothesized trajectory of the sensory canals, with no ethmoid commissure, extension of the supraorbital canal, and three nasal bones; **D,** hypothesized trajectory of the sensory canals with the no ethmoid commissure and the sensory canals extending into a rostral membrane from the premaxillo-lachrymal to the nasal bones. Illustrations and bone identifications are modified from Pearson and Westoll, 1979. Bone names in bold are new reinterpretations, bone names in parentheses and italics are original names that have been changed in this paper, bone names in roman type set are unchanged from the original descriptions. The hypothesis in **B** is favored here. Abbreviations: see previous figures and: **?-Pmx-La**, cannot determine if premaxillo-lachrymal or ventral rostral-premaxillo-lachrymal bone; **?R**, cannot determine if rostral bone or dorsal rostral bone; **ec,** ethmoid commissure; **Nv2**, second ventral nasal bone; **rom**, rostral membrane.

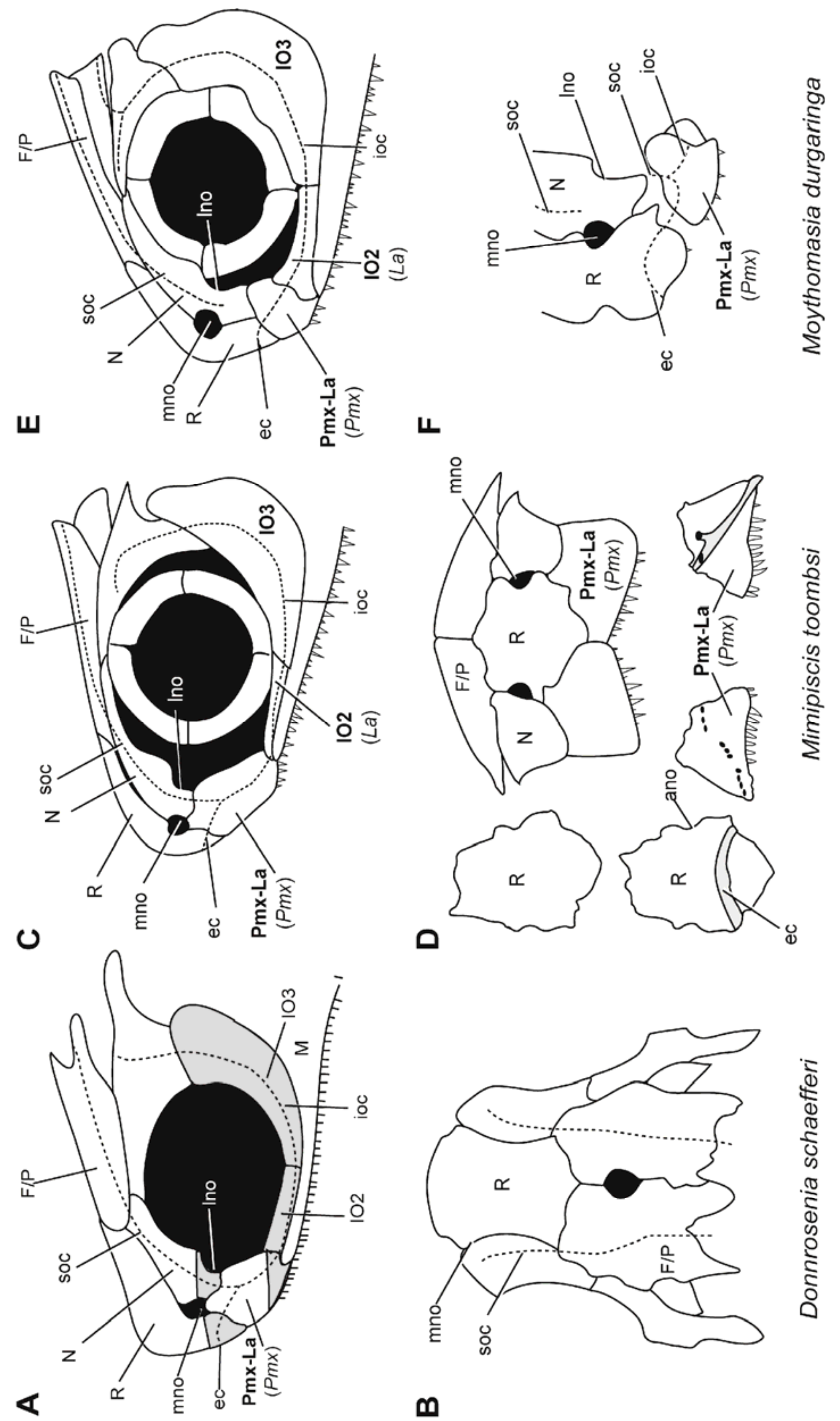


Gogosardina coatesi

Kalops monophrys

Paratarrasius hibbardi

Figure 4 (Previous page)—Illustrations of the snout region of Devonian and Carboniferous fishes depicting a snout pattern of either a single rostral bone (**A–B**) or dorsal and ventral rostral bones (**C–F**). **A,** lateral and **B,** dorsal views of the snout region of *Gogosardinia coatesi;* **C,** lateral and **D,** dorsal views of the snout region of *Kalops monophrys*; **E,** lateral and **F,** dorsal views of *Paratarrasius hibbardi.* Illustrations and bone identifications modified from Choo et al., 2009 (**A, B**); Poplin and Lund, 2002 (**C, D**) and Lund and Melton, 1982; Lund and Poplin, 2002 (**E, F**). Bones infilled with gray are reconstructed on the basis of other Devonian fishes. Bone names in bold are new reinterpretations, bone names in parentheses and italics are original names that have been changed in this paper, bone names in roman type set are unchanged from the original descriptions. **Abbreviations:** See previous figures and **Ao,** antorbital bone; **La,** lachrymal bone; **LPr,** lateral postrostral bone, **N1, N2, N3**, nasal bone 1, 2, and 3; **Pmx**, premaxilla; **Pmx-La**, premaxillo-lachrymal bone, **VR**, ventral rostral bone.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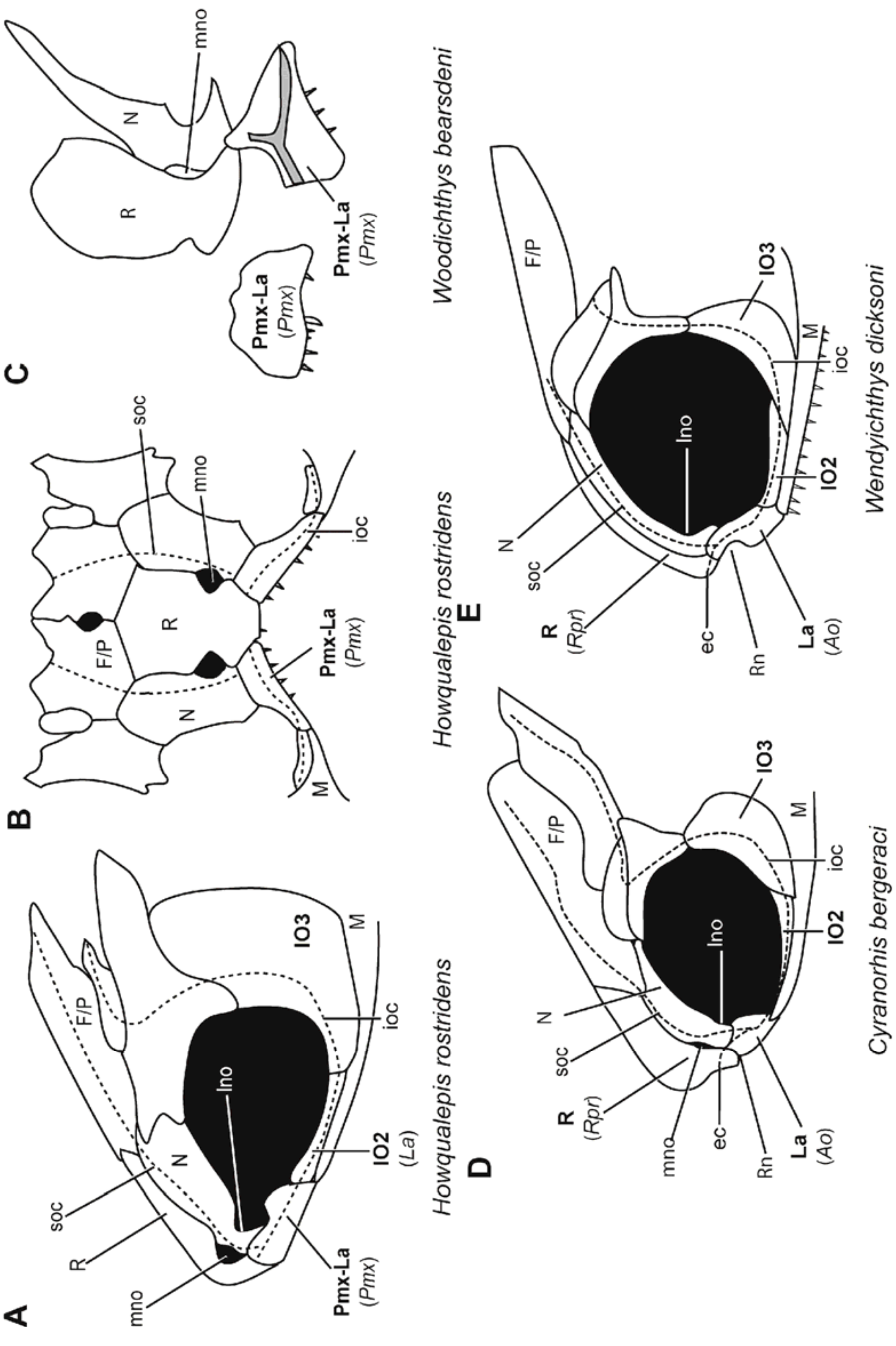
Moythomasia durgaringa

Figure 5 (Previous page)—Illustrations of the snouts of Devonian fishes depicting a snout pattern of a single rostral bone. **A–C,** single rostral bone and a premaxillo-lachrymal complex bone; **D–E,** single rostral bone and a separate lachrymal bone, premaxillae lost. **A,** lateral and **B,** dorsal views of *Donnrosenia schaefferi*; **C,** lateral and **D,** anterior views of *Mimipiscis toombsi,* external view of premaxilla on the left, internal view on the right; **E,** lateral and **F,** anterolateral view of *Moythomasia durgaringa*. Illustrations and bone identifications modified from Long et al., 2008 (**A, B**); Gardiner, 1984 (**C-F**). Bones infilled with gray are reconstructed on the basis of other Devonian fishes. Bone names in bold are new reinterpretations, bone names in parentheses and italics are original names that have been changed in this paper, bone names in roman type set are unchanged from the original descriptions. **Abbreviations:** See previous figures.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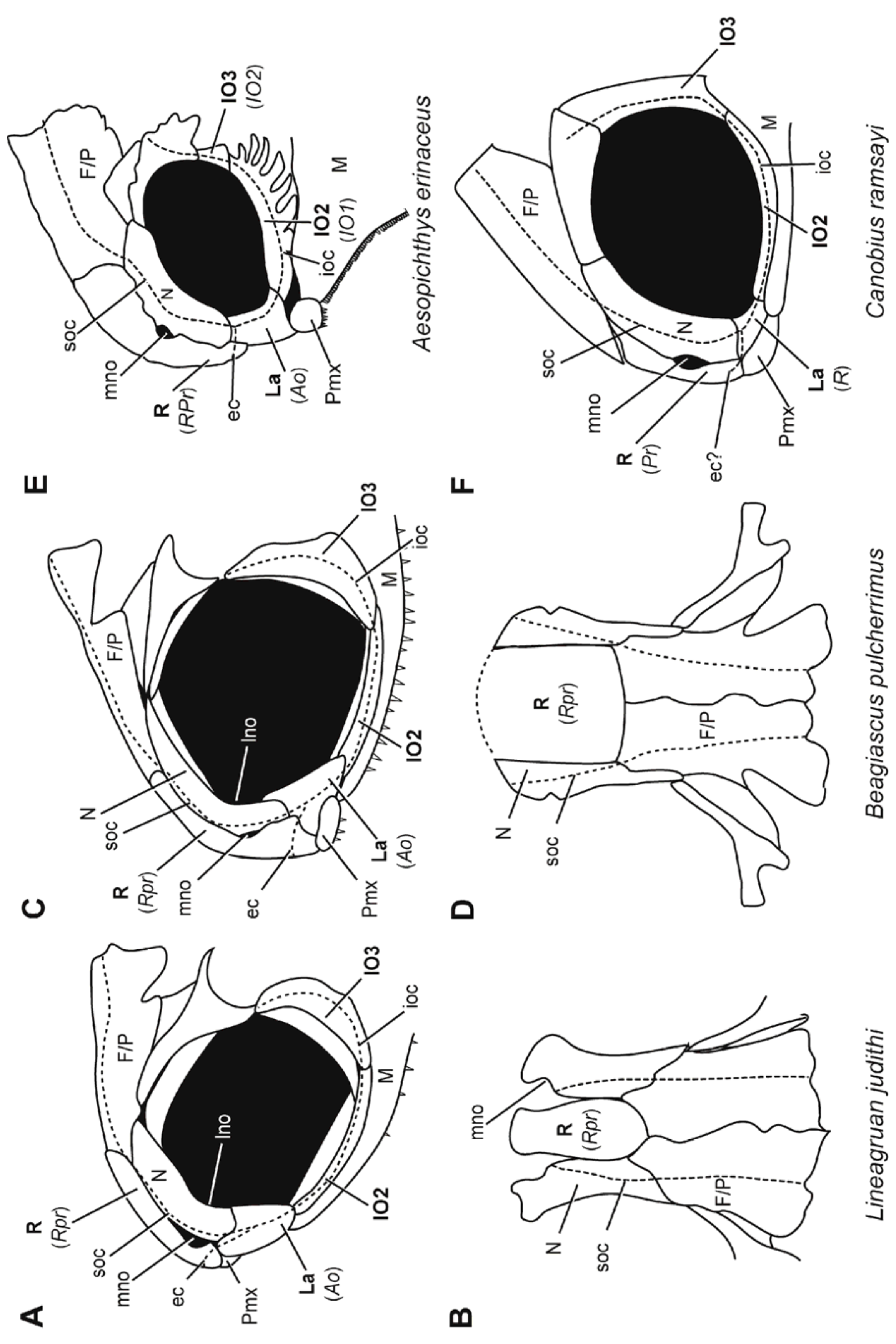
Wendyichthys dicksoni

Figure 6 (Previous page)—Illustrations of the snouts of Devonian and Carboniferous fishes depicting a snout pattern of a single rostral bone. **A,** lateral and **B,** dorsal views of *Howqualepis rostridens*; **C,** close up of the snout of *Woodichthys bearsdeni*; **D,** lateral view of *Cyranorhis bergeraci*; and **E,** lateral view of *Wendyichthys dicksoni.* Illustrations and bone identifications modified from Long, 1988b (**A, B**), Coates, 1998 (**C**), Lund and Poplin, 1997 (**D, E**). Bone names in bold are new reinterpretations, bone names in parentheses and italics are original names that have been changed in this paper, bone names in roman type set are unchanged from the original descriptions. **Abbreviations:** See previous figures and **rn,** rostral notch.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Canobius ramsayi

Figure 7 (Previous page)—Illustrations of the snouts of Carboniferous fishes depicting a snout pattern of a single rostral bone and separate premaxillary and lachrymal bones. **A,** lateral and **B,** dorsal views of *Lineagruan judithi*; **C,** lateral and **D,** dorsal views of *Beagiascus pulcherrimus*; **E,** lateral view of *Aesopichthys erinaceus* **F,** lateral view of *Canobius ramsayi.* Illustrations and bone identifications modified from Mickle et al., 2009 (**A–D**), Poplin and Lund, 2000 (**E**), Moy-Thomas and Bradley Dyne, 1938 (**F**). Bone names in bold are new reinterpretations, bone names in parentheses and italics are original names that have been changed in this paper, bone names in roman type set are unchanged from the original descriptions. **Abbreviations:** See previous figures and **Rpr**, rostro-postrostral bone.

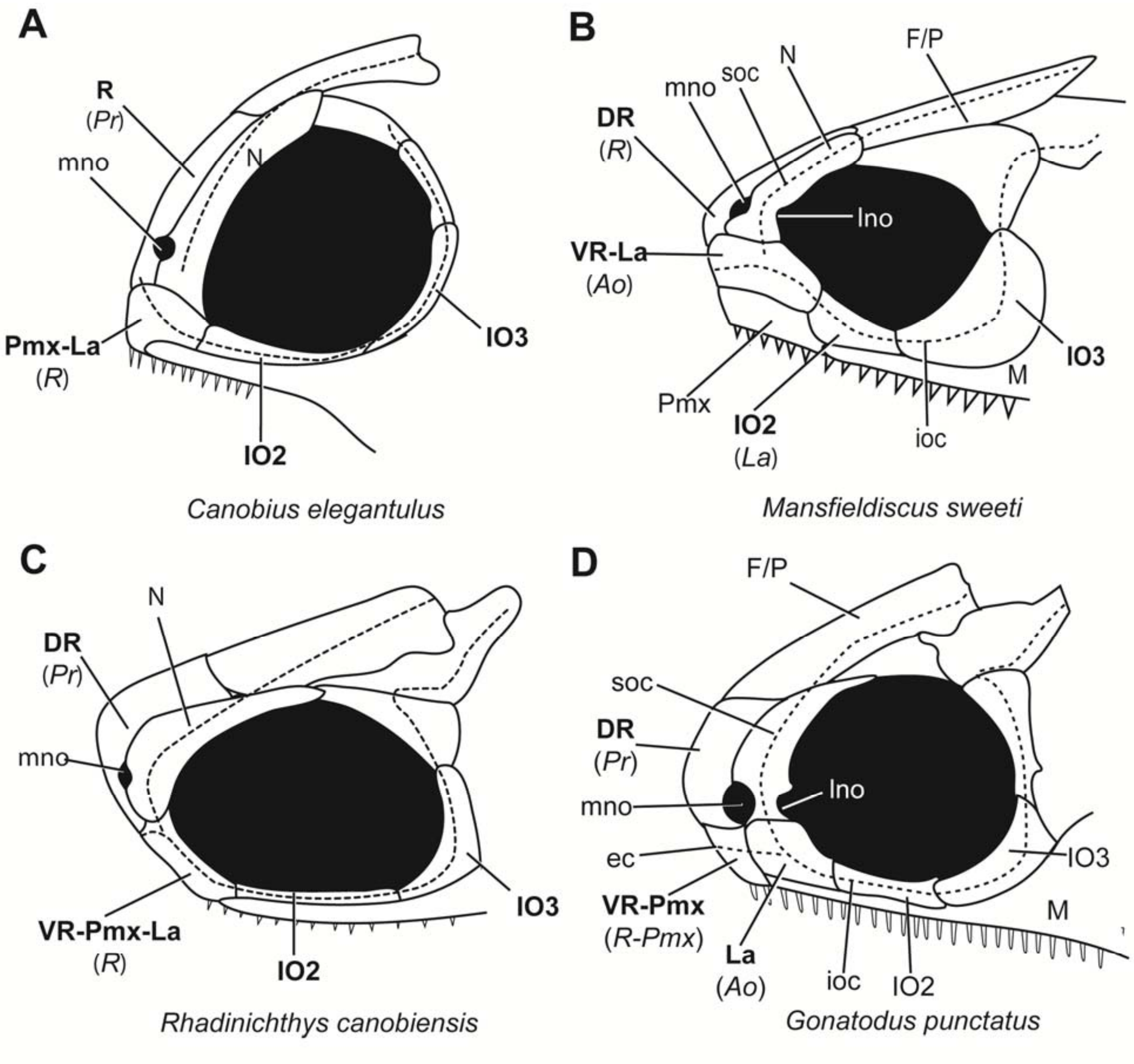


Figure 8—Illustrations of the snouts Carboniferous fishes depicting snout patterns of either a single rostral bone (**A**) or two rostral bones (**B–D**). **A,** lateral view of lateral view of *Canobius elegantulus,* **B,** lateral view of *Mansfieldiscus sweeti*; **C**, lateral view of *Rhadinichthys canobiensis,* and **D,** *Gonatodus punctatus.* Illustrations and bone interpretations modified from Moy-Thomas and Bradley Dyne, 1938 (**A, C**), Long, 1988b (**B**), and Gardiner, 1967a (**D**). Bone names in bold are new reinterpretations, bone names in parentheses and italics are original names that have been changed in this paper, bone names in roman type set are unchanged from the original descriptions. **Abbreviations:** See previous figures and **VR-La**, ventral rostro-premaxillo bone; **VR-Pmx**, ventral rostro-premaxillo bone.

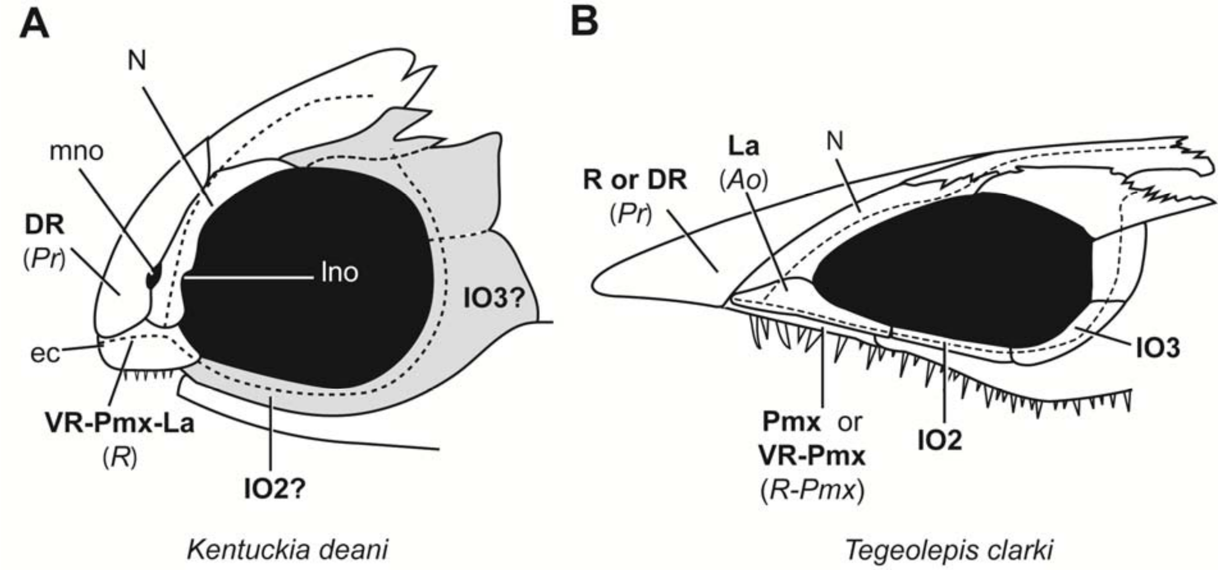


Figure 9—Illustrations of the snout of Devonian fishes. **A,** lateral view of *Kentuckia deani,* **B,** lateral view of *Tegeolepis clarki*. Illustrations and bone interpretations modified from Rayner, 1951 (**A**) and Dunkle and Schaeffer, 1973 (**B**). Bone names in bold are new reinterpretations, bone names in parentheses and italics are original names that have been changed in this paper, bone names in roman type set are unchanged from the original descriptions. **Abbreviations:** See previous figures.

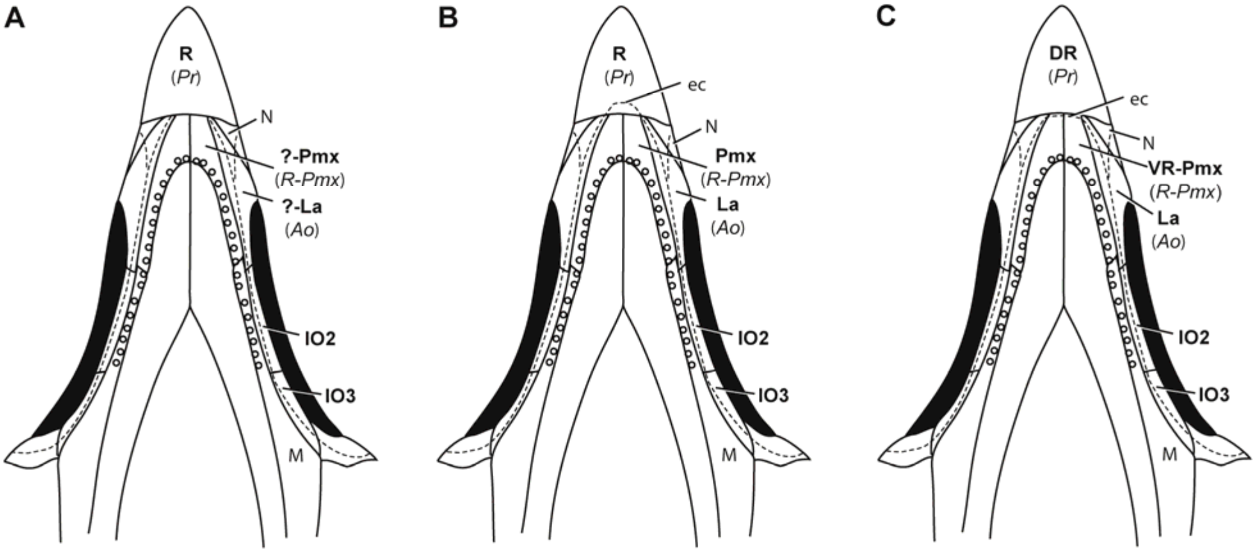


Figure 10--Hypotheses regarding the trajectory of canal lines in *Tegeolepis clarki* and subsequent bone identifications. **A**, known paths of the sensory canals of the snout; **B,** hypothesized trajectory of the sensory canals, with the ethmoid commissure exiting the lachrymal bone and entering the rostral bone; **C,** hypothesized trajectory of the sensory canals, with the ethmoid commissure exiting the lachrymal bone and entering the ventral rostro-premaxilla. Illustrations and bone identifications are modified from an illustration from Dunkle and Schaeffer, 1973. Bone names in bold are new reinterpretations based on that particular proposed canal trajectory, bone names in parentheses and italics are original names that have been changed in this paper, bone names in roman type set are unchanged from the original descriptions. Abbreviations: see previous figures.

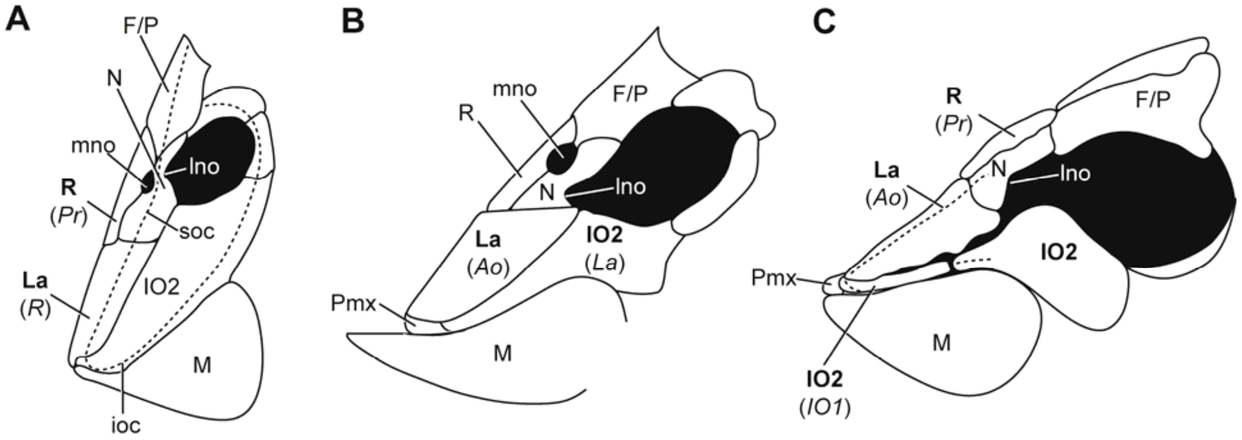


Figure 11—Illustrations of the snout of some Carboniferous deep-bodied fishes. **A,** lateral view of *Platysomus superbus,* **B,** lateral view of *Platysomus schultzei,* **C,** lateral view of *Platysomus swaffordae*. Illustrations and bone interpretations modified from Moy-Thomas and Bradley Dyne, 1938 (**A**), Zidek, 1992 (**B**), and Mickle and Bader, 2009 (**C**). Bone names in bold are new reinterpretations, bone names in parentheses and italics are original names that have been changed in this paper, bone names in roman type set are unchanged from the original descriptions. **Abbreviations:** See previous figures.

CHAPTER 3—REVISITING THE ACTINOPTERYGIAN PREOPERCULUM

ABSTRACT

The preoperculum has been a closely studied character among actinopterygians. Previous studies have identified the preopercular conditions of palaeoniscoids as primitive, ‘subholosteans’ as intermediate, and holosteans as advanced. Changes in the preoperculum across actinopterygians are thought to have functional implications regarding the jaw suspensorium and feeding mechanisms. Here, a wider study of the preoperculum in Paleozoic, Mesozoic, and Recent fishes reveals that the conventional wisdom that there is a gradual and progressive change from the palaeoniscoid condition to a more advanced condition in holostean and teleost fishes is an oversimplification. For instance, there are numerous palaeoniscoid fishes with vertical preopercula and specialized feeding regimes. When the preopercular conditions of Paleozoic and Mesozoic fishes are examined within a phylogenetic context, the original hypothesis is also not supported. Lastly, this character study highlights the need for strong phylogenetic hypotheses of relationships for a broad sampling of Paleozoic and Mesozoic actinopterygians.

INTRODUCTION

The preoperculum has been considered a particularly important bone in the evolution of actinopterygians. Different configurations of preopercular bones have been proposed for the pre-phylogenetic grade levels of Paleozoic palaeoniscoids, more advanced ‘subholosteans,’ and holosteans (Brough, 1939; Schaeffer, 1956; Schaeffer and Rosen, 1961; Gardiner, 1967b). These differences have been attributed to changes in the jaw suspensorium and in turn, feeding mechanisms (Schaeffer, 1956; Schaeffer and Rosen, 1961; Gardiner; 1967). Traditionally, palaeoniscoids have been described as having the most “primitive” preopercular condition with a tight association between the preopercular bone, maxilla, and palate—a characteristic generally used to define palaeoniscoids (Brough, 1939; Schaeffer, 1956; Schaeffer and Rosen, 1961; Gardiner, 1967b). It is hypothesized that this tight association is gradually lost, allowing for a change in the feeding mechanism.

Goals

A primary problem with this hypothesis is that it never has been investigated in a systematic or phylogenetic fashion. Past publications dealing with the importance of the preopercular bone provide few examples of the preopercular condition of Paleozoic, Mesozoic, and Recent fishes. These publications do not take into account or investigate the great diversity the preoperculum shows in these fishes, nor do they investigate this diversity within a phylogenetic framework. Here, a literature review of the hypotheses regarding the importance of the actinopterygian preoperculum is presented. This paper also seeks to test the strength of these hypotheses via a broader examination of the preopercular condition of actinopterygians from the Devonian to the Recent, and to include newly described forms in this analysis. Though some readers may feel that the results of the previous preopercular studies are outdated and incorrect, no official refutation of these papers has been published. These previous hypotheses are addressed here for the first time. Lastly, a major goal of this paper is to point out that morphological characters must be examined within a phylogenetic context. Right now, it is difficult to do so because strong hypotheses of relationships are lacking for Paleozoc, Mesozoic, and especially Paleozoic and Mesozoic fishes. A concerted effort to include a larger diversity of fossil fishes in phylogenetic analyses is necessary.

The importance of the preoperculum—a literature review

Brough (1939), Schaeffer (1956), Schaeffer and Rosen (1961), and Gardiner (1967) recognized functional implications of changes in the preoperculum across various actinopterygians. Though an external dermal bone, the preoperculum typically overlies the hyomandibula and can be used as a proxy for information on the jaw suspensorium itself (Schaeffer, 1956). Changes in the shape, inclination, and position of the preoperculum are all informative (Gardiner, 1967b).

Numerous authors have described the changes in the preopercular condition from palaeoniscoid, to 'subholostean,' to holostean fishes. Below is a synopsis of the findings of four main papers on the importance of the preoperculum in actinopterygian evolution. Palaeoniscoids have been considered representative of the most primitive condition with an anteriorly inclined preoperculum firmly fixed to the maxilla and infraorbital bones (Brough, 1939; Schaeffer, 1956; Schaeffer and Rosen, 1961; Gardiner, 1967b). A rigid cheek has implications to the underlying musculature, specificially the adductor mandibulae. The fixed external cheek bones combined with the palatoquadrate formed a narrow chamber in which the adductor mandibulae muscle was housed (Gardiner, 1967b). This chamber could either be open or closed dorsally, though the majority of palaeoniscoids with inclined preopercula were considered to have a closed dorsal margin (Schaeffer and Rosen, 1961, Gardiner, 1967b). This narrow chamber would limit the origin of the adductor mandibulae muscle to the palatoquadrate (Gardiner, 1967b). In these fishes, the adductor mandibulae would originate on the palatoquadrate, pass through the Meckelian fossa and insert anterior to the jaw articulation (Schaeffer and Rosen, 1961). The resulting biting mechanism was considered to be less efficient than that in holosteans or 'subholosteans' (Schaeffer and Rosen, 1961).

Palaeoniscoids with oblique preopercula and suspensoria were considered to have limited ability to expand the orobranchial chamber laterally (Schaeffer and Rosen, 1961; Gardiner, 1967b). The vertical articulation of the hyomandibula and the braincase would only allow the hyomandibula to swing anteriorly (Schaeffer and Rosen, 1961). This movement was assisted by the levator and adductor arcus palatine muscles, which attached to the hyomandibula itself. The pressure these muscles created on the overlying dermal bones is thought to have caused the bones to fragment and form the suborbital series. In fact, it is hypothesized that the anterior rim of the preoperculum itself fragmented to form the suborbital bones, a trend more common in long jawed forms (Gardiner, 1967b).

The "less efficient" adduction power of the adductor mandibulae, limited ability to laterally expand the orobranchial cavity, deep gape of the mouth, and typical pointed dentition of these palaeoniscoid fishes has led to the feeding regime of these early actinopterygians being reconstructed as predatory, with predator overpowering prey whole or repeatedly catching, biting, and releasing prey (Schaeffer and Rosen, 1961). The variety of feeding mechanisms seen today such as filter or suction feeding would not be expected in these fishes (Schaeffer and Rosen, 1961). Changes in the feeding mechanisms in actinopterygians resulted from the change in the jaw suspensoria in fishes (Schaeffer and Rosen, 1961; Gardiner, 1967b).

The transition from the palaeoniscoid to the holostean condition deals with a change in the angle of the suspensorium and a maxillary-palatoquadrate chamber that is open dorsally (Schaeffer and Rosen, 1961; Gardiner, 1967b). The existence of palaeoniscoid-grade fishes with vertical preopercula is considered a minority, but Schaeffer and Rosen (1961) and Gardiner (1967) mention an assemblage of fishes loosely referred to as 'subholosteans' which also show a vertical suspensorium (Schaeffer and Rosen, 1961; Gardiner, 1967b). In many of these so called ‘subholostean’ fishes, the maxillary-palatoquadrate chamber that housed the adductor mandibulae muscle was open dorsally, allowing the adductor mandibulae muscle to originate on the hyomandibula and the braincase (Schaeffer and Rosen, 1961; Gardiner, 1967b). The increase in the mass of the adductor mandibulae could mean there was an increase in its power (Schaeffer and Rosen, 1961). The more vertical suspensorium would allow for the hyomandibula to swing in a vertical plane, not just anteriorly like earlier palaeoniscoids, resulting in an increased ability to laterally expand the orobranchial chamber (Schaeffer and Rosen, 1961). Suborbital bones may or may not be present in these fishes, but it is noted that several taxa with vertical preopercula do not have suborbital bones (Gardiner, 1967b).

Many changes to the jaw suspensorium occurred in the Late Permian and Early Triassic and resulted in the holostean condition (Schaeffer and Rosen, 1961). One of the biggest changes from the palaeoniscoid condition to the holostean condition was the decoupling of the maxilla and the preoperculum and infraorbital bones. Concurrent with this was a reduction in the size of the preoperculum, modifications to the palatoquadrate and hyomandibula, and a coronoid process on the lower jaw (Schaeffer and Rosen, 1961). These changes resulted in the elimination of the maxillary-palatoquadrate chamber and the opening of the cheek region. This would allow for further expansion of the adductor mandibulae muscle and a stronger bite (Schaeffer and Rosen, 1961). It is hypothesized that these changes led to an adaptive radiation of feeding mechanisms so that some holosteans are characterized by crushing dentition (semionotids and pycnodonts) and long snouted forms (lepisosteids) (Schaeffer and Rosen, 1961).

MATERIALS AND METHODS

The preopercular conditions of Paleozoic and Mesozoic fishes were examined via a literature review and direct examination of specimens. Table 1 details taxa and literature examined for this chapter. Data collected included the number, shape, and inclination of preopercular bone(s), associations between the preoperculum and other bones, and paths of sensory canals.

Fishes from numerous publications are examined in this paper. As a result, it is necessary to try to standardize the naming of certain bones. Some of the identities of certain bones have been changed from the original publications. Naming of bones of importance for this publication has been standardized using the criteria detailed below and in Figure 1.

Preoperculum—The preoperculum is the bone anterior to the operculum and suboperculum that bears the preopercular canal (Figure 1A). Typically, the preoperculum is posterior to and separated from the orbit by the infraorbital series; and when present, the suborbital bones.

Preopercular canal—The preopercular canal runs down the depth of the preopercular bone (Figure 1A). Ventrally, the canal exits the preoperculum and continues into the lower jaw as the mandibular canal, dorsally, the preopercular canal joins the otic canal in the skull roof (Schultze, 1993, 2008).

Suborbital bones—Suborbital bones are typically anterior to the preoperculum and posterior to the infraorbital bones and orbit (Figure 1B). Most importantly, suborbitals are anamestic (Jollie, 1986). Suborbitals are absent in Devonian actinopterygians and can be characterized by variation in the numbers of individual elements among species, within species, and between the left and right sides of the same specimen.

Infraorbital bones—Infraorbitals are the circumorbital bones that bear the infraorbital canal (Figure 1A). Following sarcopterygians terminology, the first infraorbital bone is often referred to as the lachrymal, whereas the infraorbital bone in the posteroventral corner of the orbit is referred to as the jugal (Jollie, 1986). Here, the circumorbital bones bearing the infraorbital canal are all referred to as infraorbitals (with the exception of the dorsal-most bone, see below).

Dermosphenotic—The dermosphenotic is problematic—so problematic that there is an entire paper dedicated to discussing the nomenclatural dilemma this bone presents (Poplin, 2004). Here, the term dermosphenotic is used sensu Poplin (2004) to refer to the dermal bone in the posterodorsal corner of the orbit, dorsal to the infraorbitals and bearing the uppermost portion of the postorbital section of the infraorbital canal as well as the junction (when present) of the infraorbital canal with the supraorbital canal (Figure 1A). Poplin (2004) identified three different patterns of dermosphenotic bones—presence of a single dermosphenotic, two dermosphenotics (Figure 1A), or absence of a separate bone. These patterns are further broken down into subcategories (Poplin, 2004) that are used throughout this work. This definition is different from that used to describe the bones in the posterodorsal corner of the orbit and consequently subsequent bones in the otic region of numerous Bear Gulch palaeoniscoids (Lund and Melton, 1982; Lund and Poplin, 1997; Mickle et al., 2009). These fishes are presented here following the nomenclatural rules proposed by Poplin (2004).

Dermopterotic—Along with the dermosphenotic, the dermopterotic is problematic. There is variation amongst fossil actinopterygians regarding the number of lateral skull roofing bones that carry the otic canal. There are examples of fishes with one, two, or (rarely) three separate bones. Along with variation in the number of individual elements, there is variation in naming of these elements (See Poplin, 2004 figure 2). Some authors use the sarcopterygian nomenclature of intertemporal and supratemporal, implying homology (Poplin, 2004). Here, actinopterygian nomenclature is used to refer to the lateral skull roofing bones. Instead of supratemporal, the term dermopterotic is used to refer to the lateral skull roofing bone that carries the otic canal (Figure 1A). Bones anterior to the dermopterotic are named following the categories detailed by Poplin (2004)—dermosphenotic, dorsal dermosphenotic, and ventral dermosphenotic (Figure 1A). Actinopterygian nomenclature is used here when discussing only the actinopterygian fishes, but see the section concerning the homology of this bone to the bone in sarcopterygians in Chapter 6.

Dermohyal—The dermohyal is an anamestic bone located posterior to the preoperculum and anterior to the operculum (Figure 1A). This bone may be separated from the operculum by antopercular bone(s).

Antopercular bones—Antopercular bones are located anterior to the operculum and posterior to the dermohyal and preoperculum (Figure 1B). These bones can be singular, or present in a series of smaller bones.

Features of the maxilla—The term postorbital plate is used to describe the expanded region of the maxilla posterior to the orbit (Figure 1A). The postorbital plate is seen in numerous Paleozoic actinopterygians. The term posteroventral process is used to refer to the posteroventral portion of the maxilla that overlaps, or occludes, the posterodorsal portion of the dentary bone (Figure 1A).

Quadratojugal—Many deep-bodied fishes such as *Platysomus*, *Ebenaqua*, *Ecrinesomus*, and *Bobasatrania* have a large bone posterior to the maxilla and anterior to the preoperculum. This bone has been referred to as a suborbital (Campbell and Phuoc, 1983), quadratojugal (Zidek, 1992), and a supramxillaquadratojugal (Nielsen, 1952; Lehman, 1956; Schaeffer and Mangus, 1976). This bone is referred to here as a quadratojugal following the justification of Mickle and Bader (2009).

Palaeoniscoid, ‘subholostean,’ and holostean—The terms palaeoniscoid, ‘subholostean,’ and holostean were used by Schaeffer and Rosen (1961). This paper is a review of that work, so these terms are used for comparison purposes knowing fully well that the term ‘subholostean’ does not referring to natural groupings, whereas Holostei has recently been resurrected by both morphological and molecular studies (Kikugawaa et al*., 2*004; Chenhong *et al., 2*008; Grande, 2010). Based on the results of Chapter 6, the term palaeoniscoid does seem to refer to a natural grouping, but one for which is different than that of Schaeffer and Rosen (1961).

While numerous palaeoniscoid and holostean fishes are identified by Schaeffer and Rosen (1961), there is ambiguity regarding which fishes were considered to be ‘subholosteans.’ Schaeffer and Rosen (1961) described ‘subholosteans’ as “a heterogenous assemblage of advanced chondrosteans” and gave only one example—*Boreosomus* (p. 191, figure 1B). Complicating this further is that in Gardiner (1967), *Boreosomus* is identified as a palaeoniscoid. In a paper discussing the evolution of ‘subholostean’ fishes, Schaeffer (1956) defines ‘subholosteans’ as advanced chondrosteans that have a combination of palaeoniscoid and holostean characters and only the families, Dictyopygidae and Perleididae are named as belonging to the Subholostei.

Romer (1945) defines palaeoniscoids as “primitive forms, mainly Paleozoic” (pg. 89) and ‘subholosteans’ as Triassic fishes “transitional to the holosteans” (pg. 89). Romer (1945) included fusiform fishes from the genera *Cheirolepis, Rhadinichthys, Elonichthys, Canobius,* and *Tarrasius* as well as deep bodied fishes from the genera *Platysomus* and *Amphicentrum* within the grade palaeoniscoids, whereas ‘subholosteans’ were identified as primarily Triassic actinopterygians including Redfieldiids, perleididae, and parasemionotids. Holosteans were considered to include genera like *Lepidotes, Dapedium, Lepidosteus,* and amiids (Romer, 1945).

Following the definitions of Romer (1945), Paleozoic fishes are identified as being palaeoniscoids, whereas Mesozoic fishes are identified as being either 'subholosteans' or holosteans. When there is ambiguity, the definitions of palaeoniscoid, 'subholostean,' and holostean fishes from Romer (1945) are used.

The hypothesis regarding the evolution of the actinopterygian preoperculum is critiqued by mapping the preopercular condition for various fishes onto previously published phylogenetic trees from Cloutier and Arratia (2004) and Mickle et al. (2009).

Institutional Abbreviations—ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia, PA, U. S. A.; **KU**, University of Kansas Natural History Museum Ichthyology Collection, Lawrence, KS, U. S. A.

RESULTS

Paleozoic palaeoniscoids

Devonian palaeoniscoids—The preopercular condition of ten Devonian actinopterygians—*Cheirolepis canadensis* (Pearson and Westoll, 1979; Arratia and Cloutier, 1996), *Cheirolepis trailli* (Pearson and Westoll, 1979, Pearson, 1982), *Moythomasia durgaringa* (Gardiner, 1984), *Mimipiscis toombsi* (Gardiner, 1984), *Gogosardinia coatesi* (Choo et al., 2009), *Limnomis delaneyi* (Daeschler, 2000), *Kentuckia deani* (Rayner, 1951), *Howqualepis rostridens* (Long, 1988b), *Stegotrachelus finlayi* (Swartz, 2009), and *Tegeolepis clarki* (Dunkle and Schaeffer, 1973) are covered here (Figure 2). The preopercula of these fishes are all anteriorly inclined, but there is variation regarding the degree of inclination amongst different genera. For example, *Cheirolepis, Howqualepis, Limnomis,* and *Moythomasia* all have strongly oblique preopercula and suspensoria, whereas the preoperculum in *Mimipiscis* is not as dramatically inclined (Figure 2).

The preoperculum in all of these Devonian taxa contacts the posterior and dorsal margins of the maxilla, making the preoperculum curved and wider anterodorsally than posteroventrally (Figure 2). Fishes such as *Moythomasia, Mimipiscis, Gogosardinia, Limnomis, Kentuckia, Stegotrachelus,* and *Tegeolepis* have prominent postorbital plates to their maxillae that overlap the preoperculae, giving the preopercular bones in these fishes a cinched middle and characteristic "hatchet shape" commonly used to describe 'palaeoniscoids.' This is not the case within the genus *Cheirolepis* where the postorbital plate of the maxilla gradually tapers to form the posteroventral process (Figure 2A-B).

Generally, the anterior margin of the preoperculum contacts the infraorbital series, but there are differences in the particulars. All the fishes except *Tegeolepis,* and perhaps *Kentuckia,* are characterized by the presence of a single infraorbital posterior to the orbit (Figure 2). *Tegeolepis,* and possibly *Kentuckia,* have an additional infraorbital bone dorsal to the infraorbital in the posteroventral corner of the orbit (Figure 2G, J). The preoperculum is only in contact with the posterior border of the infraorbital located in the posteroventral corner of the orbit in *Moythomasia, Mimipiscis, Gogosardinia, Limnomis,* and *Stegotrachelus* (Figure 2C-F, I). In *Tegeolepis*, the anterior margin of the preoperculum is only in contact with the infraorbital dorsal to the bone in the posteroventral corner of the orbit, whereas in *Cheirolepis canadensis, C. trailli,* and *Howqualepis*, the anterior border of the preoperculum contacts the infraorbital in the posteroventral corner of the orbit, as well as posteroventral border of the dermosphenotic (Figure 2A-B, H, J).

In all of the fishes where canal information is preserved, the preopercular canal is located close to the posterior margin of the preoperculum (Figure 2). This margin comes in contact with the anterior margin of the dermohyal in all of the Devonian fishes except *Tegeolepis* (Figure 2J).

Moythomasia, *Mimipiscis*, *Gogosardinia*, *Limnomis*, and *Howqualepis* are characterized by a single dermohyal located along the posterodorsal margin of the preoperculum (Fig 2C-F, H), whereas *Cheirolepis canadensis, C. trailli, Kentuckia,* and *Stegotrachelus* have a dorsal and a ventral dermohyal (Figure 2A-B, G, I). No dermohyal bones have been reported from *Tegeolepis* (2J).

In all of the Devonian fishes, the dermosphenotic is dorsal to the preoperculum. There are two dermosphenotic bones—a dorsal and ventral dermosphenotic, in *Cheirolepis trailli, Moythomasia, Mimipiscis, Gogosardinia, Limnomis, Howqualepis, Stegotrachelus, Tegeolepis,* and possibly in *Kentuckia* and (Figure 2B-F, H-J, G), whereas *Cheirolepis canadensis* is characterized by a single dermosphenotic (Figure 2A). Regardless of whether one or two dermosphenotic bones are present, posterior to these bones is a single dermopterotic (Figure 2).

With the exception of *Stegotrachelus*, *Gogosardinia,* and to a degree, *Mimipiscis,* the maxillae have long, and deep posterior plates (Figure 2). Except for *Howqualepis, Cheirolepis canadensis,* and *C. trailli,* the maxillae of the Devonian fishes are characterized by prominent posteroventral processes (Figure 2).

Two Devonian fishes that differ from the above mentioned taxa are *Moythomasia nitida* (Jessen, 1968) and Osorioichthys marginis (Taverne, 1997). These two taxa differ from all other Devonian fishes in the presence of suborbital bones. *Moythomasia nitida* is described as having one or two intervening suborbital bones between the circumorbital series and the preoperculum (Jessen, 1968); *Osorioichthys* is described as having a single suborbital bone (Taverne, 1997). These are the only Devonian fishes with suborbital bones described.

Overall, Devonian fishes are good representatives of the palaeoniscoid condition described by Schaeffer (1956), Schaeffer and Rosen (1961), and Gardiner (1967). While there may be differences in the angle of inclination and relative size, there is not a lot of diversity in the preopercular condition of Devonian forms. The Devonian preopercular condition can be summarized as a hatchet shaped preoperculum that is wider anterodorsally than anteroventrally that contacts the posterior and dorsal margins of the maxilla, as well as the posterior margin of the infraorbital bone(s).

Carboniferous fishes—Actinopterygians are abundant and diverse in the Carboniferous, suggesting a radiation of these fishes occurred at the end of the Devonian or the beginning of the Carboniferous (Janvier, 1996). An attempt to cover a broad portion of this diversity is made here. The Carboniferous fishes presented here have been divided into four different categories—fusiform palaeoniscoid fishes with anteriorly inclined preopercula (Figure 3), fusiform palaeoniscoid fishes with more vertically inclined preopercula (Figure 4), deep-bodied fishes with vertical preopercula (Figure 5), and haplolepids (Figure 6).

Fusiform palaeoniscoid fishes with anteriorly inclined preopercula—The majority of Carboniferous fusiform palaeoniscoids are characterized by an anteriorly inclined hatchet-shaped preoperculum similar to that in Devonian actinopterygians (Figure 3). Examined here are *Rhadinichthys canobiensis* and *Elonichthys serratus* (Moy-Thomas and Bradley Dyne, 1938); *Mansfieldiscus sweeti* (Long, 1988b); *Wendyichthys dicksoni*, *W. lautreci* and *Cyranhoris bergeraci* (Lund and Poplin, 1997); *Kalops diophrys* and *K. monophrys* (Poplin and Lund, 2002) and *Lineagruan snowyi* (Mickle et. al., 2009). As in the Devonian forms, a dermohyal is present along the posterodorsal margin of the preoperculum, but some Carboniferous forms such as *Lineagruan snowyi* (Figure 3I) have an additional series of antopercular bones posterior to the dermohyal and anterior to the operculum (Figure 3I).

A difference between the Carboniferous and Devonian forms minus *Moythomasia nitida* and *Osorioichthys* is the presence of suborbital bones that separate the preoperculum from the infraorbital series (Figure 3). While uncommon in the Devonian, suborbital bones are common and diverse starting in the Carboniferous. The diversity of suborbital bones includes the presence of a single suborbital bone (*Mansfieldiscus sweeti* Long, 1988b; *Wendyichthys lautreci* Lund and Poplin, 1997), two suborbital bones (*Rhadinichthys canobiensis* and *Elonichthys serratus* Moy-Thomas and Bradley Dyne, 1938; *Wendyicthys dicksoni* and *Cyranhoris bergeraci* Lund and Poplin, 1997), or a mosaic of smaller bones (*Kalops monophrys* and *K. diophrys* Poplin and Lund, 2002; *Beagiascus pulcherrimus,* and *Lineagruan snowyi* (Mickle et al., 2009).

Typically, the Carboniferous palaeoniscoids with strong oblique preopercula and suspensoria are those with long postorbital plates and posteroventral processes to their maxillae (Figure 3). The preoperculum contacts both the posterior and dorsal margins of the maxilla. If the postorbital plate is lengthened, the preoperculum that lies on the dorsal margin of the maxilla is also lengthened. This lengthening of the maxilla and preoperculum is commonly seen in fishes with strongly oblique preopercula and suspensoria.

Fusiform palaeoniscoids with vertical preopercula—Unlike the Devonian forms, there are Carboniferous palaeoniscoids with almost vertical preopercula (Figure 4). This was mentioned by Schaeffer and Rosen (1961) and Gardiner (1967), but not examined in depth. Fusiform fishes with more vertically oriented preopercula (Figure 4A-B) include *Mesopoma pulchellum, M. politum* (Moy-Thomas and Bradley Dyne, 1938) and *Lineagruan judithi* (Mickle et al., 2009). These fishes retain the association of the preoperculum with the posterior and dorsal margins of the maxilla, but have much shorter postorbital plates than fishes with strongly oblique preopercula (Figure 4A-B). The preopercula retain the same hatchet shape seen in other palaeoniscoids because the bone extends from the posterior to the dorsal margin of the maxilla and is overlapped by the maxilla (Figure 4A-B).

Some Carboniferous palaeoniscoids such as *Canobius ramsayi*, *C. elegantulus,* and *Proteurynotus traquairi* (Moy-Thomas and Bradley Dyne, 1938) are characterized by a vertical preoperculum and a different association between the preoperculum and maxilla (Figure 4D-F). In *Canobius ramsayi,* the dorsal margin of the postorbital plate is peaked and the preoperculum only contacts the descending portion of this margin (Figure 4D). In *Canobius elegantulus*, the postorbital plate is rounded and the preoperculum only contacts the posterior margin of the maxilla (Figure 4E). In *Proteurynotus traquairi*, the maxilla is triangular and the preoperculum contacts its posterior margin (Figure 4F).

Deep-bodied Carboniferous fishes—The numerous Carboniferous deep-bodied fishes present many different preopercular conditions (Figure 5). Examined here are *Proceramala montanensis* and *Aesopichthys erinaceus* (Poplin and Lund, 2000: Figure 7B); *Paramesolepis tuberculata* and *Cheirodopsis geikiei* (Moy-Thomas and Bradley Dyne, 1938); *Platysomus gibbosus* (Campbell and Phuoc, 1983); *Platysomus superbus* (Moy-Thomas and Bradley Dyne, 1938); *Platysomus schultzei* (Zidek, 1992); *Platysomus swaffordae* (Mickle and Bader, 2009); *Amphicentrum granulosum* (Zidek, 1992); and *Guildayichthyes carnegiei* and *Discoserra pectinodon* (Lund, 2000).

One deep-bodied Carboniferous fish, *Proceramala montanensis* (Poplin and Lund, 2000) retains a hatchet-shaped preoperculum and a maxilla with a short postorbital plate (Figure 5A). Like the fusiform palaeoniscoids with abbreviate postorbital plates, the preoperculum is nearly vertical (Figure 5A). A mosaic of suborbital bones is present anterior to the preoperculum.

Another deep-bodied fish, *Aesopichthys erinaceus* (Figure 5B) has a short maxilla with a rounded postorbital plate that gives the bone a tear-drop shape (Poplin and Lund, 2000). The preoperculum is tall, nearly vertical, hatchet shaped, and firmly attached to the maxilla via an internal flange (Poplin and Lund, 2000). A single suborbital separates the preoperculum from the infraorbital series and the dermosphenotic (Figure 5B). A coronoid process is present on the mandible (Poplin and Lund, 2000).

The deep bodied fishes *Paramesolepis* and *Cheirodopsis* (Moy-Thomas and Bradley Dyne, 1938) have vertical preopercula that only contact the posterior margin of the maxillae (Figure 5C-D). The maxillae in both of these fishes have absent or reduced posteroventral processes and reduced postorbital plates. Unlike *Proceramala* and *Aesopichthys*, the hatchet shaped preoperculum is not retained in these genera (Figure 5C-D).

There is a great deal of preopercular diversity within the deep-bodied genus *Platysomus* (Figure 5E-H) with species differing in the number of preopercular bones and associations to other cheek bones. The type species, *Platysomus gibbosus* (Figure 5E) has two preopercular bones—dorsal and ventral preopercular bones that form a crescent shaped preopercular complex (Campbell and Phouc, 1983). This preopercular complex is vertical to slightly posteriorly inclined. The ventral preopercular bone does not contact the maxilla, rather it contacts the platysomid quadratojugal (Campbell and Phouc, 1983). The preopercular bones are separated from the infraorbital bones by three large intervening suborbital bones.

Platysomus superbus differs from *P. gibbosus* in that it has a single vertical preopercular bone contacting the posterior margin of the maxilla (Figure 5E-F). The maxilla has a rounded postorbital plate and no posteroventral process. The platysomid quadratojugal is not present or externally visible.

Though the preoperculum is not well preserved in *Platysomus schultzei* (Zidek, 1992), enough is preserved to see that the ventral portion of the preoperculum contacts the platysomid quadratojugal and not the maxilla (Figure 5G). The preoperculum in this fish is either vertical or slightly posteriorly inclined. Likewise, *P. swaffordae* (Mickle and Bader, 2009) has a tall, narrow, posteriorly inclined preoperculum in tight association with the platysomid quadratojugal. Interestingly, the preopercular canal of *Platysomus swaffordae* is located on the anterior margin of the preoperculum—not the posterior margin as in the other fish discussed so far (Figure 5H).

Amphicentrum granulosum (Zidek, 1992) has a vertical club shaped preoperculum that contacts the posterior margin of the maxilla (Figure 5I). The maxilla is triangular in shape and lacks a posteroventral process. The preoperculum is separated from the orbit by an infraorbital bone and the dermosphenotic. The preopercular canal is along the posterior border of the bone. *Amphicentrum* is characterized by the presence of robust toothplates (Zidek, 1992).

Two deep-bodied fishes are in the order Guildayichthyiformes—*Guildayichthys carnegiei* and *Discoserra pectinodon* (Lund, 2000). *Guildayichthys carnegiei* (Figure 5J) has two preopercular bones—dorsal and ventral bones that both carry the preopercular canal (Lund, 2000). The preopercular bones are separated from the infraorbital series by a mosaic of small suborbital bones (Figure 5J). The suborbital bones also separate the ventral preopercular bone from the maxilla. Posterodorsally, the ventral preoperculum contacts the large operculum; posteroventrally, the ventral preoperculum contacts a series of interopercular bones. Together, the dorsal and ventral preopercular bones form a crescent shaped complex that is posteriorly inclined (Figure 5J).

Discoserra pectinodon also has two narrow preopercular bones (Lund, 2000). The ventral preoperculum is taller and wider than the dorsal preoperculum, but together the two preopercula form a crescent-shaped complex (Figure 5K). This complex is posteriorly inclined and separated from the series of small infraorbital bones by a mosaic of suborbital bones. The maxilla is triangular and short—the posterior end of the maxilla does not reach the midpoint of the orbit. Consequently, the gape is also short. The preoperculum is decoupled from the maxilla and overall, the cheek is more flexible because of the mosaic of small, loosely associated suborbital bones (Figure 5K). The dentary is longer than the maxilla. Both the dentary and maxilla bear long, thin teeth on just the anterior third of the bones (Lund, 2000). Here is a Carboniferous fish with narrow, fragmented preopercula decoupled from the maxilla and a more flexible cheek.

Haplolepids—Schaeffer and Rosen (1961) and Gardiner (1967) discussed how certain Carboniferous fishes, such as haplolepids, have almost vertical suspensoria. It is unclear whether these fishes would have been considered palaeoniscoids or 'subholosteans' in the previous papers (Schaeffer and Rosen, 1961; Gardiner, 1967b). Within the Haplolepidae, there is diversity in preopercular and maxillary shapes; the conditions of *Microhaplolepis ovoidea*, *Parahaplolepis tuberculata*, and *Haplolepis corrugata* (Westoll, 1944; Lowney, 1980) are discussed here (Figure 6). *Microhaplolepis ovoidea* (Westoll, 1944) has an almost vertical preoperculum contacting the dorsal and posterior margins of the maxilla (Figure 6A). The maxilla is low, curved, has a concave dorsal margin, a rounded posterior margin, and lacks a posteroventral process. Two large suborbital bones separate the preoperculum from contacting the skull roof (Figure 6A). A similar preopercular shape is seen in *Parahaplolepis tuberculata*, but the shape of the maxilla is different from that in *M. ovoidea*. Unlike *M. ovoidea,* the postorbital plate of *M. tuberculata* is drawn up into a high peak (Figure 6B). Again, the preoperculum of *M. tuberculata* is nearly vertical (Figure 6B).

Haplolepis corrugata has a broad preoperculum that is widest midbone, and narrows both dorsally and ventrally (Figure 6C). The anterodorsal corner of the preoperculum is covered by an overlapping suborbital bone. Like *Microhaplolepis ovoidea,* the preoperculum does not contact the skull roof. Unlike *Microhaplolepis ovoidea,* the maxilla of *H. corrugata* has a tall triangular postorbital plate. Again, the suspensorium and preoperculum is described as almost vertical (Westoll, 1944).

Mesozoic fishes

The preopercular bone is diverse in Carboniferous fishes, but it is even more diverse in the Mesozoic. A variety of 'subholostean' and holostean Mesozoic fishes and their preopercular conditions will be dealt with here. 'Subholostean' fishes include Redfieldiids, Ptycholepiforms, Pholidopleurids, and Perleidids, whereas holostean fishes include Semionotiformes, Lepisosteiformes, Macrosemiiformes, Amiids, and *Dapedium*. Acipenseriformes, the cladistian *Polypterus,* and a representative basal teleost, *Leptolepis*, are also discussed.

'Subholosteans'

Redfieldiids—Redfieldiid fishes generally resemble Paleozoic palaeoniscoids with hatchet-shaped preopercula that come in contact with the posterior and dorsal margins of the maxilla (Figure 7). The maxillae of *Redfieldius gracilis* and *Dictyopyge macrurus* (Schaeffer and McDonald, 1978) and *Daedalichthys higginsi*, *Brookvalia gracilis*, and *Atopocephala watsoni* (Hutchinson, 1973) lack, or have very reduced, posteroventral processes (Figure 7A-E). Like in the palaeoniscoids, there are fishes with either elongated or reduced postorbital plates. Redfieldiids with elongated postorbital plates—such as *Redfieldius gracilis* and *Brookvalia gracilis* (Figure 7A, D) have preopercula that are more anteriorly inclined than *Dictyopyge macrurus* and *Atopocephala watsoni,* which have reduced postorbital plates (Figure 7B, E).

Dictyopyge macrurus and *Atopocephala watsoni* are characterized by vertical or near vertical preopercula (Figure 7B. E).

Suborbital bones are present in *Redfieldius gracilis, Dictyopyge macrurus, Daedalichthy higginsis*, *Atopocephala watsoni*, and *Brookvalia gracilis* but these bones differ in their placement. In *Daedalichthys higginsi, Brookvalia gracilis,* and *Atopocephala watsoni,* the suborbital bones are anterior to the preoperculum and posterior to the infraorbital bones (Figure 7C-E). The suborbitals separate the preoperculum from the infraorbital series as in numerous Paleozoic palaeoniscoids. The suborbital bones of *Redfieldius gracilis* and *Dictyopyge marcurus* are anterior and dorsal to the preopercular bones. In these taxa, the suborbital bones separate the preoperculum from the skull roofing bones and incompletely separate the preoperculum from the infraorbital series (Figure 7A-B).

Ptycholepiformes—Three species of *Ptycholepis* are examined here—*Ptycholepis barboi* (Bürgin, 1992), *P. bollensis*, and *P. curta* (Wenz, 1968). Within the genus *Ptycholepis*, a variety of preopercular shapes exist. *Ptycholepis barboi* (Figure 8A) is characterized by a hatchet shaped preoperculum with an elongated anterodorsal process (Bürgin, 1992). *Ptycholepis bollensis* (figure 8B, C) has been described with a single preopercular bone, or a preoperculum fragmented into two separate portions that both bear the preopercular canal (Wenz, 1968). In both *Ptycholepis barboi* and *P. bollensis*, the anterior margin of the preoperculum contacts a series of small suborbital bones. Though both *P. barboi* and *P. bollensis* have vertical preopercula, they differ in the contact between the maxillae and preoperculae. The preoperculum in *Ptycholepis barboi* contacts the posterior and dorsal margins of the maxilla, whereas the preoperculum in *P. bollensis* only contacts the dorsal margin of the maxilla (Figure 8B). In both of these species, the preopercular canal is more anteriorly placed (Figure 8A, B). *Ptycholepis curta* (figure 8D) is a curious fish in that there is no preopercular bone visible externally. The majority of the cheek is filled with a series of large suborbital bones (Wenz, 1968).

Wenz (1968) described the preopercular conditions in the genus *Ptycholepis* as representative of a pattern of fragmentation of the preopercular bone and a difference between palaeoniscoids and holosteans. Wenz (1968) discusses two types of preopercular bones—the palaeoniscoid type with a single anteriorly inclined preoperculum and a preopercular canal along the posterior portion of the bone, and the 'holostean' type where the preoperculum is vertical with an anteriorly placed canal. Wenz (1968) also reviews previous discussions (Brough, 1939, Stensiö, 1947) regarding the transition from a palaeoniscoid preoperculum to a 'holostean' preoperculum. There are two ways this transition is thought to have occurred—either through a fragmentation of the preoperculum into separate elements or by an enlargement of the suborbitals into the space formerly occupied by a large preoperculum (Brough, 1939; Stensiö, 1947; Wenz, 1968). Wenz (1968) describes *Ptycholepis curta* as being an extreme example of the reduction of the preoperculum and expansion of the suborbital bones into the area of the cheek the preoperculum is typically positioned in, whereas *P. bolesnsis* supports the fragmentation hypothesis.

Pholidopleuriformes—The pholidopleurid *Pholidopleurus ticinensis* (Bürgin, 1992) has a narrow, vertical, hatchet-shaped preoperculum that contacts the posterior and dorsal margins of the maxilla (Figure 9). There are no suborbital bones, only infraorbitals. A large open space separates the preoperculum from the skull roof and infraorbital bones. This open space is found in all pholidopleurid species and allowed for a more open flexible cheek (Bürgin, 1992).

Perleidiformes—Within the Perleidiformes, fishes are characterized by differences in preopercular shape, contact between the preoperculum and the skull roof, and the presence of suborbital bones (Figure 10). *Platysiagum minus*, *Meridensia meridensis*, *Peltoperleidus bellipinnis*, and *Ctenognathichthys bellottii* (Bürgin, 1992) are examined here. *Platysiagum minus* has a broad preoperculum that is wider dorsally than ventrally (Figure 10A). The preopercular canal is close to the posterior margin of the bone. The postorbital plate of the maxilla is low and the posteroventral process is weakly developed. There are no suborbital bones so the anterior margin of the preoperculum contacts the infraorbital and dermosphenotic bones. The preoperculum is almost vertical (Figure 10A).

Peltoperleidus bellipinis (Figure 10B) and *Meridensia meridensis* (Figure 10C) have vertical preopercula, but differ in the shape of the bone. *Peltoperleidus bellipinis* has a preoperculum with a tall narrow dorsal process that extends to the skull roof, a narrow process that extends posterior to the maxilla, and a spiked anterior process that extends along the dorsal margin of the maxilla (Figure 10B) *Meridensia meridensis* has an anterior rectangular expansion posterior to the infraorbital series and narrow dorsal and ventral processes (Figure 10C). The preopercula in both of these taxa contact the dorsal and posterior margins of the maxilla (Figure 10B-C). *Meridensia meridensis* differs from *Peltoperleidus bellipinis* with the presence of a single suborbital bone overlapping the anterodorsal margin of the preoperculum (Figure 10B-C). Both taxa are characterized by weakly developed posteroventral processes on the maxilla, but *Meridensia meridensis* has a taller but shorter postorbital plate than *Peltoperleidus bellipinis* (Figure 10B-C).

Ctenognathichthys bellottii (Bürgin, 1992) differs in that the preoperculum is roughly crescent shaped and contacts the rounded posterior margin of the maxilla (Figure 10D). Two suborbital bones contact the anterior margin of the preoperculum, separating the preoperculum from the dermosphenotic and infraorbital bones. The maxilla and dentary are short and bear long pointed teeth (Figure 10D).

The Triassic *Luganoia lepidosteoides* (family Luganoiidae) is characterized by a broad, plate-like preoperculum with a rounded dorsal border (Bürgin, 1992). Anteroventrally, the preoperculum is extended out ventral to the orbit as a narrow arm (Figure 10E). The preopercular canal and pit lines are located near the posterior margin of the bone. Anteriorly, the preoperculum is in contact with the infraorbital series, posteriorly the ventral half of the operculum and the suboperculum. The narrow anteroventral arm of the preoperculum is in contact with the dorsal border of the maxilla. Two suborbital bones, identified as anamestic postorbitals by Bürgin (1992) are located dorsal to the preoperculum. Posterior to the suborbital series, and still in contact with the dorsal margin of the preoperculum, is a dermohyal. Ventral to the preoperculum is a series of block-like anamestic bones. These bones are posterior to the maxilla and identified by Bürgin (1992) as postmaxillary bones. These bones, and a quadratojugal, separate the preoperculum from the lower jaw and the posterior margin of the maxilla (ibid.).

Holosteans

Semionotiformes—Semionotids from the genus *Lepidotes—L. lennieri* and *L. elvensis* (Wenz, 1968) are examined here (Figure 11). In both species, the preoperculum is crescent-shaped and wider ventrally than dorsally (Figure 11). Dorsally, the preoperculum extends up to the skull roof and is vertical. Ventrally, the wider section of the preoperculum extends anteriorly and is situated ventral to the suborbital bones (Figure 11). Ventral to the preoperculum is an interopercular bone (Figure 11). The preoperculum is decoupled from the maxilla but retains a firm connection to a series of suborbital bones (Wenz, 1968).

As in *Lepidotes,* the preoperculum of *Semionotus kanabensis* (Figure 11C) is crescent-shaped (Schaeffer and Dunkle, 1950). Preopercular contact with the infraorbital series is limited because of the presence of a large ovoid suborbital bone along the anterodorsal border of the preoperculum (Schaeffer and Dunkle, 1950). As in *Lepidotes*, the preoperculum of *Semionotus kanabensis* is decoupled from the maxilla. Ventral to the preoperculum are the suboperculum and interoperculum. The preopercular canal is situated near the posterior border of the bone (Schaeffer and Dunkle, 1950).

Amiiformes—Fishes from the Families Amiidae and Caturidae have been examined. The amiid *Amia calva* (Figure 12A) has a crescent shaped preoperculum that is attached to the hyomandibula (Grande and Bemis, 1998). The preoperculum is narrow, and the preopercular canal is positioned at about midbone with pore lines positioned posteriorly (Grande and Bemis, 1998). The preoperculum is posteriorly inclined and the posterior margin of this bone contacts the operculum, suboperculum, and interoperculum. The preoperculum is decoupled from the maxilla and supramaxilla. Infraorbital, or postorbital bones, are present, but do not contact the preoperculum. Because the preoperculum does not contact the maxilla or suborbital bones, *Amia* is characterized by an open cheek that allows for a much larger area for the adductor mandibulae muscle (ibid.).

The caturid *Caturus furcatus* (Figure 12B) also has a crescent shaped preoperculum (Grande and Bemis, 1998). The preopercular canal is positioned near the anterior border with pore lines extending towards the posterior margin of the bone. As in *Amia calva,* the preoperculum contacts the opercular series posteriorly and is decoupled from the maxilla. Unlike *Amia calva,* there are infraorbital and suborbital bones. Anteriorly, the preoperculum contacts two large anamestic suborbital bones. These bones separate the preoperculum from contacting the infraorbital bones (Grande and Bemis, 1998). The cheek of *Caturus furcatus* is not as open as that in *Amia calva* (Figure 12).

Lepisosteiformes—The classification scheme of Grande (2010) is used here for extant and extinct gars. As detailed by Grande (2010) the preoperculum in the lepisosteid gar *Lepisosteus osseus* is a crescent shaped bone with a ventral horizontal portion and a dorsal vertical portion (Figure 13). The horizontal arm is visible externally, whereas the majority of the vertical arm is overlain by the suborbital series, making the preoperculum seem smaller than it actually is (Grande, 2010). The hyomandibula is attached to the mesial side of the dorsal half of the vertical arm of the preoperculum. The preoperculum is situated anteroventral to the operculum and the suboperculum and does not contact the maxilla (ibid.). The anterodorsal margin of the horizontal arm of the preoperculum contacts the infraorbitals, whereas the posterodorsal margin contacts the mosaic of suborbital bones. The contact between the preoperculum, infraorbital, and suborbital bones makes for a rigid cheek.

As shown by Grande (2010) the interoperculum is absent in *Lepisosteus osseus* and other lepisosteid gars, but is present and prominent in the non-lepisosteid fossil gars *Obaichthys decoratus* and *Dentilepisosteus laevis* (Figure 13 D). In these non-lepisosteid gars, the preoperculum is similar in shape to that in lepisosteid gars, but differ in that the ventral margin of the preoperculum contacts the dorsal margin of a triangular interopercular bone (ibid.). It is suggested that in lepisosteid gars, the large horizontally oriented limb of the preoperculum invades the space previously occupied by an interoperculum; but it is unknown whether the interoperculum fuses to the preoperculum or if it is lost as a distinct bone (ibid.).

Macrosemiiformes—The macrosemiid *Macrosemius rostratus* (Figure 14) has an L shaped preoperculum that has large fenestra around the preopercular canal (Bartram, 1977). The horizontal arm is more robust than the posteriorly inclined arm. The preoperculum is decoupled from the maxilla, infraorbital series, and skull roof. The cheek is flexible because the infraorbital series is reduced to a chain of triangular bones that in the cheek region, do not contact any other bones ventrally. Anterior and ventral to the orbit, these bones are thin with a thickened region covering the infraorbital canal. Posterior to the orbit, the infraorbital bones are complete tubes that house the infraorbital canal (Bartram, 1977). An ovoid interopercular bone is present posterior to the preoperculum and anterior to the suboperculum.

Dapedium—*Dapedium pholidotus* and *D. punctatus* (Wenz, 1968) are round deep-bodied fishes. Consequently, the maxillae and mandibles of these fish are very different from other Mesozoic fishes. The short maxilla has a rounded posterior portion that only reaches the anterior half of the orbit. The lower jaw is deeper than the maxilla and tear drop shaped (Wenz, 1968). Posterior to the orbit is a series of infraorbital bones (interpreted to include the bones bearing pore canals in *Dapedium pholidotus*). In *Dapedium pholidotus*, a series of suborbital bones are ventral to the infraorbitals, whereas in *D. punctatus,* suborbitals are posterior and ventral to the suborbital bones. In both species, the infraorbital and suborbital bones form a rather rigid cheek.

In both *Dapedium pholidotus* and *D. punctatus*, the preoperculum is reduced to a narrow rectangular bone that is almost horizontal in orientation (Figure 15). Pore canals from the preopercular canal are present in *D. pholidotus* (Figure 15A). This narrow preoperculum is situated ventral to the suborbital bones and dorsal to an elongate interopercular bone. The preoperculum is decoupled from the maxilla. There seems to be a space anterior to the preoperculum and posterior to the lower jaw in both *D. pholidotus* and *D. punctatus*. The preoperculum does not contact the skull roof and overall, has a ventral postion on the side of the head. It is difficult to imagine how this preopercular bone overlies the hyomandibula.

Pachycormus—*Pachycormus macropterus* (Wenz, 1968) has a crescent shaped preoperculum that is slightly wider ventrally than dorsally. The preoperculum is decoupled and separated from the maxilla by a large suborbital bone and the supramaxilla (Figure 16). Ventrally, the preoperculum contacts the dorsal margin of a narrow interopercular bone. Anteroventrally, the preoperculum contacts the angular of the lower jaw. Two large suborbital bones are present posterior to a series of rectangular infraorbital bones. The preopercular canal is along the anterior border of the preoperculum.

Acipenseriformes

Cranial bones in recent and fossil members of Acipenseriformes are reduced, especially in the cheek region. No ossified preopercular bones are present in members of Polyodontidae, but there are small ossifications around the preopercular canal in extant members of Acipenseridae (Grande and Bemis, 1991; Hilton, 2005 see figure 1b, 1e, 3b; Grande and Hilton, 2006).

Cladistia

***Polypterus*—**A large portion of the cheek in polypterids is formed by a club shaped bone with a narrow vertical canal bearing portion and an expanded anterior portion that contacts the maxilla (Figure 17A, shaded, 17B). The identity of this bone has caused a great deal of controversy which must be summarized before looking at the preoperculum in polypterids. The bone in question was identified as a preoperculum by Müller (1846) and Agassiz (1833-43), whereas Traquair (1871) identified it as a cheek-plate and doubted the presence of a preopercular bone in polypterids (Allis, 1922). Huxley (1861) also doubted that this bone was a preoperculum, but identified two portions to the bone—these portions were called the supratemporal and the hyomandibula (Allis, 1922). Collinge (1893) also identified two portions to this bone—he considered the expanded anterior portion to be an infraorbital bone fused to the tall and narrow preoperculum and identified a groove and suture between these two bones in young specimens (Allis, 1922). Pollard (1892) termed the bone a preoperculum, but also identified two portions—a preopercular portion and a portion homologous to the postorbital in *Amia* (Allis, 1922).

Allis (1922) is in agreement with Huxley (1861), Pollard (1892), and Collinge (1893) in that there seems to be two separate portions to this large cheek bone in adult specimens, but disagreed with Collinge (1893) in that Allis (1922) could not identify a suture between the two components. The expanded plate-like portion that contacts the maxilla is more superficial than the posterior portion that bears the preopercular canal. The horizontal and vertical pit lines are present in this expanded portion. The grooves that house the pit lines are considered by Allis (1922) to be the groove Collinge (1893) saw separating the two portions of the "preopercular bone." Allis (1922) concludes that the superficial expanded portion housing the pit lines is homologous to the squamosal, whereas the deeper portion of the bone that bears the preopercular canal is homologous to the preoperculum. Collectively, this bone was referred to as the cheek plate (Allis, 1922).

Pehrson (1947) was able to examine adult and 24 mm long specimens of *Polypterus* and came to a different conclusion than Allis (1922). In the 24 mm long specimen, Pehrson (1947) identified two portions to the developing preopercular bone—a dorsal and ventral component. The ventral component bears the preopercular canal, whereas the dorsal component forms the expanded plate like region anterior to the canal bearing portion. Pehrson (1947) states that there is nothing to indicate that this dorsal component is anything but an anterior process off the preopercular bone and that the larval stages he has examined do not support the assertion that the expanded anterior portion of the preoperculum is homologous to the squamosal.

Bartsch (1997) disagrees with Pehrson (1947) and agrees with Allis (1922) in regards to the presence of a squamosal in polypterids and identifies the large cheek bone in question as a squamoso-preopercular. Based on detailed larval studies, Bartsch (1997) describes how the squamosal (the expanded anterior region) develops independently of the two, if not more, preopercular canal bearing bones. The squamosal portion, which is in contact and interdigititated with the posterior end of the maxilla, develops before the posteriorly placed preopercular canal bearing bones. The preoperculum fuses secondarily to the squamosal to form the distinct club shaped cheek bone in polypterids (Bartsch, 1997).

Though there is controversy over the identity of the large dermal cheek bone in polypterids, a few things are clear. First, it is clear that it is not a single bone, but formed by at least two fused portions. This was identified by Huxley (1861), Pollard (1892), Allis (1922), and Bartsch (1997). Second, the posterior portion of this bone that carries the preopercular canal is the preoperculum. The question is the identity of the expanded dermal plate that is in contact with the posterior margin of the maxilla. This bone does not bear the infraorbital canal so it is clearly not an infraorbital, or postorbital. Bartsch (1997) has the most comprehensive developmental series of polypterids and the most complete understanding of the ontology of these fishes. Bartsch (1997) describes these two elements as being originally separate, and fusing secondarily. This is accepted here, but with some changes. Instead of the more superficial cheek plate component being identified as a squamosal as it was by Bartsch (1997) and Allis (1922), it is identified here as a suborbital. In *Polypterus ornatapinnis,* there are anemestic bones, identified as suborbitals (Grande, 2010) between the infraorbital canal bearing bone (identified by Grande, 2010 as a postorbital) and the preoperculum + cheek plate. It seems more parsimonious to consider the superficial cheek plate portion of the preopercular complex to be one or many suborbital bones than a squamosal. Here, the preopercular complex is considered to be a suborbital-preoperculum.

The suborbital-preoperculua have been examined in *Polypterus ornatipinnis* (KU 23147), *P. endlicheri* (ANSP 78303, Figure 17B), and; from the literature, *P. bichir* (Allis, 1922) and *P. senegalus* (Bartsch, 1997). While there are no obvious suture lines between the two portions, there is a clear demarcation between the more superficial suborbital component and the deeper preopercular component in the form of a sloping ridge or ledge (Allis, 1922, KU 23147, ANSP 78303, Figure 17B). The deeper preopercular portion carries the preopercular canal and four pores are present; one on the anteroventral portion of the preoperculum, two on the posterior border, and one on the posterodorsal margin of the preoperculum (Bartsch, 1997 figure 2D). The suborbital portion articulates with the posterior margin of the maxilla. The preopercular portion does not bear any ornamentation, whereas the suborbital portion is heavily ornamented with closely spaced tubercles (Allis, 1922, KU 23147, ANSP 78303, Figure 17B).

The hyomandibula is shaped as an inverted L with the horizontal portion rostrally directed. The preopercular portion of the cheek bone overlies the vertical arm of the hyomandibula and the dorsal margin of the preopercular component corresponds to the opercular process of the hyomandibula (Allis, 1922, KU 23147, ANSP 78303). The posterodorsal corner of the suborbital overlies a portion of the rostrally directed arm (KU 23147, ANSP 78303). In *P. endlicheri* (ANSP 78303) and *P. bichir* (Allis, 1922) there is an accessory hyomandibula on the dorsal margin of the horizontal arm of the hyomandibula. In both of these species, this accessory hyomandibula and the anteriomost portion of the horizontal arm extend above the dorsal margins of both the preopercular and suborbital portions of the cheek plate. Overall, the hyomandibula is slightly posteriorly inclined, similar to the preopercular element itself (Allis, 1922, KU 23147, ANSP 78303). Along with overlying the hyomandibula, this cheek plate is external to the masseter portion adductor mandibulae muscle (Allis, 1919).

Teleosts

Basal teleosts *Leptolepis coryphaenoides*—Basal teleosts are only mentioned briefly in this chapter. *Leptolepis coryphaenoides* (Arratia, 1996) is characterized by a broad crescent shaped preoperculum that does not contact the maxilla because of an intervening posteroventral process of the quadrate and the symplectic (Figure 18). Ventral to the preoperculum is an elongate interopercular bone (Figure 18). Posterior to the infraorbital series and overlapping the dorsal margin of the preoperculum is a large suborbital bone. Suborbital bones are not common in Jurassic teleosts (Arratia, 1996). A suborbital bone is present in *Varasichthys ariasi*, but this bone is much smaller and in a different position than that in *L. coryphaenoides* (Arratia, 1996). The main preopercular canal is along the anterior border of the bone and prominent branches come off the main canal and extend towards the posterior margin of the bone (Figure 18). The shape of the preoperculum in *L. coryphaenoides* is similar to that found in the Jurassic teleosts *Anaethalion knorri*, *Ascalabos voithii*, *Leptolepides sprattiformis*, and *Orthogonikleithrus leichi* (Arratia, 1996).

Previous hypotheses within a phylogenetic context

The preopercular condition of various actinopterygians can be placed onto previously published phylogenetic trees to determine if there is support for the previous hypotheses of a smooth transition from a palaeoniscoid condition, to a ‘subholostean’ condition, to a holostean condition. Two phylogenetic trees that resulted from analyses of lower actinopterygian fishes are used—Mickle et al. (2009) and Cloutier and Arratia (2004). These trees were chosen over other published trees because of their taxonomic breadth, in regard to both number and diversity of the included taxa. Figure 19 shows the tree from Mickle et al. (2009). This tree was specifically chosen because of the presence of numerous Carboniferous deep-bodied fishes. Intermixed among the palaeoniscoids are fishes with anteriorly inclined preoperculum as well as vertical preoperculum. The same pattern is seen for the Mesozoic forms (Figure 19). If the tree from Cloutier and Arratia (2004) is considered, a similar pattern is revealed (Figure 20). Neither of these trees support the hypothesis of a gradational change from one preopercular condition to another.

If the shape of the preoperculum is mapped onto the tree presented here in Chapter 6 that resulted from parsimony analyses with recent fishes included (Chapter 6, Figure 9), a similar pattern to what is presented above is recovered. This tree is presented here in Figure 21. Within the Palaeonisci, all preopercular orientations are seen—anteriorly inclined, vertical, and posteriorly inclined. Within the Paleonisciformes, again, anteriorly inclined, vertical, and vertical to posteriorly inclined preopercula are present. A monophyletic Palaeonisciformes includes the deep bodied Platysomidae, as well as the Carboniferous Haplolepidae and Mesozoic Redfieldiidae (Figure 21). These fishes are often not included in analyses, were not considered in depth by Schaeffer and Rosen (1961) and Gardiner (1967), or fall under their heading of 'subholostean.' With the recovery of these fishes within the Palaeonisciformes, there is not a transition from one preopercular shape to another from palaeoniscoids, Late Paleozoic to Mesozoic 'subholosteans', and holosteans. Instead, a greater diversity of preopercular shapes are seen within the palaeoniscoids. The different preopercular shapes among lower actinopterygians may have functional signifigance and not necessarily part of a phylogenetic sequence.

This said, what is missing from all of these trees are a high representation of Mesozoic forms. There are a few Mesozoic fishes, but many of the advanced Mesozoic forms are not included in analyses. Though we can see that within the palaeoniscoids, there is a greater diversity of preopercular shapes than originally discussed by Schaeffer and Rosen (1961) and Gardiner (1967), there cannot be a strong comment made regarding the condition of the preoperculum among Mesozoic and Paleozoic forms at this time. Phylogenetic trees with a greater sampling of Paleozoic and Mesozoic fishes are necessary for this to be accomplished.

DISCUSSION

Unspecialized versus specialized feeding regimes—In some publications, early actinopterygians were described as primarily predaceous fishes that fed by overtaking and biting its prey—feeding was not assisted by current actions (Schaeffer and Rosen, 1961). This may be an over generalization and goes against how fish feed (and respire). The act of a fish opening its mouth, regardless of its feeding mechanism, will result in an increase in the volume of the oral cavity and water rushing into the mouth. This is also the first step in respiration. There have not been drastic changes in how basic respiration occurs in actinopterygians—water must enter the orobranchial chamber and run across the gills. It can be assumed that this is how palaeoniscoid fishes respired as well. Following this reasoning, when a fish opens its mouth to capture prey, regardless of whether it is a palaeoniscoid, a ‘subholostean,’ or a holostean, there will be a subsequent suction force. This said, the strength of the suction force should be expected to be different amongst different types of fishes—palaeoniscoids with immobile maxilla would have a less powerful suction force than a teleost with a mobile premaxilla.

On top of this, a broader survey of Paleozoic fishes suggests that the idea that early actinopterygians were characterized by unspecialized feeding mechanisms may not be correct. While the Devonian actinopterygians are representative of the ‘primitive palaeoniscoid’ condition, there is a greater diversity of preopercular shapes among Paleozoic actinopterygians. Often the Paleozoic fishes with different preopercular conditions have other morphological differences that suggest Paleozoic fishes were characterized by specialized feeding mechanisms. A clear example of this is the deep-bodied Carboniferous fishes.

Deep-bodied Carboniferous fishes provide evidence for an array of feeding mechanisms. As mentioned by Poplin and Lund (2000), the deep-bodied *Aesopichthys* has a modified feeding mechanism compared to the typical fusiform palaeoniscoids. The nearly vertical preoperculum and suspensorium, short gape, coronoid process on the mandible, and dentition have led Poplin and Lund (2000) to describe the biting mechanism of this fish as being strong and sharp. This specialization, combined with the specialized body shape and a possible suction mechanism described by Poplin and Lund (2000) led to a reconstruction of a specialized feeding regime—*Aesopichthys* is hypothesized to have fed on shrimp, and worms that were engulfed or sucked into the oral cavity. An additional hypothesized feeding regime was that *Aesopichthys* could have browsed on bryozoans and algae (Poplin and Lund, 2000).

The Carboniferous Guildayichthyiformes have also been described to have highly specialized feeding mechanisms (Lund, 2000). With its two narrow preopercular bones that are not associated with the maxilla and its flexible cheek, *Discoserra pectinodon* has quite a different preopercular condition than other Paleozoic fishes. Combined with its long teeth and short gape, the feeding regime of this fish is reconstructed as involving plucking and grazing (Lund, 2000). The loosening of the bones in the cheek, as well as changes to the operculogular apparatus is hypothesized to have allowed for suction feeding (Lund, 2000).

There are Paleozoic fishes that have ‘specialized’ feeding mechanisms in the form of crushing dentition. Some species of *Platysomus,* such as *Platysomus schultzei* (Zidek, 1992) have phyllodont tooth plates supported on the parasphenoid and vomer and lack teeth on the upper and lower jaws (Zidek, 1992). These tooth plates are hypothesized to have crushed crustaceans (Zidek, 1992). Other Paleozoic deep-bodied fishes, like *Amphicentrum*, have conical teeth on large robust tooth plates that have been hypothesized to crush mollusc shells (Zidek, 1992). It should be noted that *Platysomus*, *Amphicentrum*, and the previously mentioned deep-bodied fishes with hypothesized specialized feeding regimes all have different preopercular configurations.

CONCLUSIONS

A wider study of the actinopterygian preoperculum has revealed that there is a greater diversity of preopercular conditions in both Paleozoic and Mesozoic fishes than originally described. While Schaeffer and Rosen (1961) and Gardiner (1967) are correct in the statement that a large number of Paleozoic palaeoniscoids are characterized by anteriorly inclined preoperculum, by concentrating mainly on these fishes, a greater diversity of preopercular conditions among Paleozoic fishes is missed. When a wider array of Paleozoic fishes is examined, it is clear that, like the Mesozoic, the Paleozoic was a time of experimentation in preopercular conditions and feeding regimes. This is especially true for deep-bodied forms. If results from Figures 19–21 are examined, the palaeoniscoid fishes are characterized by more than just anteriorly inclined preoperculum (Figures 19–21). The diversity of the actinopterygian preoperculum cannot be pigeon holed into three distinct categories.

The only way the importance of certain characters such as the preoperculum can be tested is to look for a pattern within a phylogenetic framework. When the preopercular conditions of Paleozoic and Mesozoic fishes are examined within a phylogenetic context, the previously proposed gradational change from one preopercular condition to the next is not recovered. It is not as easy as the story of the existence of a primitive condition, an intermediate condition, and a “perfected’ condition. This said, the availability of phylogenetic trees that include a broad array of Paleozoic and Mesozoic fishes is poor, and the testing of the hypothesis regarding the importance of the preoperculum in this paper is a first attempt with the data at hand.

Unfortunately, broad analyses are not common in the field of paleoichthyology. It is more common for phylogenetic analyses to be focused in on one subset of the fossil fish diversity. Take investigations into the relationships of Paleozoic fishes into consideration. Recently, phylogenetic analyses into the relationships of Paleozoic lower actinopterygians commonly focus on Devonian fishes, with the ingroup including only, or a majority of, Devonian taxa (Friedman and Blom, 2006; Long et al., 2008, Swartz, 2009). Multiple deep bodied Paleozoic fishes such as *Platysomus* and *Amphicentrum* are commonly excluded (with the exceptions of Lund, 2000; Mickle et al., 2009). The Haplolepidae, Redfieldiidae, Aeduellidae, and Amblypteridae are usually not included in analyses with more “typical” palaeoniscoid taxa unless these families are the focus of the analysis (Dietze, 2000; Poplin and Dutheil, 2005). Extant lower actinopterygians are often not investigated with extinct lower actinopterygians even though they have been clearly shown to be influential in changing hypotheses of relationships (Cloutier and Arratia, 2004). The number of analyses that include both Paleozoic and Mesozoic fishes is low, and those that do, do not provide a thorough sampling of the Mesozoic diversity. Until such hypotheses exist, we cannot look at characters such as the preoperculum in any depth. Larger phylogenetic analyses with broader taxon sampling across the Devonian to the recent are not only necessary for understanding the evolution of specific characters, but as will be pointed out in Chapter 6, seem to be necessary in forming a stronger understanding of specific taxa. Such analyses are necessary to form stronger insight into actinopterygians as a whole.

Table 1—Investigated taxa and literature or specimens examined.

Taxon	Source	Examined Specimens
Aesopichthys erinaceus	Poplin and Lund, 2000	CM 48550
Amia calva	Grande, Bemis, 1998	
Amphicentrum granulosum	Zidek, 1992	–
Atopocephala watsoni	Hutchinson, 1973	–
Brookvalia gracilis	Hutchinson, 1973	–
Canobius elegantulus	Moy-Thomas and Bradley Dyne, 1938	–
Canobius ramsayi	Moy-Thomas and Bradley Dyne, 1938	–
Cheirodopsis geikiei	Moy-Thomas and Bradley Dyne, 1938	–
Cheirolepis canadensis	Pearson and Westoll, 1979; Arratia and Cloutier, 1996	–
Cheirolepis trailli	Pearson and Westoll, 1979; Arratia and Cloutier, 1996	–
Ctenognathichthys bellottii	Bürgin, 1992	–
Cyranhoris bergeraci	Lund and Poplin, 1997	CM 40991
Daedalichthys higginsi	Hutchinson, 1973	–
Dapedium pholidotus	Wenz, 1968	–
Dapedium punctatus	Wenz, 1968	–
Dentilepisosteus laevis	Grande, 2010	–
Dictyopyge macrurus	Schaeffer and McDonald, 1978	–
Discoserra pectinodon	Lund, 2000	CM 30621, CM 27292
Elonichthys serratus	Moy-Thomas and Bradley Dyne, 1938	–
Gogosardinia coatesi	Choo et al., 2009	–
Guildayichthyes carnegiei	Lund, 2000	CM 41071
Haplolepis corrugata	Westoll, 1944; Lowney 1980	–
Howqualepis rostridens	Long,1988	–
Kalops diophrys	Poplin and Lund, 2002	CM 40914, CM 35426
Kalops monophrys	Poplin and Lund, 2002	CM 27372
Kentuckia deani	Rayner, 1951	–
Lepidotes elvensis	Wenz, 1968	–
Lepidotes lennieri	Wenz, 1968	–
Lepisosteus osseus	Grande, 2010	
Leptolepis coryphaenoides	Arratia, 1996	–
Limnomis delaneyi	Daeschler, 2000	–
Lineagruan judithi	Mickle et al., 2009	CM 35412, CM 62743
Lineagruan snowyi	Mickle et al., 2009	MV 2980, ROM 41809
Macrosemius rostratus	Bartram,1977	–
Mansfieldiscus sweeti	Long, 1988b	–
Meridensia meridensis	Bürgin, 1992	–
Mesopoma politum	Moy-Thomas and Bradley Dyne, 1938	–

Taxon	Source	Examined Specimens
Mesopoma pulchellum	Moy-Thomas and Bradley Dyne, 1938	–
Microhaplolepis ovoidea	Westoll, 1944; Lowney, 1980	–
Mimipiscis toombsi	Gardiner, 1984	–
Moythomasia durgaringa	Gardiner, 1984	–
Obaichthys decoratus	Grande, 2010	–
Pachycormus macropterus	Wenz, 1968	–
Parahaplolepis tuberculata	Westoll ,1944; Lowney, 1980	–
Paramesolepis tuberculata	Moy-Thomas and Bradley Dyne, 1938	–
Peltoperleidus bellipinnis	Bürgin, 1992	–
Pholidopleurus ticinensis	Bürgin, 1992	–
Platysiagum minus	Bürgin, 1992	–
Platysomus gibbosus	Campbell and Phuoc, 1983	–
Platysomus schultzei	Zidek, 1992	NMMNH P-19195
Platysomus superbus	Moy-Thomas and Bradley Dyne, 1938	–
Platysomus swaffordae	Micke and Bader, 2009	KUVP 141977
Polypterus bichir	Allis, 1922	–
Polypterus endlicheri		ANSP 78303
Polypterus ornatipinnis	Grande, 2010	KU 23147
Polypterus senegalus	Bartsch, 1997	–
Proceramala montanensis	Poplin and Lund, 2000	CM 41011
Proteurynotus traquairi	Moy-Thomas and Bradley Dyne, 1938	–
Ptycholepis barboi	Bürgin,1992	–
Ptycholepis bollensis	Wenz, 1968	–
Ptycholepis curta	Wenz, 1968	–
Redfieldius gracilis	Schaeffer and McDonald, 1978	–
Rhadinichthys canobiensis	Moy-Thomas and Bradley Dyne, 1938	–
Stegotrachelus finlayi	Swartz, 2009	–
Tegeolepis clarki	Dunkle and Schaeffer, 1973	–
Wendyichthys dicksoni	Lund and Poplin, 1997	CM 48580
Wendyichthys lautreci	Lund and Poplin, 1997	–

Table 1 (Continued)—Investigated taxa and literature or specimens examined.

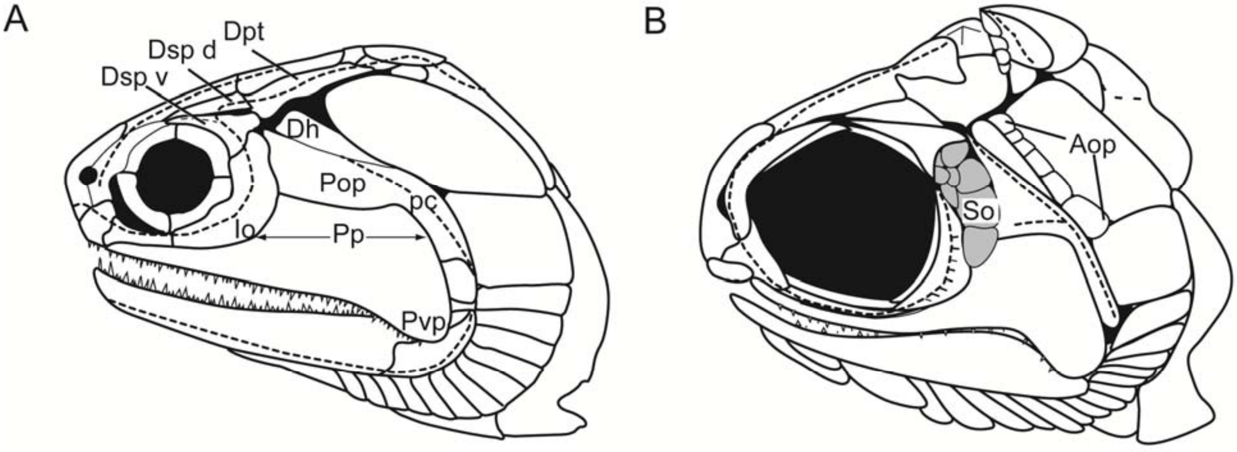
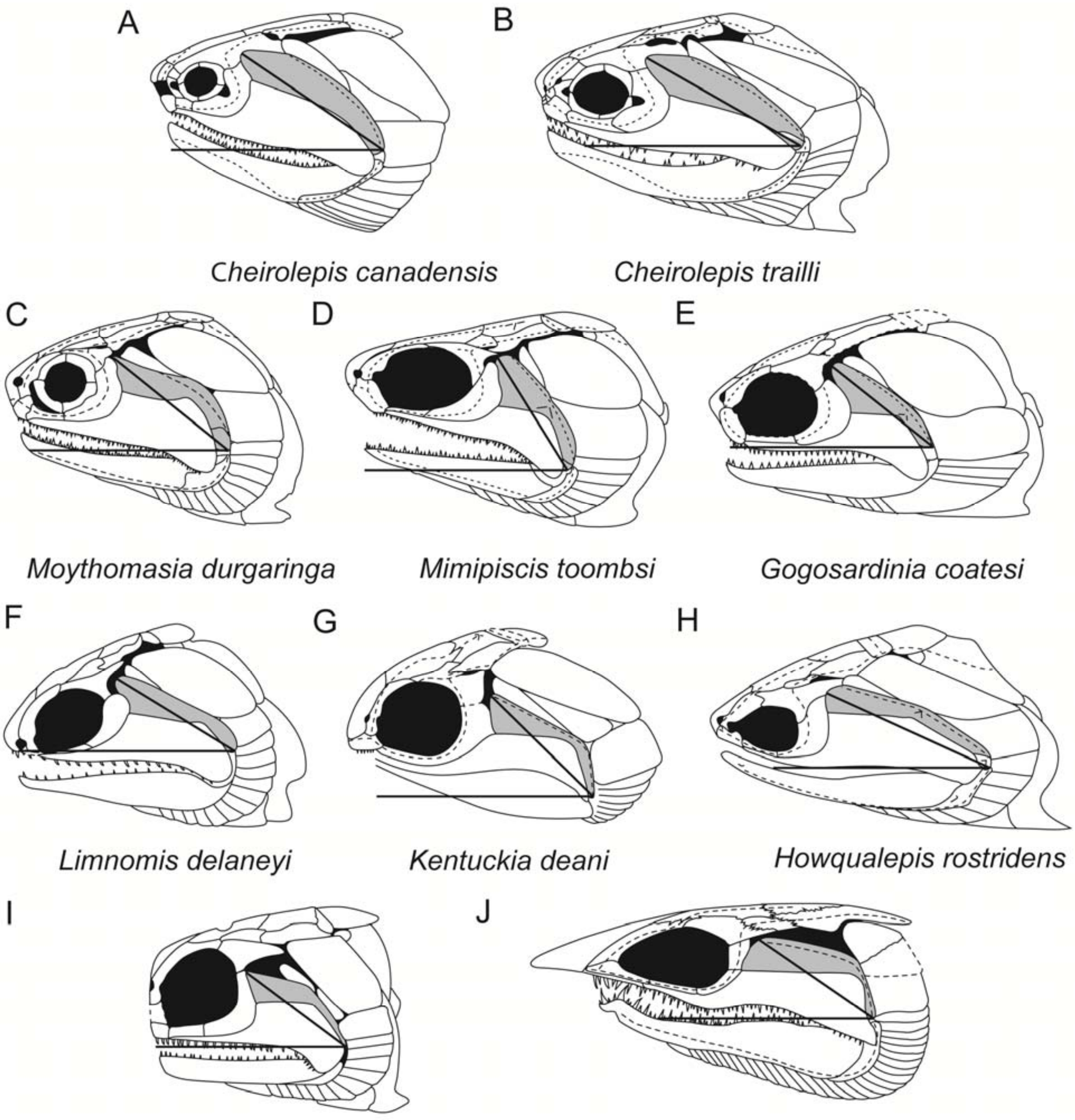


Figure 1—Explanation of bone terminology used throughout the paper using **A,** *Moythomasia durgaringa* (after Gardiner 1984: figure 103) and **B,** L*ineagruan pulcherrimus* (after Mickle et. al. 2009: figure 12A) as representatives. **Abbreviations: Aop**, antopercular bones; **Dh,** dermohyal; **Dpt,** dermopterotic; **Dsp d,** dorsal dermosphenotic; **Dsp v,** ventral dermosphenotic; **Io,** infraorbital bone; **pc,** preopercular canal; **Pop,** preoperculum; **Pp,** postorbital plate of maxilla; **Pvp,** posteroventral process of maxilla; **So,** suborbital bones (shaded in light gray).



Cheirolepis canadensis *Cheirolepis traillí*

Moythomasia durgaringa *Mimipiscis toombsi* *Gogosardinia coatesi*

Limnomis delaneyi *Kentuckia deani* *Howqualepis rostridens*

Stegotrachelus finlayi *Tegeolepis clarki*

Figure 2—Devonian palaeoniscoids with anteriorly inclined preopercula and corresponding preopercular angles **A,** *Cheirolepis canadensis* (after Arratia and Cloutier 1996: figure 6A), 34°; **B,** *Cheirolepis trailli* (after Pearson and Westoll 1979: figure 20a), 30°; **C,** *Moythomasia durgaringa* (after Gardiner 1984: figure 103), 39°; **D,** *Mimipiscis toombsi* (after Gardiner 1984: figure 101), 55°; **E,** *Gogosardinia coatesi* (after Choo et al. 2009: figure 13B), 39°; **F,** *Limnomis delaneyi* (after Daeschler 2000: figure 13), 32°; **G,** *Kentuckia deani* (after Rayner 1951: figure 2B), 44°; **H,** *Howqualepis rostridens* (after Long 1988: figure 14A), 25°; **I,** *Stegotrachelus finlayi* (after Swartz 2009: figure 3), 37°; **J,** *Tegeolepis clarki* (after Dunkle and Schaeffer 1973: figure 3), 35°. Preopercula shaded dark gray in this and subsequent figures.

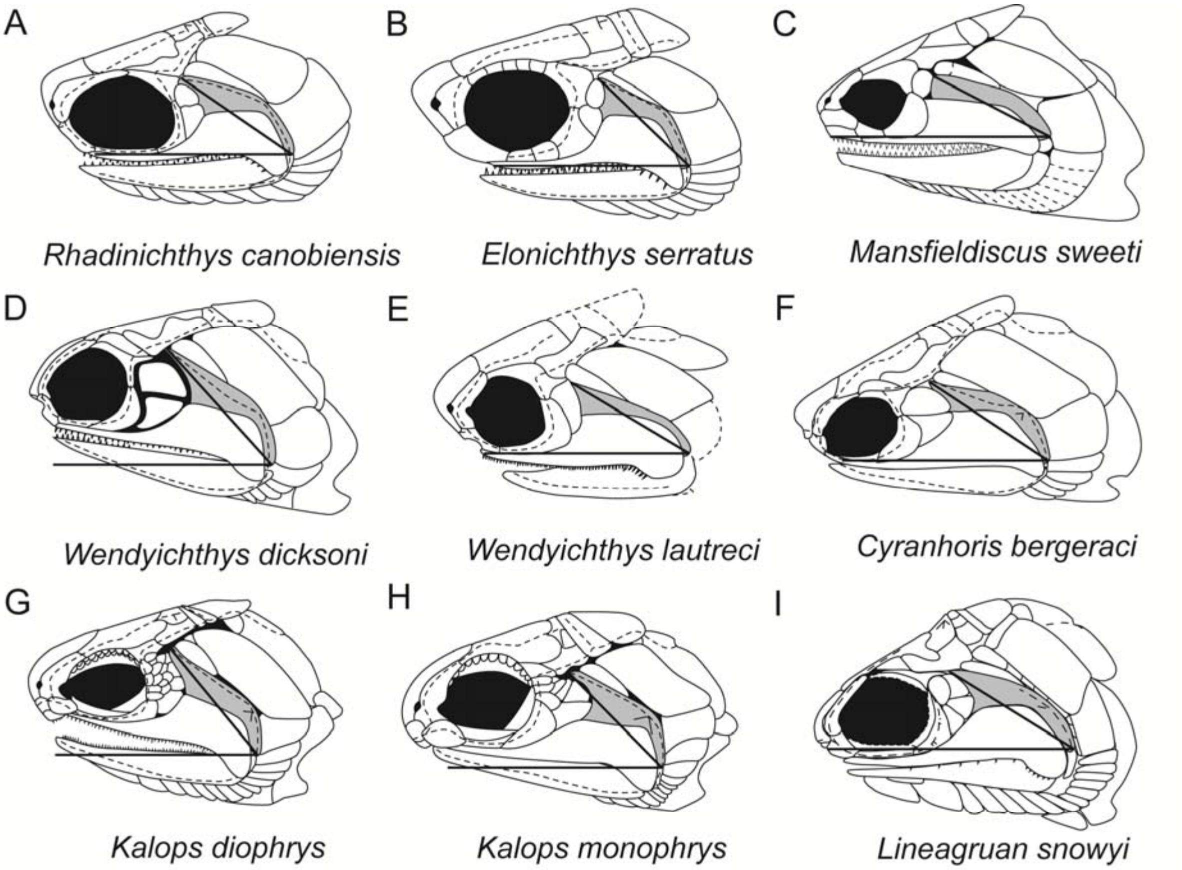


Figure 3—Fusiform Carboniferous palaeoniscoids with anteriorly inclined preopercula and corresponding preopercular angles **A,** *Rhadinichthys canobiensis* (after Moy-Thomas and Bradley Dyne 1938: figure 14), 34°; **B,** *Elonichthys serratus* (after Moy-Thomas and Bradley Dyne 1938: figure 22), 43°; **C,** *Mansfieldiscus sweeti* (after Long 1988: figure 39B), 27°; **D,** *Wendyichthys dicksoni* (after Lund and Poplin 1997: figure 2B), 48°; **E,** *Wendyichthys lautreci* (after Lund and Poplin 1997: figure 10), 31°; **F,** *Cyranhoris bergeraci* (after Lund and Poplin 1997: figure 15B), 34°; **G**, *Kalops diophrys* (after Poplin and Lund 2002: Figure 5:1), 48°; **H,** *Kalops monophrys* (after Poplin and Lund 2002: figure 2:4), 45°; **I,** *Lineagruan snowyi* (after Mickle et al. 2009: figure 9A) 32°.

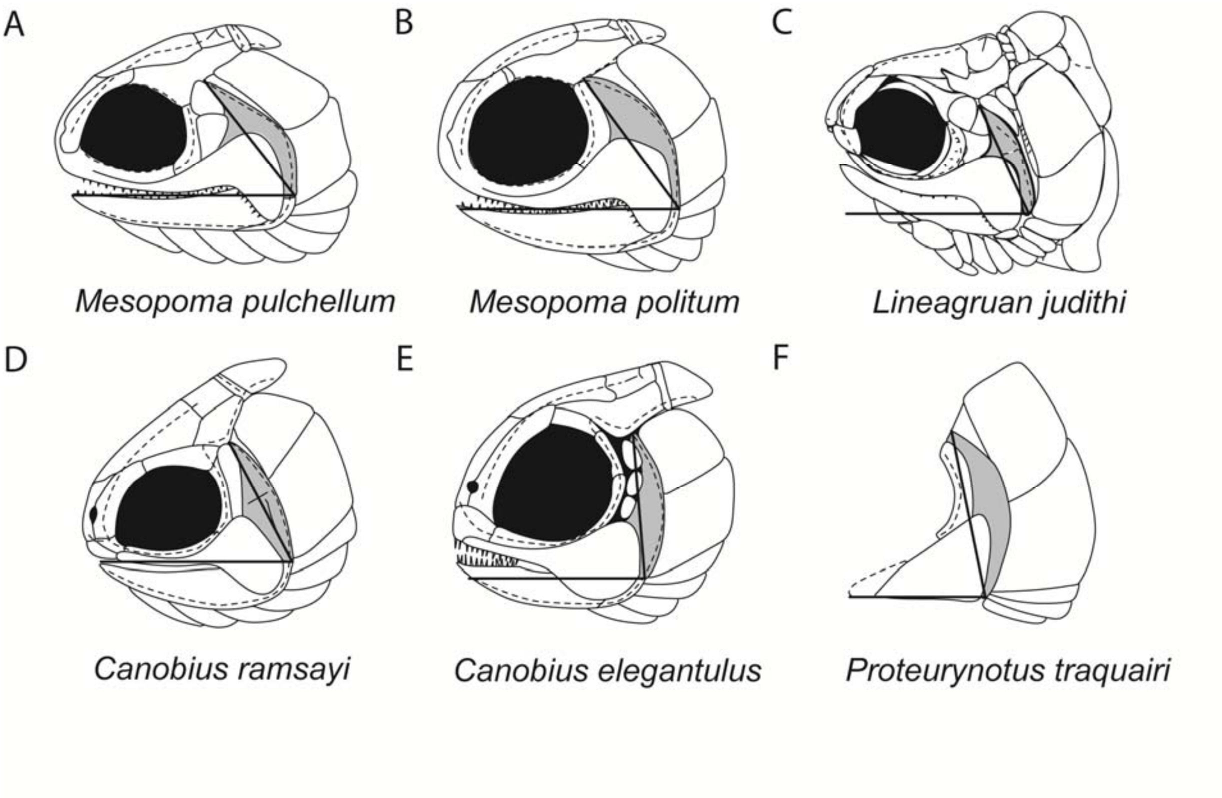
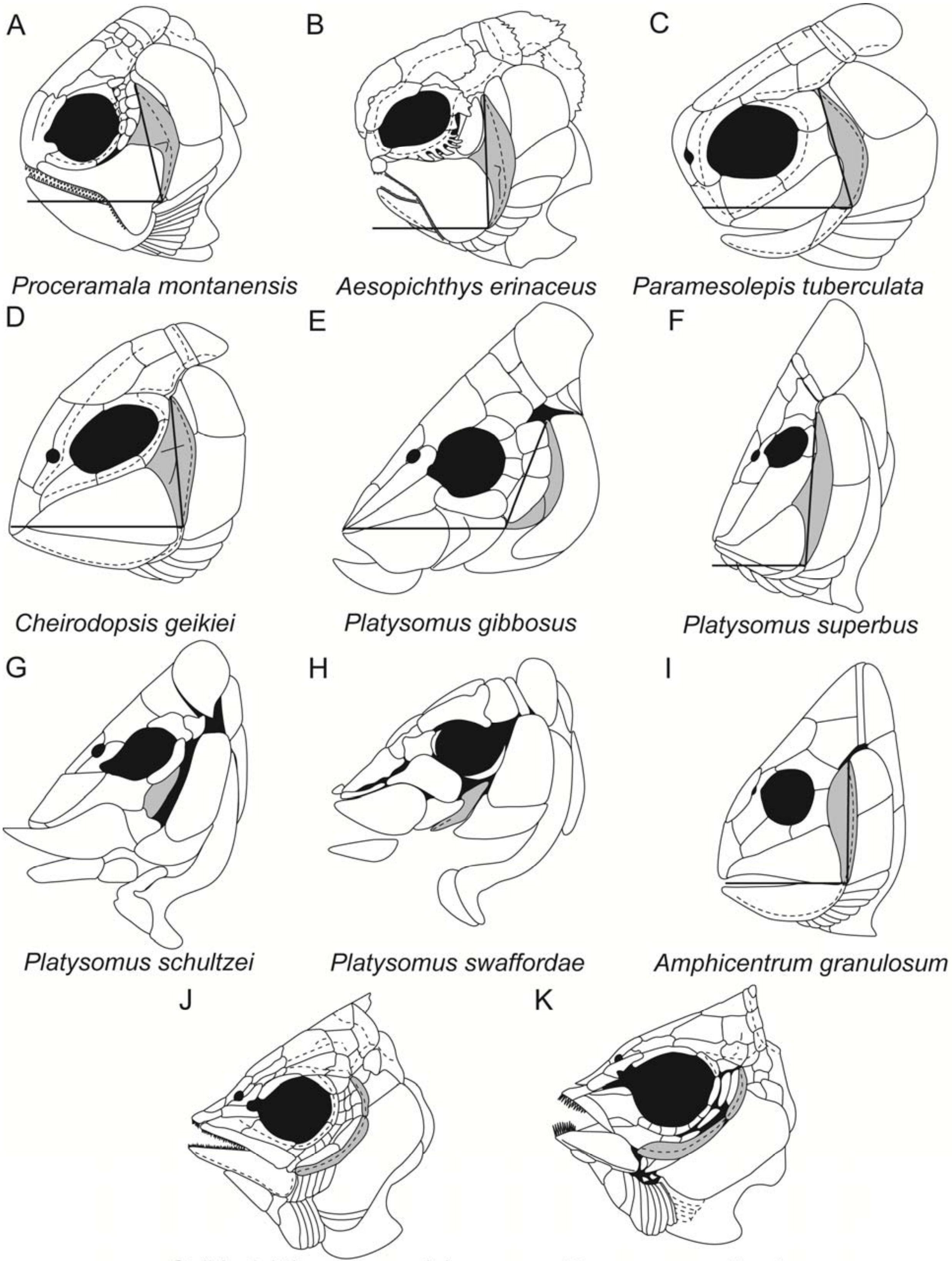


Figure 4—Fusiform Carboniferous palaeoniscoids with vertical preopercula and corresponding preopercular angles **A,** *Mesopoma pulchellum* (after Moy-Thomas and Bradley Dyne, 1938: figure 8), 52°; **B,** *Mesopoma politum* (after Moy-Thomas and Bradley Dyne, 1938: figure 10), 54°; **C,** *Lineagruan judithi* (after Mickle et al., 2009: Figure 4A), 65°; **D,** *Canobius ramsayi* (after Moy-Thomas and Bradley Dyne, 1938: figure 1), 63°; **E,** *Canobius elegantulus* (after Moy-Thomas and Bradley Dyne, 1938: figure 4), 86°. **F,** *Proteurynotus traquairi* (after Moy-Thomas and Bradley Dyne, 1938: figure 29), 79°.



Proceramala montanensis

Aesopichthys erinaceus

Paramesolepis tuberculata

Cheirodopsis geikiei

Platysomus gibbosus

Platysomus superbus

Platysomus schultzei

Platysomus swaffordae

Amphicentrum granulosum

Guildayichthyes carnegiei

Discoserra pectinodon

Figure 5 (Previous page)—Deep-bodied Carboniferous palaeoniscoids with either vertical or posteriorly inclined preopercula and corresponding preopercular angles **A,** *Proceramala montanensis* (after Poplin and Lund, 2000: Figure 16), 77°; **B,** *Aesopichthys erinaceus* (after Poplin and Lund, 2000: Figure 7B), 88°; **C,** *Paramesolepis tuberculata* (after Moy-Thomas and Bradley Dyne, 1938: figure 31), 75°; **D,** *Cheirodopsis geikiei* (after Moy-Thomas and Bradley Dyne, 1938: figure 35), 85°; **E,** *Platysomus gibbosus* (after Campbell and Phuoc, 1983 : figure 17), 111°; **F,** *Platysomus superbus* (after Moy-Thomas and Bradley Dyne, 1938: figure 37), 94°; **G,** *Platysomus schultzei* (after Zidek : figure 24C), NA; **H,** *Platysomus swaffordae* (after Mickle and Bader, 2009: figure 4), NA; **I,** *Amphicentrum granulosum* (after Zidek, 1992: figure 14), 90°; **J,** *Guildayichthyes carnegiei* (after Lund, 2000: figure 3); **K,** *Discoserra pectinodon* (after Lund, 2000: figure 7).

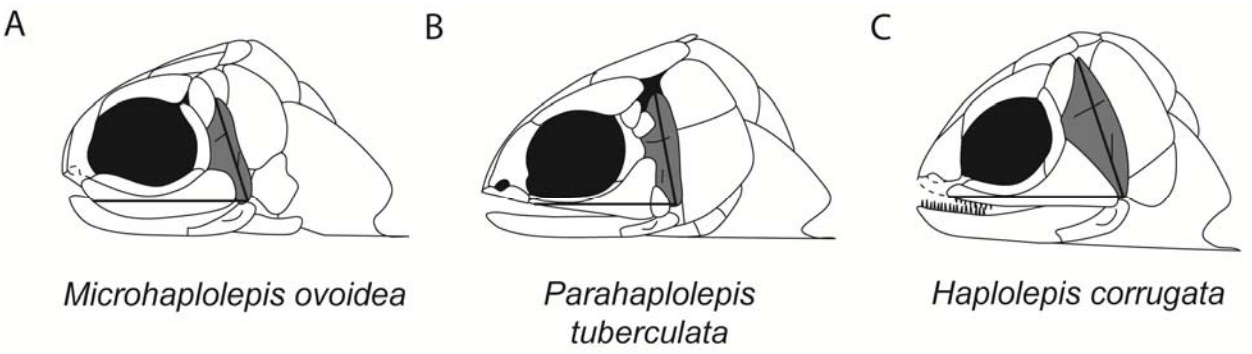
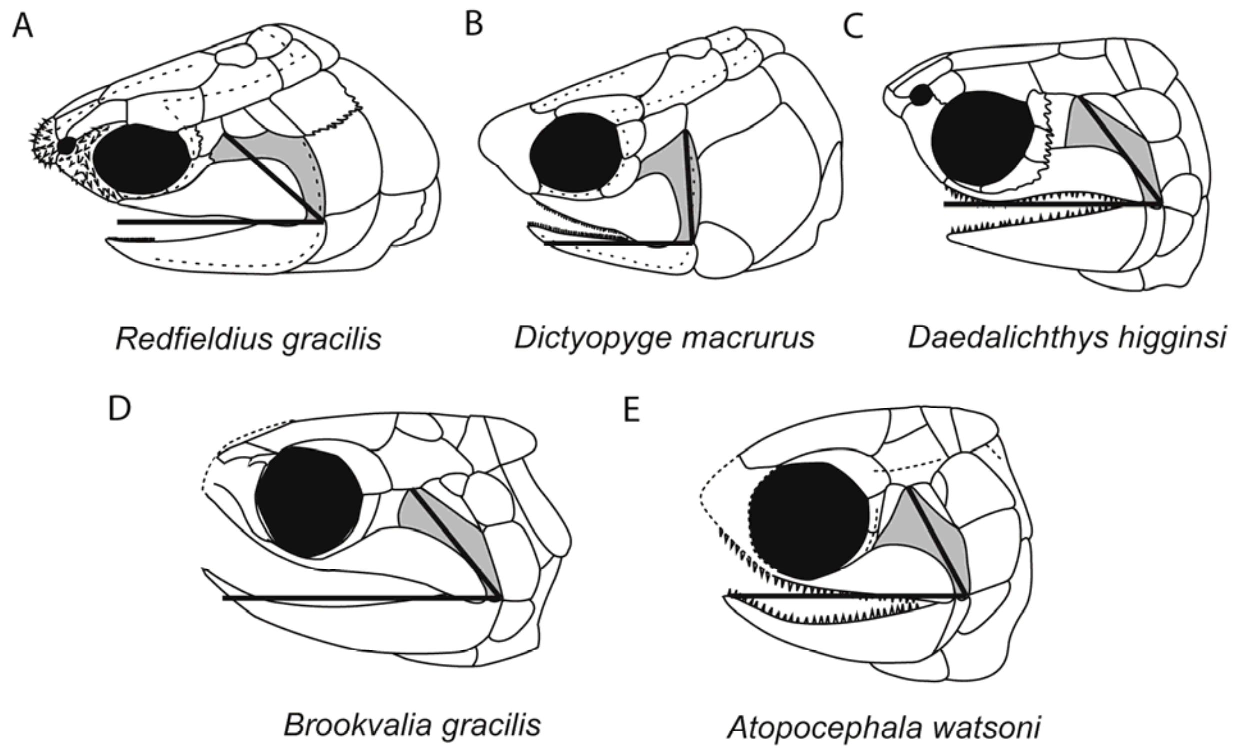


Figure 6—Haplolepids with vertically inclined preopercula and corresponding preopercular angles **A,** *Microhaplolepis ovoidea* (after Westoll, 1944: figure 2C), 72°; **B,** *Parahaplolepis tuberculata* (after Westoll, 1944: figure 14C), 79°; **C,** *Haplolepis corrugata* (after Westoll, 1944: figure 8C), 72°



Redfieldius gracilis

Dictyopyge macrurus

Daedalichthys higginsi

Brookvalia gracilis

Atopocephala watsoni

.

Figure 7—Preopercular condition of Redfieldiid fishes and corresponding preopercular angles **A,** *Redfieldius gracilis* (after Schaeffer and McDonald, 1978: figure 6B), 41°; **B,** *Dictyopyge macrurus* (after Schaeffer and McDonald, 1978: figure 15B), 86°; **C,** *Daedalichthys higginsi* (after Hutchinson, 1973: figure 19), 53°; **D,** *Brookvalia gracilis* (after Hutchinson, 1973: figure 9), 50°; **E,** *Atopocephala watsoni* (after Hutchinson, 1973: figure 7A), 62°.

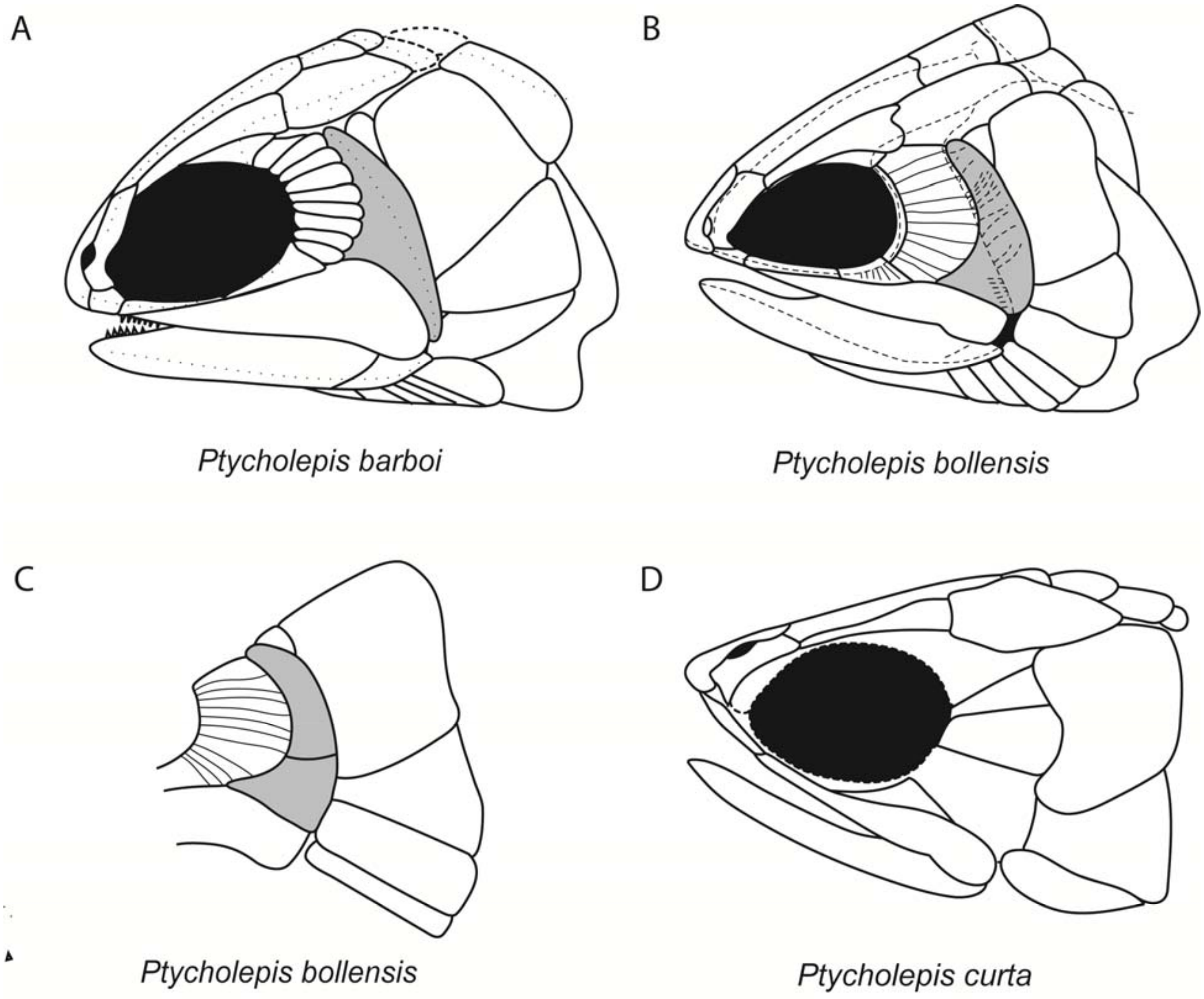


Figure 8—Preopercular conditions of various species of *Ptycholepis* **A,** *P. barboi* (after Bürgin, 1992: figure 15); **B**, *P. bollensis* with a single preoperculum (after Wenz, 1968: figure 13); **C,** *P. bollensis* with two preopercula (after Wenz, 1968: figure 16); **D,** *P. curta* (after Wenz, 1968: figure 19).

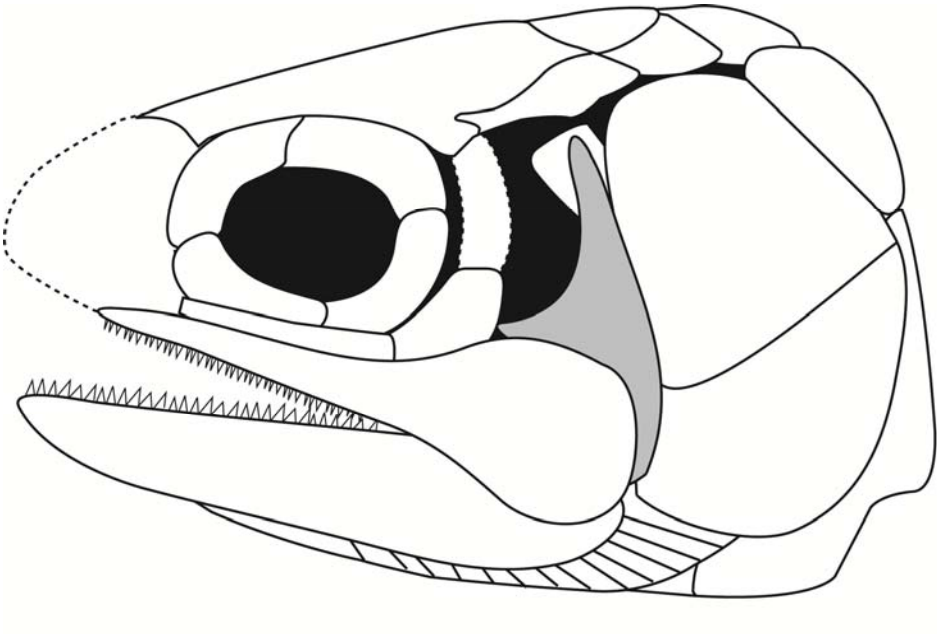
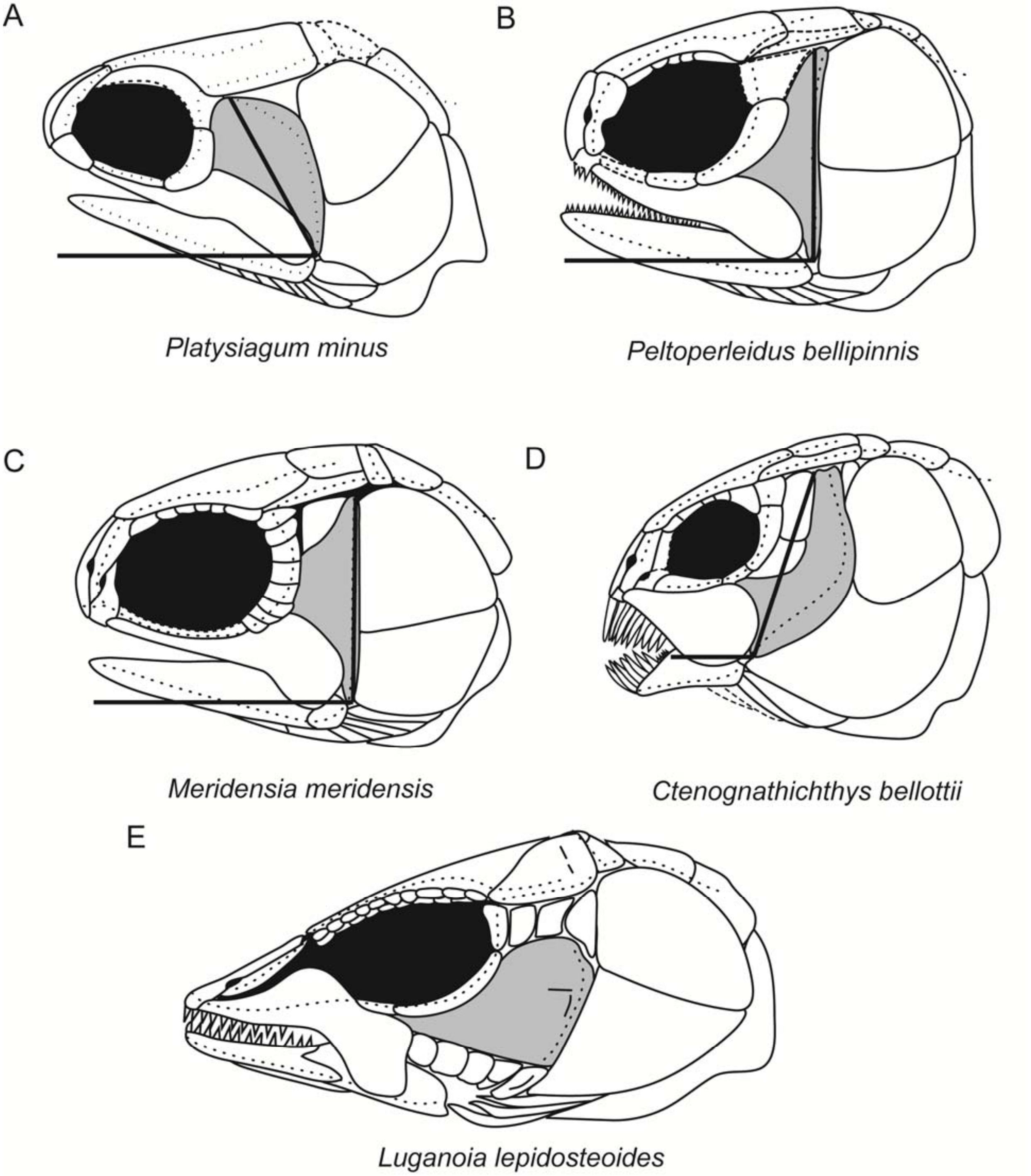


Figure 9—Preopercular condition of *Pholidopleurus ticinensis* (after Bürgin, 1992: figure 41).



Platysiagum minus

Peltoperleidus bellipinnis

Meridensia meridensis

Ctenognathichthys bellottii

Luganoia lepidosteoides

Figure 10—Preopercular condition of **A,** *Platysiagum minus* (after Bürgin, 1992: figure 57), 62°; **B,** *Peltoperleidus bellipinnis* (after Bürgin, 1992: figure 101), 90°; **C,** *Meridensia meridensis* (after Bürgin, 1992: figure 72), 90°; **D,** *Ctenognathichthys bellottii* (after Bürgin, 1992: figure 89), 108°; **E,** *Luganoia lepidosteoides* (after Bürgin, 1992: figure 134).

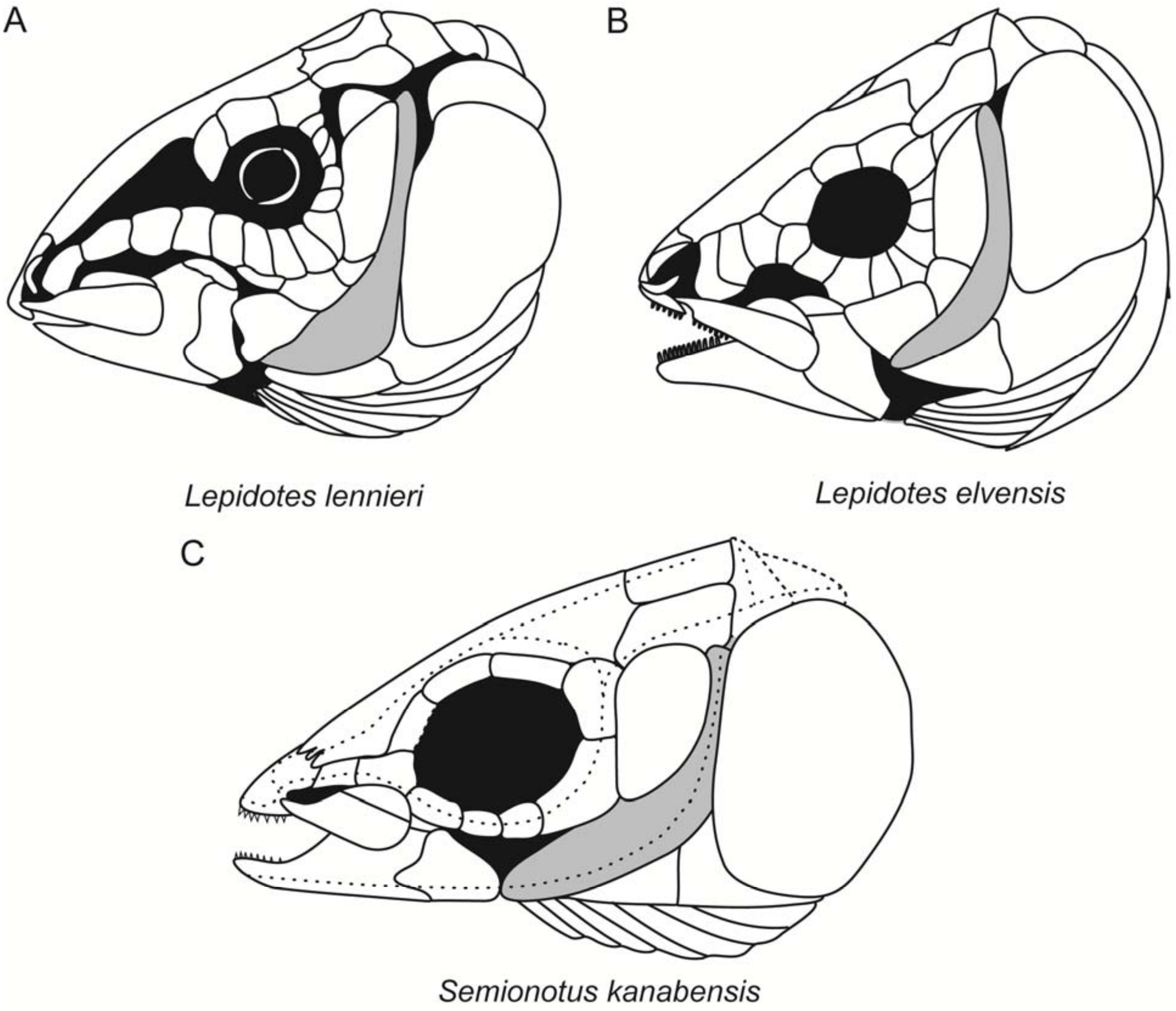


Figure 11—Preopercular condition of **A,** *Lepidotes lennieri* (after Wenz, 1968: figure 40); **B,** *Lepidotes elvensis* (after Wenz, 1968: figure 45); **C,** *Semionotus kanabensis* (after Schaeffer and Dunkle, 1950: figure 2).

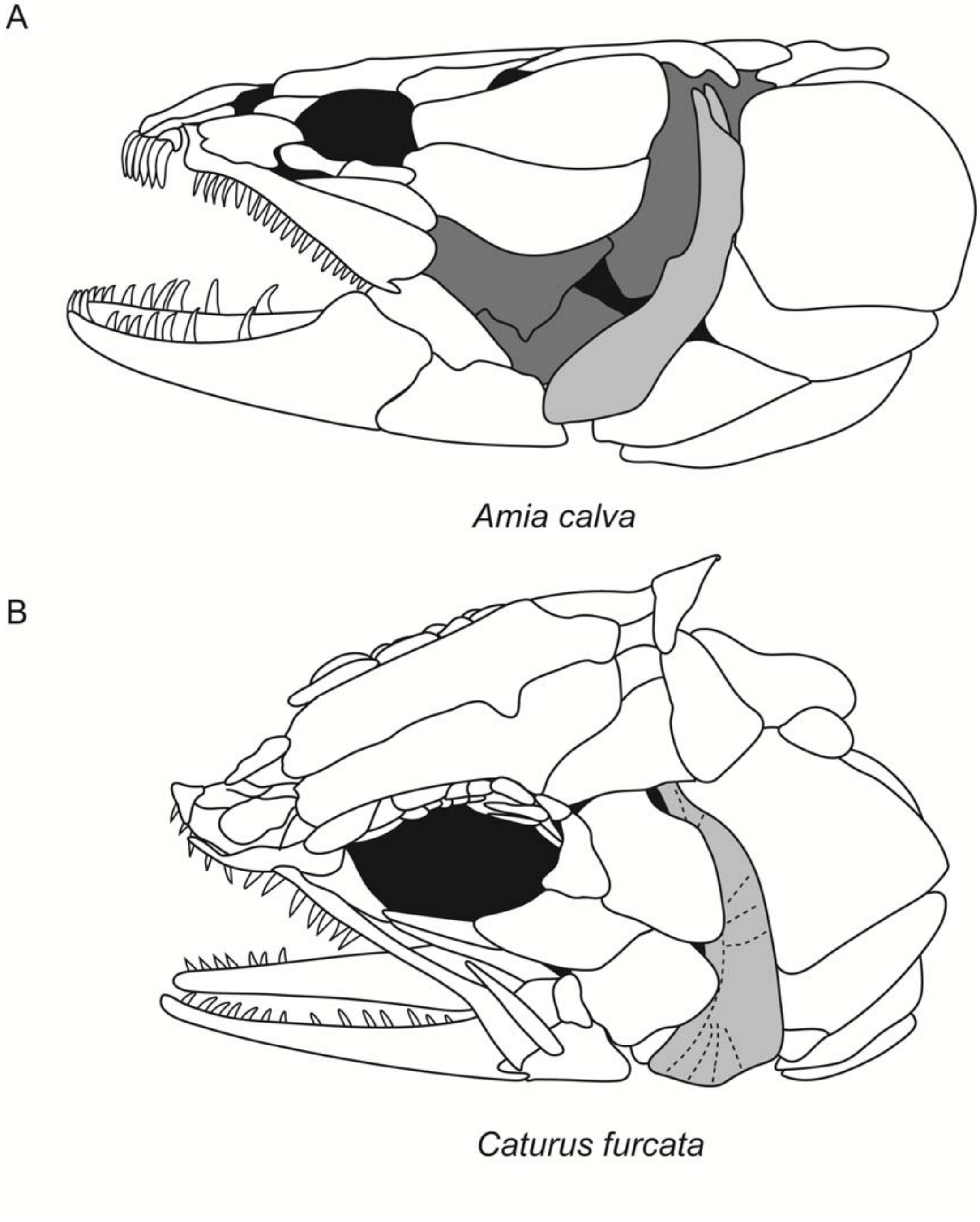


Figure 12—Preopercular condition of **A,** *Amia calva* (after Grande and Bemis, 1998: figure 16B); **B,** *Caturus furcata* (after Grande and Bemis, 1988: figure 401A).

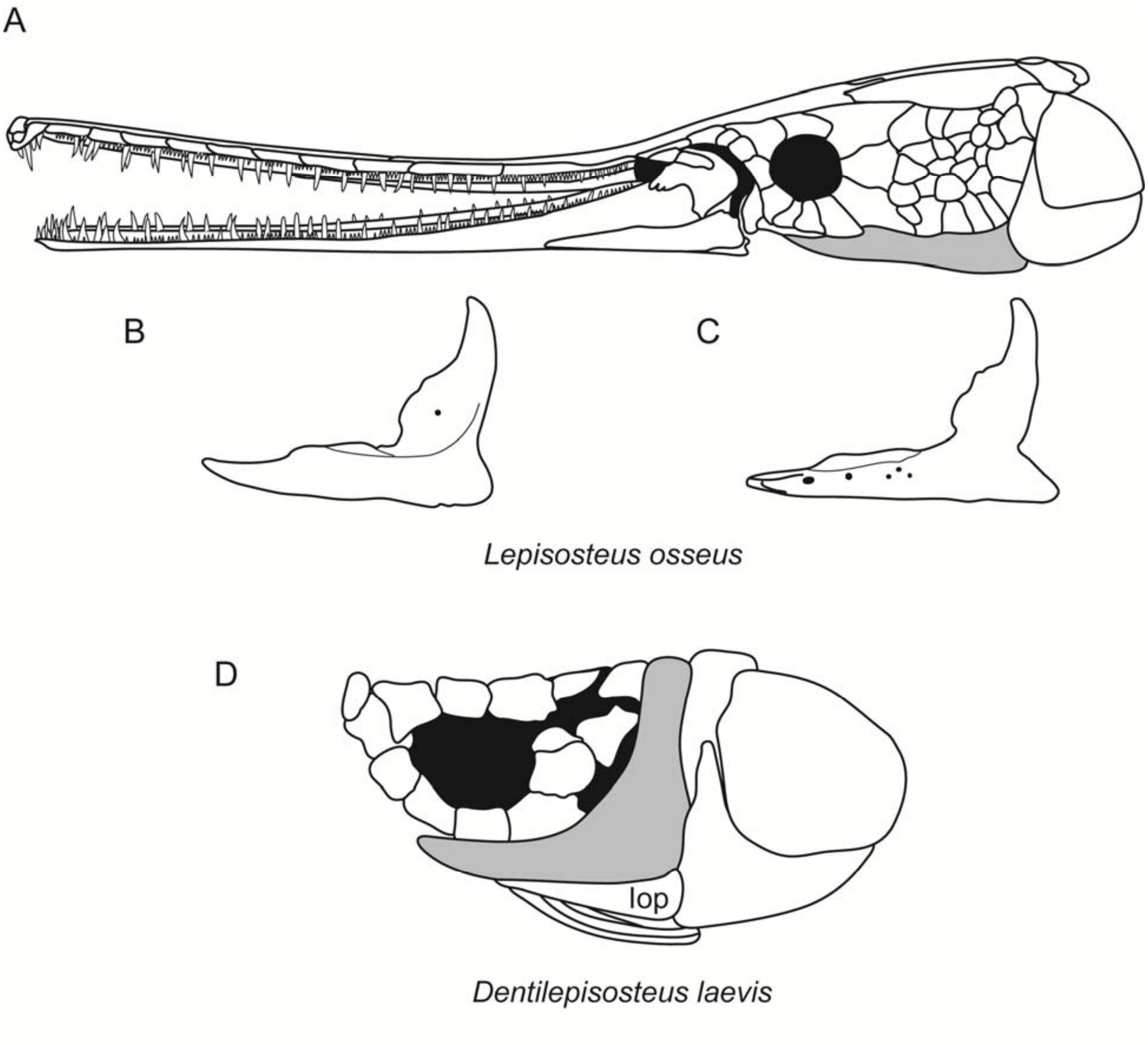


Figure 13—Preopercular condition of Lepisosteiformes **A,** *Lepisosteus osseus* (after Grande, 2010: figure 23); **B,** isolated preoperculum from *L. osseus*, lateral view (after Grande, 2010: figure 60); **C,** isolated preoperculum from *L. osseus,* medial view (after Grande, 2010: figure 61); **D,** *Dentilepisosteus laevis* (after Grande, 2010: figure 490). Abbreviations: **Iop,** interoperculum.

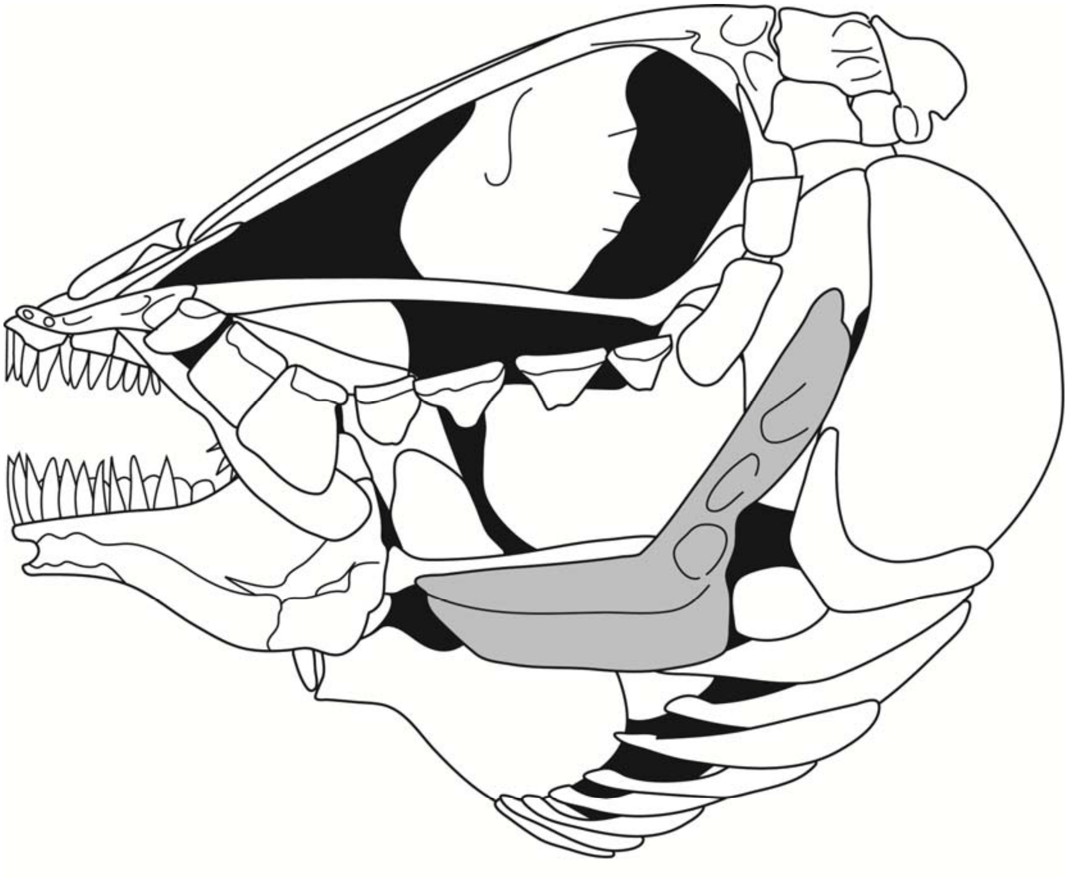
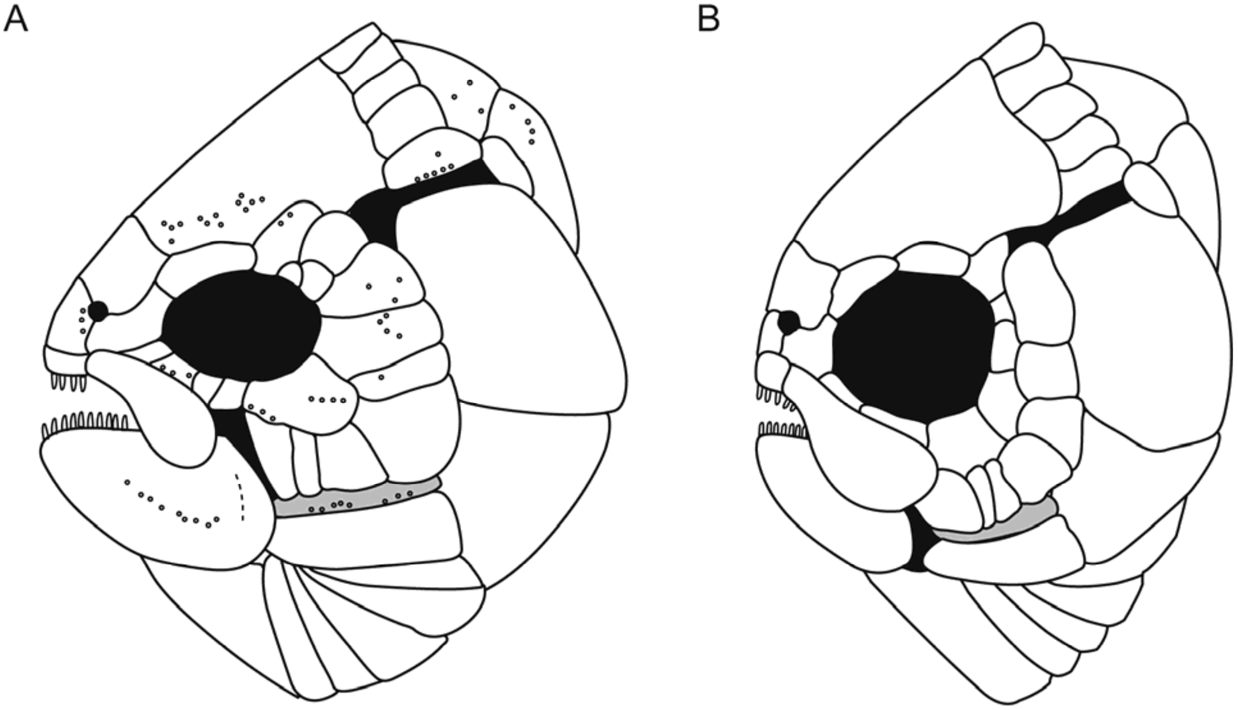


Figure 14—Preopercular condition of *Macrosemius rostratus* (after Bartram, 1977: figure 13).



Dapedium pholidotus

Dapedium punctatus

Figure 15—Preopercular condition of **A,** *Dapedium pholidotus* (after Wenz, 1968: figure 30); **B,** *Dapedium punctatus* (after Wenz, 1968: figure 35).

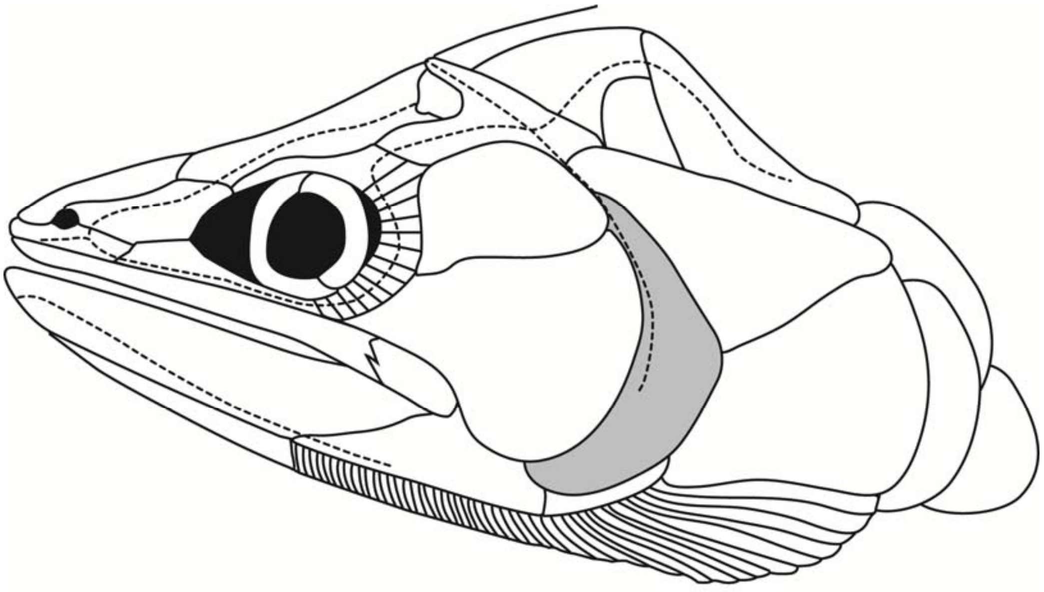
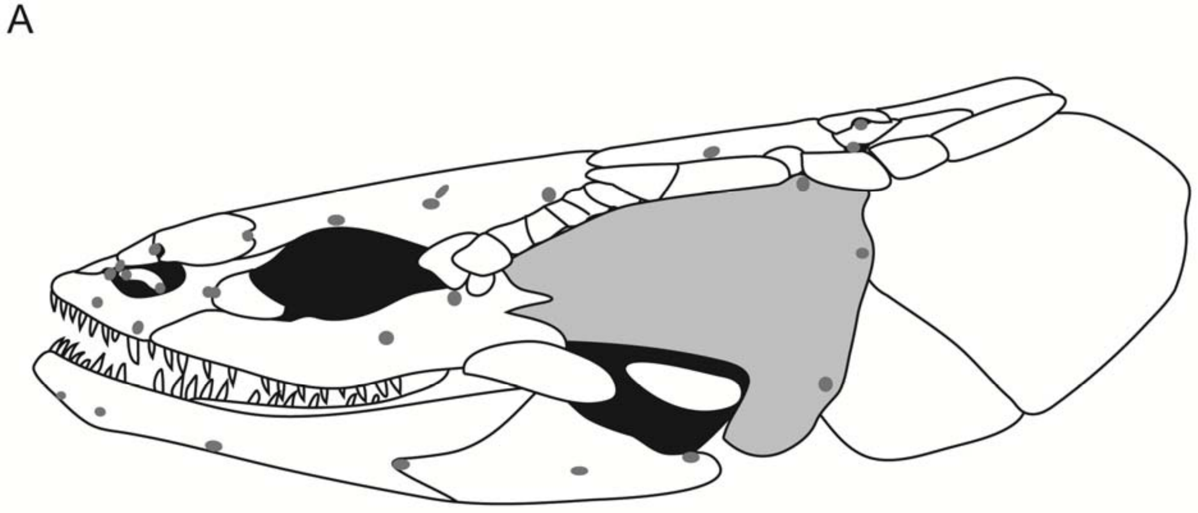
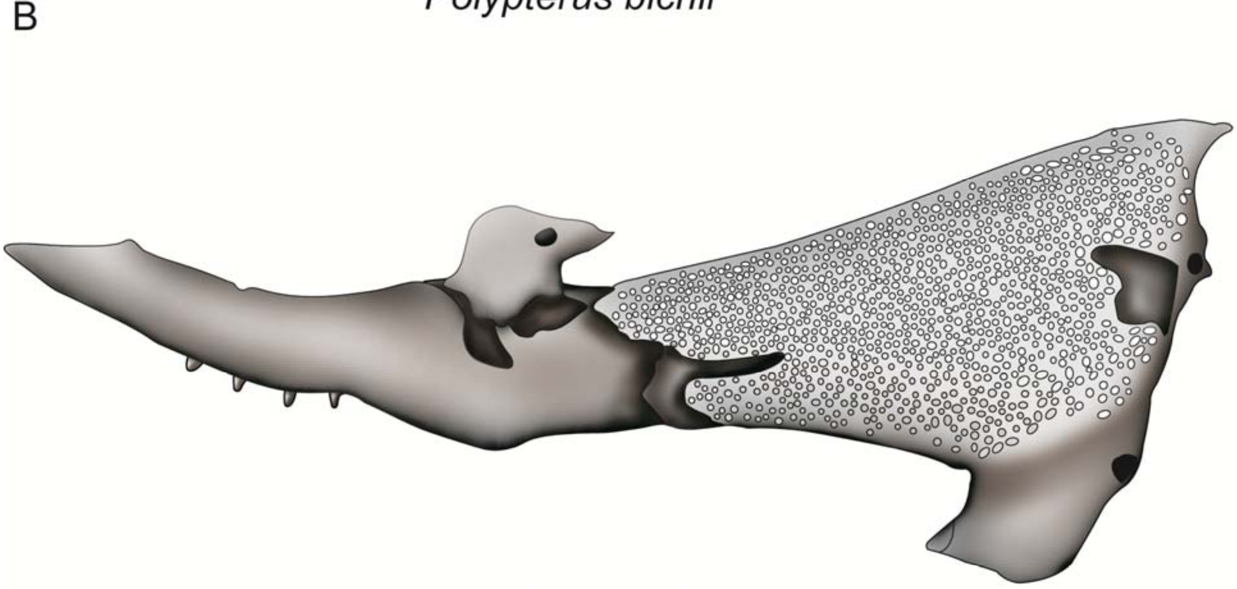


Figure 16—Preopercular condition of *Pachycormus macropterus* (after Wenz, 1968: figure 52).



Polypterus bichir



Polypterus endlicheri

Figure 17—A, preopercular condition of *Polypterus bichir* (after Allis, 1922: plate 5 figure 5); **B,** preopercula + suborbital of *P. endlicheri* (ANSP 78303), drawn from right side of specimen, illustration reflected.

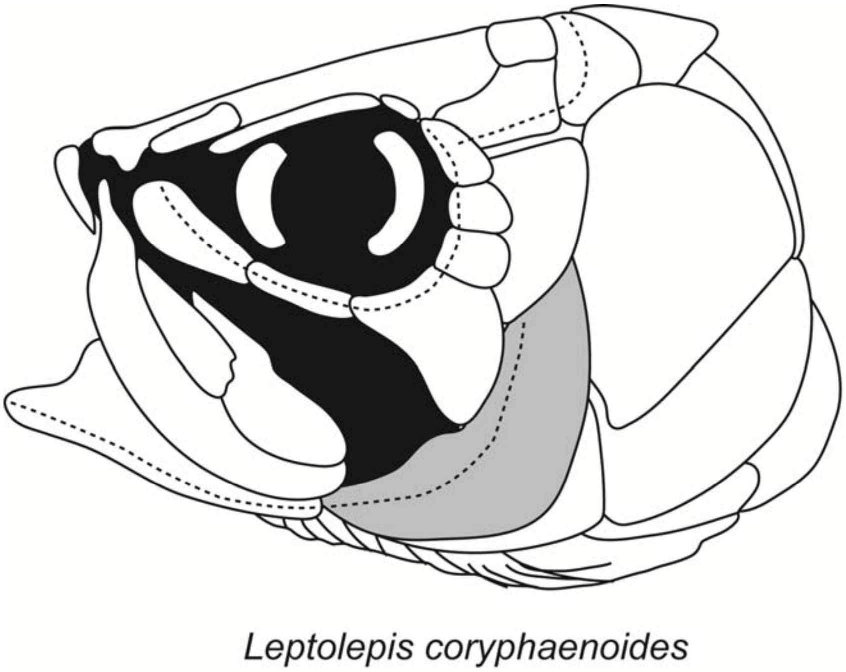


Figure 18—Preopercular condition of *Leptolepis coryphaenoides* (after Arratia, 1996: figure 1D).

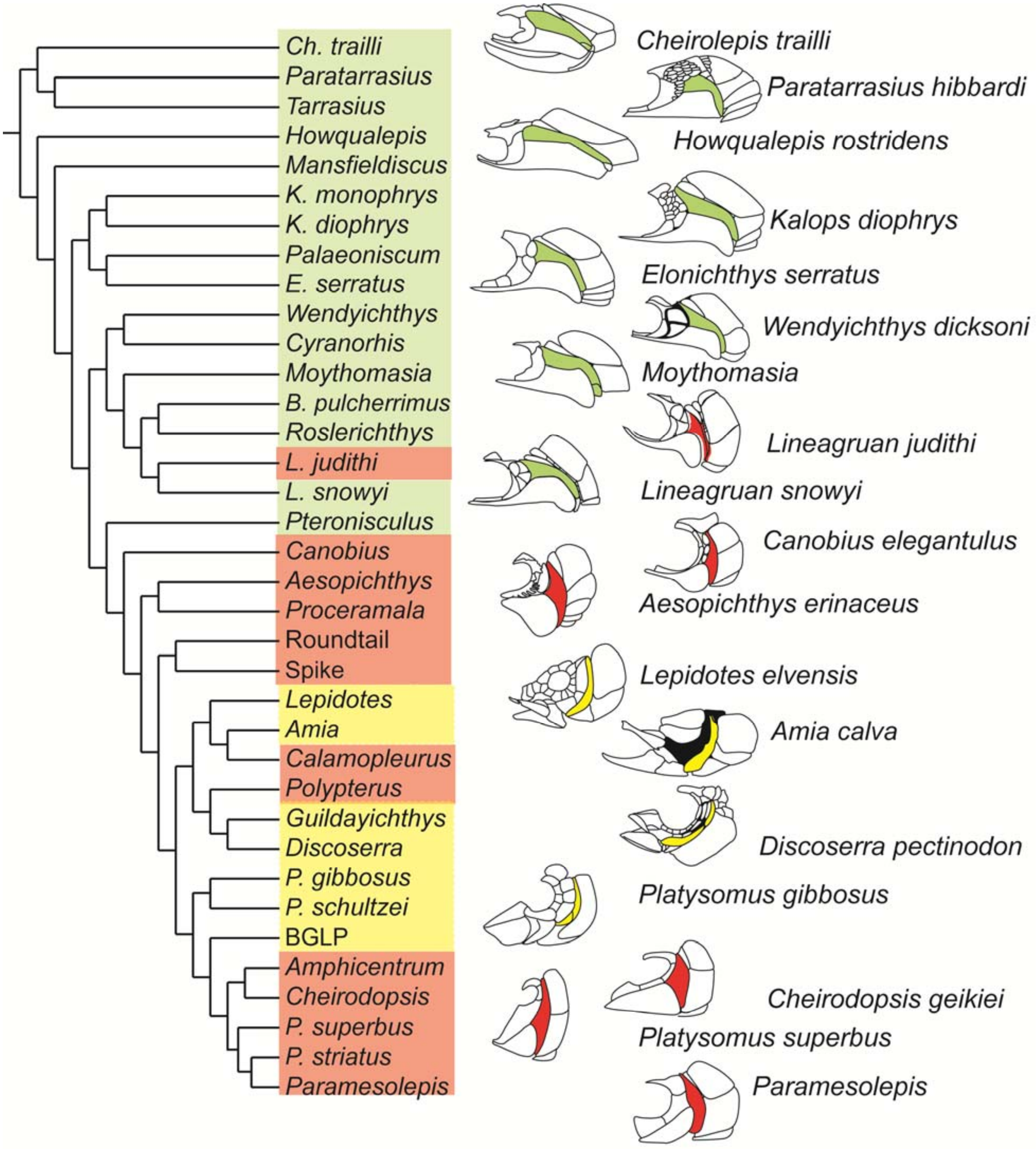


Figure 19—Preopercular conditions mapped onto a phylogenetic tree from Mickle et al., 2009 (figure 16). Taxa shaded to signify preopercular condition-green' anteriorly inclined; red, vertically inclined; yellow, posteriorly inclined. Outlines of preopercular conditions for selected taxa from Figures 2-5, 11-12 and *Paratarrasius hibbardi* (after Lund and Poplin, 2002: fig 1D).

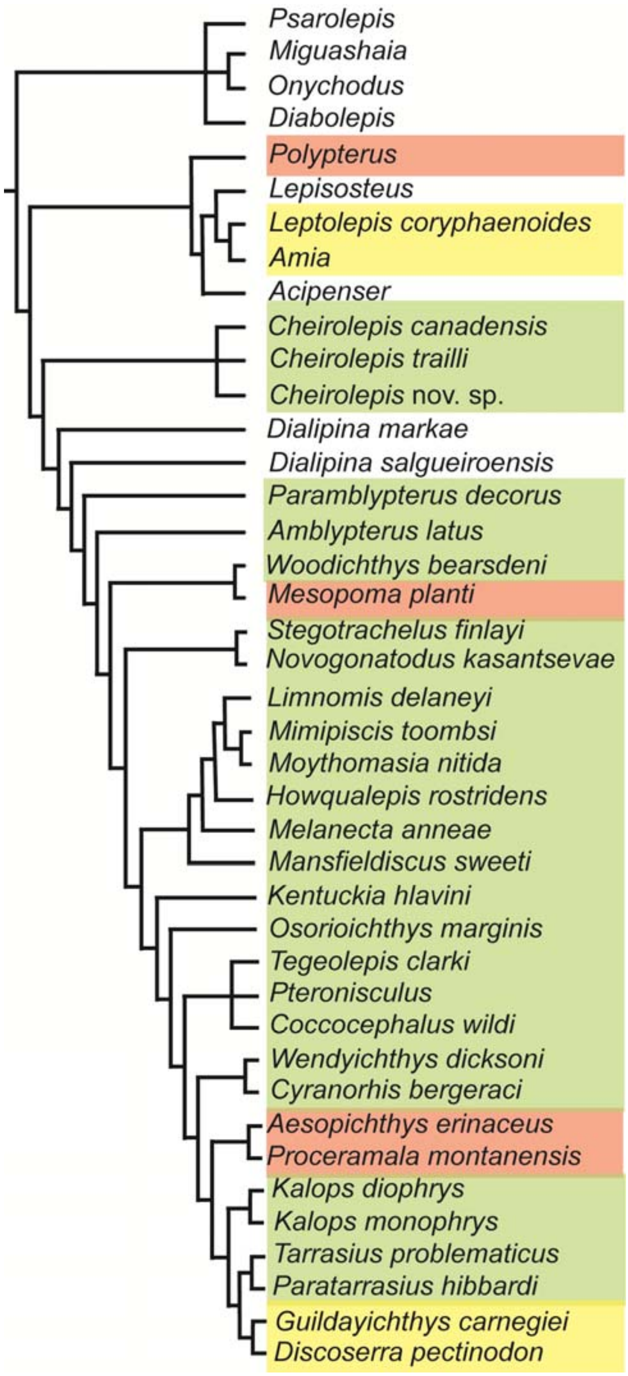


Figure 20—Preopercular conditions mapped onto a phylogenetic tree from Cloutier and Arratia (2004: figure 13D). Color codings are the same as Figure 19.

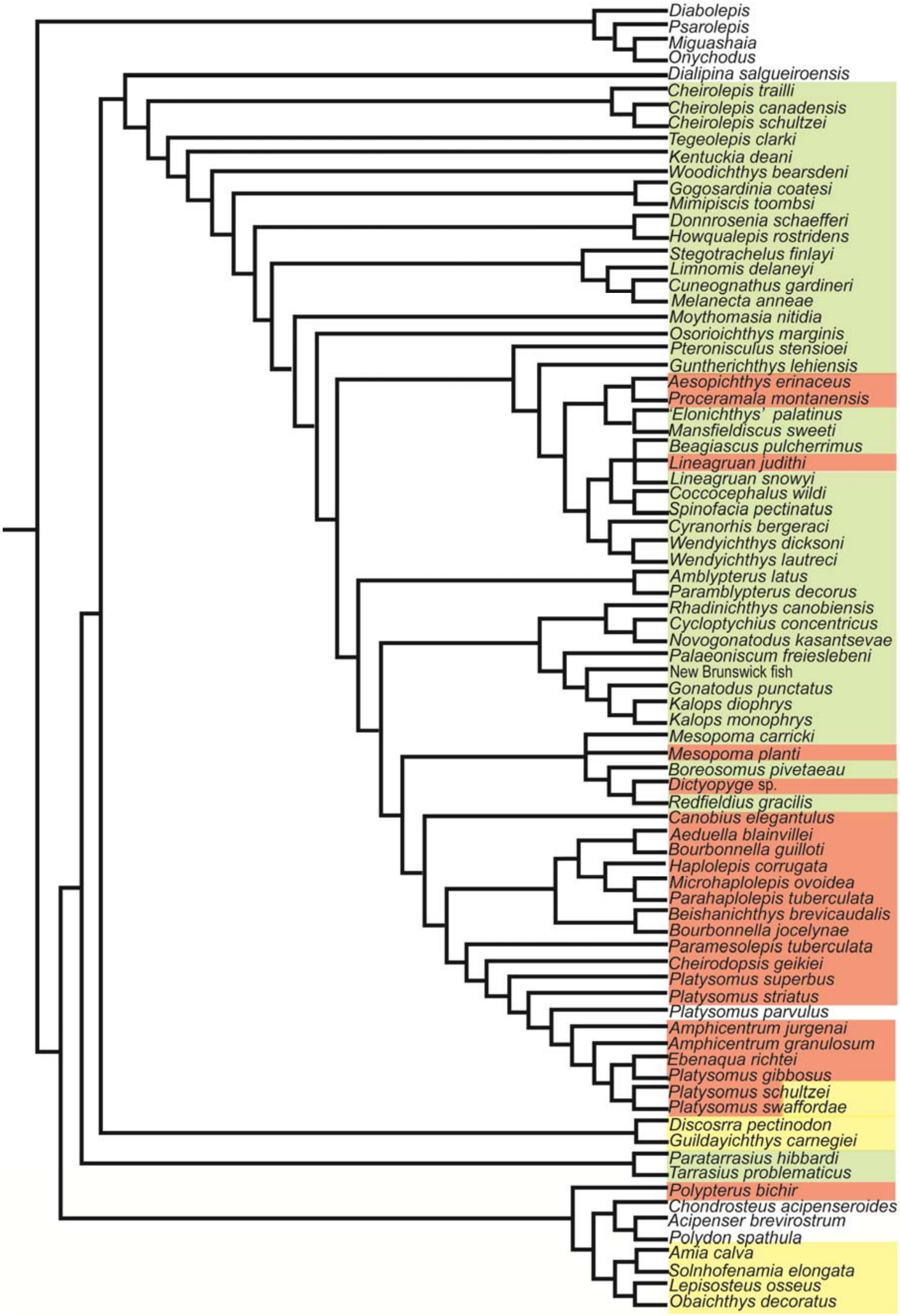

Diabolepis
Psarolepis
Miguashaia
Onychodus
Dialipina salgueiroensis
Cheirolepis trailli
Cheirolepis canadensis
Cheirolepis schultzei
Tegeolepis clarki
Kentuckia deani
Woodichthys bearsdeni
Gogosardinia coatesi
Mimipiscis toombsi
Donnrosenia schaefferi
Howqualepis rostridens
Stegotrachelus finlayi
Limnomis delaneyi
Cuneognathus gardineri
Melanecta anneae
Moythomasia nitidia
Osorioichthys marginis
Pteronisculus stensioei
Guntherichthys lehiensis
Aesopichthys erinaceus
Proceramala montanensis
'Elonichthys' palatinus
Mansfieldiscus sweeti
Beagiascus pulcherrimus
Lineagruan judithi
Lineagruan snowyi
Coccocephalus wildi
Spinofacia pectinatus
Cyranorhis bergeraci
Wendyichthys dicksoni
Wendyichthys lautreci
Amblypterus latus
Paramblypterus decorus
Rhadinichthys canobiensis
Cycloptychius concentricus
Novogonatodus kasantsevae
Palaeoniscum freieslebeni
New Brunswick fish
Gonatodus punctatus
Kalops diophrys
Kalops monophrys
Mesopoma carricki
Mesopoma planti
Boreosomus pivetaeau
Dictyopyge sp.
Redfieldius gracilis
Canobius elegantulus
Aeduella blainvillei
Bourbonnella guilloti
Haplolepis corrugata
Microhaplolepis ovoidea
Parahaplolepis tuberculata
Beishanichthys brevicaudalis
Bourbonnella jocelynae
Paramesolepis tuberculata
Cheirodopsis geikiei
Platysomus superbus
Platysomus striatus
Platysomus parvulus
Amphicentrum jurgenai
Amphicentrum granulosum
Ebenaqua richtei
Platysomus gibbosus
Platysomus schultzei
Platysomus swaffordae
Discosrra pectinodon
Guildayichthys carnegiei
Paratarrasius hibbardi
Tarrasius problematicus
Polypterus bichir
Chondrosteus acipenseroides
Acipenser brevirostrum
Polydon spathula
Amia calva
Solnhofenamia elongata
Lepisosteus osseus
Obaichthys decoratus

Figure 21 (Previous page)—Preopercular conditions mapped onto a phylogenetic tree from Chapter 6 (figure 9). Color codings are the same as Figure 19 plus yellow and red, vertical to posteriorly inclined.

CHAPTER FOUR--THE EARLY ACTINOPTERYGIAN FAUNA OF THE MANNING CANYON SHALE FORMATION (UPPER MISSISSIPPIAN, LOWER PENNSYLVANIAN) OF UTAH, U.S.A.

ABSTRACT

The Manning Canyon Shale Formation (upper Mississippian/lower Pennsylvanian) of Central Utah is well known for its diverse flora, but not its vertebrate fauna. The previously described vertebrates from the Manning Canyon Shale are a tooth from a cladodont shark, an acanthodian, and a microsaur. Here, the known vertebrate diversity is expanded with the description of early actinopterygian fishes. The actinopterygian ichthyofauna consists of two new species of palaeoniscoid fishes, *Spinofacia pectinatus* and *Guntherichthys lehiensis,* and a new aeduellid species, *Bourbonnella jocelynae*. *Spinofacia pectinatus* is characterized by the presence of extra lateral gulars (the only documented case outside the Bear Gulch Limestone of Montana) and extra-oral denticles on various dermal bones of the skull, whereas *Guntherichthys lehiensis* is distinguished by scales with slightly rounded posterior margins. The new aeduellid, *Bourbonnella jocelynae*, is now the earliest known aeduellid and the second occurrence of this genus and family in North America. Its discovery supports biogeographical and paleoecological findings of a marine connection between North America and Europe. The previously proposed freshwater paleoenvironment of the Manning Canyon Shale Formation is called into question, especially when the ichthyofauna of the site is considered. It is also important to note that although not many actinopterygian specimens have been collected from the Manning Canyon Shale, those that have reveal a previously unknown diversity.

INTRODUCTION

The Manning Canyon Shale Formation of central Utah is late Mississippian to early Pennsylvanian in age and traditionally, has been interpreted as a swampy lowland with small ponds and riparian habitats (Tidwell, 1967; Nelson and Tidwell, 1987; Carroll et al., 1991). Though this site contains the remains of the most diverse and complete flora from the Carboniferous, faunal remains are sparse (Nelson and Tidwell, 1987; Schultze, 1990; Carroll et al., 1991). Three genera of sponges are described from the Manning Canyon Shale Formation (Rigby and Moyle, 1959), along with a tooth from a cladodont shark attributed to *Cladodus* sp. (Miller, 1981), the acanthodian *Utahacanthus guntheri* (Schultze, 1990), and the microsaur *Utaherpeton franklini* (Carroll et al., 1991; Carroll and Chorn, 1995). Actinopterygian scales and isolated bones from this site have been mentioned in the literature, but until now, articulated specimens have not been described (Schultze, 1990). Here, the ichthyofauna of the Manning Canyon Shale, which consists of two new genera and species of palaeoniscoid actinopterygians, and one new species belonging to the family Aedeullidae.

The family Aeduellidae includes actinopterygian fishes from eight genera and thirteen species that have a primarily European distribution (Heyler, 1969; Poplin, 2001; Poplin and Dutheil, 2005). Multiple aeduellid specimens have been recovered from the Czech Republic (Štamberg, 2007), Germany (Uhl, 1997), France (Westoll, 1937; Heyler, 1969; 1980; Poplin, 2001), Spain (Forey and Young, 1985), and Switzerland (Bürgin, 1990). There is only one previously described occurrence of a North American aeduellid from New Mexico (Gottfried, 1987). A recent phylogenetic investigation of the Aeduellidae by Poplin and Dutheil (2005) recovered a monophyletic Aeduellidae, but the relationships within Aeduellidae and with other basal actinopterygians were not resolved.

The goal of this chapter is to describe two new genera of palaeoniscoid actinopterygians and a new species of the aeduellid *Bourbonnella* from the Manning Canyon Shale Formation, and to discuss their potential paleogeographic and paleoenvironmental importance. The phylogenetic relationships of these fishes and other early actinopterygians will be investigated and discussed in Chapter 6. Little is understood about the diversity of Paleozoic actinopterygians and there is no consensus regarding their relationships. Because of this, descriptions of new taxa and characters are vital steps toward a greater understanding of these fishes. Better resolution of these groups will occur as new fishes are studied and described.

MATERIALS AND METHODS

The fishes described here were collected from different exposures in the Manning Canyon Shale Formation (upper Mississippian/lower Pennsylvanian) of Central Utah (Figure 1). The two specimens of *Spinofacia pectinatus*, were collected from the upper part of the Manning Canyon Formation exposure from the “clay pit” localities in the Lake Mountains of Utah, southwest of Lehi, Utah, near Highway 68 (Tidwell, 1967; Dorka, 1998) and the Traverse Mountains of Utah (Figure 1), approximately 3 km north of Highway 73 and 16 km west to northwest of Lehi (Tidwell, 1967; Dorka, 1998). The *Guntherichthys lehiensis* specimen was collected west of Lehi, central Utah, whereas the specimen of *Bourbonnella jocelynae* was collected from a clay pit locality west of Utah Lake of central Utah.

A total of four specimens was examined by stereomicroscopy. Specimens were viewed in 70% ethanol to aid in the visualization of features. A camera lucida and a Canon XSi Digital SLR camera were used to prepare illustrations and figures. Digital images and illustrations were prepared using Adobe Photoshop and Illustrator software programs and pen and ink.

Bone Nomenclature—Two naming conventions have been used to refer to the pairs of bones in the skull roof of actinopterygians—frontal and parietal, or parietal and postparietal. The first naming convention is based on tradition, whereas the second is based in homology (Jollie, 1962; Wiley, 2008). The problems posed by the two different conventions to phylogenetic analyses are discussed by Schultze (2008) and Wiley (2008). The literature consists of a mixture of both naming schemes. Accordingly, to prevent confusion when comparing the newly described fish to previously described fishes (as pointed out by Friedman and Blom, 2006), and confusion caused by not using names based on homology, both names are given here and Chapter 5. The paired skull roofing bones are referred to as the frontal (parietal) bone and the parietal (postparietal) bone. Providing both names is a convention previously used by Arratia and Herzog (2007) and Mickle and Bader (2009), among others.

Anatomical Abbreviations—**An**, angular; **B**, branchiostegal rays, **C**, cleithrum; **Cl**, clavicle; **D**, dentary; **Dbr,** displaced branchiostegal ray; **Dh**, dermohyal; **Dp**, dermopterotic; **Ds**, dermosphenotic; **Ec**, ethmoid commissure; **Eg**, extralateral gular; **Ex**, extrascapula; **H**, hyomandibula; **F(P)**, frontal (parietal) bone; **Io**, infraorbital bone; **In**, otic infilling; **La,** lachrymal; **Lg**, lateral gular; **Llc**, lateral line canal; **M**, maxilla; **Mg**, median gular; **N**, nasal bone; **O**, operculum; **Pa**, parasphenoid; **Pf**, pelvic fin; **Po**, preoperculum; **P(Pp)**, parietal (postparietal) bone; **Ps**, presupracleithrum; **Pl**, scaled pectoral lobe; **Pt**, posttemporal; **R,** rostral bone; **S**, suborbital bone; **Sc**, supracleithrum; **Sl**, sclerotic bone; **So**, suboperculum.

Institutional Abbreviations—**BYU**, Brigham Young University, Provo, Utah; **KUVP**, Division of Vertebrate Paleontology, Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, Kansas.

SYSTEMATIC PALEONTOLOGY

Class Osteichthyes Huxley, 1880

Subclass Actinopterygii Cope, 1871

Family incertae sedis

Genus *Spinofacia* n. gen.

Diagnosis—As for the type and only species.

Type and Only Species—*Spinofacia pectinatus*

Etymology—*Spinofacia*, or "spiny face" referring to the extra-oral denticles on the cheek bones that define the genus. After the Latin "spino" for spine and "facia" for face.

Spinofacia pectinatus n. gen. n. sp.

(Figures 2–5)

Etymology—*pectinatus,* referring to the pectinated scales, after the latin "pectin" for comb.

Diagnosis—Based on the following unique combination of characters: Tooth-like denticles on surfaces of dermal cranial bones and the presence of extralateral gulars; median rostral bone; two infraorbital bones posterior to orbit bearing ganoine tuberculations; two large suborbital bones anterior to expanded region of preoperculum; single wedge-shaped dermohyal;

rectangular operculum more than twice the depth of suboperculum; pectinated scales; short fringing fulcra on dorsal fins, longer fringing fulcra on pectoral fins.

Holotype—KUVP 150475 (Figures 2, 3, 5)

Referred Specimens—BYU M 5001ab (Figures 4, 6)

Locality—Lower Pennsylvanian exposures of the Manning Canyon Shale Formation of central Utah. Specimen KUVP 150475, was collected by Lloyd and Frieda Gunther from an exposure in the Lake Mountains of Utah (Figure 1), southwest of Saratoga Springs (Dorka, 1998). This fish was collected from the "clay pits" locality in the Lake Mountains, approximately 20 km southwest of Lehi, Utah, near Highway 68 (Tidwell, 1967; Dorka, 1998). The second specimen, BYU M 5001ab, was collected by Thomas Black at another exposure in the Traverse Mountains of Utah (Figure 1), approximately 3 km north of Highway 73 and 16 km to the west to northwest of Lehi (Tidwell, 1967; Dorka, 1998). This fish was collected from the same section as the microsaur described by Carroll et al. (1991) and Carroll and Chorn (1995) and the acanthodian described by Schultze (1990).

Description

Specimens—The type specimen KUVP 150475 is preserved in lateral view (Figure 2A, B). Various bones, including suborbital and opercular bones from both sides are visible. There is a complete dorsal fin and fragmentary scraps of pectoral and pelvic fins. The dorsal lobe of the caudal fin is present but the ventral lobe is absent. The anal fin is not preserved. Whereas the body of specimen BYU M 5001ab is almost complete, most of the dermal bones of the head are missing. Some are present as disarticulated and displaced bones, whereas others are preserved as faint impressions. Specimen BYU M 5001b preserves most of the caudal, pectoral, and pelvic fins and poorly preserved dorsal and anal fins.

Snout—The bones of the snout are only preserved in KUVP 150475 (Figure 3A–D). These include the nasal, rostral, and lachrymal bones (Figure 3C). The nasal bone, visible from both sides of the skull, is narrow and bears the supraorbital canal. The bone is notched anteroventrally, forming the posterior margin of the anterior narial opening. Above this anteroventral notch, there is a slight process extending from the bone anteriorly. The bone is also slightly notched posteroventrally to form the anterior margin of the posterior narial opening.

Between the nasal bones lies a single median rostral bone that bears the ethmoid commissure on its ventralmost portion (Figure 3C). The rostral is notched on the left and right sides, forming the anterior margins of the anterior narial openings. The rostral is widest ventral to these notches and narrows dorsal to these. The dorsal margin cannot be determined.

The lachrymal bone lies posterior and ventral to the nasal bone (Figure 3C). The lachrymal has two portions—a narrow band of bone that runs dorsal to the anterior margin of the orbit and posterior to the nasal bone, and a horizontal band that runs ventral to the nasal bone and sutures to the ventrolateral margin of the rostral bone. The Y-shaped junction of the infraorbital and supraorbital canals can be seen in the lachrymal bone (Figure 3C).

Skull Roof—Remnants of some skull roof bones are preserved in BYU M 5001ab (Figure 4A–C). Anteriorly, the frontal (parietal) bones bear a series of short diagonal ridges of ganoine. Horizontal ridges are present from mid-length to the posterior margin of the frontal (parietal) bone. Some evidence of the parietal (postparietal) bones is seen, notably in the holotype. In KUVP 150475 the parietal (postparietal) is a rectangular bone with an undulating ventrolateral margin that sutures with the dorsomedial margin of the dermopterotic. The posttemporal bone is ovoid, and in lateral view bears vertical ridges of ganoine anteriorly and curved ridges near the posterior margin (Figures 3C, 4C).

Cheek—Unless noted, information on the cheek bones is from KUVP 150475 (Figure 3A–D). The infraorbital bone in the posteroventral corner of the orbit is large and crescent-shaped. Numerous short canals branch off of the posterior margin of the infraorbital canal. Scale-like tuberculations of ganoine also are present. An ovoid-shaped and heavily tuberculated infraorbital bone lies dorsal to the infraorbital bone in the posteroventral corner of the orbit. Dorsal to this infraorbital bone is the dermosphenotic. The dermosphenotic contributes to the posterodorsal margin of the orbit. It is narrow anteriorly and wider posteriorly. The posterior margin of the dermosphenotic is concave and houses the dorsal margin of the infraorbital bone. Another infraorbital bone is present ventral to the orbit and anterior to the infraorbital bone in the posteroventral corner of the orbit. The infraorbital canal is seen in this region.

The posterior portion of the maxilla is preserved in KUVP 150475 and BYU M 5001ab (Figures 3C, 4C) but the anterior portion is broken in both specimens. Posteriorly, the maxilla is expanded into a posterior plate which is low and squat. There is a posteroventral process extending from this expanded region which covers most of the depth of the lower jaw, but this process is narrow. The teeth along the maxilla are recurved anteriorly. Teeth are also present along the oral margin of the posteroventral process of the maxilla. On BYU M 5001ab, the in situ maxilla is preserved in internal view, but another maxilla, preserved as a disarticulated bone, shows the bone in external view.

There is a single hatchet-shaped preoperculum (Figures 3C, 4C) with a narrow vertical section posterior to the maxilla. This narrow portion curves anteriorly and widens as the preoperculum extends along the dorsal margin of the maxilla. Two suborbital bones are situated anterior to the expanded region of the preoperculum and posterior to the infraorbital bones (Figure 3C). These suborbital bones are clearly visible in KUVP 150475 but displaced and faint in BYU M 5001. The dorsalmost suborbital bone from the right side of the holotype is visible. Posterodorsal to the preoperculum is a single wedge shaped dermohyal that is widest dorsally, tapers to a point ventrally, and has a rounded dorsal margin (Figures 3C, 4C).

The lower jaw is deeper posteriorly and tapers anteriorly to a point. Conical teeth are located along the length of the lower jaw. The anterior teeth are vertically oriented, whereas the posterior teeth are recurved anteriorly. Some horizontal ganoine ridges are preserved in BYU M 5001ab. The angular is visible in KUVP 150475 posterior to the dentary and posteroventral to the preoperculum (Figure 3C).

Operculo-gular Apparatus—The operculum is an anterodorsally inclined rectangular bone that is more than twice the depth of the suboperculum (Figures 3C, 4C). The ventral margin of the operculum is convex and rounded. Based on BYU M 5001ab, the suboperculum is deeper posteriorly than anteriorly (Figure 4C). The posterior margin of the suboperculum is rounded and convex and the dorsal margin of the suboperculum is concave. No ganoine ridges or tuberculations are visible on the suboperculum, but concentric rings that may represent growth lines are present (Figure 4A, B).

In BYU M 5001ab, the complex of branchiostegal rays and gulars has been displaced from the head and preserved in ventral view below the lower jaw (Figure 4 A, C). There is an ovoid median gular that tapers to a narrow point anteriorly, widens, and then tapers to a blunt, rounded point posteriorly. The paired lateral gulars are similar in size and shape to the median gular. A pair of extralateral gulars is located lateral to the posterior half of the median gular and the anterior half of the lateral gulars. Posterior to the left lateral gulars, five branchiostegal rays are preserved. Specimen KUVP 150475 preserves the brachiostegal rays and gulars in lateral view (Figure 3C). Here, a single median gular, lateral gular, and nine branchiostegal rays are visible.

Squamation—The scales of *Spinofacia pectinatus* are pectinated (Figure 4D). An internal view of the scales is preserved (KUVP 150475), but there are a few scales for which external information is available. The scales with their external surfaces preserved are pectinate and bear similar ganoine ornamentation as those of BYU M 5001ab. Based on BYU M 5001ab, the anterior flank scales are rectangular, pectinate with seven or eight serrations, and bear horizontal ridges of ganoine that are inclined anteroventrally. The deepest flank scales are those carrying the lateral line canal. These scales are notched in the middle of the posterior margin. Infilled portions of the lateral line canal are visible at the level of these notches. The infilled portions of the lateral line canal are located between the posterior border of the anterior scale and in front of the free field of the posterior scale. More anterior scales are rhombic, but their posterior margins are serrated. Scales positioned mid-flank, anterior to the origin of the dorsal fin, are rhombic. Anterior to the dorsal fin, the scales positioned closer to the ventral and dorsal margins of the body are rectangular. Posterior to the dorsal fin, the scales are diamond shaped, regardless of their position on the body.

Fins—The dorsal fin is intact in KUVP 150475 (Figures 2, 5). The triangular dorsal fin bears short, closely packed fringing fulcra along its anterior margin. It comprises 31 fin rays and is placed at Scale Row 23. The fin rays are distally bifurcate. The dorsal lobe of the caudal fin is present in KUVP 150475, but the ventral lobe is absent. There are at least two dorsal scutes anterior to the dorsal lobe of the caudal fin in KUVP 150475 and BYU M 5001b. These dorsal scutes are anterior to a series of four other elements, but it cannot be determined whether these elements are scutes or basal fulcra. The caudal fin rays in BYU M 5001b are narrow, closely packed and distally bifurcate. There are fringing fulcra along the leading edge of the ventral lobe of the caudal fin. The caudal fin in BYU M 5001b is positioned at Scale Row 42. Enough of the pectoral fin is preserved in BYU M 5001 to determine that the anterior margin of the pectoral fin bore fringing fulcra. These are closely packed and are longer than those seen on the dorsal fin of KUVP 150475. A small pectoral fin is positioned at Scale Row 11 in BYU M 5001b.

Denticles—A unique characteristic of *Spinofacia pectinatus* is the presence of pointed denticles on the maxilla, preoperculum, operculum, dermohyal, and suborbital bones (Figure 6A–C). In specimen KUVP 150475, whole and broken denticles are preserved. The intact extra-oral denticles resemble the shape of the teeth on the oral margins of the maxilla and dentary—they are conical with a wide base that narrows to a pointed tip. There is no evidence of an apical cap of acrodin on these structures. Remnants of broken denticles appear as hollow rings with thick walls. The presence and orientation of these hollow rings suggest that these denticles were attached to the underlying bone. The type of attachment—whether there was a hinge of connective tissue connecting the denticle to the underlying bone—cannot be determined based on the available specimens. Most of the denticles appear to be arranged in rows on the various bones of the skull. Evidence of these denticles is also preserved on BYU M 5001, but they are not as numerous or apparent as those on KUVP 150475.

Discussion—Two diagnostic characters of *Spinofacia pectinatus* are the presence of extralateral gulars and denticles on the dermal bones of the head. This combination of characters has not been seen in other palaeoniscoids and the presence of either of these characters is uncommon in palaeoniscoids in general. These characters are discussed in more detail below.

Extralateral gulars—These small bones (Figure 4B, C) were defined by Lund and Poplin (1997) as the thin, lateralmost gulars that extend from the anterior tip of the median gular to the third branchiostegal; comparable to the submandibular bones in sarcopterygians. These small gulars are hidden between the dentary and the lateral edges of the other gular bones (Lund and Poplin, 1997). Lund and Poplin (1997) proposed that extralateral gulars could allow for a greater widening of the oral-branchial cavity during respiration and feeding, functioning in a similar manner as proposed by Pearson (1982) for the sarcopterygian submandibular bones.

Extralateral gulars are rarely recognized in palaeoniscoids, but they have been found in various taxa from the Lower Carboniferous (Mississippian, Serpukhovian) Bear Gulch Limestone (Montana, USA). Bear Gulch palaeoniscoids with extralateral gulars include *Cyranorhis bergeraci* (Lund and Poplin, 1997), *Wendyichthys dicksoni* (Lund and Poplin, 1997), *Lineagruan judithi* and *L. snowyi* (Mickle et al., 2009), and *Beagiascus pulcherrimus* (Mickle et al., 2009). *Spinofacia pectinatus* represents the only described example of a palaeoniscoid outside of the Bear Gulch Limestone with these bones. The extralateral gulars in *Spinofacia pectinatus* are unique in that these bones begin at the midpoint of the median gular and extend the whole length of the lateral gular (Figure 4C). This differs from the extralateral gulars in *Wendyichthys dicksoni* and *Cyranorhis bergeraci*, which begin at the anteriormost tip of the median gular (Lund and Poplin, 1997: figure 4B, 16B).

The shared presence of extralateral gulars does not necessarily signify a close relationship between the extralateral bearing Bear Gulch palaeoniscoids and *Spinofacia pectinatus.* There are multiple differences that clearly distinguish the Bear Gulch genera from *Spinofacia pectinatus.* The placement of the extralateral gulars differs between *Spinofacia* and the Bear Gulch taxa. Also, there are many differences in cranial bones. *Spinofacia pectinatus* can be distinguished from *Wendyichthys* and *Cyranorhis* by the number and/or shapes of the infraorbital bones, dermosphenotic, dermohyal, and maxilla (Lund and Poplin, 1997). *Spinofacia* differs from *Lineagruan* and *Beagiascus* based on characteristics of the maxilla, opercular, anteopercular, preopercular, suborbital, and dermosphenotic bones (Mickle et al., 2009).

Denticles—There is a large amount of literature detailing denticles from the scales and/or dermal bones of extant basal actinopterygian fishes such as *Lepisosteus osseus* (Hertwig, 1879, figure 13; Nickerson, 1893; Goodrich, 1909, figure 192; Kerr, 1952) and *Polypterus* (Agassiz, 1833–43; Hertwig, 1879; Goodrich, 1909, figure 265; Sewertzoff, 1932; Kerr, 1952). In these extant fishes, the denticles have apical caps of acrodin, which are not seen in *Spinofacia* (Hertwig, 1879; Nickerson, 1893; Kerr, 1952). Tooth-like denticles also are well known on the dermal skull bones and/or scales of various teleosts, including the clupeomorph *Denticeps clupeoides* (Clausen, 1959; Greenwood, 1960, 1968; Sire et al., 1998); the atheriniform *Atherion elymus* (Sire and Allizard, 2001); xiphioid swordfish and billfish (Sire et al., 1998), numerous armored catfish (Bhatti, 1938; Sire and Huysseune, 1996); and the fossil *Pholidophorus granulatus* (Egerton, 1855; Schultze, 1966). Denticles on scales and dermal bones in fossil basal actinopterygians are less commonly known. The Carboniferous *Whiteichthys greenlandicus* (Goodrich, 1942) has been described as having extra-oral denticles. Goodrich (1942) stated that the lack of denticles on more fossil early actinopterygians was a "remarkable fact" and that "we should certainly expect to find them" (Goodrich, 1942:459). *Spinofacia pectinatus* is an additional fossil early actinopterygian that preserves evidence of denticles on the surfaces of dermal bones.

It is unfortunate that the preservation of the denticles in *Spinofacia pectinatus* does not allow for histological studies. All discussions of the nature of these elements must be made on their gross anatomical structure, nevertheless; they can be compared to the denticles in fishes for which detailed histological and morphological studies have been done.

Structures on the scales and bones in the Carboniferous *Whiteichthys greenlandicus* are considered true denticles, with a conical cap of dentine surrounding a pulp cavity that may become fused to underlying bony structures (Goodrich, 1942). There is no evidence of apical caps of acrodin on these structures in *Whiteichthys*. The denticles appear as rounded tubercles on the head, and sharp elongated spines on the body scales (Goodrich, 1942). The conical denticles are prominent on the posterior edge of the scale, but it does seem that they were present in regular rows on the flat surfaces of the scales (Goodrich, 1942). This situation is similar to what is found on the dermal bones of *Spinofacia pectinatus.* Though the denticles are similar between the two genera, *Spinofacia pectinatus* can be easily distinguished from *Whiteichthys greenlandicus* on the basis on numerous morphological details. *Whiteichthys* differs from *Spinofacia* on the basis of the absence of suborbital bones, a larger suboperculum than operculum, lack of a posteroventral process on the maxilla, and differences in the shapes of the preoperculum, dermohyal, and infraorbital bones. The shared presence of these denticles does not support a close relationship between these genera.

The round hollow rings found close to the intact denticles in *Spinofacia pectinatus* may resemble structures found in the clupeomorph *Denticeps clupeoides.* In *Denticeps,* the denticles are elongated spine-shaped elements firmly fixed to a bony support. When the denticles are broken off or shed, the basal region is left as a hollow ring still attached to the underlying bone (Sire et al., 1998). As with teeth, these structures are referred to as pedicels and are morphologically similar to the rings seen in *Spinofacia pectinatus.* These hollow rings also occur in the extant basal actinopterygian, *Lepisosteus osseus* (Hertwig, 1879; Goodrich, 1909, figure 192; Kerr, 1952). Because of these general similarities in morphology, the extra-oral tooth-like structures found on the bones of *Spinofacia pectinatus* are considered to be true denticles.

Family incertae sedis

Genus *Guntherichthys* n. gen.

Diagnosis—As for the type and only species.

Type and Only Species—*Guntherichthys lehiensis*.

Etymology—after Lloyd Gunther for his contributions to the paleontology of Utah, specifically the Manning Canyon Shale.

Guntherichthys lehiensis n. gen. n. sp.

(Figures 7–10)

Diagnosis—Based on the following unique combination of characters: Anterior scales with slightly rounded posterior, dorsal, and ventral margins; scales with curved ridges of ganoine; scales rhombic at level of caudal peduncle; lack of serrations on posterior margin of scales; maxilla with posteroventral process; operculum twice the depth of the suboperculum; dorsal fin originating at the same level as the anal fin; continuous dorsal scutes between dorsal and caudal fins; ventral scutes between pelvic and anal fins; ventral scutes between anal and caudal fins; large conical teeth anteriorly on mandible; horizontal ridges of ganoine on mandible.

Holotype—KUVP 124570ab (Figures 7–10).

Locality— Manning Canyon Shale Formation, west of Lehi, central Utah.

Etymology—after the town of Lehi, which is close to the locality.

Description

Specimen—The type and only specimen is preserved in lateral view. It is difficult to determine the margins of the skull bones but the body and fins are preserved in detail. The fish is relatively small and most of the snout is missing, but the standard length is estimated to be a little over 7.5 cm. Though small, the specimen is completely scaled and bears ganoine ornamentation on both bones and scales.

Snout—The snout region of the fish is not well preserved. Remnants of the nasal bone are preserved in KUVP 124570b (Figure 7A, B, E). The nasal bone is wide ventrally, notched on its anterior and posterior margins, and tapers dorsally. Ventrally, the nasal bone sutures to a poorly preserved bone, which is considered to be a lachrymal, based on its position and probable canal lines.

Skull Roof—The margins of the anterior portion of the frontal (parietal) bone are poorly preserved on KUVP 124570b (Figure 7A, B, E). Enough of the bone is preserved to determine that the frontal (parietal) bone is wider posteriorly than anteriorly and is notched on its posteroventral margin. An anterior extension of the dermopterotic is situated within this notch. A portion of the supraorbital canal is visible running close to the lateral margin of the frontal (parietal) bone. Posterior to the frontal (parietal) bone is a rhombic parietal (postparietal) (Figure 7E); both bones bear short ridges and tuberculations of ganoine.

Ventral to the frontal (parietal) and parietal (postparietal) bones is the dermopterotic (Figure 7A, B, E). The portion of the dermopterotic that is ventral to the parietal (postparietal) bone is wide and rhombic. Anteriorly, the dermopterotic is drawn out into a thinner process which lies ventral to the frontal (parietal) bone, with the anteriormost portion of this process situated within a notch of the frontal (parietal) bone. The ventral margin of this bone is difficult to determine, but it appears rounded.

Cheek—The hyomandibula is visible on KUVP 124570b. It is anteriorly inclined, wider dorsally and ventrally, but tapered, or cinched, in the middle. The dermohyal lies on the posterodorsal portion of the hyomandibula (Figure 7A–E).

The posterior portion of the maxilla is preserved on KUVP 124570 (Figure 7A–E). It has a pronounced posteroventral process, but this process may actually be larger than preserved because the specimen is broken ventrally. The anterior arm of the maxilla is not preserved. The preserved posterior portion bears diagonal ridges of ganoine on the posteroventral process and horizontal ridges anteriorly on the expanded portion of the maxilla.

Most of the mandible is preserved in KUVP 124570b, whereas only the anterior portion of the mandible is visible in KUVP 124570a (Figure 7A–E). Large conical teeth are present on the mandible. A few horizontal ridges of ganoine are preserved in KUVP 124570b. At least two sclerotic bones are visible in the orbit. The parasphenoid is displaced and exposed (Figure 7A, B, E).

Otic Region—In the otic region, there is a large three-dimensional bulge that appears to be made of the same material as the rock matrix (Figure 7A, B, E). The anterodorsal portion of the hyomandibula comes in contact with this bulge. This bulge is not bone, but appears to represent an otic infilling, similar to those seen in acanthodians, osteostracans, and chondrichthyans (Sahney and Wilson, 2001).

Operculo-gular Apparatus—The operculum is a rectangular bone that is anteriorly inclined and deeper than wide (Figure 7A, B, E). The suboperculum is about half the depth of the operculum and rhombic (Figure 7A–E). Unlike the operculum, the suboperculum is slightly posteriorly inclined. The dorsal margin of the suboperculum is concave and houses the convex ventral margin of the operculum.

The median gular is visible ventral to the mandible in KUVP 124570-b (Figure 7). Directly posterior to the median gular, there is evidence of the rest of the branchiostegal series, but individual elements cannot be distinguished. Toward the posterior end of the dentary, four branchiostegal rays can be distinguished (Figure 7C–E)

Pectoral Girdle—The cleithrum is partially preserved on KUVP 124570a (Figure 7A, B, E). The dorsal arm extends slightly past the ventral margin of the operculum, narrows to a blunt point, and sutures with the ventral margin of the supracleithrum. The supracleithrum is ovoid and slightly constricted mid-bone along its posterior margin.

There is a small, round presupracleithrum anterior to the supracleithrum and posterior to the operculum, that bears curved ridges of ganoine. Posterior to the parietal (postparietal) bone is the posttemporal (Figure 7A, B, E). In lateral view, the posttemporal is an ovoid-shaped bone that bears curved ridges.

Squamation—Overall, the anterior scales have a more rounded appearance owning to the slightly rounded posterior, dorsal, and ventral margins (Figure 8B). These scales bear curved ridges of ganoine. Ventral scales are narrower than flank or dorsal scales. At the level of the dorsal fin, the scales are more rhombic in shape and narrower than those just posterior to the pectoral girdle. This trend continues posteriorly so that the scales on the caudal peduncle are even narrower and rhombic (Figure 8A). The scales on the heterocercal lobe are narrow and diamond shaped.

Fins—There is no evidence of the pectoral fins, but the dorsal and anal fins are superbly preserved in both part and counterpart (Figure 9A–C). The dorsal fin seems to be missing some of the anterior rays, but both the dorsal and anal fins are triangular. There are at least 23 fin rays in the dorsal fin and 29 in the anal fin. The dorsal and anal fins are positioned at Scale Rows 22 and 18, respectively. The dorsal fin is slightly taller than the anal fin. There are a few of the baseosts visible ventral to the dorsal fin in KUVP 124570a. Fringing fulcra appear to be absent on the dorsal and anal fins. A small pelvic fin is found at scale row nine; again, with no fringing fulcra. There are five pre-anal fin scutes between the pelvic and anal fins, creating a continuous row of scutes between the fins.

The caudal fin is present in KUVP 124570b (Figure 10) at Scale Row 40. Although the caudal fin is heterocercal, it is not forked. The caudal fin rays form a single triangular series—there are no distinct ventral and dorsal portions to the caudal fin as is typically seen in palaeoniscoids. Fringing fulcra are absent on the caudal fin. Continuous dorsal scutes are present between the dorsal fin and the caudal fin and continuous ventral scutes are between the anal and caudal fins

Discussion—The combination of rounded, anteriorly placed scales and rhombic, posteriorly placed scales is unusual in palaeoniscoids, which typically are characterized by rhombic scales. Rounded scales are present in a few genera of early actinopterygians such as *Cryphiolepis* and *Sphaerolepis* (Fritsch, 1875; Traquair, 1907; Gardiner, 1967a). As in *Guntherichthys, Cryphiolepis* and *Sphaerolepis* have anterior scales with rounded posterior, dorsal, and ventral margins (Gardiner, 1967a). In both *Guntherichthys* and *Sphaerolepis,* these rounded scales bear concentric curved ridges of ganoine. The posterior scales in these three genera are similarly rhombic. In *Sphaerolepis,* the first three to four rows of scales posterior to the cleithrum have pectinate posterior margins, that are absent in *Guntherichthys* (Gardiner, 1967a).

The shape of the caudal fin is similar in *Guntherichthys* and *Sphaerolepis*. The caudal fin in *Sphaerolepis* is long, heterocercal, and uncleft (Gardiner, 1967a). Although incomplete in *Guntherichthys,* enough is preserved to determine that the caudal fin was also heterocercal and uncleft (Figures 9, 10). Like the scales, an uncleft heterocercal caudal fin is not typical of palaeoniscoids which generally have a cleft heterocercal fin with distinct dorsal and ventral lobes.

According to Gardiner (1967), other early actinopterygians that share this characteristic with *Guntherichthys* and *Sphaerolepis* include *Phanerorhynchus* (Gill, 1923), *Palaeoniscinotus* (Rohon, 1890), *Holorus* (Traquair, 1881), and *Holuropsis* (Berg, 1947). Unlike *Guntherichthys* and *Sphaerolepis*, these fishes do not have scales with rounded posterior margins.

The new genus and species *Guntherichthys lehiensis* is erected because though the type specimen KUVP 124570 shares scale and fin characteristics with *Sphaerolepis* and *Cryphiolepis,* there are numerous differences between these fishes. *Cryphiolepis* is characterized by the "typical palaeoniscoid" cleft heterocercal caudal fin, rather than the uncleft caudal fin seen in *Guntherichthys* (Traquair, 1907). There are numerous differences in the skull bones of *Sphaerolepis* and *Guntherichthys. Sphaerolepis* has a large fossa in the skull roof ventral to the frontal (parietal) bone and parietal (postparietal) bone and dorsal to the dermopterotic (Fritsch, 1893; Gardiner, 1967a). Though *Guntherichthys* does not have a perfectly preserved skull roof, enough of the frontal (parietal), parietal (post parietal), and dermopterotic bones are preserved to document the absence of a large fossa (Figure 7). The maxilla of *Sphaerolepis* is interpreted as being rounded dorsally, but lacking the posteroventral process that is seen in most palaeoniscoids (Gardiner, 1967a). The maxilla of *Guntherichthys lehiensis* is rounded dorsally and has the posteroventral process that overlaps the posterior portion of the lower jaw (Figure 7). The sizes of the opercular bones differ in *Sphaerolepis* and *Guntherichthys.* The operculum in *Sphaerolepis* is described as being more than three times the depth of the suboperculum whereas in *Guntherichthys,* the operculum is only twice the depth of the suboperculum (Figure 7). Based on the reconstruction of *Sphaerolepis* in Gardiner (1967) and Štamberg (2006), this difference is attributable to the suboperculum being smaller in *Sphaerolepis* than in *Guntherichthys.* The suboperculum is only slightly deeper than the branchiostegal rays in *Sphaerolepis.*

Differences involving the postcranial skeletons of *Guntherichthys* and *Sphaerolepis* include the presence of continuous dorsal scutes between the dorsal and caudal fin, ventral scutes between the pelvic and anal fins, and between the anal and caudal fin in *Guntherichthys* and an absence of all of these structures in *Sphaerolepis* (Gardiner, 1967a). The dorsal fin of *Guntherichthys* originates at about the same level as the anal fin whereas the dorsal fin originates far in advance of the anal fin in *Sphaerolepis* (*ibid.*). Though the two genera have scales with rounded posterior margins, *Sphaerolepis* differs from *Guntherichthys* in the presence of three or four rows of pectinate scales posterior to the pectoral girdle (*ibid.*).

At first glance, the shared presence of scales with rounded posterior margins and an uncleft caudal fin seem to closely align *Guntherichthys* and *Sphaerolepis.* A closer examination of these two genera reveals that there are numerous differences regarding the cranial and postcranial skeletons. Though not well preserved, the head does provide valuable information that separates this specimen from *Sphaerolepis.* The lack of a prominent fossa in the skull roof, the presence of a prominent posteroventral process on the maxilla, and the larger suboperculum justifies the description of a new genus and species for specimen KUVP 124570. Though some of the cranial characteristics are not diagnostic by themselves—for instance, the presence of a posteroventral process on the maxilla is common for early actinopterygians—it is the combination of cranial and postcranial characteristics that is unique to the new genus and species *Guntherichthys lehiensis*. There are some similarities regarding the postcranial characteristics of *Guntherichthys, Cryphiolepis,* and *Sphaerolepis,* but until phylogenetic analyses are completed, there can be no comment on the relationships of these genera. What should be noted is that characteristics of the scales and caudal fin characteristics shared by both genera are uncommon amongst early actinopterygians in general.

Order Aeduelliformes Heyler, 1969

Family Aeduellidae Romer, 1945

Diagnosis—After Štamberg (2007), emended. Fusiform or elevated-fusiform body; total length approximately three to four times depth of body anterior to dorsal fin; head and orbit large; large tuberculated rostral bone; large nasal with longitudinal ridges; supraorbital canal passes along lateral margin of frontal (parietal), traverses onto dermopterotic as a "pit line" or canal interconnected with infraorbital canal; medial and posterior pit lines on parietal (postparietal); infraorbitals either all small or a few large; premaxillae absent; maxilla with elevated postorbital region; vertical preoperculum; operculum large, nearly vertical; suboperculum nearly same depth as operculum; one to few branchiostegal rays; elongated median gular; predorsal ridge scales not complete to occiput; no ridge scales between dorsal and caudal fins; one anal plate; dorsal and anal fins originating at about the same scale row; heterocercal caudal fin.

Genus *Bourbonnella* Heyler, 1969

Diagnosis—After Štamberg (2007), emended. Total length of 15–30 cm; total length 3.5–5.5 times length of head; one long and narrow infraorbital bone; posterior region of maxilla deeper than in other Aeduellidae; deep and subequal opercula and subopercular bones with rectilinear common suture; operculum slightly anteriorly inclined; three to six ridge scales anterior to dorsal fin; pectoral fin with scaled lobe.

Bourbonnella jocelynae n. sp.

(Figures 11–14)

Diagnosis—Based on the unique combination of characters: An aeduellid with horizontal ridges of ganoine on frontal (parietal) bones; short ganoine ridges and tuberculations on parietal (postparietal) bones; lateral extrascapulae; elongated dermosphenotic bone; rectangular operculum and suboperculum; suboperculum deeper than operculum; slightly concave dorsal margin of suboperculum; prominent clavicle visible in lateral view; three elements anterior to dorsal fin, including two dorsal scutes, one dorsal basal fulcrum.

Holotype—KUVP 150476ab (Figures 11–14).

Locality—Collected by David Stricklan in the "clay pits" location of the upper Mississippian/lower Pennsylvanian Manning Canyon Shale Formation, west of Utah Lake of central Utah (Latitude 40.254354°, Longitude –111.870288°).

Etymology—*jocelynae,* in the memory of Jocelyn Stricklan, daughter of the collector of the holotype, David Stricklan.

Description

Body Form—*Bourbonnella jocelynae* is a relatively small fish, but because the anterior portion of the head is missing in both part and counterpart, the standard length is estimated to be slightly more than 3 cm. There is little information on the snout (Figure 11A–E). Overall, there is a vertical orientation to the cheek and opercular bones that gives *Bourbonnella jocelynae* a short, but deep head that is diagnostic of Aeduellidae.

Snout and Skull Roof—The only remnant of the snout is a heavily tuberculated section considered to be the median rostral bone (Figure 11A, C, E), which is a characteristic of Aeduellidae. Remnants of the frontal (parietal) bone are present in the part and counterpart. The frontal (parietal) bone is not well preserved, but the anterior portion of this bone is narrower than the posterior end. When observed in lateral view, the bone primarily bears horizontal ridges of ganoine, but some cross-vertical ridges are present posterodorsally. Posterior to the frontal (parietal) bone is a large rectangular parietal (postparietal) bone (Figure 11A–E), bearing short ridges and tuberculations of ganoine.

An elongated dermosphenotic is present posterodorsal to the orbit (Figure 11A–E). The dermosphenotic is narrowest anteriorly and becomes progressively wider posteriorly. A dermopterotic bone lies posterior to the dermosphenotic. In KUVP 150476a, there is a slight process extending from the ventral border of the dermopterotic (Figure 11C, E). The dermopterotic has an undulating dorsal margin and bears short ganoine ridges.

Posterior to the parietal (postparietal) bone are the lateral extrascapulae (Figure 11A–E). The lateral extrascapula is present as a narrow band of bone and when observed in lateral view, bears cross-vertical ridges of ganoine. Posterior to the extrascapular bones are the paired posttemporal bones (Figure 11A–E) that are slightly ovoid and bear curved ridges of ganoine.

Cheek—Both maxillae are visible on the part and counterpart (Figure 11A–E). The maxilla lacks a posteroventral process. There is an expanded posterior region, but no process arises from the ventral margin of the maxilla. This shape of the maxilla characterizes fishes within the order Aeduelliformes. The maxilla in *Bourbonnella jocelynae* has a short, narrow anterior arm that tapers anteriorly. Though most of the anterior portion of the head is not preserved, the full length of the maxilla seems to be preserved because a complete mandible of almost the same length is seen in KUVP 15047 b. The mandible is low and bears horizontal ridges of ganoine, whereas the maxilla bears dramatically curved ridges of ganoine (Figure 11B, D, E).

The preoperculum has a narrow vertical portion and an expanded anterior portion. The latter is dorsal to the posterodorsal margin of the maxilla (Figure 11 A, C, E). The preopercular canal extends up the vertical portion of the preoperculum and curves around the dorsal margin of the expanded region. The horizontal pit line comes off of the main preopercular canal and extends onto the expanded region of the preoperculum.

Dorsal to the preoperculum, there is a part of an apparently vertical hyomandibula (Figure 11A–E), posterodorsal to which a slight impression of a wedge shaped dermohyal is preserved (Figure 11A, C, E).

Operculo-gular Apparatus—Both the operculum and suboperculum are rectangular (Figure 11A–E). The ventral margin of the operculum is slightly concave. Overall, the suboperculum is taller than the operculum and the posteroventral border of the bone is slightly rounded. The ventral margin of the suboperculum is diagonal, whereas the upper margin is slightly concave. This margin makes the posterodorsal portion of the suboperculum slightly taller than the anterodorsal portion. There are no signs of any anteopercular bones anterior to the operculum or suboperculum. There are no gulars or branchiostegal rays preserved in lateral view under the lower jaw, but one branchiostegal ray is preserved ventral to the suboperculum (Figures 11A–E, 14).

Pectoral Girdle—The supracleithrum is present posterior to the operculum (Figure 11A–E). It is slightly deeper than the operculum and notched about at about the midpoint of its posterior margin. A canal can be seen running through the dorsal portion of the supracleithrum and exiting at the notch. The dorsal margin of the supracleithrum is blunt and rounded, the ventral margin tapered to a blunt point.

Ventral to the supracleithrum and posterior to the suboperculum is the cleithrum (Figure 11A–E). The cleithrum has a tall vertical portion that extends to about the upper margin of the suboperculum. The cleithrum is notched posteroventrally and the pectoral fin is located in this notch. Ventral to this notch, the cleithrum widens. The cleithrum bears vertical ridges of ganoine on the tall vertical portion and curved ridges at the level of the notch. The clavicle is present anterior to this widened portion of the cleithrum (Figure 11A–E), and is triangular with horizontal ridges of ganoine.

Fins—The caudal fin is not preserved in the part or counterpart. Triangular dorsal and anal fins are positioned at Scale Rows 20 and 17, respectively (Figures 12, 13). The dorsal fin originates slightly anterior to the origin of the anal fin. In the dorsal fin, there are 24 fin rays, whereas there are 17 fin rays in the anal fin. There is no sign of fringing fulcra on the leading edges of either of these fins. Small pelvic fins are preserved on KUVP 150476a at scale row 9. There are large scutes in front of the anal fin. Anterior to the dorsal fin, there are three elements. Two of these elements are dorsal scutes—median structures that lie in dorsal midline (Arratia, 2008). The third element that abuts against the leading edge of the dorsal fin is oriented more vertically, and is paired. These characteristics indicate that this element a dorsal basal fulcrum (Arratia, 2008). There are a few pectoral fin rays that are borne upon a short scaled lobe (Figure 14). This scaled lobe is evidenced by the curved scale rows situated at the notch of the cleithrum and resembles that previously described for *Bourbonnella* (Heyler, 1969; Poplin, 2001; Poplin and Dutheil, 2005; Štamberg, 2007).

Discussion—*Bourbonnella jocelynae* has been placed within Aeduellidae because it exhibits numerous diagnostic characteristics of this family (Heyler, 1969; Poplin and Dutheil, 2005; Štamberg, 2007). These shared characteristics include a deep, broad head; large orbits without a sclerotic ring; a median rostro-postrostral that bears strong tuberculations; a row of extrascapular bones; a short and vertically oriented preoperculum and a vertical suspensorium; a large suboperculum; ridge scales (dorsal scutes) anterior to the dorsal fin; and few branchiostegal rays. KUVP 150476 is placed with the genus *Bourbonnella* on the basis of the shared presence of a postorbital portion of the maxilla that is deeper than those of other genera of Aeduellidae; deep and subequal operculum and suboperculum; a slightly anteriorly inclined operculum; three to six large ridge scales anterior to the dorsal fin; and a pectoral fin borne on a scaled lobe place (Poplin, 2001; Poplin and Dutheil, 2005; Štamberg, 2007).

Specimen KUVP 150476 represents a new species, *Bourbonnella jocelynae*, based on the presence of more intricate ornamentation on the skull bones, different shapes of both the dermopterotic and dermosphenotic bones, and a prominent clavicle visible in lateral view that has not seen in other previously described species of *Bourbonnella.*

COMMENTS ON PALEOENVIRONMENT

The Manning Canyon Shale has previously been considered a freshwater site. Recently, many Carboniferous European sites that were originally considered to be freshwater have been reinvestigated and reinterpreted as marine, primarily based on evidence from the autochthonous fauna (see Soler-Gijón, 1993, 1997; Poplin, 2001; Schultze and Soler-Gijón, 2004). The Manning Canyon Shale, hypothesized to be freshwater on the basis of allochthonous terrestrial plants (Tidwell, 1975; Carroll *et al.*, 1991), could also be open to reinterpretation. The following discussion is not intended to be a complete revision of the paleogeography or paleoenvironment of the Manning Canyon Shale, but rather it is meant to highlight why it may not be freshwater and the need for a deeper investigation into its paleoenvironment.

Aeduellids

The presence of an aeduellid in the Manning Canyon Shale raises some questions regarding the interpretation of the paleogeography and paleoenvironment of this site. Historically, aeduellids have historically been described as endemic European freshwater fishes because they came from sites that were considered to be freshwater (Heyler, 1969). Aeduellids of the genus *Bourbonnella* have been described from the Upper Carboniferous Konservat-Lagerstätte Montceau-les-Mines of France (Heyler, 1969) and the Puertollano Basin of Spain (Schneider et al., 2000). Both of these sites were previously described as freshwater and without a marine connection (Wagner, 1985), but have been revised and are now considered to be marine-connected (Soler-Gijón, 1993, 1997; Poplin, 2001; Schultze and Soler-Gijón, 2004). Gottfried (1987) described an aeduellid, *Bourbonnella* sp. indet., from the upper Pennsylvanian Kinney Brick Quarry from the Wild Cow Formation of New Mexico. The Kinney Brick Quarry is a near shore marine deposit (Feldman et al., 1992; Kues and Lucas, 1992) and so, the discovery of an aeduellid at this site raises questions as to how a fish from a family of endemic freshwater European fishes could be recovered from a marine site in North America (Gottfried, 1987). Gottfried (1987), Schultze and Soler-Gijón (2004), and Schultze (2009) suggested that presence of aeduellids in North America necessitates a marine connection between the localities. Poplin (2001) stated that based on the present knowledge, the genus *Bourbonnella* is euryhaline. Aeduellids should not necessarily be considered endemic freshwater fishes and the discovery of a second North American aeduellid further supports this hypothesis (discussed below).

It should be noted that the presence of aeduellids in New Mexico and Utah are not the only evidence suggesting a marine connection to sites like the Puertollano Basin or Montceau-les-Mines. Since Gottfried's 1987 publication, there have been many published works describing taxa as well as investigating paleoecological data. Schultze (2009) compiled a long list of recent studies that provide paleoecological, sedimentological, and geochemical evidence for the Puertollano Basin being a coastal, estuarine, or lagoonal environment (see Schultze, 2009 and citations therein).

Recent descriptions of autochthonous aquatic taxa from the Montceau-les-Mines Basin have led to reassessments and reinterpretations regarding the paleoenvironment of this site (Schultze, 2009; Schultze and Soler-Gijón, 2004; Poplin et al., 2001). Numerous taxa have been described from Montceau-les-Mines that suggest a marine influence. One of the most telling is the description of *Myxineidus gononorum*, a myxinoid (Poplin et al., 2001). As pointed out by Poplin et al. (2001), Schultze and Soler-Gijón (2004), and Schultze (2009), extant hagfish are strictly marine fishes that show no indication of a prior freshwater existence. A previously described fossil myxinoid, *Myxinikela* (Bardack, 1991) is also from a marine site, the Essex fauna in Mazon Creek, U.S.A. (Bardack, 1991). This, combined with the presence of marine polychaetes from the genus *Palaeocampa* in both the Montceau-les-Mines and Mazon Creek, supports the current interpretations of a marine Montceau-les-Mines and justifies the earlier comparisons of this site to Mazon Creek (Rolfe, et al., 1982; Schultze, 2009). Aeduellids, originally regarded as freshwater endemics because the sites they were recovered from were considered freshwater, have been reinterpreted as euryhaline and now are known from marine sites. The presence of an aeduellid in the Manning Canyon Shale does necessarily support a freshwater interpretation, but does support a marine connection between the Manning Canyon Shale of Utah and other Carboniferous European sites.

Paleoenvironment of the Manning Canyon Shale

The flora of the Manning Canyon Shale has been used to reconstruct the paleoenvironment as a swampy lowland with ponds and riparian habitats; suggesting a freshwater habitat (Tidwell, 1975; Carroll, et al., 1991). Following the argument of Schultze (1996; 2009), terrestrial plants cannot be used to determine if an aquatic environment is freshwater or marine because the plants are allochthonous to the aquatic environment in question. Instead, aquatic environments should only be defined by the organisms that lived in that habitat (Schultze, 1996, 2009).

The fauna of the Manning Canyon Shale consists of a cladodont shark (Miller, 1981), actinopterygian fishes, an acanthodian (Schultze, 1990), a microsaur (Carroll et al., 1991; Carroll and Chorn, 1995), and three genera of sponges (Rigby and Moyle, 1959). The presence of a single cladodont shark tooth is not strong support for or against a marine influence to the locality. At first glance, the presence of palaeoniscoid and acanthodian fishes also does not seem to be informative because both types of fishes have been found in marine and freshwater environments (Schultze, 2009). However, the presence of the aeduellid, is informative. As Schultze (2009:133) pointed out, "the occurrence of similar or the same fishes in two or more localities indicates a marine connection, meaning the fishes could migrate using a marine route." The presence of aeduellids in Utah, New Mexico, and numerous European sites demonstrates that there was at least a marine connection between Europe and North America through which these fishes were able to migrate. Also, aeduellids have been recovered from sites currently considered to be marine (Schultze, 2009 and citations therein).

The presence of the microsaur, *Utaherpeton franklini* (Carroll et al., 1991; Carroll and Chorn, 1995) does not necessarily point to a freshwater habitat. Numerous microsaur specimens have been recovered from the marine Mississippian Kinkaid Formation of Illinois, which also contains the remains of edrioasteroid echinoderms and crinoids (Gutschick, 1965; Kammer et al., 1987; Schultze and Bolt, 1996; Lombard and Bolt, 1999). Microsaurs also have been recovered from the Pennsylvanian Joggins Formation of Nova Scotia from poorly drained coastal plains that have been interpreted as brackish-influenced coastal shallows (Falcon-Lang et al*.,* 2006).

The sponges recovered from the Manning Canyon Shale Formation are the most informative with regard to the aquatic environment. Sponges from the marine genera *Wewokella*, *Talpaspongia*, and *Annulispongia* have been recovered in association with bryozoans, crinoids, and corals, from the Manning Canyon Shale Formation (Rigby and Moyle, 1959; Finks and Rigby, 2004 a, b). This suggests that, not only was there a marine connection, but that the Manning Canyon Shale itself was marine, or marine influenced. The earliest undisputed freshwater sponges have been recovered from Mesozoic rocks, with the oldest genera, *Eospongilla* (Dunagan, 1999) and *Spongilla* (Hinde, 1883) found in the Upper Jurassic (Reitner and Wörheide, 2002; Finks and Rigby, 2004c; Schindler et al., 2008). Recently, Schindler et al. (2008) described purported freshwater sponges from the Permo-Carboniferous Saar-Nahe Basin, but it seems that these sponges have been classified as freshwater on the basis of the locality being considered a freshwater lake deposit. Thus, there is controversy over whether the Saar-Nahe Basin is actually a freshwater lake deposit (Schultze, 2009).

When the fauna that lived in the aquatic environment are considered, a different hypothesis regarding the paleoenvironment of the Manning Canyon Shale Formation can be reached. Based on the autochthonous taxa, the Manning Canyon Shale Formation could be considered, in the least, marine connected and/or marine influenced.

CONCLUSIONS

While the fishes from this site do not match the sheer number or diversity of the flora for which this formation is famous, it is important to note that the few fish specimens that are available for study have in fact been quite diverse. Based on four specimens, a total of two new genera and three new species of Paleozoic actinopterygian fishes have been described. The newly described aeduellid, *Bourbonnella jocelynae,* is the earliest known aeduellid and only the second occurrence of this family in North America. A review of the fauna recovered from the Manning Canyon Shale, especially the aeduellid and sponges, suggests that a reinvestigation and perhaps reinterpretation of the paleoenvironment of the site is necessary. The Manning Canyon Shale may be similar to numerous European sites that were originally considered to be freshwater on the basis of allochthonous taxa, but that were later determined to be marine when autochthonous taxa were considered. That said, further paleoecological, sedimentological, and geochemical evidence are necessary before any firm statements regarding the paleoenvironment of the Manning Canyon Shale are made.

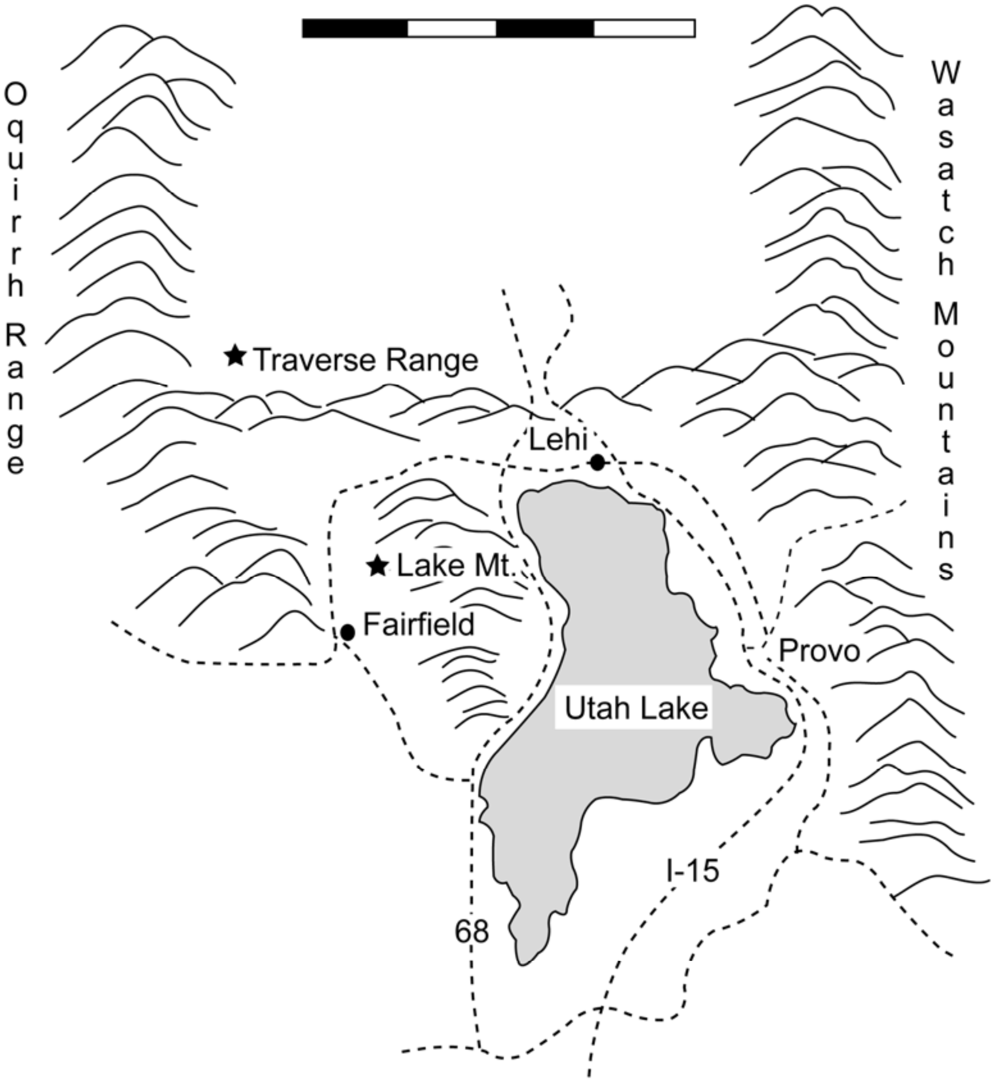


Figure 1—Locality map. Stars represent areas specimens were collected. Modified from Carroll et al., 1991. Scale bar equals 25 mi, 40 km.

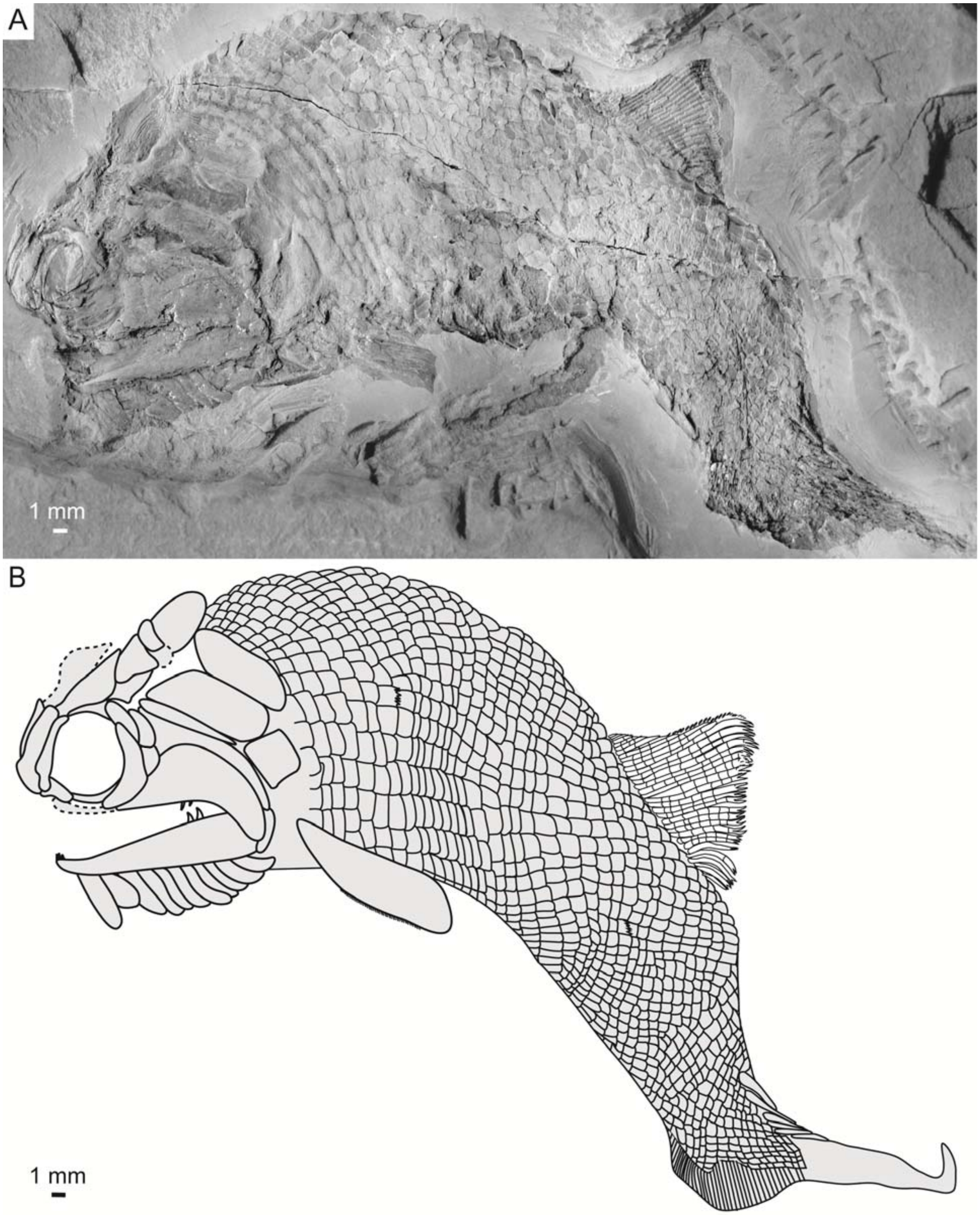


Figure 2—*Spinofacia pectinatus* n. gen. n. sp. **A,** photograph of holotype KUVP 150475. Lateral view of the whole fish, natural cast; **B,** reconstruction based upon holotype KUVP 150475. Scale bars equal 1 mm.

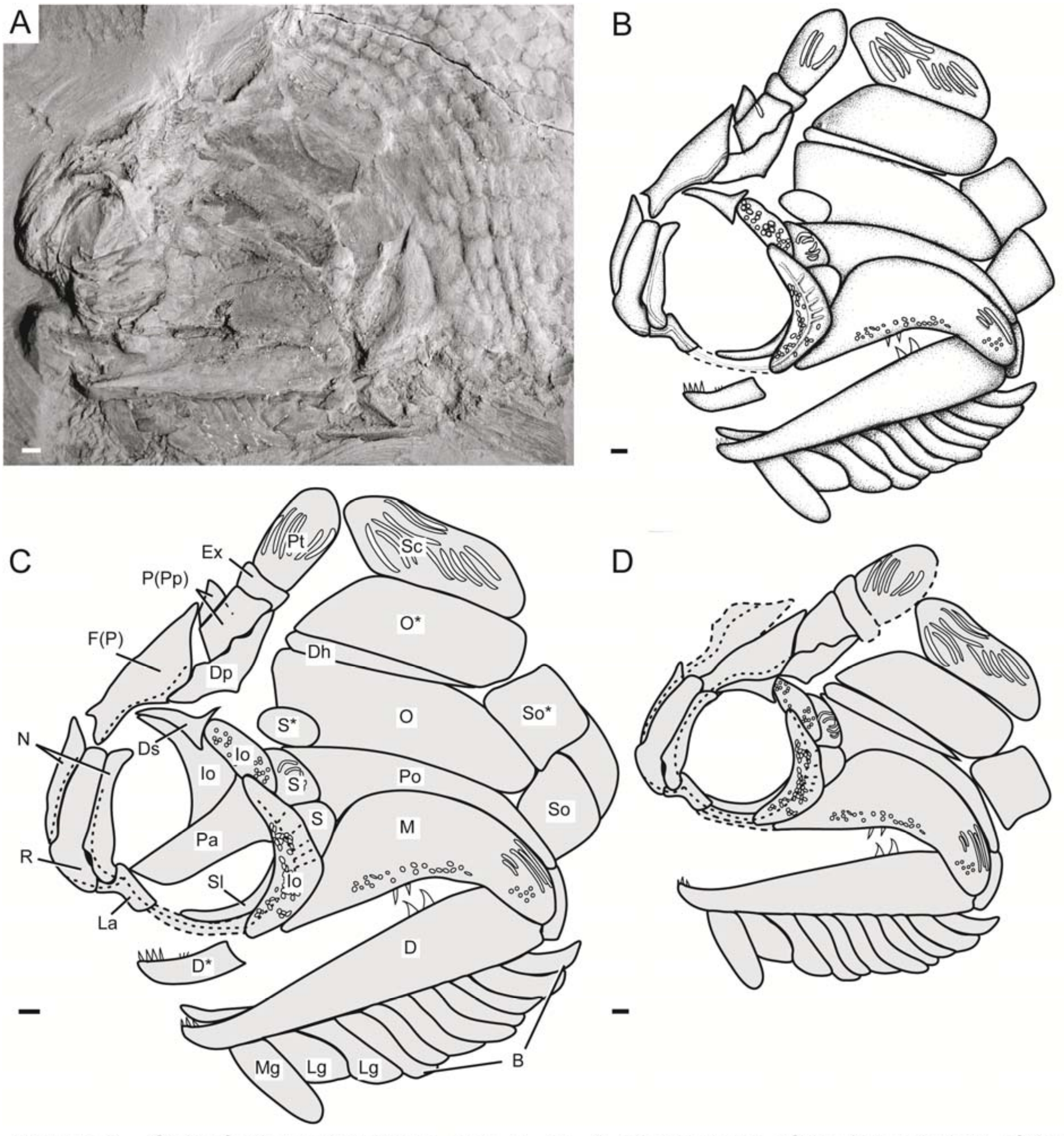


Figure 3—*Spinofacia pectinatus* n. gen. n. sp. **A,** photograph of the lateral view of the head of holotype KUVP 150475; **B, C,** illustrations of the head of holotype. **D**, reconstruction of the head of *Spinofacia pectinatus* in lateral view. **Abbreviations: B,** branchiostegal rays; **D,** dentary; **Dh,** dermohyal; **Dp,** dermopterotic; **Ds,** dermosphenotic; **Ec,** ethmoid commissure; **Ex,** extrascapula; **F(P),** frontal (parietal) bone; **Io,** infraorbital bone; **La,** lachrymal; **Lg,** lateral gular; **M,** maxilla; **Mg,** median gular; **N,** nasal bone; **O,** operculum; **Pa,** parasphenoid; **Po,** preoperculum; **P(Pp),** parietal (postparietal); **Pt,** posttemporal; **R,** rostral bone; **S,** suborbital bone; **Sc,** supracleithrum; **Sl**, sclerotic; **So,** suboperculum. Scale bars equal 1 mm. Dashed lines represent areas of ambiguity, dotted canal lines. Bones with * after abbreviation are bones visible from the right side.

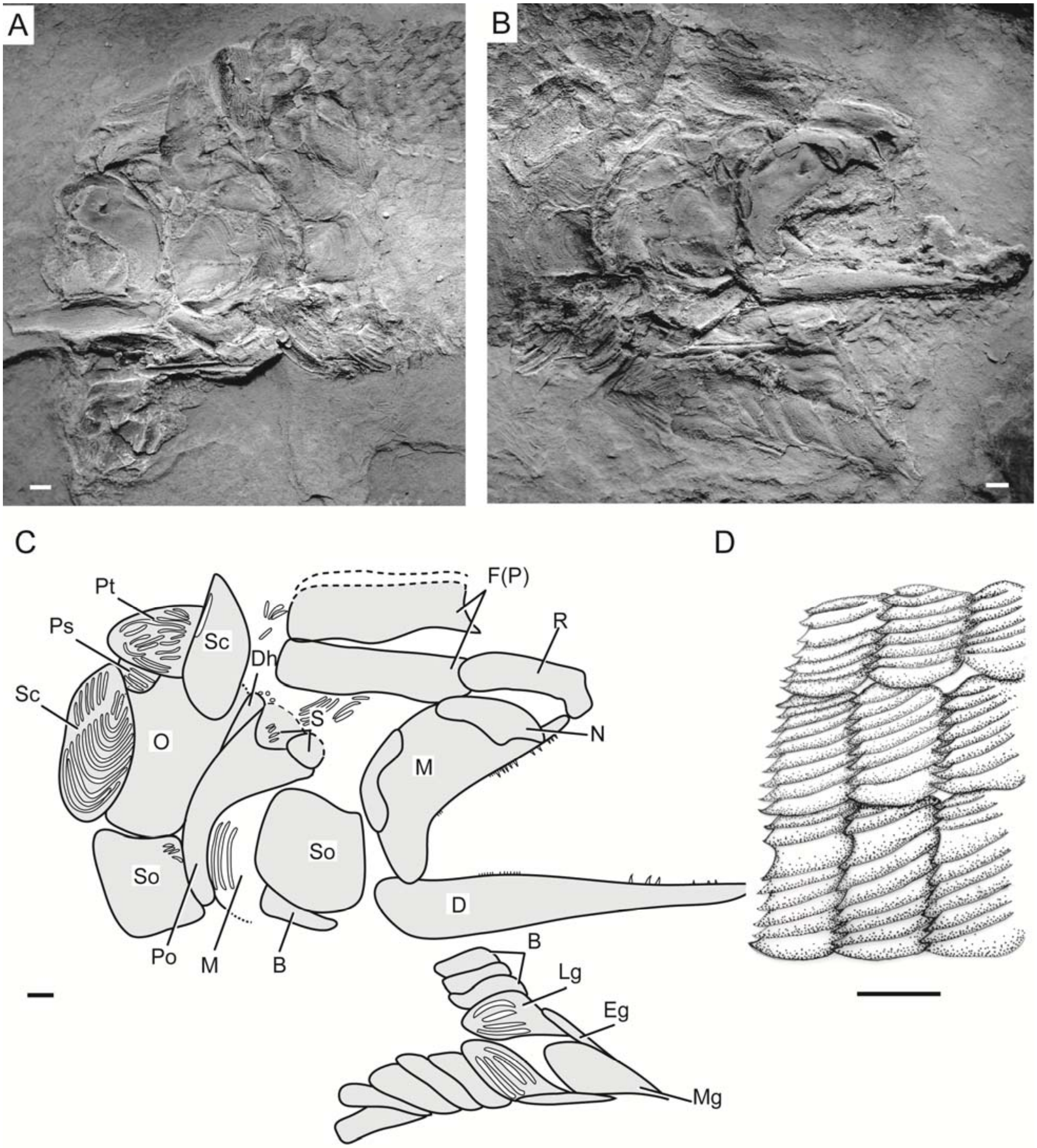


Figure 4—*Spinofacia pectinatus* n. gen. n. sp., referred specimen BYU M 5001a,b. **A,** photograph of BYU M 5001a, lateral view of the left side of head; **B,** photograph of BYU M 5001b, lateral view of right side of head; **C,** illustration based on BYU M 5001a,b; **D,** free field of anterior trunk scales of BYU M 5001b. **Abbreviations:** See Figure 3 and **Eg**, extralateral gular; **Ps,** presupracleithrum. Dotted lines represent areas of ambiguity. Scale bars equal 1 mm.

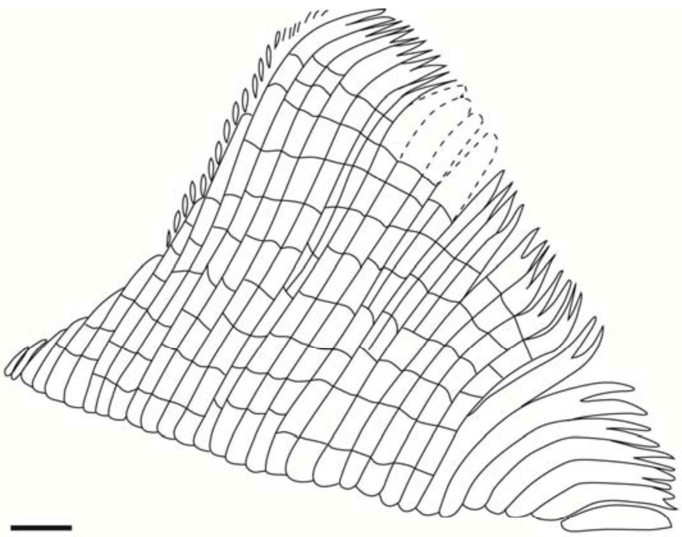


Figure 5—Dorsal fin of *Spinofacia pectinatus* n. gen. n. sp. from the holotype KUVP 150475. Scale bar equals 1 mm.

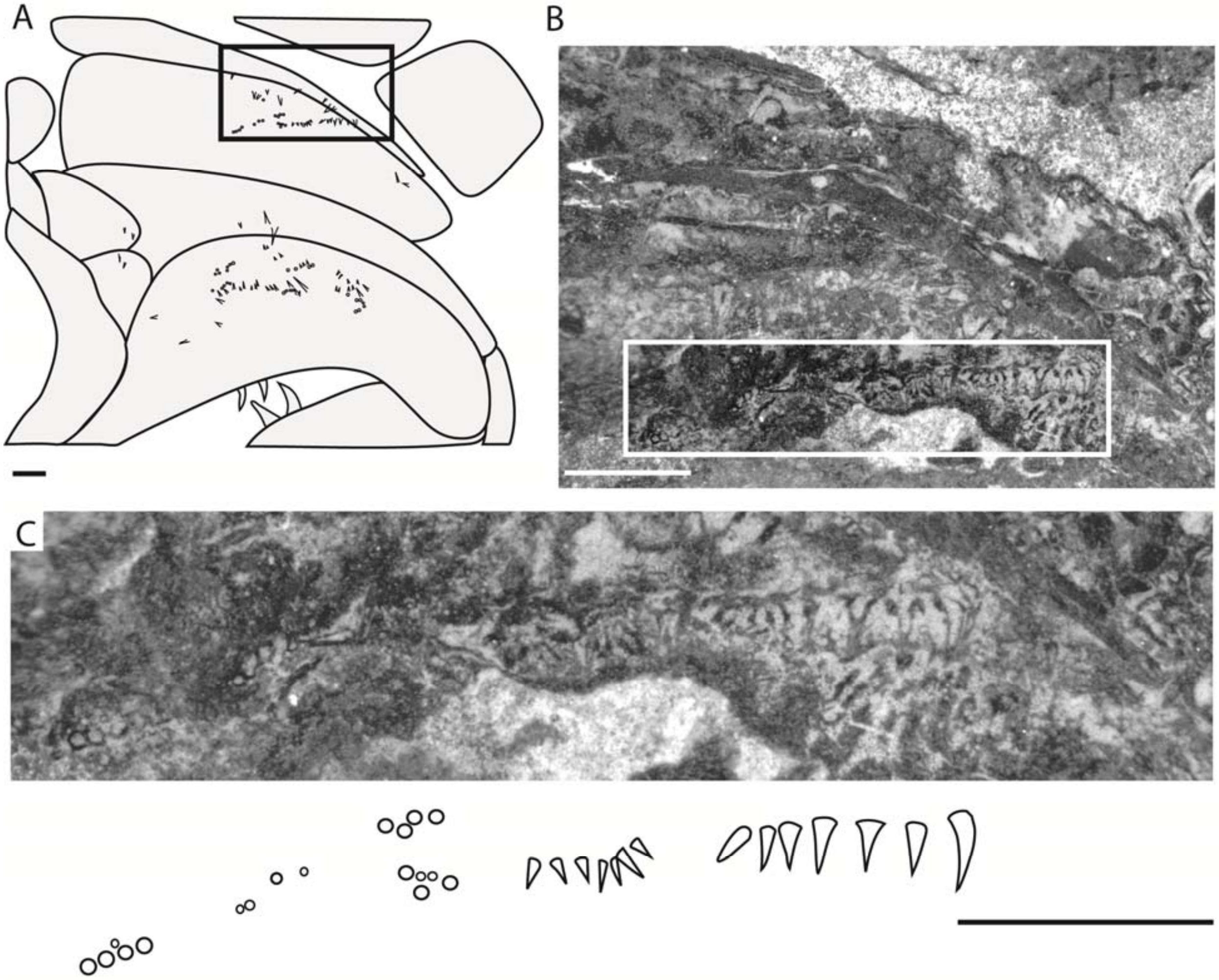


Figure 5—Dermal denticles on the holotype KUVP 150475 of *Spinofacia pectinatus* n. gen. n. sp. **A.** Illustration of denticles on cheek bones. **B.** Photograph of denticles found on operculum, photograph represents an enlarged view of the black box in **A. C.** Magnified photograph and illustration of denticles detailed in the white box in **B.** Scale bars equal 1 mm.

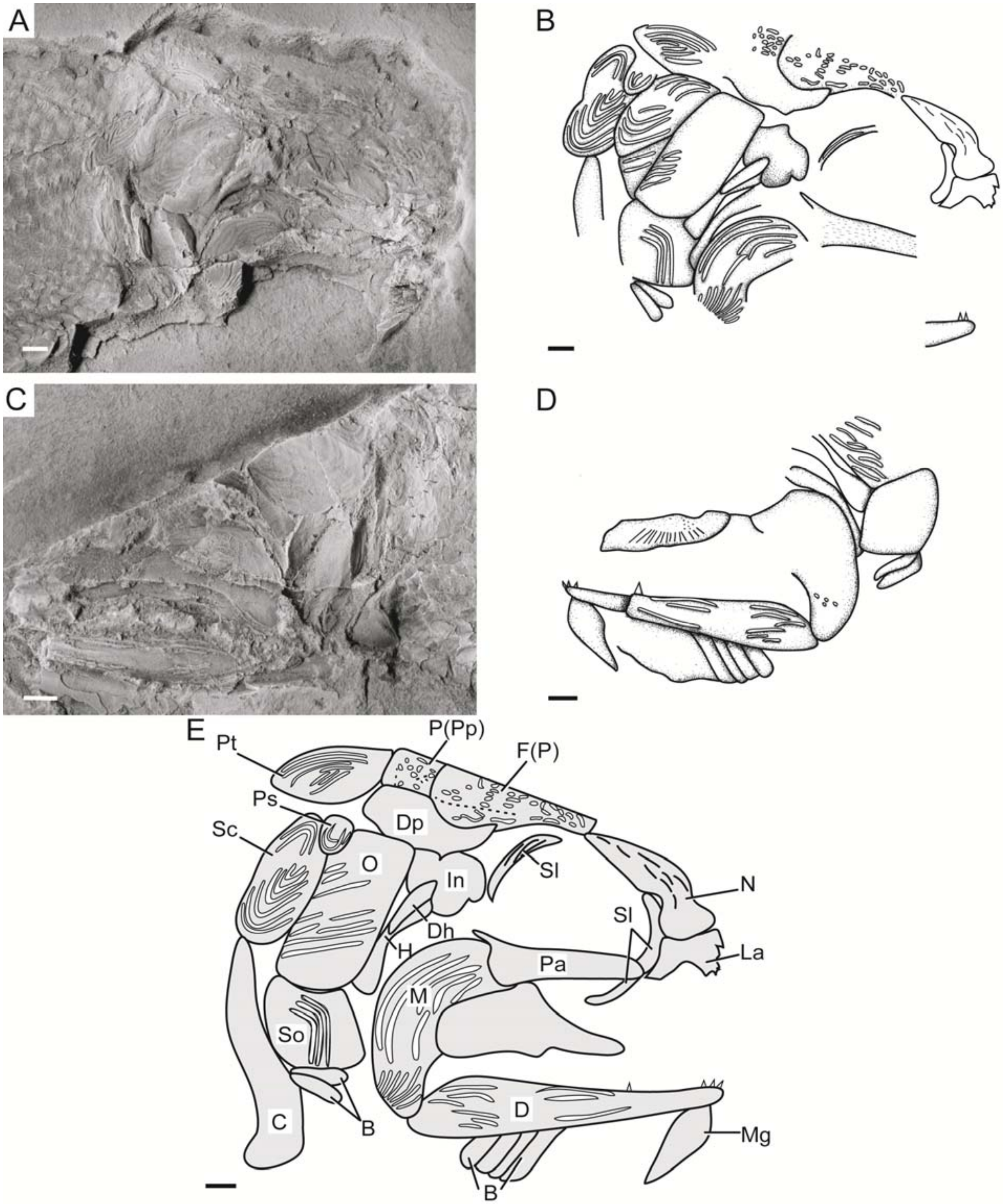


Figure 7—*Guntherichthys lehiensis* n. gen. n. sp. **A–E,** head of holotype KUVP 124570. **A, B,** lateral view of the right side of KUVP 124570a; **A,** photograph; **B,** illustration of A; **C, D**, lateral view of left side of KUVP 124570b; **C,** photograph; **D,** illustration of C; **E,** reconstruction of right lateral side of the head based on KUVP 124570a,b. **Abbreviations:** See Figures 3 and 4 and **C,** cleithrum; **In,** otic infilling; **H,** hyomandibula; **Sl,** sclerotic bone. Scale bars equal 1 mm.

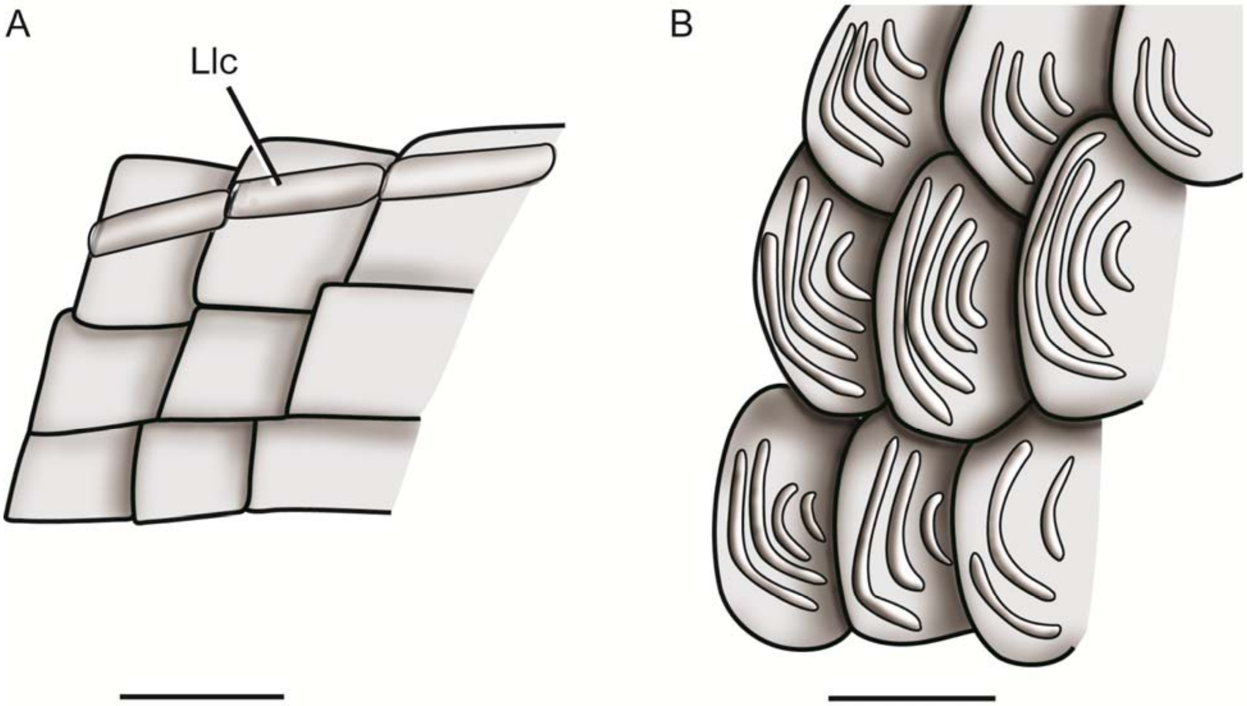


Figure 8—Illustrations of scales from *Guntherichthys lehiensis* n. gen. n. sp. holotype KUVP 124570a. **A,** rhombic scales located posterior to the dorsal fin; **B,** scales located posterior to the pectoral girdle that have rounded posterior, dorsal, and ventral margins. **Abbreviations: Llc,** lateral line canal. Scale bars equal 1 mm.

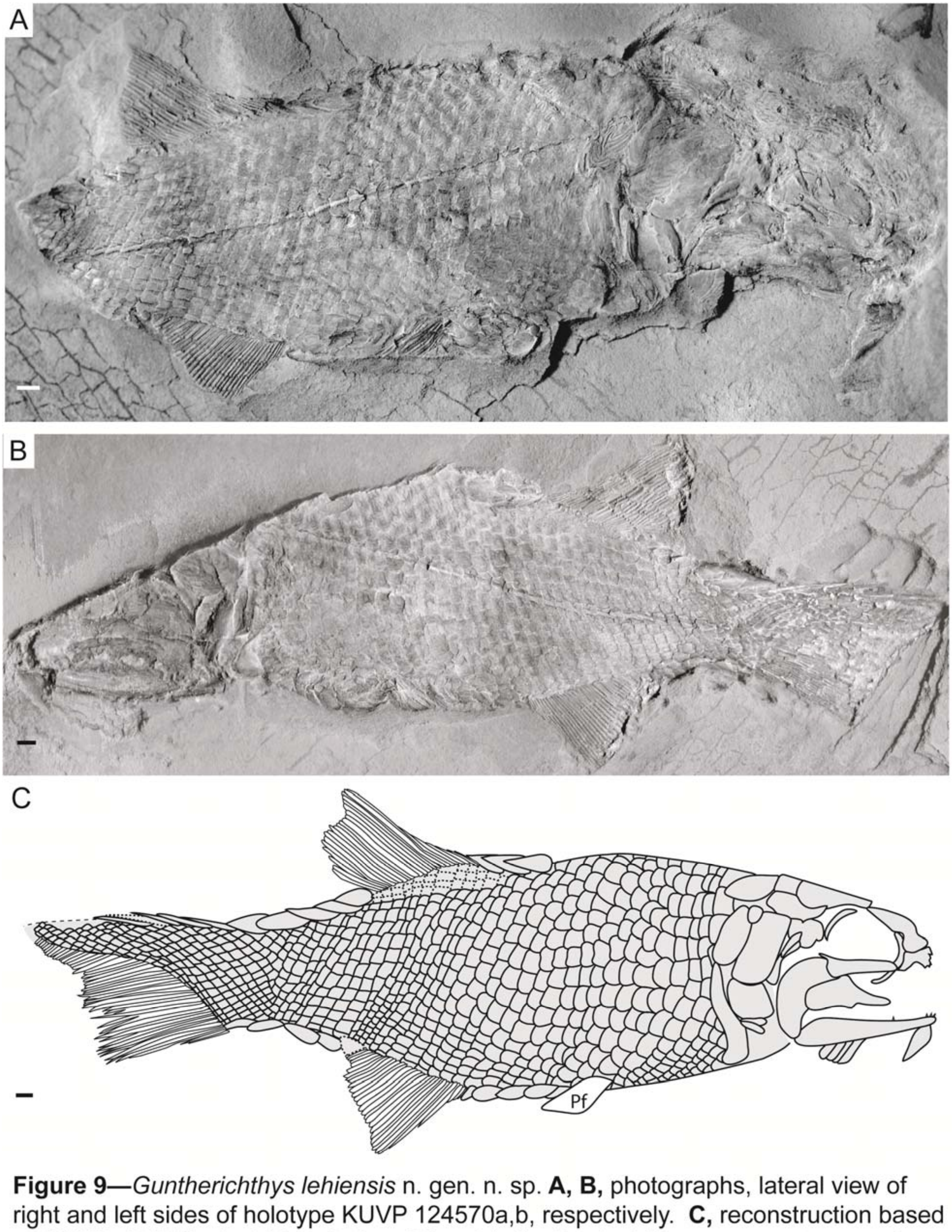


Figure 9—*Guntherichthys lehiensis* n. gen. n. sp. **A, B,** photographs, lateral view of right and left sides of holotype KUVP 124570a,b, respectively. **C,** reconstruction based on KUVP 124570a,b. **Abbreviation: Pf,** pelvic fin. Dashed lines represent areas of ambiguity. Scale bars equal 1 mm.

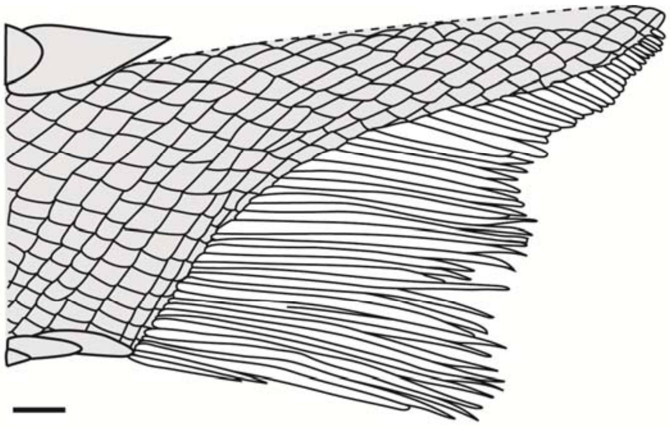


Figure 10—Caudal fin of *Guntherichthys lehiensis* based on holotype KUVP 124570b. Dashed line represents areas of ambiguity. Scale bar equals 1 mm.

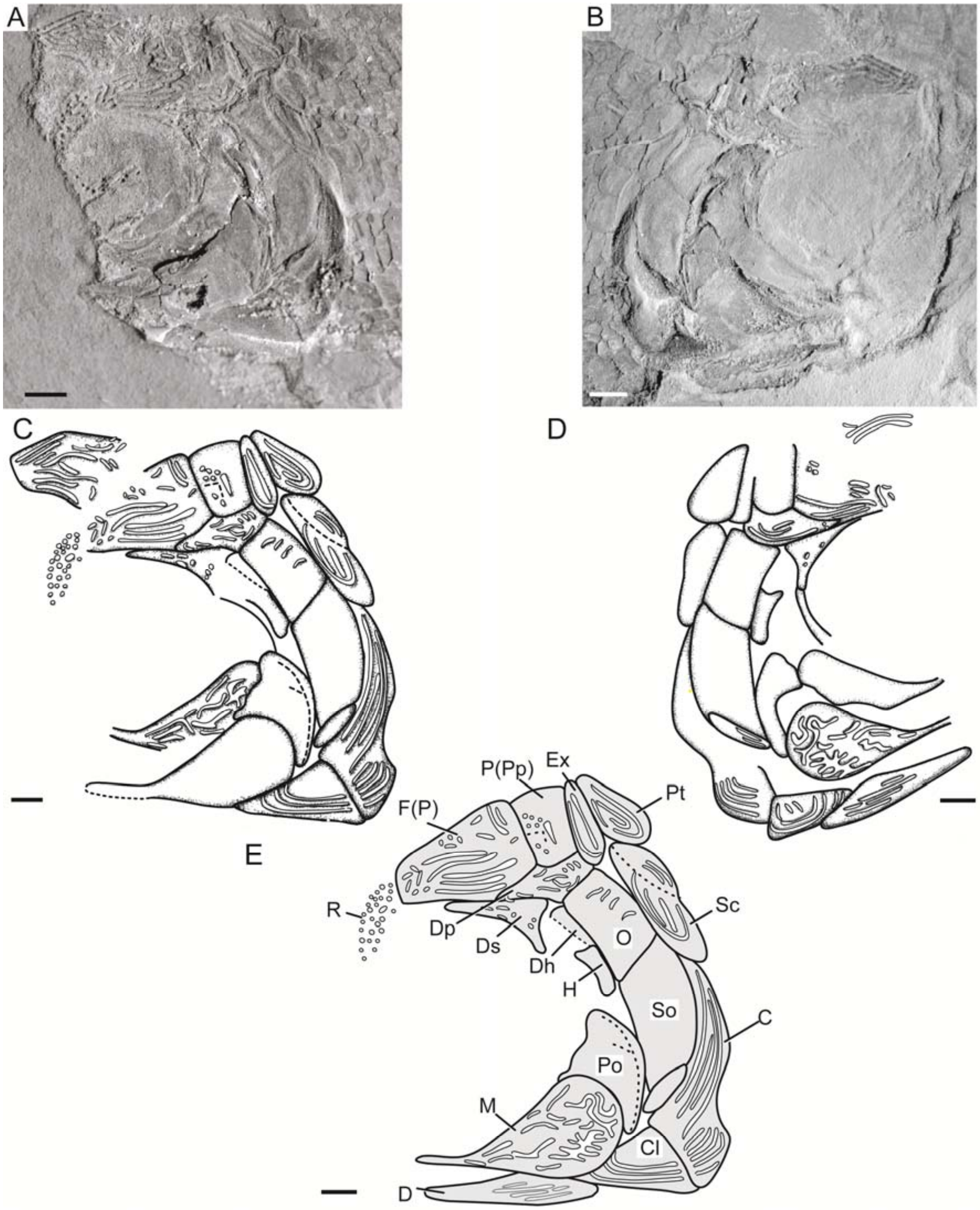


Figure 11—*Bourbonnella jocelynae* n. sp. **A, B** photographs, lateral view of left and right side of head of the holotype KUVP 150476a,b, respectively. **C, D,** illustrations of left and right side of head of KUVP 150476a,b; **E,** reconstruction based on KUVP 15076a,b. **Abbreviations:** See Figures 3, 4, and 6 and **Cl,** clavicle. Dashed lines represent areas of ambiguity; dotted, canal lines. Scale bars equal 1 mm.

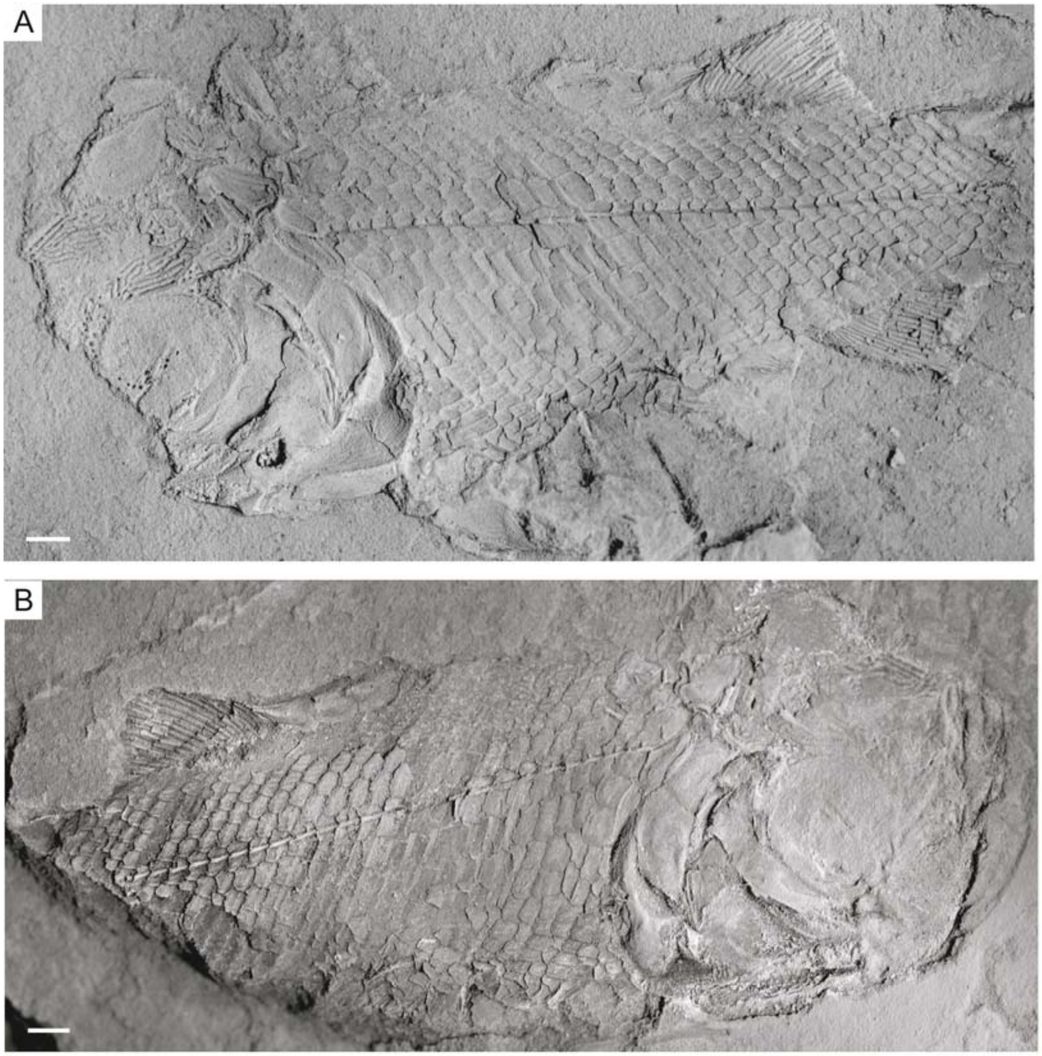


Figure 12—*Bourbonnella jocelynae* n. sp. **A, B** photographs of holotype KUVP 150476a, b, lateral view of the left and right side of the whole body, respectively. Scale bars equal 1 mm.

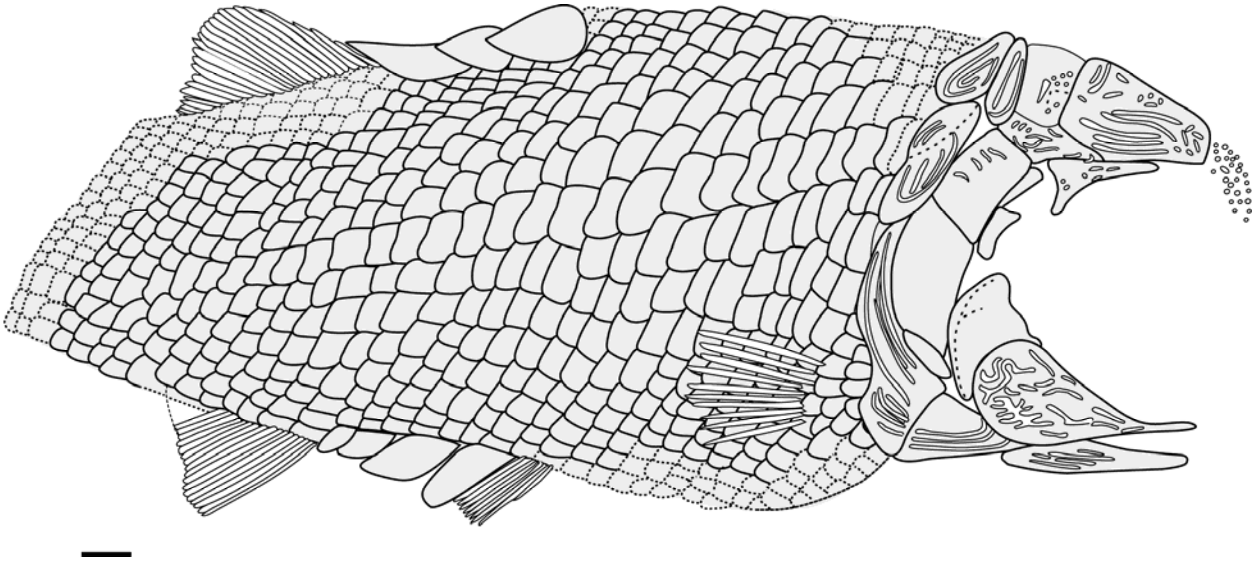


Figure 13—Reconstruction of *Bourbonnella jocelynae* based on holotype KUVP 150476ab. Scale bar equals 1 mm. Scales with dashed lines are reconstructions.

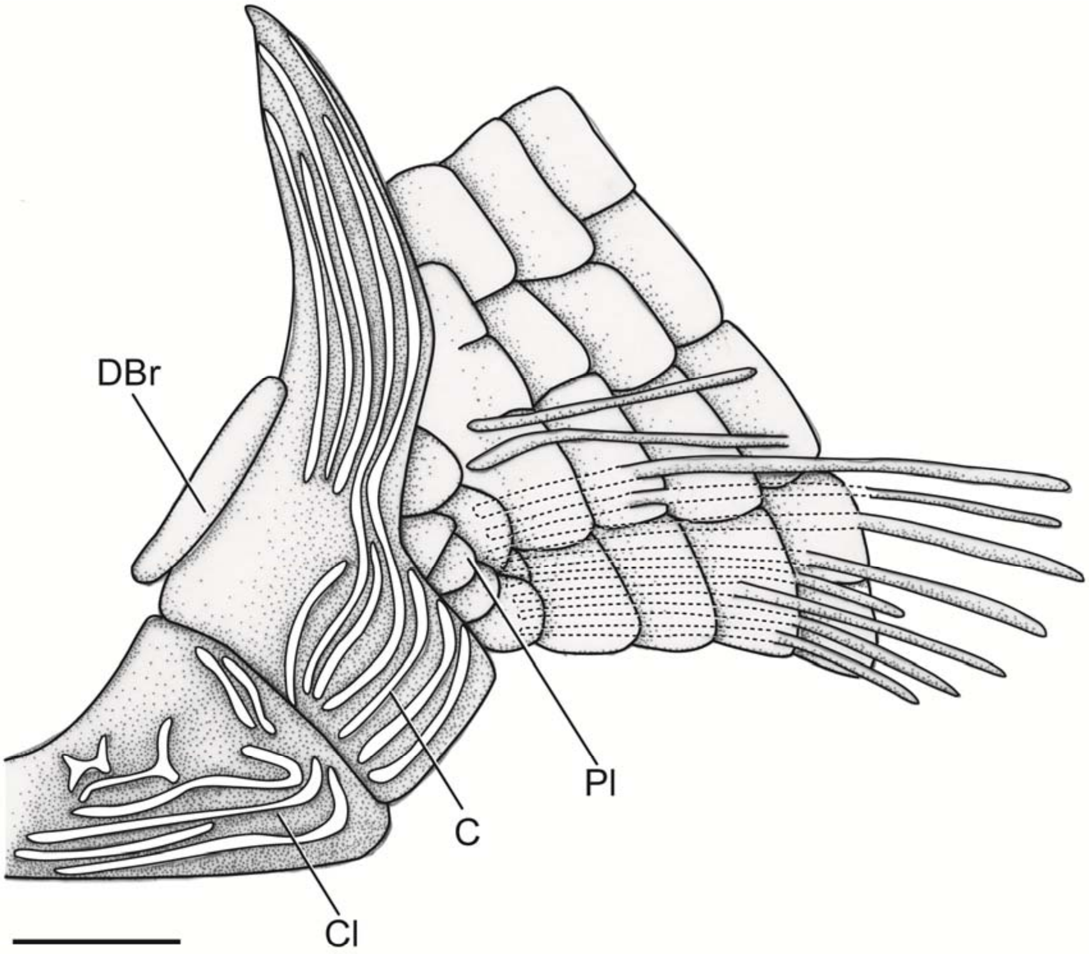


Figure 14—Pectoral girdle of *Bourbonnella jocelynae* n. sp. based on KUVP 150476a, highlighting the pectoral fin lobe and fin rays. Dashed lines are reconstructed fin rays. **Abbreviations:** See Figures. 6, 10, **Dbr,** displaced branchiostegal ray; and **Pl,** scaled pectoral lobe. Scale bar equals 1 mm.

CHAPTER FIVE—PALAEONISCOID FISHES FROM THE LOWER CARBONIFEROUS ALBERT SHALE FORMATION OF NEW BRUNSWICK, CANADA

INTRODUCTION

The term Albert Shales has been used informally to refer to the Albert Formation in southeastern New Brunswick, Canada (Greiner, 1962) (Figure 1). The Albert Formation is the middle formation of the Horton Group between the basal Memramcook Formation and the overlying Weldon Formation (Gussow, 1953; Greiner, 1962) (Figure 2). Greiner (1962) and Utting (1987) present the Albert Formation itself as being composed of three members—the Dawson Settlement, Frederick Brook, and Hiram Brook members (Figure 2). St. Peter (1993) presents the Albert Formation as being composed of six stacked lithofacies—conglomerate, sandstone, mudstone, mudstone/sandstone, kerogenous mudstone, and evaporate facies.

Since the 1800s, there has been controversy over the age of the Albert Formation. While an Early Carboniferous age was supported by the fossil fish and plants (Bailey and Ells, 1878; Lambe, 1909, 1910), some cautioned that the Albert Formation could be Devonian in age (Bailey et al., 1880; Ells, 1903). This trend continued into the late 1900's. Greiner (1962, 1974) had originally described the Albert Formation as Lower Carboniferous in age, but after the description of an osteolepid, "*Latvius porosus*," he considered the lower part of the Albert Formation to be Devonian (Greiner, 1977). Recent reassessments of the Albert Formation sarcopterygian material do not support Greiner's assignment of the material to the Devonian genus *Latvius,* but rather suggest megalichthyid and Carboniferous affinities (Miller and Brazeau, 2007). Today, based on spore analyses, the Albert Formation is considered to be Tournaisian

(Lower Carboniferous) in age, near the Devonian and Lower Carboniferous boundary (Utting, 1987; St. Peter, 1993; Miller and Brazeau, 2007).

Though known for its oil shales and veins of the solid hydrocarbon albertite, the Albert Formation is paleontologically famous for its countless articulated palaeoniscoid actinopterygian specimens (Greiner, 1977). This chapter concentrates on the palaeoniscoid lower actinopterygians from the Albert Formation. These fishes are important because they are Early Carboniferous in age, close to the boundary between the Devonian and Carboniferous. There is a higher diversity of actinopterygian fishes in the Carboniferous than the Devonian, both in terms of the number of species and morphologies. There also are morphological differences between Carboniferous and Devonian fishes. It would seem that Albert Formation actinopterygians may bridge morphological gaps between Devonian and Permo-Carboniferous forms. Unfortunately, these fishes have not been dealt with in any great detail for over a hundred years. Because of this, these fishes must be reinvestigated and compared to fishes that have since been described. The goals of this chapter are to review the taxonomic history of the described palaeoniscoids, present photographs and detailed illustrations of the previously described taxa, discuss obstacles faced when redescribing these forms, and to describe a new taxon actinopterygian from the Albert Formation.

PREVIOUSLY DESCRIBED PALAEONISCOIDS

Review of the Taxonomic History of the Albert Formation palaeoniscoids

The palaeoniscoid fishes from the Albert Formation of New Brunswick have been a taxonomic nightmare for over 150 years. Lambe (1909, 1910) provided a taxonomic history of these fishes in his redescription of some of the New Brunswick fishes. This information is updated and provided below.

In 1851, Jackson described the first palaeoniscoid fishes from the Albert Shales in papers titled "Report on the Albert Coal Mine" (1851a) and "Descriptions of five new species of fossil fishes" (1851b). Though the second title claims to include the descriptions of five new taxa, only three new species were described and named—*Palaeoniscus[m] alberti, P. brownii*, and *P. cairnsii.* Four additional specimens were described but never named. No type material was designated and though plates and figures are referenced in this publication, they were never included with the text.

Though Jackson's plates and figures were never published with the original descriptions, a few must have been distributed to leading paleontologists of the time because the plates were referenced by other scientists (see Traquair, 1877, p. 49; Dawson 1877, p. 338). In 1877, Dawson described two new palaeoniscoid species from the Albert Formation—*Palaeoniscus[m] modulus* and *Palaeoniscus[m] jacksonii.* Again, no type material was designated. Dawson (1877) also provided additional comments on Jackson's original species and referenced particular specimens figured by Jackson (1851).

In the late 1800s and early 1900s, many scientists commented on how the Albert Formation palaeoniscoids were more closely aligned with species within the genera *Rhadinichthys* and *Elonichthys.* Traquair (1877) commented that *Palaeoniscus[m] alberti* and *P. cairnsii* are closely allied to *Rhadinichthys carinatus* (Agassiz), a reassignment he upheld in 1911. Also in 1877, Traquair reassigned *Palaeoniscus[m] brownii* to *Elonichthys brownii.* Newberry (1889) followed Traquair's (1887) reassignments. In Woodward's catalogue (1891), *Palaeoniscus[m] alberti, P. cairnsii,* and *P. modulus* were reassigned to *Rhadinichthys alberti, R. cairnsii,* and *R. jacksoni* (1891). Woodward (1891) also reassigned *Palaeoniscus[m] brownii* to *Elonichthys brownii,* but also noted that he felt this was a "doubtful" and ill defined species

(Lambe, 1910). Eastman (1908) also reassigned the species to the genera *Rhadinichthys* and *Elonichthys.* In the same publication, Eastman described a new species from the Albert Shales—*Elonichthys elegantulus.* Again, no type specimen was designated. It must be noted that these reassignments were done without detailing the justifications of these reidentifications.

Sometime before 1909, Jackson's original unpublished plates were discovered by Eastman in the Yale Peabody Museum (Lambe, 1910). Using these plates, it was possible to identify Jackson's original type and figured specimens in the collections of the Museum of Comparative Zoology, Harvard, and the Boston Society of Natural History. With the discovery of these plates, Jackson's 1851 type specimens were identified. Using this new information, Lambe (1909, 1910) was able to redescribe the Albert Mine fishes and describe a new taxon, *Elonichthys ellsi*. Agreeing with Traquair (1877, 1911), Woodward (1891), and Newberry (1908), Lambe reassigned *Palaeoniscum alberti* to *Rhadinichthys alberti* and *P. brownii* to *Elonichthys brownii.* Lambe also determined *Palaeoniscum cairnsii* (Jackson) was not a valid species, nor was *Elonichthys* (*Palaeoniscum*) *jacksoni* (Dawson). Lambe (1909, 1910) also reassigned *Palaeoniscum modulus* (Dawson) to *Canobius modulus*. The validity of *Elonichthys elegantulus* Eastman, 1908 was called into question (Lambe, 1909, 1910).

Westoll in Moy-Thomas (1938) commented that *Canobius modulus* is just a curiously preserved specimen of *R. alberti*. Sternberg (1939) studied newly collected specimens from the Albert Formation that he assigned to *R. alberti.* Sternberg (1939) concluded that there were differences in measurements and ratios between the specimens designated as *R. alberti*, suggesting that either there is more than one species within this taxon, or the species is characterized by a great degree of variation. Gardiner commented on the Albert Formation fishes in his catalog of Canadian fossil fishes (1966). In 1997, Miller and McGovern published a preliminary report describing palaeoniscoids tentatively identified as *Elonichthys* from the Albert Shales in Norton, New Brunswick, Canada. This has been the last work that has investigated the actinopterygian fauna of the Albert Shale Formation.

In summary, a total of six species of palaeoniscoid fishes have been described from the Albert Shale Formation. Currently, there are three recognized species from the Albert Mines—*Rhadinichthys alberti* (Jackson, 1851), *Elonichthys brownii* (Jackson, 1851), and *Elonichthys ellsi* (Lambe, 1910). *Elonichthys elegantulus* (Eastman, 1908) and *Canobius modulus* (Dawson, 1877) have been considered questionable. Jackson's original taxa—*Rhadinichthys alberti, R. cairnsii,* and *Elonichthys brownii* are investigated here, as well as new material and new taxa. Some of these specimens have a long history of moving from one museum collection to another and have changed catalog numbers over the years. This makes identifying specimens mentioned in older literature difficult. Tables 1 and 2 detail the numerous identities of the original Jackson and Lambe specimens, respectively. The two questionable taxa from the Albert Formation—*Rhadinichthys elegantulus* (Gardiner 1966 states that the type is in MCZ, no number given) and *Canobius modulus* (Gardiner 1966 states that the type is in Redpath Museum, McGill University, no number given) have never had type specimens designated. The statuses of these taxa are examined here.

One problem encountered while working on the Albert Formation palaeoniscoids, is the fact that they have been described as belonging to genera that are all in need of revision. An additional problem involves the original descriptions themselves and the quality of the preservation of the type specimens. Both of these problems are discussed below.

Problem of generic assignment of the Albert Formation Palaeoniscoids

The majority of the fishes from the Albert Formation have been described as belonging to the genera *Palaeoniscum, Elonichthys,* or *Rhadinichthys*. This is problematic because these genera are poorly defined and paraphyletic. These problems are intensified by the fact that the type specimens of some of these genera are poorly preserved and uninformative. The specific problems with these genera are described below, as well as suggestions on how to deal with these problems.

***Palaeoniscum*—**

> "The genus *Palaeoniscus*[*m*] has been made to include an immense number of species, which are, indeed, referable to more than one generic type, some of them actually not being Palaeoniscidae at all. Authors have, in point of fact, been only too apt to refer nearly every small rhombic-scaled fusiform-shaped ganoid fish from Upper Palaeozoic rocks to *Palaeoniscus[m]*, without inquiring too narrowly into how far its structure agrees with that of the original type of the genus…" –Traquair, 1877, p. 557.

Originally described in 1818 by Blainville, the genus *Palaeoniscum* has been a problematic one. After Blainville's original description, Agassiz (1833) found no distinction between *Palaeoniscum* and another genus described by Blainville, *Paleothrissum*. Agassiz combined the two genera into a new genus, *Palaeoniscus,* keeping the same type species as Blainville (1818). Jordan (1917) regarded Agassiz's use of the term *Palaeoniscus* as a misspelling and called for the use of the name *Palaeoniscum* and authority going to Blainville (1818). It should be noted that de Blainville's original specific epithet was *Palaeoniscum freieslebenense* (Blainville, 1818), not the spelling that is used today, *Palaeoniscum freieslebeni.*

In 1857, Troschel recognized that Agassiz's *Palaeoniscum* could probably be divided into two different genera based on scale morphologies. After Agassiz, many species of *Palaeoniscus[m]* were described, though as Traquair (1877) pointed out, many of these species are dubious.

Traquair (1877) recognized the problem with the genus *Palaeoniscum* early on and made the above comments regarding the status of this genus. Traquair attempted to remedy the problem by restricting the species included in this genus to *Palaeoniscum freieslebeni, P. magnus, P. macropomus, P. elegans, P. comptus, P. longissimus,* and *P. macrophthalmus* (ibid.). Though a step towards constraining and defining just what constitutes *Palaeoniscum*, Traquair's diagnosis is problematic in that it provides a list of characteristics that are not diagnostic, not even when taken as a unit. The diagnosis of *Palaeoniscum* includes characters common to Paleozoic actinopterygians (fusiform body, jointed fin rays in the pectoral fin, small fulcra on pectoral fin, dorsal fin originates anterior to anal fin, oblique suspensorium, small conical teeth) and characters that are difficult to determine or compare amongst specimens ("fins of comparatively small size"). Even with restricting which species are included within *Palaeoniscum*, the genus is still in need of redescription. Woodward (1891) followed Traquair (1877) by restricting which species were included in the genus *Palaeoniscum.* While Traquair recognized the problem with *Palaeoniscum* early, his above statement still describes the situation today.

Rhadinichthys—The genus *Rhadinichthys* was erected by Traquair (1877) to house species that were once considered to belong to the genus *Palaeoniscum*. The type species of *Rhadinichthys*, *R. ornatissimus,* was originally described as a species of *Palaeoniscus* by Agassiz (1835). Traquair's original diagnosis of *Rhadinichthys* includes characteristics such as a slender body, very oblique suspensorium, dorsal fin originating almost opposite the anal fin, and the principal rays of the pectoral fin being unarticulated till towards their terminations (Traquair, 1877). Again, these characters are not diagnostic and quite general among palaeoniscoids.

After describing four species of *Rhadinichthys* from the Carboniferous of Glencartholm, Moy-Thomas and Bradley Dyne (1938) remarked that the genus could be divided into two different types—one with long thin bodies and small fins and the other with deeply fusiform bodies with large fins. They concluded that *Rhadinichthys* "requires complete revision" and that the forms that they discussed will be more accurately described after revisionary work was done (1938, p. 457). In 1945, Romer erected a family, the Rhadinichthyidae, for which *Rhadinichthys* is the type genus. This work was done without a reinvestigation of the genus as called for by Moy-Thomas and Bradley Dyne (1938).

Gardiner and Schaeffer (1989) attempted to divide lower actinopterygians into different groups. Different *Rhadinichthys* species are placed in different groups and the genus is placed in shutter quotes, suggesting that it is paraphyletic. For example, '*Rhadinichthys' canobiensis* is placed in the *Australichthys* group whereas '*Rhadinichthys' carinatus* is placed within the *Belichthys* group and the type species of *Rhadinichthys, R. ornatissimus,* is placed within the *Amblypterus* group (ibid.)

Lund and Poplin (1997) attempted to reappraise the Rhadinichthyidae and the genus, which gives this family its name, primarily based on newly described Bear Gulch fishes they placed within the Rhadinichthyidae. They recognized the following features as diagnostic of Rhadinichthyidae: prominent snout and subterminal mouth; two suborbital bones; operculum higher but narrower than suboperculum; triangular dorsal fin with an origin almost equal to that of the anal fin; deeply cleft and inequilobate caudal fin, fin rays distally bifurcated in all fins; reverse L-shaped 'antorbital' bone; rostropostrostral not contributing to the rim of the mouth, no premaxillae; absence of premaxillae results in a rostral notch below the rostropostrostral and between the 'antorbitals'; no supraorbital bones; an anamestic anocleithrum; elongated clavicles;

low ventrolateral abdominal scale rows (Lund and Poplin, 1997). While this was a step in the right direction, the redescription of *Rhadinichthys*, the type genus of the family Rhadinichthyidae, had not been done prior to Lund and Poplin's (1997) redescription of the Rhadinichthyidae. *Rhadinichthys* should be viewed as a paraphyletic genus and should be the focus of future revisionary work.

Elonichthys—The genus *Elonichthys* was described by Giebel in 1848. The type species of *Elonichthys*, *E. germari* is represented by a poor type specimen (Schultze and Bardack, 1987; Malabarba, 1988; Long, 1988b; Schindler, 1993). As pointed out by Schultze and Bardack (1987), the type specimen of *Elonichthys germari* does not allow for confirmation of generic designation. Malabarba (1988) also commented on the poor quality of the type species of this genus, and our poor understanding of the genus as a whole. Schindler (1993) described *Elonichthys* as being a "summary" genus that cannot be clearly defined.

Schultze and Bardack (1987) and Malabarba (1988) have both discussed the paraphyletic/polyphyletic nature of the genus *Elonichthys.* Long (1988, p. 39) cautioned that many Carboniferous species of *Elonichthys* have been erected on characters of "dubious phylogenetic value" and that the genus could be paraphyletic. Long (1988) also identified a further problem with this genus, primarily that many of the specimens assigned to this genus are too poorly preserved.

Gardiner and Schaeffer (1989) placed various species of *Elonichthys* in different groups and have shutter quotes around the genus name, suggesting they also thought that the genus was paraphyletic. Recognizing the problems with this genus, Schindler (1993) avoided phylogenetic discussion of *Elonichthys* and also placed the name in shutter quotes. A further problem with this genus is the fact that according to Malabarba (1988) and Gardiner (1988, cited as pers.

comm. in Malabarba, 1988) *Elonichthys serratus* is more similar to *Palaeoniscum freieslebeni* than to *Elonichthys germani*. Schindler mentioned an ongoing revision of the genus *Elonichthys* based on the original type material and new material from the type locality. This revision has not been completed and so our present understanding of this genus does not allow for much confidence when placing a species within this genus (Schindler, 1993). To date, our understanding of *Elonichthys* is that it is a paraphyletic, if not polyphyletic, genus represented by a poorly preserved type species.

Overall, *Palaeoniscum, Rhadinichthys,* and *Elonichthys* represent paraphyletic genera that are in need of revision. This revisionary work is beyond the scope of this study. Recognizing the problems with these genera, and the high likelihood that revisionary work may lead to the erection of multiple new genera, it has been decided to not place any new species from the Albert Formation or elsewhere within these genera. Species cannot be confidently assigned to these taxa because it is unclear what defines these genera to begin with. This also hinders redescriptions of the New Brunswick fishes, which have been moved from one poorly understood genus to another.

Previous descriptions of Albert Formation Palaeoniscoids

***Rhadinichthys alberti*—**Jackson's original description of *Palaeoniscum alberti* is based on the specimen figured in Plate I, Figure 1 (Jackson, 1851). This specimen was later identified as BSNH 7899, which was changed to catalog number MCZ 1960, and then MCZ 5082 (Table 1). Accordingly, the holotype is currently housed in the Museum of Comparative Zoology, Cambridge as MCZ 5082. The type specimen is illustrated in Figure 3A. Below is Jackson's original 1851 description:

> 'Fish, four diameters of its body long; head, obtuse or blunt, as if obliquely compressed on upper and front part; whole length, 3 3/10 inches, width, in middle

> of body 85/100 inch; fins, one dorsal, opposite anal, small triangular, 3/10ths of an inch at base, jointed, drooping as if the fish was dead before it was enclosed in the mud, (now shale). Anal, small, triangular, a little larger than dorsal; Pectoral, small, compressed into mass of scales of body of the fish; Tail, bifurcated, unequal, very long, and tapering in upper division, which extends to a fine point. The scales run down on upper division of tail, and become gradually smaller to tip; caudal rays come exclusively from under side of upper, and form lower division of tail. Scales of body brilliant, rhomboidal, wavy, serrated on posterior margins, colour light brown. This fish is embalmed and not petrified. No ridge of bone is seen to indicate the vertebral column, hence the bones must have been cartilaginous and compressible. The gill plates are too confusedly compressed to be dissected. I cannot find in any published book any figure of a fossil fish identical with this. It is evidently *Palaeoniscus[m],* and is probably a young individual, as seems to be indicated by its small size, and the delicacy of its scales. We will name it, provisionally, *Palaeoniscus[m] alberti,* in commemoration of its being the first fossil fish discovered in Albert County, in New Brunswick'

There are many problems with this original description. First, many of the features included in the description are common to palaeoniscoids (such as a single triangular dorsal fin and bifurcated caudal fin) and therefore uninformative. Other details, such as the color of the scales and absence of information on the gill plates or the vertebral column, do not add relevant information to the description.

Another problem deals with the holotype itself. As pointed out by Lambe (1909, 1910), MCZ 5082 is a poorly preserved specimen. Overall, there is no information about the skull. The holotype consists of a body with poorly preserved fins—pelvic fins are absent and the pectoral, dorsal, and anal fins are incomplete. Though the fulcra of the caudal fin are preserved, the caudal fin itself is highly fragmentary. Even the scales are poorly preserved—the posterior margins of the majority of the scales are broken and the ganoine ornamentation on these scales is hard to determine. The type specimen itself barely preserves any diagnostic characters (Figure 3A).

The reassignment of *Palaeoniscus[m] alberti* to *Rhadinichthys alberti* by Traquair (1877; 1911), Woodward (1891), Hay (1902), Eastman (1908) and Lambe (1909, 1910) was not justified or explained other than the statement that the specimens seemed to be closer aligned to

Rhadinichthys (Traquair, 1877). It is assumed that it is the placement of the dorsal and anal fins relative to each other that justified the movement of this species to *Rhadinichthys*. Lambe's redescription does provide more diagnostic characters, but, these characters are not based on what is preserved in the type specimen itself. Lambe (1909, 1910) does not identify the other specimens included in this species, nor did he detail which specimens preserve these new diagnostic characters. This reclassification also has problems. As discussed above, the question of what defines the genus *Palaeoniscum* is a valid one; as is the question of what defines the genus *Rhadinichthys.*

In the redescription of *R. alberti,* Lambe (1909, 1910) concluded that there were no differences between *R. alberti* and *R. cairnsii.* Jackson (1851) had identified differences in the ganoine ornamentation on the scales that distinguish *R. alberti* from *R. carnsii.* Lambe (1909, 1910) said these differences did not exist and so *R. carnsii* was dismantled and the specimens originally described in this species were placed into *R. alberti.* The type specimen of *R. carnsii* is more complete than the type specimen of *R. alberti.* The type of *R. carnsii* preserves cranial information, including a tuberculated snout. Using information from the type specimen of *R. carnsii* to redescribe the taxon *R. alberti* is problematic, especially when the character that is supposed to join the two taxa, ganoine ornamentation, is so unclear and poorly preserved in the type of *R. alberti.*

Gardiner (1966) stated that *Rhadinichthys alberti* may belong to the genus *Rhadinoniscus* White because of features of the branchiostegal rays. This statement is problematic because the type specimen of *R. alberti* does not preserve any clear information about the branchiostegal rays. Gardiner (1966) also agreed with Lambe (1909, 1910) that *R. elegantulus* may be a juvenile of *R. alberti*.

Rhadinichthys cairnsii**—**Jackson's original type for *R. cairnsii* is illustrated in Figure 3B based on MCZ 5084. Below is Jackson's original 1851 description of *P. cairnsii*, which was later reassigned to the genus *Rhadinichthys.*

> 'Fish, long and slender, 4 ½ diameters of its body long, length of head, a little less than the largest diameter of the body; the head has the shape of an equilateral spherical triangle; tip of nose, or snout curiously tuberculated and dotted; gill plates cannot be dissected, they are so brittle and confused with the head; fins, pectoral a little behind gill plates, and extend below the fish 3-10ths of an inch—it is a narrow-pointed fin, well marked with its rays, Dorsal fin far back towards the tail, a little anterior to anal; it is half an inch long and 2-10ths of an inch high, and is well marked with its rays. Anal fin somewhat larger than dorsal, a little posterior to it. Abdominal fin very small, situate a very little in advance of the middle of the body; tail unequally bifurcated or heterocercal; scales run down on it becoming smaller and more and more acutely rhomboidal or lozenge shaped as they recede; caudal rays come exclusively from under side of upper division of tail. Scales obtusely rhomboidal on anterior and middle of body, and are distinctly striated parallel to anterior and lower margins, while they are smooth and very brilliant towards and upon the tail; dorsal scales large and in form of obtuse spherical triangles pointing backwards towards the dorsal fin. This species is not described in any book I have examined, and believing it to be new, I shall take the liberty of naming it *Palaeoniscus[m] cairnsii…..*'

The distinction between *P. cairnsii* and *P. alberti* were attributed to differences in the ganoine ornamentation of the flank scales, with the scales of *P. cairnsii* being described as having striae running parallel to the anterior and lower margins of the scales (Jackson, 1851). Though the scales are not well preserved in the type of *R. alberti*, Lambe determined that the same striation pattern existed in *R. alberti* and *R. cairnsii,* and so *R. cairnsii* was not a distinct and separate species. Lambe included the former type specimen of *R. cairnsii* in *R. alberti* (1909, 1910). The problems with this have been discussed above.

Elonichthys brownii**—**The type specimen of *E. brownii* is illustrated in Figure 3C. Jackson's (1851) original description is provided below:

> 'Fish nearly whole. It is one of the largest species yet found, and its length is three times the greatest width of its body; whole length 5 3/10 inches; breadth, 1 7/10 inches; head broken off just in front of pectoral fin; extremity of tail broke;

> abdominal fin missing, it having been broken in getting out the specimen. Dorsal fin, a little behind middle of body, opposite, or rather a little in front of anal.'

Though the type specimen of *E. brownii* is incomplete, the fins and scales are well preserved, making description of this fish possible (Figure 3C). The Albert Formation specimens were most likely placed within this genus by Traquair (1877) on the basis of the large size of the fins in comparison to the other Albert Formation specimens that were placed within the genus *Rhadinichthys.* As mentioned above, there is a large problem with this assignment to *Elonichthys* because of our understanding of what this genus represents.

The type specimen of *Palaeoniscum jacksonii* (Dawson) could not be located, but based on Jackson's figure 4, plate 1, which illustrates the type of *P. jacksonii,* Lambe (1909, 1910) determined it to be the same as *Elonichthys brownii.*

***Elonichthys ellsi*—**Lambe (1909, 1910) described a new species from the Albert Shales based on the type and only specimen, CMN 4379. Lambe (1909, 1910) describes a unique pattern of ganoine on the anterior flank scales that defines this species. The anterior flank scales bear ridges of ganoine that "have the appearance of rows of connected tubercles" (Lambe, 1909, pg. 171). Again, its placement within *Elonichthys* is dubious, but the ganoine ornamentation makes it clear that this specimen is unique and different from the other previously described Albert Mine fishes. This pattern of ganoine ornamentation has not been seen in any other specimen.

Elonichthys (Rhadinichthys) elegantulus—The most abundant fish from the Albert Shales is represented by small fusiform fishes that preserve much information regarding the scales, but not much regarding the head (Lambe, 1910). These fishes were originally described by Eastman in 1908 as *Elonichthys elegantulus* with the following description:

> "may be readily distinguished by its small size, slender and graceful proportions, and decidedly prominent, even coarse details of scale ornament. The scales are traversed longitudinally by a number of closely crowded raised ridges, smooth, continuous, glistening, and the whole presenting an appearance not distantly recalling *Ptycholepis*, from a much later horizon. In addition, the lateral line is very conspicuous. The head and fin structures are not clearly revealed in any individual that has thus far come to light…"

On reexamination, Lambe (1909, 1910) found the description of this fish problematic. Lambe proposed that these small and abundant specimens represent the young of one of the taxa represented by the larger specimens. Lambe (1910) concluded this on the basis of its small size and imperfect preservation, especially in regard to the head. Lambe proposed that these specimens were more similar to the body shape of *Rhadinichthys alberti* than *Canobius modulus* and warned that these specimens may be juvenile *Rhadinichthys* (Lambe, 1909, 1910), a statement Gardiner (1966) supported. This species was later listed as *Rhadinichthys elegantulus* by Hay (1929) and Gardiner (1966).

Also problematic is the lack of type material for this species. Though there are countless small fishes with well preserved scales, prominent lateral lines, and poorly preserved heads, we do not know which specimen Eastman used in his description. In the description of *E. elegantulus*, Eastman refers to an "extensive suite of material from the Lower Carboniferous of Albert County" as well as Jackson's original descriptions, but no specific specimens are mentioned (1908, pg. 274). There are no illustrations of *E. elegantulus* figured, therefore, we cannot determine which small fish specimens were studied by Eastman or which is the holotype. Gardiner (1966) mentions that the type specimen is in the Museum of Comparative Zoology, Harvard, but does not give a specimen number.

***Canobius modulus*—**Originally described by Dawson (1877, 1878) as *Palaeoniscus (Rhadinichthys) modulus,* this species is figured by Dawson in 1877 as Figure 1 and 1878 as

Figure 18. Dawson (1877) stated that the specimen figured in Jackson's Plate II, Figure 5 "probably belongs" to this species (p. 338). Important characters noted by Dawson include ten large oval dorsal ridge scales with serrated posterior margins between the head and the dorsal fin,

Woodward (1891) and Eastman (1908) reassigned *Palaeoniscum modulus* to *Rhadinichthys modulus* because of the reassignment of the other Albert Formation palaeoniscoids to the genus *Rhadinichthys.* Eastman (1908) stated that Dawson's original description is a composite based upon two individuals preserved on the same slab of shale. One of the specimens is incomplete and poorly preserved in comparison to the second specimen on the same rock. The more complete specimen is figured by Dawson (1878), but this specimen does not preserve the dorsal ridge scales that are illustrated and described in the description. The information on the dorsal ridge scales comes from the more incomplete second specimen. Eastman (1908) provided a photograph of two specimens on a single slab of shale and described them as cotypes of *Canobius modulus.* Eastman (1908) also mentioned that this specimen is housed in the Peter Redpath Museum of McGill University. Attempts to locate this specimen have so far failed.

Lambe (1909, 1910) redescribed this species as *Canobius modulus.* He placed the species in the genus *Canobius* on the basis of the near vertical suspensorium, blunt snout, and dorsal ridge scales complete to the occiput that are seen in *Canobius* but not in *Rhadinichthys.* Three specimens from the Redpath Museum were examined by Lambe. Westoll (in Moy-Thomas, 1938) remarked that *Canobius modulus* may be *R. alberti.* Gardiner (1966) agreed with Westoll and stated that *C. modulus* is considered to be a "peculiarly preserved specimen of *Rhadinichthys alberti*" and then synonymized the two taxa (1966, p. 61). While Eastman, Lambe, and Gardiner agree that the type specimen of *C. modulus* is in the Redpath Museum, McGill University, there is no record of a specimen number.

Concluding remarks on redescriptions of the Albert Formation palaeoniscoids

Six species have been described from the Albert Formation, but the validity of the majority of these species has been questioned. The type specimens are either unknown, or poorly preserved. On top of this, the Albert Formation palaeoniscoids have been assigned to genera that are poorly understood, represented by poor type material, and are known to be paraphyletic. Even more problematic is how every described species has been moved from one poorly described genus to another without much justification. What we are left with is a situation where the palaeoniscoids from the Albert Shale Formation cannot be redescribed at this time.

I examined hundreds of Albert Formation palaeoniscoids at the Museum of Comparative Zoology, Harvard; Yale Peabody Museum; Canadian Museum of Nature, Ottawa, Canada; and the New Brunswick Natural History Museum, St. John, Canada. Some of these specimens are well preserved and have been previously placed within *Rhadinichthys alberti, Elonichthys brownii,* or even *Rhadinichthys cairnsii.* The problem with this is that these better preserved specimens show features that are not visible in the type specimens of the species they have been assigned to. Compounding the problem is that the features they do preserve that are absent in the type specimen of the species have been used in redescriptions of the taxa. When faced with this, I sat down to look at the descriptions of the type specimens of the genera they have been placed within and moved from. It became clear that I could not confidently determine whether these forms were species within *Rhadinichthys, Palaeoniscum,* or *Elonichthys.* Currently, it is impossible to determine if any of the Albert Shale Formation actinopterygians belong to any of these genera because it is impossible to determine what defines these genera.

Problems with the paraphyly of *Rhadinichthys, Elonichthys,* and *Palaeoniscum* have far reaching effects beyond our understanding of the palaeoniscoids from the Albert Formation of New Brunswick, Canada. Our understanding of the systematics of lower actinopterygians in general is also impaired. Multiple species have been placed within these genera, meaning we do not understand a large portion of the lower actinopterygian diversity. Also, though many species have been described as belonging to *Rhadinichthys, Elonichthys,* and *Palaeoniscum,* investigations into the relationships of lower actinopterygian fishes may include one representative species from each genus, if any. By including only one taxon from a genus known to be paraphyletic excludes a large amount of diversity and impedes recognizing problems with these genera. Future work on lower actinopterygians will necessitate redescriptions of *Rhadinichthys, Elonichthys,* and *Palaeoniscum.* Until such work is done, we do not understand a large portion of the Carboniferous and Permian actinopterygian diversity.

Problems with these genera have been known since the late 1800's. A concerted effort must be made to address the problems with *Rhadinichthys, Elonichthys,* and *Palaeoniscum.* Problems with the condition of the type specimens may necessitate that the types are the type and only specimen of each genus. The other species placed within *Rhadinichthys, Elonichthys,* and *Palaeoniscum* may then have to be reevaluated and placed in new genera that can be described on the basis of informative type species. This may be the only prudent way to deal with large cosmopolitan genera described on the basis of uninformative type species. Such an undertaking is beyond the scope of this study, but must be done in the near future.

Though the fishes from the Albert Formation subscribed to the genera *Rhadinichthys, Elonichthys,* or *Palaeoniscum* cannot be commented on further here, one specimen can. While examining specimens of palaeoniscoids from the Albert Formation, specimens which represent forms quite different from the type specimens of the previously described fishes were uncovered. These specimens are well preserved and can be differentiated from the previously described taxa, regardless of the condition of those type specimens. One specimen, which constitutes a new taxon from the Albert Formation, is described below.

DESCRIPTION OF A NEW GENUS AND SPECIES FROM THE ALBERT FORMATION

Materials and Methods

The new taxon is represented by a single specimen from the Yale Peabody Museum (YPM). The fossil specimen and its latex peel were examined by steromicroscopy. The latex peel allowed for three dimensional views of the specimen preserved as a negative impression. The fossil and peel were examined side by side. Photographs were taken with a Canon XSi digital camera equipped with a macro lens. Illustrations were prepared using a camera lucida and digital illustrations were prepared using Adobe Photoshop and Illustrator programs. This specimen was included in phylogenetic analyses presented in Chapter 6 to determine if it constituted a new taxon and its affinities.

Nomenclature—Two naming conventions have been used in reference to the two paired bones in the skull roof of actinopterygians—frontal and parietal or parietal and postparietal. The first set of names is based on tradition, whereas the second is based on homology (Jollie, 1962; Schultze, 2008; Wiley, 2008). For further discussion on the problems the traditional naming convention pose, especially to phylogenetic analyses, see Schultze, 2008 and Wiley, 2008. Though it is recognized that the second convention of parietal and postparietal is based on homology, we are left with a literature that uses both schemes. In order to prevent confusion when comparing newly described fishes to previously described fishes, both names are given here. The paired skull roofing bones are referred to as the frontal (parietal) bone and the parietal (postparietal) bone. The use of both names is a convention previously used by Arratia and Herzog (2007), Mickle and Bader (2009), and Mickle (2011) among others.

Bones are identified as the dermosphenotic(s) and dermopterotic following the criteria of Poplin (2004). See Chapter 6 for more discussion of these bones. The bone in the anteroventral corner of the orbit is identified as the lachrymal rather than an antorbital following the rationale of Schultze (2006). To clarify, this bone has also been identified as the first infraorbital in the literature.

Anatomical Abbreviations—Aop, accessory opercular bone; **Bsi,** inserted body scales; **D,** dentary; **Df,** dorsal fin; **Dh,** dermohyal; **Dpt,** dermopterotic; **Drs,** dorsal ridge scales; **Dsp,** dermosphotic bone; **Ex,** extrascapular; **F/P,** frontal/parietal bone; **Io,** infraorbital bone; **MDR,** median dorsal rostral bone; **Mg,** median gular; **N,** nasal bone; **La,** lachrymal; **Lg,** lateral gular; **Op,** operculum; **Pop,** preoperculum; **P/Pp,** parietal/postparietal bone; **Ps,** presupracleithrum; **Pt,** posttemporal bone; **Sc,** sclerotic bone; **Scl,** supracleithrum; **So,** suborbital bone; **Sop,** suboperculum; **Sup**, supraorbital bone; **VR-Pmx,** ventral rostro-premaxillary bone;

Institutional Abbreviations—YPM, Yale Peabody Museum, Yale University, New Haven, Connecticut;

SYSTEMATIC PALEONTOLOGY

Class Osteichthyes Huxley, 1880

Subclass Actinopterygii Cope, 1871

Family incertae sedis

Genus “New Brunswick Fish” n. gen.

Diagnosis—As for the type and only species

Type and Only Species—“New Brunswick Fish” n. sp.

Etymology—A name will not be given to this new genus until it is published in a scientific journal. Until then, it is referred to with the code name “New Brunswick Fish”, or the catalog number of the type and only specimen, YPM 8664.

“New Brunswick Fish” n. gen. n. sp.

(Figs. 4–10)

Etymology—A specific epithet will not be given until this taxon is published in a scientific journal.

Diagnosis—Based on the unique combination of characters: large edentulous tuberculated ventral rostro-premaxilla; median dorsal rostral bone; maxilla with broad postorbital plate; complex ganoine ornamentation on maxilla; nasal bones with ganoine ornamentation of tubercles and short ridges ventrally, longer diagonally oriented ridges midbone; single rectangular shaped supraorbital bone; numerous suborbital bones; dermopterotic as long as the frontal/parietal plus parietal/post-parietal bone; presupracleithrum; dermohyal; series of accessory opercular bones; 12 branchiostegal rays; two lateral gular plates; six dorsal ridge scales beginning at scale row 20; first three dorsal ridge scales with pectinated posterior margins; dorsal ridge scales occupy the space of two body scale rows; body scales rows intermittently inserted between adjacent dorsal ridge scales; anal fin almost opposite dorsal fin; dorsal and anal fins posteriorly placed on the body; body depth dramatically decreases posterior to dorsal fin; large pectoral and pelvic fins; body scales with pectinated posterior margins and horizontal ganoine ridges; ventrally placed scales from scale row five to the end of pelvic fin have pectinated posterior and ventral margins.

Holotype and only specimen—YPM 8664 (Figures 4–10)

Locality—Lower Carboniferous Albert Formation, New Brunswick, Canada.

Description

Specimen—The holotype YPM 8664 preserves the anterior 2/3 of a rather large fish in lateral view (Figure 4). The counterpart is missing. The caudal fin and peduncle are not preserved. Though the dorsal fin is missing its distal portion, the proximal portion along the body is preserved and appears to be complete. The pectoral, pelvic, and anal fins are large and spectacularly preserved (Figure 4). Though the specimen is not complete, it is large with a length of 19.5 cm, minus the caudal peduncle and fin. It is interesting to note that this large fish is preserved on a slab with the remains of three other smaller palaeoniscoids.

Snout—The snout is prominent and heavily tuberculated. A median dorsal rostral bone forms the anterior-most portion of the snout (Figures 5–6) The posterior margin of the median rostral bone contacts the frontal/parietal bone whereas the ventral margin contacts the ventral rostro-premaxilla (Figures 5–6). The lateral margin of the median dorsal rostral bone is notched. This notch forms the median margin of the anterior narial opening. The median dorsal rostral bone bears tubercles ventrally and short ridges of ganoine dorsally. These ridges are longitudinal to diagonal in orientation (Figures 5–6).

A large nasal bone lies lateral to the median dorsal rostral bone and anterior to the orbit (Figures 5–6). The anterior margin of the nasal bone is notched. This notch forms the medial margin of the posterior narial opening. The posterior border of the nasal bone is also notched in two different locations. The ventral-most notch on the posterior margin forms the anterior margin of the lateral narial opening. Dorsal to this notch, there is a bump that extends off the posterior margin. Dorsal to this bump is the second notch on the posterior margin of the nasal bone for the supraorbital bone (Figures 5–6). The nasal bone bears a complex pattern of ganoine. Unlike many other Carboniferous palaeoniscoids that bear long vertical ridges of ganoine, YPM 8664 has a nasal bone with tubercles and short ridges ventrally, and longer diagonally oriented ridges at midbone (Figures 5–6).

One of the most striking features of this fish is the heavily tuberculated bone located ventral to the median rostral and nasal bones. This bone is identified here as the ventral rostro-premaxilla (Figures 5–6). The anterior tip of the maxilla is ventral to the posteroventral margin of the ventral rostro-premaxilla. The ventral rostro-premaxilla does not bear teeth, though it is possible that small teeth are obscured by the heavy amount of tuberculations on this bone. It should also be noted that there are no teeth visible on the anterior half of the maxilla. No canal is visible in this bone but this could also be because of the heavy ganoine tuberculations. It is termed a ventral rostro-premaxilla because the only criterion that can be used to identify this bone is its placement, information on the placement of canals in any of the snout bones is absent. The bone lies anterior to the maxilla, ventral to a median rostral bone, and separate from a lachrymal bone. The size of this bone and placement suggest that it is not simply a premaxillary bone. This bone is physically located in the area where premaxillary and rostral bones are found.

Circumorbital series—Posterior to the ventral rostro-premaxilla, posteroventral to the nasal bone, and dorsal to the anterior tip of the maxilla is a lachrymal bone. This bone is referred to as a lachrymal because of its position and the putative canals in this bone (Figures 5–6). This bone has also been referred to as the first infraorbital bone. See Chapter 2 for a discussion on this bone and the uses of the term lachrymal. The lachrymal bone is roughly triangular in shape and there is a row of sensory pores. The lachrymal forms the anteroventral margin of the orbit and abuts against the anterior margin of a thin rectangular infraorbital bone that lies ventral to the orbit (Figures 5–6). This rectangular bone, referred to as infraorbital two is large enough to bear small tubercules of ganoine. There is a large crescent-shaped infraorbital bone in the posteroventral corner of the orbit (Figures 5–6). This is infraorbital three. This large infraorbital bone bears tubercles of ganoine and traces of the main infraorbital canal near the anterior border of the bone. There are pore canals that branch off the main infraorbital canal preserved near the posteroventral margin of the bone. This bone is disturbed, broken in half by of the inward collapse of the dorsal half of the bone, but can be easily reconstructed to its original crescent shape (Figures 5–6).

Dorsal of the orbit, posteroventral to the nasal bone and behind the "bump:, is a rectangular bone (Figures 5–6). This bone is not a sclerotic bone—a separate sclerotic bone is preserved ventral to this bone in question (Figures 5–6). The rectangular bone bears short ridges of ganoine that are different in orientation and size from those on the nasal bone. This bone fills in the space created by the dorsal-most notch on the posterior margin of the nasal bone. This bone is identified as a supraorbital bone. The posterior margin of the supraorbital bone comes in contact with the anteroventral margin of the frontal/parietal bone.

Skull Roof— A single dermosphenotic bone is located in the posterodorsal corner of the orbit (Figures 5–6). The anterodorsal and posteroventral margins of this bone cannot be made out with any confidence, but it does appear that this bone is narrower anterodorsally than posteroventrally. There are thin short ridges of ganoine at about mid-bone and elongated tubercles anterodorsally. The dermosphenotic abuts against a large dermopterotic bone (Figures 5–6). The dermopterotic is ventral to the frontal/parietal and parietal/post parietal bones and practically the length of these bones combined.

The margins of the frontal/parietal bones are difficult to determine. The frontal/parietal bones contact the nasal, postrostral, and supraorbital bones anteriorly, the dermopterotic laterally, and the parietal/post parietal bones posteriorly (Figures 5–6). The frontal/parietal bones bear short ridges of ganoine along the length of the bone and a few elongated tubercles. The parietal/postparietal bone is trapezoidal in shape, with the dorsal margin of the bone being longer than the ventral margin (Figures 5–6). Pit lines are not apparent because of the heavy ganoine ridges present on this bone. The parietal/post-parietal bone is about a third of the length of the frontal/parietal bone.

A thin band of bone posterior to the parietal/post-parietal bone and the dermopterotic is interpreted as an extrascapular bone (Figures 5–6). There is no ganoine ornamentation on this bone, nor can it be determined if this is a series of bones or a single bone.

Cheek—Posterior to the circumorbital bones lies a series of suborbital bones (Figures 5–6). Though this region is disturbed by the inward collapse of the infraorbital and suborbital bones, it is clear that there are numerous suborbital bones. The suborbitals are roughly arranged in three rows—the first row is posterior to the circumorbital bones, the second is between the first and third rows of suborbital bones, and the third row contacts the anterior margin of the preoperculum (Figures 5–6). The third row of suborbitals bones is composed of two large bones (Figures 5–6). The dorsal most of the two large suborbital bones has a rounded convex anterior margin. Ventral to this is a triangular suborbital bone with rounded corners. The anterior border of this suborbital bone is slightly concave. Both of these suborbital bones bear fine diagonal ridges of ganoine.

The second row of suborbital bones is also composed of large bones. Two large bones with fine ganoine ridges are present and overlain in sections by the suborbital bones in rows three and one (Figures 5–6). The first row of suborbital bones is the area with the most disturbance. It seems that multiple smaller suborbital bones are located posterior to the dermosphenotic and infraorbital three (Figures 5–6).

The maxilla is a large bone that has a deep and broad postorbital plate (Figures 5–6). There is a posteroventral process off this postorbital plate overlapping the posterodorsal margin of the lower jaw. The maxilla tapers to a narrow arm that extends ventral to the orbit and anterior to the orbit. This narrow arm terminates ventral to the heavily tuberculated premaxilla. There are fine, minute, needle-like teeth on the oral margin of this portion of the maxilla. Large conical teeth are seen on the oral rim ventral to the postorbital plate. There are small conical teeth in between these large teeth.

The ganoine ornamentation of the maxilla is complex (Figures 5–6). The anterior-most portion of the maxilla, up to the anteriormost corner of the infraorbital in the posteroventral corner of the orbit, is heavily tuberculated with closely set tubercles. Below infraorbital three, the maxilla bears short diagonal ridges of ganoine. The pattern of ganoine on the maxilla then changes again to fine, faint, and more horizontally oriented ridges along the postorbital plate. Fine vertical ridges are present along the posteroventral process of the maxilla. Though the anteroventral margin of this process is disturbed, it appears that these vertical ridges of ganoine break down to fine tubercles at this margin. The ventral margin of the postorbital plate has its own ganoine pattern—here there are closely set, short vermiform ridges that are horizontal to vertical in orientation. Directly ventral to the orbit and posteroventral to the orbit, there is a narrow band along the dorsal-most border of the maxilla that is smooth and does not bear any ganoine ornamentation. This is an area of articulation between the maxilla and the overlying infraorbitals.

Individual bones that make up the lower jaw cannot be distinguished. Overall, the lower jaw is a large bone that is longer than the maxilla (Figures 5–6). The lower jaw extends slightly anterior to the rostro-premaxilla. Large vertically oriented conical teeth are along the oral rim of about the anterior half of the lower jaw. In between these large teeth are smaller conical teeth. There are also teeth medial to this series of large and small conical teeth. The medially placed teeth are conical, short, and closely set. Anteriorly, the lower jaw is tuberculated. These tubercles are present until about the posterior margin of the premaxilla. Posterior to the rostro-premaxilla to the posterior margin of the median gular, the lower jaw is ornamented with short diagonal ridges. Posterior to the median gular, there is a change in ganoine ornamentation on the lower jaw to fine and long horizontal ridges. Near the posterior margin of the lower jaw, these horizontal ridges curve dorsally towards the posteroventral process of the maxilla.

The preoperculum is hatchet shaped and anteriorly inclined (Figures 5–6). The preoperculum comes in contact with the dorsal and posterior margins of the postorbital plate of the maxilla. Dorsal to the maxilla, the preoperculum is expanded whereas posterior to the maxilla, the preoperculum is a tall, narrow arm. The anterior margin of the preoperculum sutures with two suborbital bones. These suborbital bones are situated within a concavity made by the arms of the expanded region of the preoperculum. There are short ganoine ridges along the posterior margin of the preoperculum and fine horizontal ridges on the expanded region of the preoperculum, dorsal to the maxilla.

Posterior to the preoperculum, and anterior to the operculum is a tall and narrow wedge shaped dermohyal (Figures 5–6). The dermohyal extends from the anterodorsal corner of the operculum to about half the depth of this bone. The dermohyal bears short horizontal ridges of ganoine, similar to those found on the expanded region of the preoperculum. Posterior to the preoperculum, ventral to the dermohyal, and along the anterior border of the operculum, is a series of accessory opercular bones. The largest bone of the series is found near the anteroventral corner of the operculum. This bone is wider ventrally than dorsally and bears diagonal ridges of ganoine. There are three accessory opercular bones dorsal to the expanded ventral bone. The dorsal accessory opercular bones are small, rhombic, and bear faint ridges of ganoine.

Operculo-Gular Apparatus—The operculum is a rectangular bone that is anteriorly inclined and about twice the height of the suboperculum (Figures 5–6). The operculum has fine diagonal ridges of ganoine that are not as closely packed as the ganoine ornamentation on other bones. The suboperculum is vertical in orientation and rhombic in shape (Figures 5–6). There are short diagonal and vertical ganoine ridges on this bone. The suboperculum is taller posterodorsally than anterodorsally.

Gulars and branchiostegal rays are visible in lateral view (Figures 5–6). The proximal portion of the median gular closest to the lower jaw is missing so that only the distal tip of this bone can be commented upon. The distal portion of the median gular bears short ridges of ganoine and a few tubercles. Posterior to the median gular is the first of two lateral gulars. Both lateral gulars are tear drop shaped and bear short ridges of ganoine. When seen in lateral view, these ridges are diagonal on the first lateral gular, but more horizontally oriented on the second lateral gular. The second lateral gular bears a prominent pit line. Posterior to the lateral gulars is a series of branchiostegal rays (Figures 5–6). The branchiostegals are obscured just anterior to the posteroventral corner of the lower jaw, making determinations of their number and shape difficult. Anterior to this point, there are two branchiostegal rays. Posterior to this point, there are seven rays. If the size of the branchiostegal rays anterior to the posteroventral corner of the lower jaw are consistent with those directly anterior and posterior to this area of ambiguity, the total number of branchiostegal rays is estimated to be around 12.

Pectoral Girdle—The posttemporal is a large bone with a rounded posterior margin (Figures 5–6). The posttemporal bears prominent ridges of ganoine that extend to the posterior border of the bone to form a serrated posterior margin. The posttemporal overlaps the dorsal border of the ventrally located supracleithrum.

A rounded presupracleithrum is situated near the posterodorsal corner of the operculum and overlaps the anterior margin of the supracleithrum (Figures 5–6). The presupracleithrum bears diagonal ridges of ganoine that extend to the posterior end of the bone, giving the presupracleithrum a serrated posterior margin. The supracleithrum lies posterior to the operculum, overlapped by the presupracleithrum, and about the same depth as the operculum (Figures 5–6). At about 2/3 down the depth of the bone, the posterior margin of the supracleithrum is concave. The posterodorsal and posteroventral margins of the supracleithrum are convex. The supracleithrum bears strong ridges of ganoine. The ridges in the posterodorsal portion of the bone are curved whereas the ornamentation on the anterodorsal portion of the bone consists of straight diagonal ridges. These ridges are more vertically oriented near the anterior border of the bone. The ridges in the ventral portion of the supracleithrum are slightly diagonal to vertical in orientation.

Ventral to the supracleithrum is a tall but narrow crescent shaped postcleithrum (Figures 5–6). The postcleithrum bears short diagonal ridges on the dorsal half of the bone and vertical ridges down the ventral half. In the dorsal half of the bone, these ridges extend to the posterior margin, giving the bone a pectinated posterior margin. The smooth area anterior to the postcleithrum and posterior to the suboperculum is the cleithrum.

Squamation—A striking characteristic is the series of large dorsal ridges scales anterior to the origin of the dorsal fin (Figures 4, 7) The dorsal ridge scales are not continuous to the occiput, rather they begin at scale row 20. The dorsal ridge scales series consists of six large scales. The posterior border of the preceding scale overlaps the posterior margin of the subsequent scale. The first dorsal ridge scale has more of an acuminate posterior margin compared to the subsequent scales with blunt rounded posterior borders (Figure 7). The first three dorsal ridge scales have pectinated posterior margins (Figure 7). These serrations are formed by ridges of ganoine that run down the center of the ridge scales. The ganoine ridges on the lateral margin of these ridge scales are curved to follow the convex lateral margin of the scale.

The first and second dorsal ridge scales correspond to two ventrally placed rows of body scales (Figure 7). Because of the overlap of the dorsal ridge scales, the second body scale row that is ventral to the posteroventral margin of the first dorsal ridge scale also overlaps the posterior margin of the second dorsal ridge scale. This gives the appearance of the body scale rows being inserted between the dorsal ridge scales (Figure 7). This pattern is seen between dorsal ridge scale one and two, as well as two and three. The third dorsal ridge scale is unique in that it is the only one of the six to only correspond to one body scale row. Dorsal ridge scales four through six all correspond to two body scale rows (Figure 7). There are no serrated posterior edges on dorsal ridge scales four through six. These ridge scales also differ in shape from the anterior three ridge scales. Ridge scales four through six do not have the same rounded appearance as the first three, and they have more pronounced convex posterior margins (Figure 7).

It is questionable whether ridge scales are present between the pectoral and pelvic fins. Between the pectoral and pelvic fins there is an area of ambiguity caused by the body of a smaller palaeoniscoid overlapping the ventral margin of the larger specimen in YPM 8664. Partially visible are two rounded structures that do not bear serrated posterior margins or ganoine ornamentation. These could potentially be ventral ridge scales between the pectoral and pelvic fins. There are enlarged scales anterior to the anal fin and potentially the vent of the fish.

In order to describe the body scales, the body has been broken down into different regions. These regions are detailed in Figure 8. In YPM 8664, scales in region A1 are heavily ornamented with ridges of ganoine and have strongly serrated posterior margins. Posterior to the posttemporal, the posteroventral margin of the scales have four to five serrations, but at the level of the supracleithrum, there is a change so that the entire posterior margin is pectinated.

In region A2, scales are generally pectinated and bear diagonal ridges of closely set ganoine. These scales are rhombic at the level of the supracleithrum. At the level of the supracleithrum, at scale rows one through three, there are diagonal ridges of ganoine dorsally and curved ridges of ganoine near the ventral border of the scale. Scales ventral to the supracleithrum at about the level of the postcleithrum are taller, rectangular and narrower. These scales only bear diagonal ridges of ganoine.

In region A3, the scales are rhombic, but there is a trend of the scales being narrower and more rectangular in shape the more ventral they are on the body. Regardless of their placement, all of the scales in the A3 region bear close set diagonal ridges of ganoine.

Scales in region B commence at scale row six. Scales in region B2 are tall, narrow, and rectangular in shape. The posterior margins are pectinated, the serrations are formed by the closely set diagonal ridges of ganoine that ornament the scales.

Scales in region B3 are very unique. Here, the ventral margins of the scales, as well as the posterior margins, are pectinated (Figure 9). The scales with pectinated ventral margins continue until the origin of the pelvic fin in region C3. These scales also bear ridges of ganoine.

Scale region C starts at scale row 13. Scales in region C1 are more tear-drop shaped in appearance as compared to the anteriorly placed rhombic and rectangular scales. These scales bear diagonal ridges of ganoine. The posterior edges are sometimes pectinated with five to six serrations.

The posterior borders of scales in region C2 are pectinated with closely packed fine serrations. The exact number is hard to determine because of how closely packed the serrations are, but there are at least a dozen serrations per scale. Those scales that are located at the level of the ventral portion of the supracleithrum are more rectangular in shape than the rhombic scales above and below this point.

Like the scales in region B3, the scales in region C3 are serrated on both the posterior and ventral borders. These scales are ornamented with fine diagonal ridges of ganoine. The more ventrally placed scales are shorter and more rectangular in shape than the more dorsally placed rhombic scales in this region.

Scale region D begins at the origin of the dorsal fin. The scales in region D1, are short, but rectangular in shape. They are closely packed and overlapping. There are faint signs of horizontal ridges of ganoine. The first four scales ventral to the dorsal fin are slightly different—these scales are about two times the depth of the others and rhombic in shape.

Scales in region D2 are rhombic and not as tall as the more anteriorly placed scales. The posterior edges of scales in region D2 are pectinated with six to seven serrations. The ganoine ornamentation is not as dramatic as that of the more anteriorly placed scales but there are faint horizontal to diagonal ridges. Scales in the region D3 are similar to those described for region C3, but the scales in D3 lack the serrations on the ventral margin. There are a few scales in D3 that have serrations on the posterior margin.

Fins—The pectoral fin is large, fan-shaped, and formed by highly bifurcated and closely packed fin rays (Figure 10). Fringing fulcra line the leading edge of the pectoral fin. The fulcra are thicker and longer proximally and decrease in size down the height of the fin so that the distal most fringing fulcra are fine and short. Proximally, the fringing fulcra from the opposite side of the fin is seen. The two sides of the fulcra meet in midline to form a V-shaped unit.

All of the fin rays that make up the pectoral fin are segmented. The fin rays are bifurcated numerous times. The first bifurcation occurs in the proximal quarter of the fin. The fin rays bifurcate at least one more time distally so that the most distal portion of the fin is made up of fine delicate fin rays. This makes determining how many times the fin rays bifurcate and detailed illustrations of the distal portion of the fin difficult. The first two fin rays do not extend down the entire depth of the fin to contribute to the distal margin, instead, the highly bifurcated fin rays posterior to the first two fin rays fill in and form the distal margin of the fin.

There is a large triangular pelvic fin that spans four scale rows (Figure 10). Like the pectoral fin, the fin rays that form the pelvic fin are highly bifurcated. The first bifurcation occurs close to the proximal margin of the fin at about the second or third segment. At about mid-depth of the pelvic fin, the fin rays bifurcate again. Because of all the bifurcations, the distal region of the pelvic fin is made of very fine closely packed fin rays. There are fringing fulcra along the leading edge of the pelvic fin, but the fulcra are not as large or dramatic as that of the pectoral fin. The most proximal structure on the leading edge of the pelvic fin is different from the distal fringing fulcra—it is a single median structure that looks more like a ridge scale than the start of the fringing fulcra series.

The anal fin originates just slightly posterior to the origin of the dorsal fin. The anal fin is large—spanning about 12 scale rows, and triangular in shape (Figure 10). Like the other fins, the anal fin has highly bifurcated fin rays and fringing fulcra. The fringing fulcra are clearest on the leading edge of the distal portion of the fin though it is presumed to be continuous along the entire anterior margin. The caudal fin is not preserved.

DISCUSSION

Comparison to other Albert Formation fishes

The new Albert Formation fish differs from the other actinopterygians described from this site in regard to scale, cranial, and fin characteristics. The scales with pectinated posterior and ventral margins are unique and set YPM 8664 apart from all other Albert Formation fishes, as well as Carboniferous fishes from other localities. The ganoine ornamentation on the nasal bones is also different from the other previously described Albert Formation fishes, which all show vertical continuous ridges of ganoine. The presence of multiple suborbital bones, a large tuberculated rostro-premaxilla, a single supraorbital bone, the size and shape of the dermopterotic, presence of accessory opercular bones, and the body shape also distinguish YPM 8664 from the other Albert Formation fishes. Other Albert Formation fishes have a series of dorsal ridge scales beginning at or just behind the occiput whereas YPM 8664 has six dorsal ridge scales that start at about midbody at scale row 20.

Elonichthys brownii is of a similar size as the new fish. Though specimens of *E. brownii* do not preserve much cranial information, there are enough characteristics regarding scales and fins to support separating YPM 8664 from *E. brownii.* These include the placement of the dorsal fin relative to the anal fin, with the dorsal fin originating slightly anterior to the anal fin in YPM 8664 and far in advance of the anal fin in *E. brownii,* the presence of scales with serrated posterior and ventral margins in YPM 8664 and the absence of this scale type in *E. brownii*.

Proposed relationships of the New Brunswick fish to other lower actinopterygians

Phylogenetic analyses including the newly described New Brunswick fish have been performed. The results are discussed in depth in Chapter 6, but both parsimony and Bayesian analyses recover a close relationship between the New Brunswick fish and the Carboniferous *Kalops, Gonatodus punctatus,* and *Palaeoniscum freieslebeni* (see Chapter 6 Figures 9–10). Some analyses have recovered the Triassic *Beishanichthys brevicaudalis* in a clade with the New Brunswick fishe (Chapter 6, Figures 10–12). In parsimony analyses, the New Brunswick fish is recovered in a clade well embedded in the topology of the trees, above the Devonian forms (Chapter 6, Figures 9–10). Regardless of the methodology used, the New Brunswick fish is recovered closely related to Carboniferous, and in some analyses, a Triassic form (Chapter 6, Figures 9–12). The New Brunswick fish is compared to these taxa below.

In parsimony analyses including recent fishes, the New Brunswick fish is united in a clade with *Palaeoniscum freieslebeni, Gonatodus punctatus,* and *Kalops* on the basis of the shared characters dealing with the presence of supraorbital bones (Chapter 6, Figure 9, Appendix 2). The New Brunswick fish is recovered in a clade containing *Gonatodus* and *Kalops* based on the shared presence of a complex premaxilla in the form of a ventral rostro-premaxilla, and a separate lachrymal bone that contacts the posterior margin of the complex premaxilla (Chapter 6, Figure 9, Appendix 2). When recent fishes are excluded, the New Brunswick fish is recovered in a clade including *Gonatodus* and *Kalops,* again supported by features of the complex premaxilla and separate lachrymal bones (Chapter 6, Figure 9, Appendix 3). A difference between the two parsimony analyses is that this clade is recovered sister to [*Palaeoniscum freieslebeni* + *Beishanichthys brevicaudalis*] when recent fishes are excluded from the analyses. This clade is supported by characters dealing with features of the supraorbital and dermosphenotic bones (Chapter 6 Figure 10, Appendix 3).

In Bayesian analysis with all taxa included, the New Brunswick fish is recovered in a clade of *Palaeoniscum freieslebeni* + [*Beishanichthys brevicaudalis*] + [*Gonatodus* + New Brunswick fish]], supported by characters dealing with the supraorbital and dermosphenotic bones (Chapter 6 Figure 11, Appendix 4). The New Brunswick fish is recovered sister to *Gonatodus* supported by the shared presence of a ventral rostro-premaxilla, a premaxilla that does not form the anterior margin of the orbit, a separate lachrymal bone in contact with the posterior margin of the complex premaxilla, and a dermopterotic bone that is longer than the dermosphenotic (Chapter 6 Figure 11, Appendix 4).

Comparison to closely related fishes

Phylogenetic analyses have suggested a close relationship between the New Brunswick fish, *Palaeoniscum freieslebeni, Kalops monophyrs* and *Kalops diophyrs, Beishanichthys,* and *Gonatodus punctatus*. Similarities and differences between these taxa and the New Brunswick fish are discussed in more detail here. *Palaeoniscum freieslebeni* shares with the New Brunswick fish the presence of suparorbital bones, though in *P. freieslebeni,* there is a series of supraorbital bones, not a single bone (Westoll, 1934). Though the placement of the dorsal fin in regard to the anal fin is similar between these two fishes, *P. freislebeni* does not have the same body shape as the New Brunswick fish (ibid.). The New Brunswick fish is much deeper anterior to the dorsal fin than *P. freislebeni* (ibid.). The New Brunswick fish has more suborbital bones arranged in more rows than *P. freislebeni.* The New Brunswick fish is distinct and different from *Palaeoniscum freislebeni.*

The New Brunswick fish YPM 8664 and the Late Mississippian *Kalops monophyrs* and *K. diophyrs* share many characters, namely the presence of supraorbital bones, numerous suborbital bones, a separate and distinct lachrymal bone forming the anteroventral corner of the orbit, a median dorsal rostral bone and ventral rostro-premaxilla, and dorsal ridge scales that occupy two body row scales (Poplin and Lund, 2002, figs. 3, 6). This said, YPM 8664 and *Kalops* can be distinguished from each other. *Kalops* is characterized by multiple small supraorbital bones whereas YPM 8664 has a single supraorbital bone (Poplin and Lund, 2002). *Kalops* has a small lobed pectoral fin whereas YPM 8664 has a large unlobed pectoral fin. Anteopercular bones are present in YPM 8664 and absent in *Kalops.* The ventral rostro-premaxilla in *Kalops* is toothed (ibid.), whereas there is no sign of teeth on the ventral rostro-premaxilla in YPM 8664 (ibid.). Neither species of *Kalops* has the ventrally placed scales with serrated posterior and ventral margins (ibid.) that are seen in YPM 8664. Ganoine ornamentation on the nasal bones differ between *Kalops* and YPM 8664. Lastly, the body of *Kalops* is not as deep anterior to the dorsal fin nor does it have the same dramatic decrease in depth posterior to the origin of the dorsal fin as in YPM 8664.

The inclusion of the Triassic *Beishanichthys* in a clade containing the New Brunswick fish and other Carboniferous taxa should be considered with some caution. In the Bayesian tree with recent fishes included in the analysis, the clade of *Beishanichthys* + [*Gonatodus punctatus* + New Brunswick fish] is supported by two characters—the presence of a horizontal pit line and an anal fin that ends close to the caudal fin (Chapter 6 Figure 11, Appendix 4). In the parsimony analysis with recent fishes excluded, the inclusion of *Beishanichthys* in a clade with

Palaeoniscum, the New Brunswick fish, *Gonatodus,* and *Kalops* is supported by features of the supraorbital and dermosphenotic bones.

When *Beishanichthys* is compared to the New Brunswick fish, many drastic differences are seen. *Beishanichthys* has numerous supraorbital bones (Xu and Gao, 2011), whereas the New Brunswick fish has a single supraorbital bone. *Beishanichthys* has two suborbital bones arranged in one row (ibid.) whereas the New Brunswick fish has numerous suborbital bones arranged in more than one row. The New Brunswick fish has a ventral rostro-premaxilla and a separate lachrymal bone whereas *Beishanichthys* has a ventral rostro-premaxillo-lachrymal bone (ibid.). Other differences exist between these taxa including differences in the shape of the preoperculum and cleithrum, the presence of a quadratojugal and a long and low dorsal fin in *Beishanichthys* (ibid.).

The New Brunswick fish has been recovered closely related to *Gonatodus punctatus.* Similarities between these two taxa include the presence of a median dorsal rostral bone and a ventral rostro-premaxilla, a separate and distinct lachrymal bone, high triangular dorsal and anal fins, and a body form where the body is deepest anterior to the dorsal fin (Gardiner, 1967a). Differences between the taxa include the presence of a lobed pectoral fin, two suborbitals arranged in one row, and scales with only pectinated posterior margins, not ventral margins, in *Gonatodus,* as well as differences in the origins of the dorsal and anal fins (Gardiner, 1967a).

Characters of note

While describing the New Brunswick fish, certain characters were uncovered that deserve more discussion. These characters include dorsal ridge scales, suborbital bones, and supraorbital bones.

Dorsal ridge scales—An interesting characteristic of the New Brunswick fish involves the dorsal ridge scales. In the New Brunswick fish, the dorsal ridge scales occupy the space of two body scale rows. A review of the literature shows that dorsal ridge scales that correspond to more than one body scale row is an often overlooked character that deserves further investigation. For example, this detail may have been overlooked in *Mansfieldiscus gibbus*—at least it is not mentioned in the description of the dorsal ridge scales that they span more than one body scale row, nevertheless the figure of this fish shows that the dorsal ridge scales occupy two body scale rows (Woodward, 1906, Plate XI, fig. 1b; Long, 1988b, p. 43, fig. 41C). The same appears to be the case in *Howqualepis rostridens,* which has dorsal ridge scales that span at least three body scale rows (Long, 1988b, p. 34–35, figures 32C, 33F). Gardiner (1984) figured *Mimipiscis toombsi* as having dorsal ridge scales that correspond to three or four body scale rows (fig. 145) but does not mention this detail in the description. The reconstructions of *Cycloptychius concentricus, Elonichthys serratus, E. pulcherrimus,* and others, show dorsal ridge scales corresponding to more than one body scale row (Moy-Thomas and Bradley Dyne, 1938, figs. 21, 24, 25).

Poplin and Lund (2002) described the dorsal ridge scales in *Kalops monophrys* as spanning two to three body scale rows and figured the dorsal ridge scales in *K. diophrys* as spanning two body row scales (ibid., fig. 6). Choo et al. (2009) comment that the dorsal ridge scales in *Gogosardinia* are 20 times larger than the adjacent flank scales, so it is not surprising that the dorsal ridge scales appear to correspond to multiple body scale rows in the figures (ibid., fig. 14, p. 205).

Lastly, another fish from the Albert Formation shows this feature. The type specimen of *R. cairnsii* also has dorsal ridges scales corresponding to more than one body row (Figure 3B)

As Arratia (2008) pointed out, the diversity of fulcra, fin rays, and ridges scales is often ignored and may provide phylogenetically informative characters. Dorsal ridge scales are not uncommon in lower actinopterygians, and are often described in figures and texts. What is needed now is for these structures to be described in depth rather than comments on their presence or absence in certain taxa. Only then can it be determined if there is phylogenetic signal in this character.

Suborbital bones—Numerous suborbital bones are present in the New Brunswick fish There are other Carboniferous fishes with multiple suborbital bones including *Kalops monophrys*, *K. diophrys* (Poplin and Lund, 2002), *Beagiascus pulcherrimus* and *Lineagruan snowyi* (Mickle et al., 2009), *Namaichthys schroederi* (Gardiner, 1962). Fishes with one to two large suborbital bones are much more common in the Carboniferous and are found in *Cyranorhis bergeraci* and *Wendyichthys dicksoni* (Lund and Poplin, 1997), *Mansfieldiscus sweeti* (Woodward, 1906; Long, 1988b); *Novogonatodus kasantsevae* (Long, 1988b); *Canobius ramsayi, Cycloptychius concentricus, Rhadinichthys canobiensis, Mesopoma pulchellum,* and *Elonichthys serratus* (Moy-Thomas and Bradley Dyne, 1938); *Mesopoma carricki* (Coates, 1993), *M. planti* (Coates, 1999); *Cosmoptychius striatus* (Gardiner, 1963); *Nozamichthys*, "*Elonichthys peltigerus,*" and *"E." hypsilepis* (Schultze and Bardack, 1987).

Suborbital bones are uncommon in Devonian fishes. The majority of Devonian fishes have a series of circumorbital bones that are anterior to the preoperculum with no intervening suborbital bones. This is the case for *Cheirolepis canadensis* (Pearson and Westoll, 1979; Arratia and Cloutier, 1996), *C. trailli* (Pearson and Westoll, 1979; Pearson, 1982), *Moythomasia durgaringa* (Gardiner, 1984), *Mimipiscis toombsi* (Gardiner, 1984), *Gogosardinia coatesi* (Choo et al., 2009), *Limnomis delaneyi* (Daeschler, 2000), *Howqualepis rostridens* (Long, 1988b), *Stegotrachelus finlayi* (Swartz, 2009), and *Tegolepis clarki* (Dunkle and Schaeffer, 1973). The only exceptions to this are *Osorioichthys marginis* (Taverne, 1997) and *Moythomasia nitida* (Gross, 1953; Jessen, 1968). *Osorioichthys* is described as having one suborbital bone and *Moythomasia nitida* with either one or two (Gross, 1953; Jessen, 1968).

The presence or absence of suborbital bones in *Kentuckia deani* is considered to be considered questionable. Rayner (1951) describes *Kentuckia* with no suborbital bones. Though the cheek is not well preserved, Rayner (1951) states that the circumorbital bones are so close to the preoperculum that there is no room for suborbital bones. Dunkle (1964) describes a suborbital bone in a *Kentuckia* specimen preserved in dorsal view. In a reconstruction of a lateral view of this fish, Dunkle (1964, fig. 4) illustrates two suborbital bones anterior to the preoperculum with dashed lines and question marks. Gardiner and Schaeffer (1989, fig. 8D) figure *Kentuckia* with a single suborbital bone with no dashed lines or question marks. The presence of suborbital bones in *Kentuckia* is not accepted here.

What can be said is that suborbital bones are commonly seen in Carboniferous fish, and rare if not absent in Devonian fishes. This is at odds with Gardiner et al. (2005), who state that suborbitals are first noticed in the Triassic *Pteronisculus* and are present in varying numbers in primitive neopterygians. This result was reached on the basis of their parsimony tree—which included few Carboniferous fishes in an investigation into the relationships of lower actinopterygians (ibid.). Suborbital bones are found in few Devonian fish, but are common in Carboniferous fishes. Carboniferous fishes can have one or two large suborbital bones, or numerous bones arranged in numerous rows.

Supraorbital bones—Gardiner and Schaeffer (1989) described the presence of supraorbitals as being a character found in advanced lower actinopterygians and some neopterygians. The presence of multiple anamestic supraorbital bones is the only stem-neopterygian apomorphy that resulted from their phylogenetic analyses (Gardiner and Schaeffer, 1989; Coates, 1999). They described the presence of these bones in the Permian *Palaeoniscum freieslebeni* and the Triassic fishes *Birgeria* and *Perleidus* (ibid.). Though Gardiner and Schaeffer concentrated on advanced lower actinopterygians, there are Carboniferous fishes with supraorbital bones. These include palaeoniscoids such as *Elonichthys serratus* (Moy-Thomas and Bradley Dyne, 1938), and *Kalops monophrys* and *K. diophrys* (Poplin and Lund, 2002). The last three named fishes have multiple supraorbital bones in a series dorsal to the orbit. The New Brunswick fish can be added to the list of Carboniferous fishes with supraorbital bones. The New Brunswick fish differs from the other Carboniferous fishes in that it possesses a single rectangular supraorbital bone in a more anterodorsal position than the supraorbital bones in other Carboniferous fishes.

The shape and placement of the supraorbital bone in the New Brunswick fish differs from other Carboniferous fishes, but is similar to what is seen in the only Devonian fish with supraorbital bones. The Devonian *Cheirolepis trailli* has a single rectangular supraorbital bone located in the anterodorsal corner of the orbit (Pearson and Westoll, 1979; Pearson, 1982), similar to the placement of the bone in the New Brunswick fish. In both fishes, the ventral margin of the supraorbital bone approaches mid-orbit. Whereas the size and extent of the nasal bones that border the supraorbital bones in *Cheirolepis trailli* and the New Brunswick fish differ, both fish possess a single bone that is not fragmented into multiple supraorbitals. Gardiner and Schaeffer's (1989) statement that supraorbital bones are only found in advanced lower actinopterygians and neopterygians is not supported, nor is the stem-neopterygian apomorphy of the presence of multiple anamestic supraorbital bones. Supraorbital bones have been found in a handful of Carboniferous fishes and a Devonian fish and should be considered common in lower actinopterygians in general.

CONCLUSIONS

The Albert Formation of New Brunswick, Canada preserves an array of palaeoniscoid fishes from the Lower Carboniferous. Much of this diversity is not understood because of the need for redescriptions. Attempts at redescribing the previously described taxa from the Albert Formation will not be successful until after the genera they have been described as belonging to—*Rhadinichthys, Elonichthys,* and *Palaeoniscum*, are themselves redescribed. Until these genera are redescribed, the palaeoniscoids from the Albert Formation cannot proceed.

Other diversity remains undescribed from the Albert Formation. Here, a new genus and species is described. This new taxon shows affinities to Carboniferous fishes. Many of the morphological features of this new taxon are typically seen in Late Carboniferous forms, not Devonian forms. The presence of a separate lachrymal bone and multiple suborbital bones arranged in many rows are two such features. It was thought that fishes from the Albert Formation, which is right above the boundary between the Devonian and the Carboniferous, may preserve forms that help bridge morphological gaps between Devonian and Carboniferous lower actinopterygians. The newly described fish from the Albert Formation does not support this. Instead, the new taxon has features that are commonly seen in later Carboniferous forms.

Table 1—Identities of Jackson's figured specimens. Plate and figure numbers, past and present museum catalog numbers, Jackson's (1851) and Lambe's (1910) identifications, and type status included. **Abbreviations:** BSNH, Boston Society of Natural History; MCZ, Museum of Comparative Zoology; Genera abbreviated—*E.*, *Elonichthys*; *P.*, *Palaeoniscum*; *R.*, *Rhadinichthys.*

Plate and Fig. # Jackson, 1851	Orig.BSNH #	Former MCZ #	Current MCZ #	Jackson, 1851 ID	Lambe, 1910 ID	Type Status
Plate I, Fig. 1	7899	1960	5082	*P. alberti*	*R. alberti*	Holotype
Plate I, Fig. 2	7900	1961	5083	*P. brownii*	*E. brownii*	Holotype
Plate I, Fig. 3	7899a	1956	5084	*P. cairnsii*	*R. alberti*	Holotype *P. cairnsii* (Jackson)
Plate I, Fig. 4	Lost?	X	X	*Palaeoniscus* sp.	*E. brownii*	Holotype *P. jacksoni* (Dawson)
Plate I, Fig. 5	7901	1957	5085	Not mentioned	*E. brownii*	Plesiotype
Plate II, Fig. 1	7902		6150	*Palaeoniscus* sp.	*E. brownii*	
Plate II, Fig. 2, 2 bis	7987	1959	5086	*Palaeoniscus* sp.	*R. alberti*	
Plate II, Fig. 3	7987a	1958	5087	*Palaeoniscus* sp.	*R. alberti*	
Plate II, Fig. 4	Lost?	X	X	Not mentioned	X	
Plate II, Fig. 5	7898		6151	Not mentioned	*R. alberti*	
Plate II, Fig. 6	Lost	X	X		X	
Plate II, Fig. 7	7903	1953	5088	*Palaeoniscus* sp.		
Plate II, Fig. 8	7898a		6152	Not mentioned	*R. alberti*	

Table 2—Identities of Lambe's (1910) figured specimens. Plate and figure numbers, past and present museum catalog numbers, and identifications included. **Abbreviations:** BSNH, Boston Society of Natural History; MCZ, Museum of Comparative Zoology; Genera abbreviated—*E.*, *Elonichthys*; *R.*, *Rhadinichthys.*

Plate and Fig. # Lambe, 1910	**Original BSNH #**	**Former MCZ #**	**Current MCZ #**	**Lambe, 1910 ID**
Plate III, Fig. 1				*R. alberti*
Plate III, Fig. 2	?	?	?	*R. alberti*
Plate III, Fig. 3	?	?	?	*R. alberti*
Plate III, Fig. 4	7899a	1956	5084	*R. alberti*
Plate III, Fig. 5	7987a	1958	5087	*R. alberti*
Plate III, Fig. 6	7987a	1958	5087	*R. alberti*
Plate IV, Fig. 1	7900	1961	5083	*E. brownii*
Plate IV, Fig. 2	7900	1961	5083	*E. brownii*
Plate IV, Fig. 3	7902		6150	*E. brownii*
Plate IV, Fig. 4	7901	1957	5085	*E. brownii*
Plate V, Fig. 2, 3, 5, 6	7900	1961	5083	*E. brownii*
Plate V, Fig. 4	7902		6150	*E. brownii*
Plate VI, Fig. 1	?	?	?	*E. brownii*
Plate VII, Fig. 1	?	?	?	*E. brownii*
Plate VIII, Fig. 1	?	?	?	*E. brownii*
Plate IX, Fig. 1	?	?	?	*E. brownii*

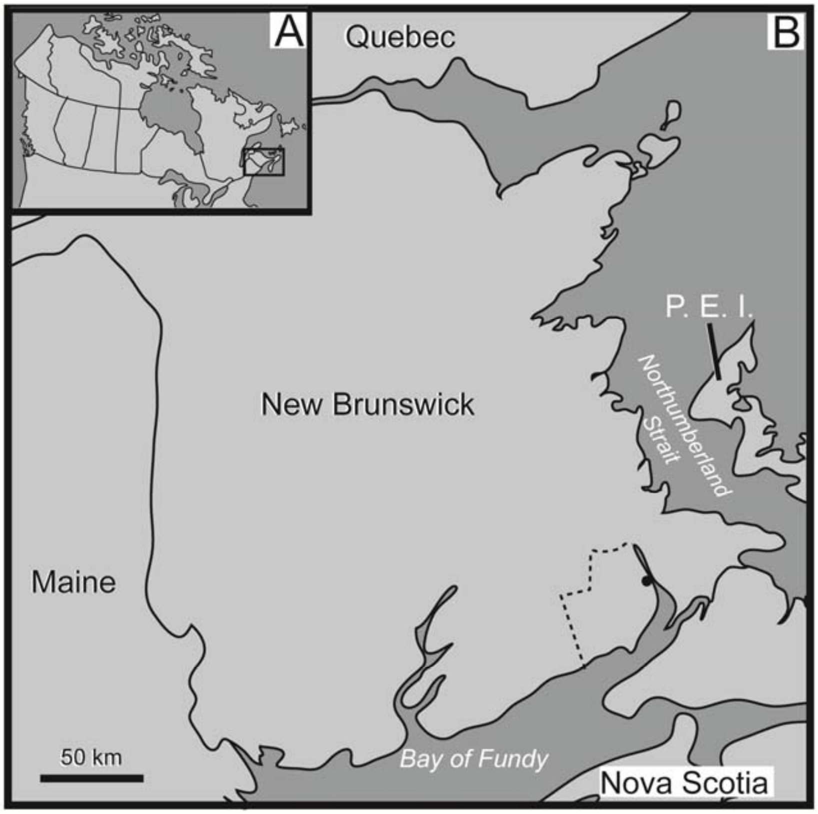


Figure 1—Map of locality. **A**, Map of North America, box highlights area enlarged in B. **B,** Close up of New Brunswick, Canada. Dashed line indicates Albert County where the majority of the specimens were collected. Black dot indicates Hillsborough, the site the original material described by Jackson was collected. Scale bar equals 50 km, **A**, not to scale. Modified from Google Maps.

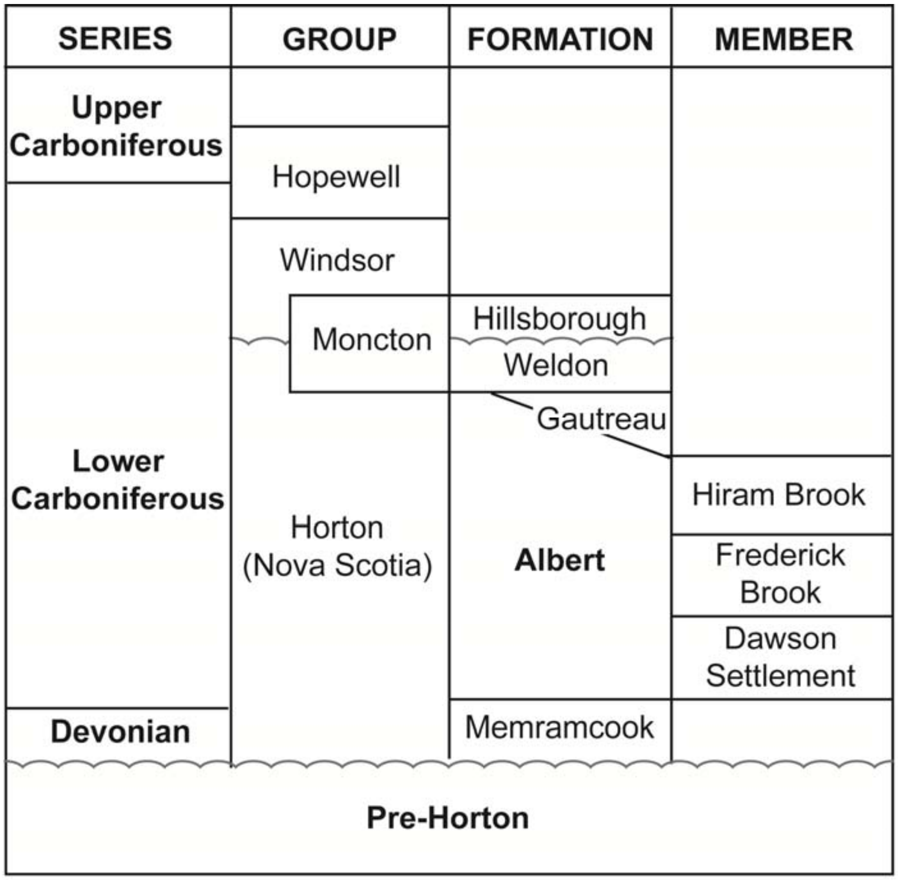


Figure 2—Stratigraphic column of the Lower Carboniferous of New Brunswick, Canada (modified after Utting, 1987).

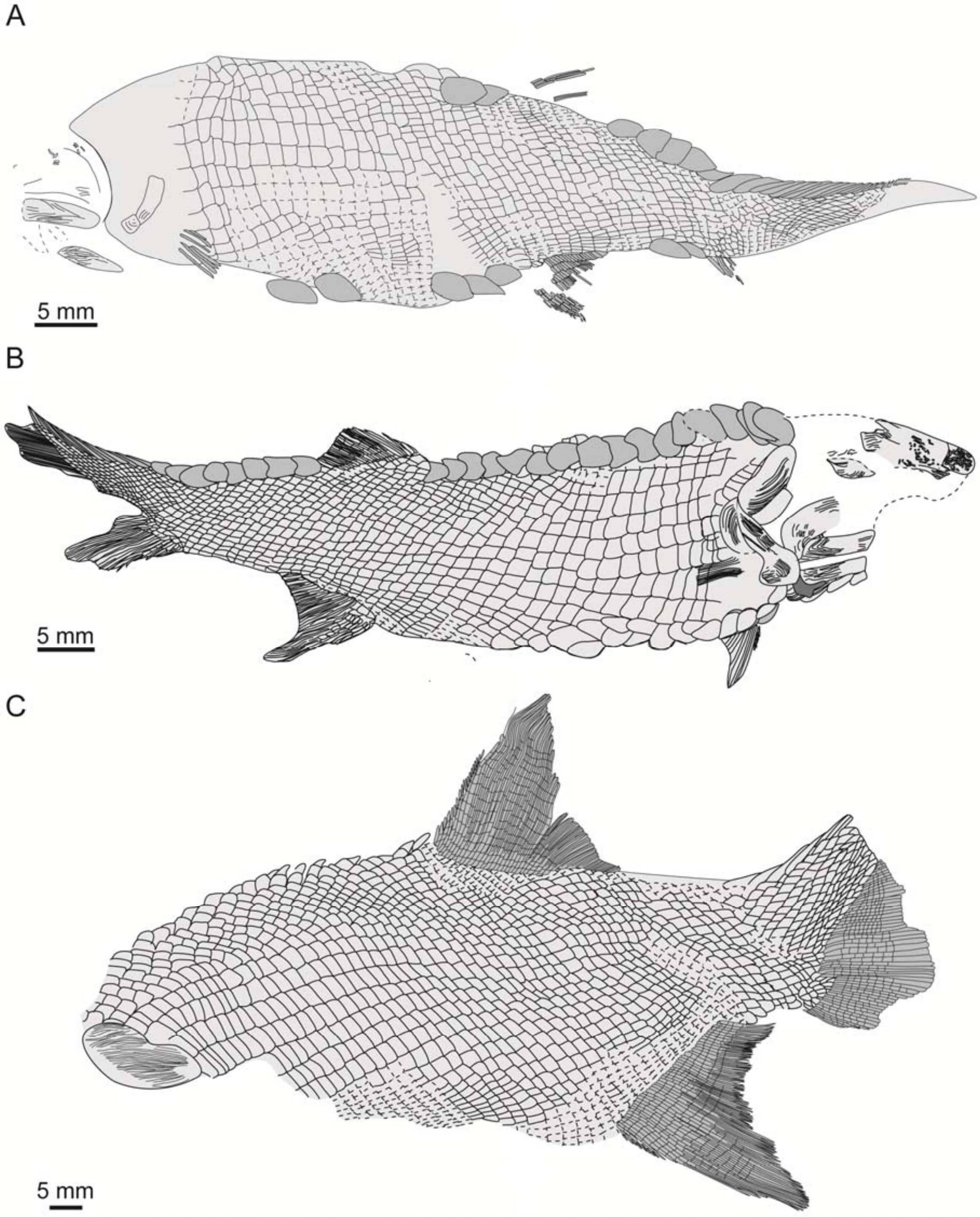


Figure 3--Illustrations of types specimens of Jackson's (1851) original species from the Albert Formation of New Brunswick, Canada. **A,** *Rhadinichthys (Palaeoniscum) alberti*, illustration of MCZ 5082; **B,** *Rhadinichthys (Palaeoniscum) cairnsii*, illustration of MCZ 5084; **C,** *Elonichthys brownii*, illustration of MCZ 5083. Scale bars equal 5 mm.

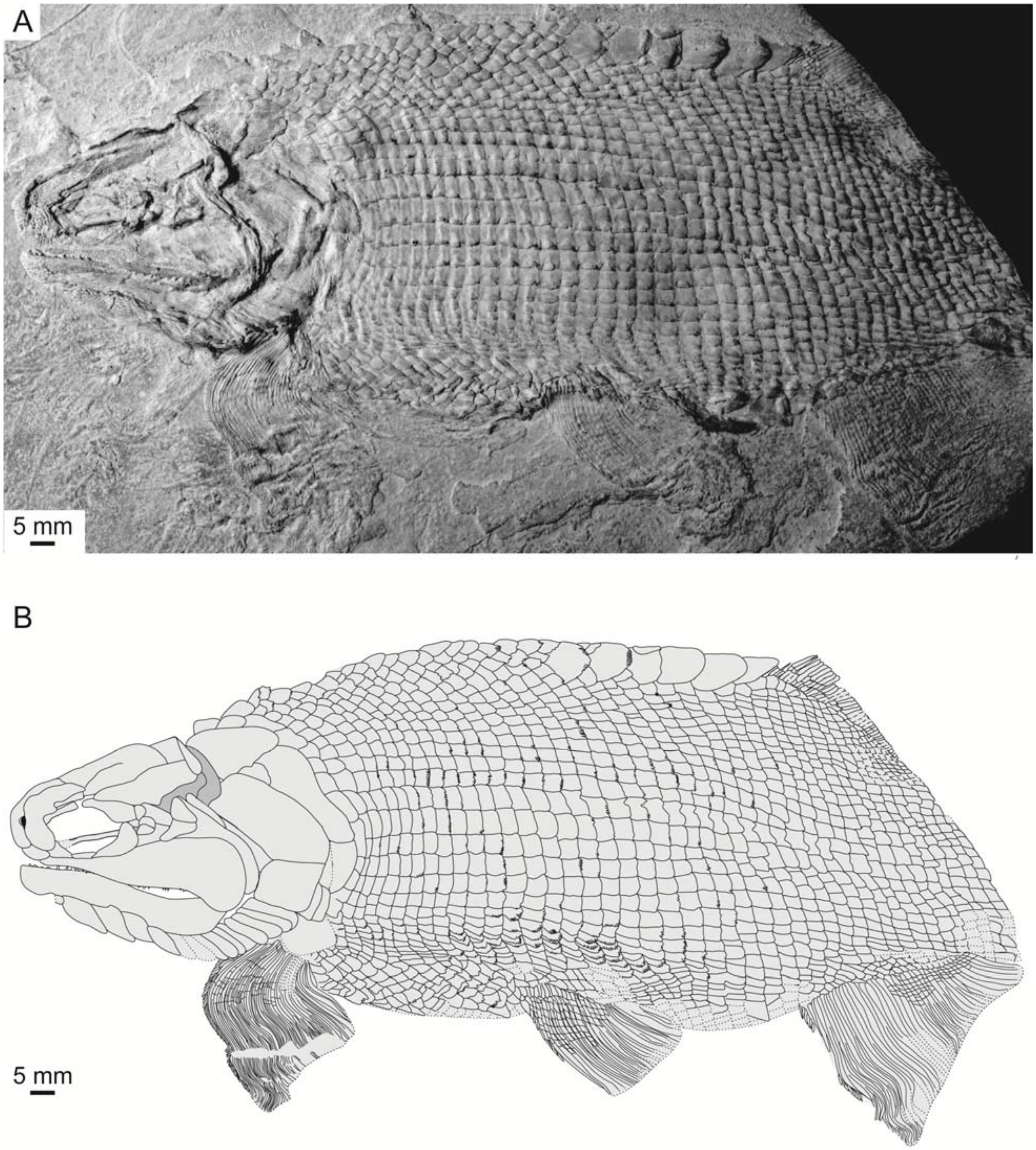


Figure 4—Type and only specimen of the New Brunswick fish. **A,** photograph of latex peel of YPM 8664; **B,** illustration based on YPM 8664. Scale bars equals 5 mm.

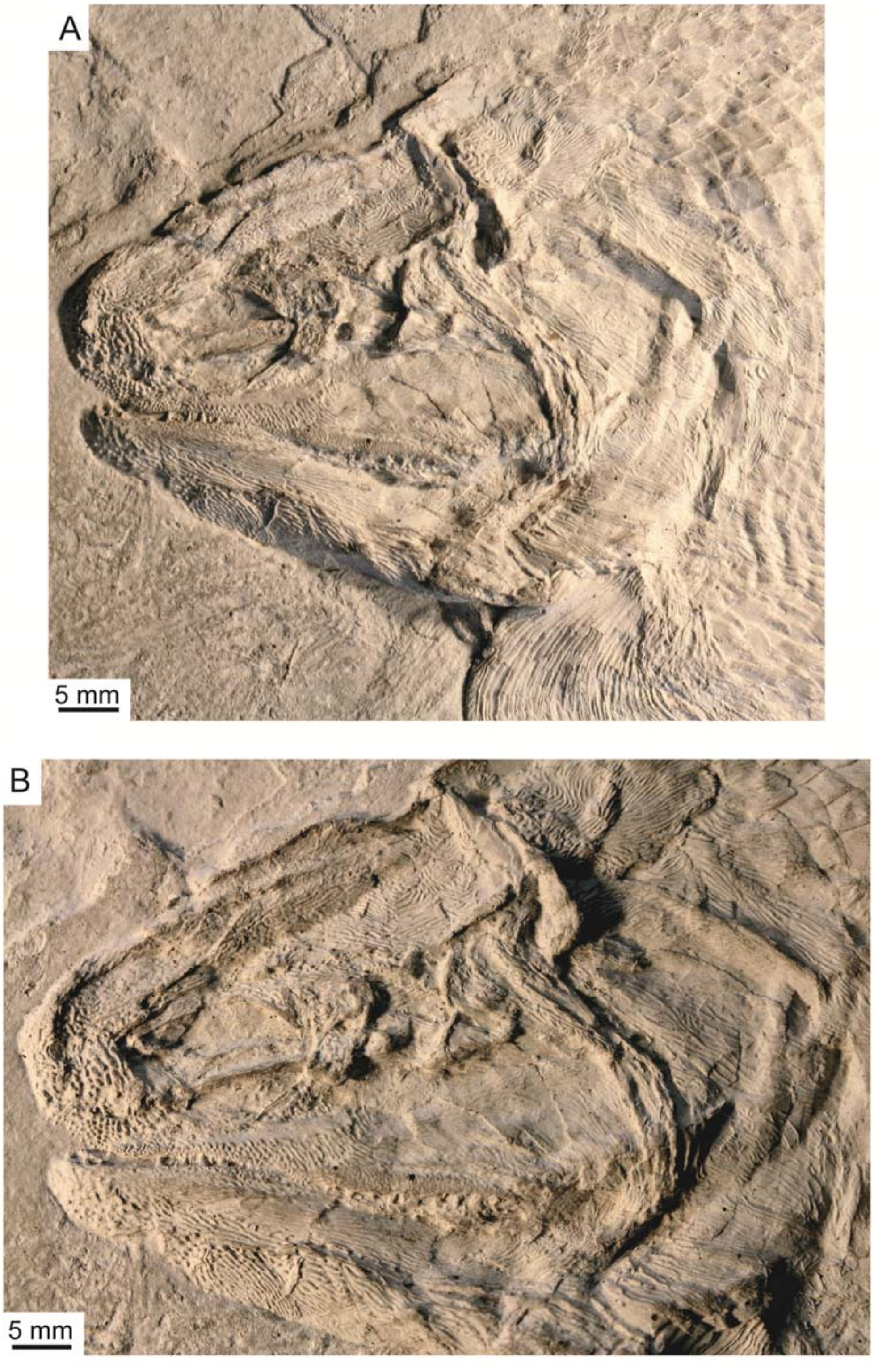


Figure 5—Photographs of the lateral view of the head of the type specimen of the New Brunswick fish YPM 8664. Scale bars equal 5 mm.

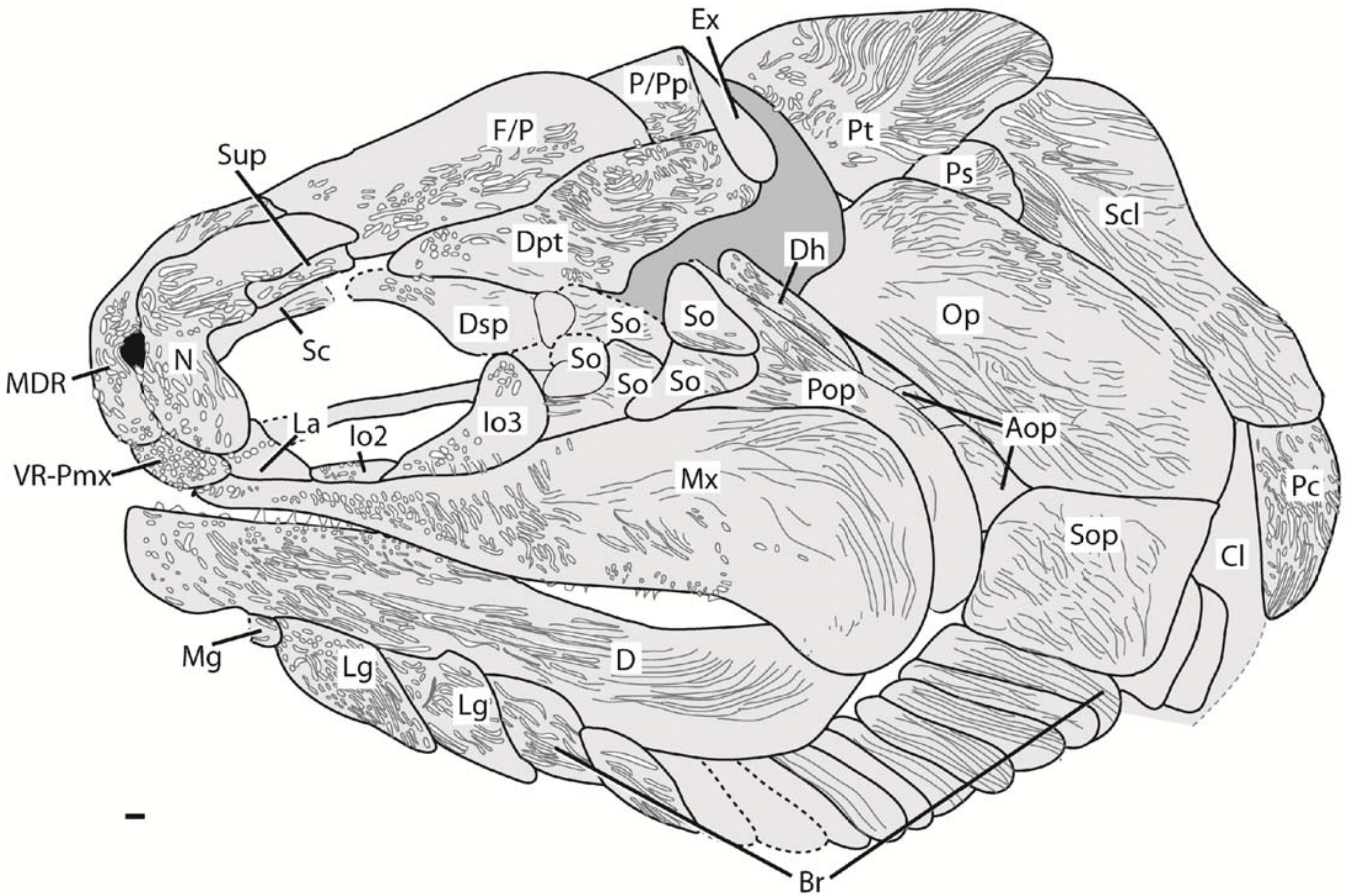


Figure 6—Reconstruction of the head of the New Brunswick fish detailing bones and ganoine ornamentation based on the type and only specimen, YPM 8664. **Abbreviations: Aop**, Anteopercular bone; **Br,** Branchiostegal rays; **Cl,** Cleithrum; **D**, Dentary; **Dh,** Dermohyal; **Dpt,** Dermopterotic; **Dsp,** Dermosphotic; **Ex,** Extrascapular; **F/P,** Frontal/Parietal bone; **Io,** Infraorbital bone; **Mx,** maxilla; **MDR,** Median dorsal rostral bone; **Mg**, Median gular; **N,** Nasal bone; **La,** Lachrymal; **Lg,** Lateral gular; **Op,** Operculum; **Pc,** postcleithrum; **Pop,** Preoperculum; **P/Pp,** Parietal/Postparietal bone; **Ps,** Presupracleithrum; **Pt,** Posttemporal bone; **Sc**, Sclerotic bone; **Scl,** Supracleithrum; **So,** Suborbital bone; **Sop,** Suboperculum; **Sup,** Supraorbital bone; **VR-Pmx,** Ventral rostro-premaxilla. Dark grey areas represent areas of infilling. Dashed lines represent areas of ambiguity.

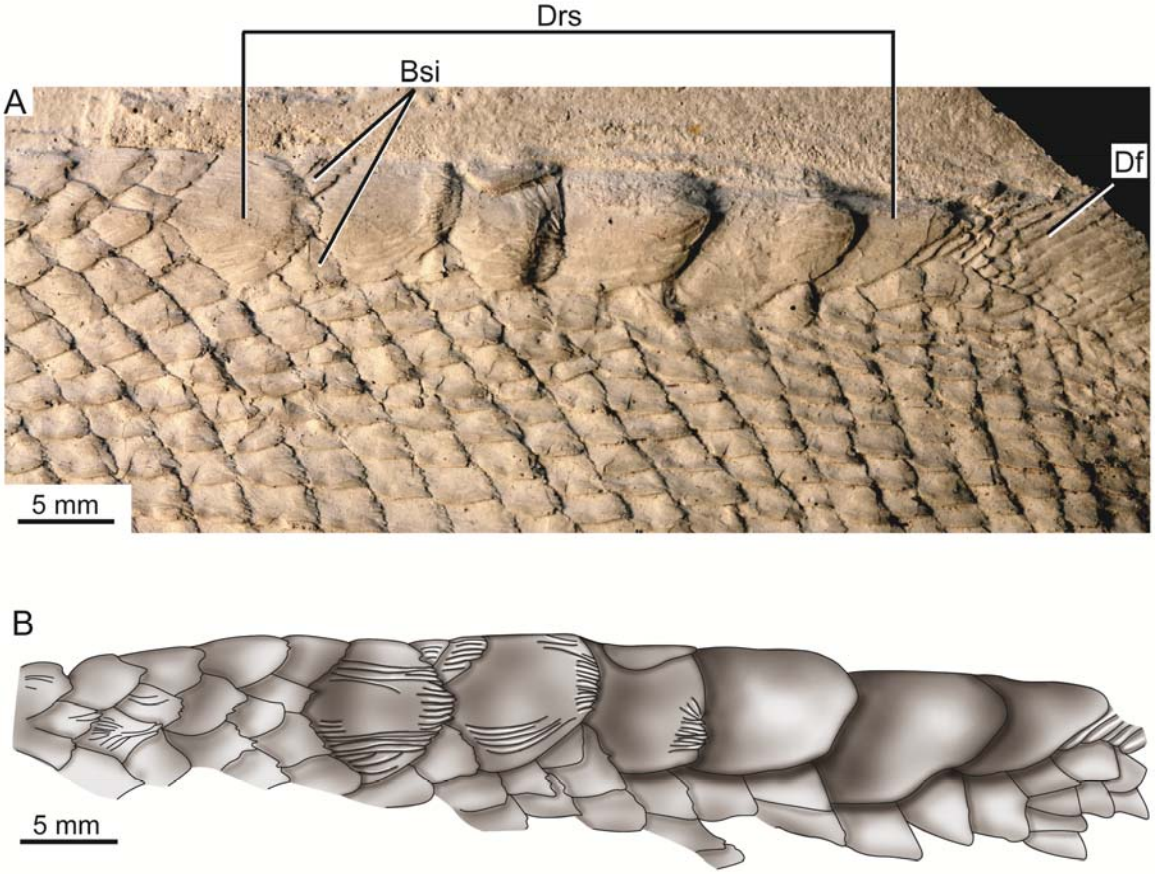


Figure 7—Dorsal ridge scales of New Brunswick fish. **A,** Photograph of dorsal ridge scales in type and only specimen YPM 8664. **B,** Illustration of dorsal ridges scales in YPM 8664. **Abbreviations: Bsi,** inserted body scales; **Df,** dorsal fin; **Drs,** dorsal ridge scales. Scale bars equal 5 mm.

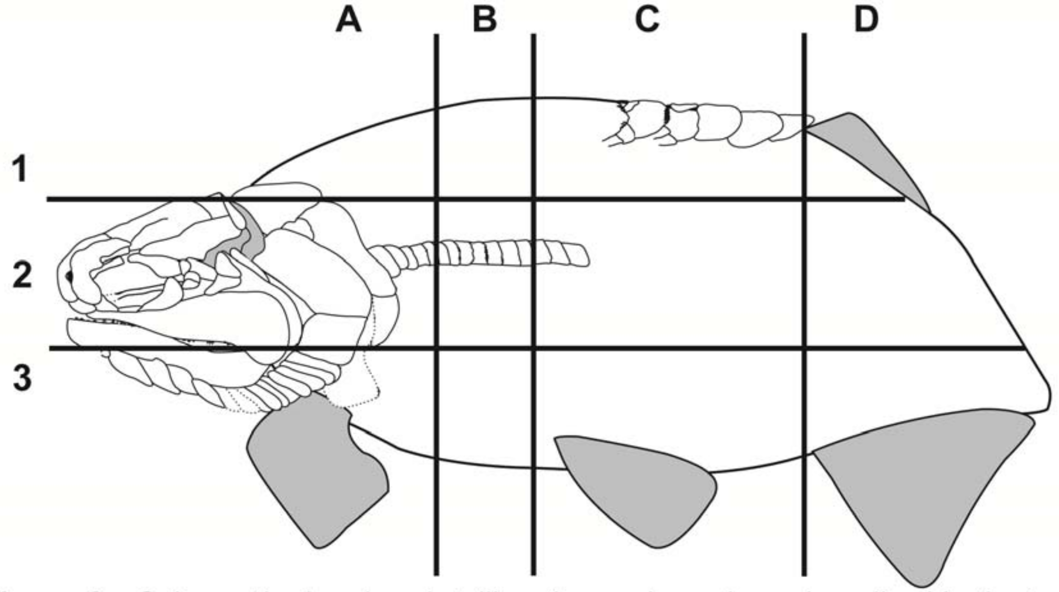


Figure 8—Schematic drawing detailing the scale regions described in the text for the New Brunswick fish YPM 8664. **A1**, **A2**, **A3**, dorsal most, midbody, and ventral most scales posterior to the pectoral girdle dorsal most scales posterior to the pectoral girdle; **B1**, **B2**, **B3**, dorsal most, midbody, and ventral most scales from scale row 6 to 12; **C1, C2, C3,** dorsal most, midbody, and ventral most scales from scale row 13 to origin of dorsal fin; **D1, D2, D3,** dorsal most, midbody, and ventral most scales from origin of dorsal fin to end of specimen.

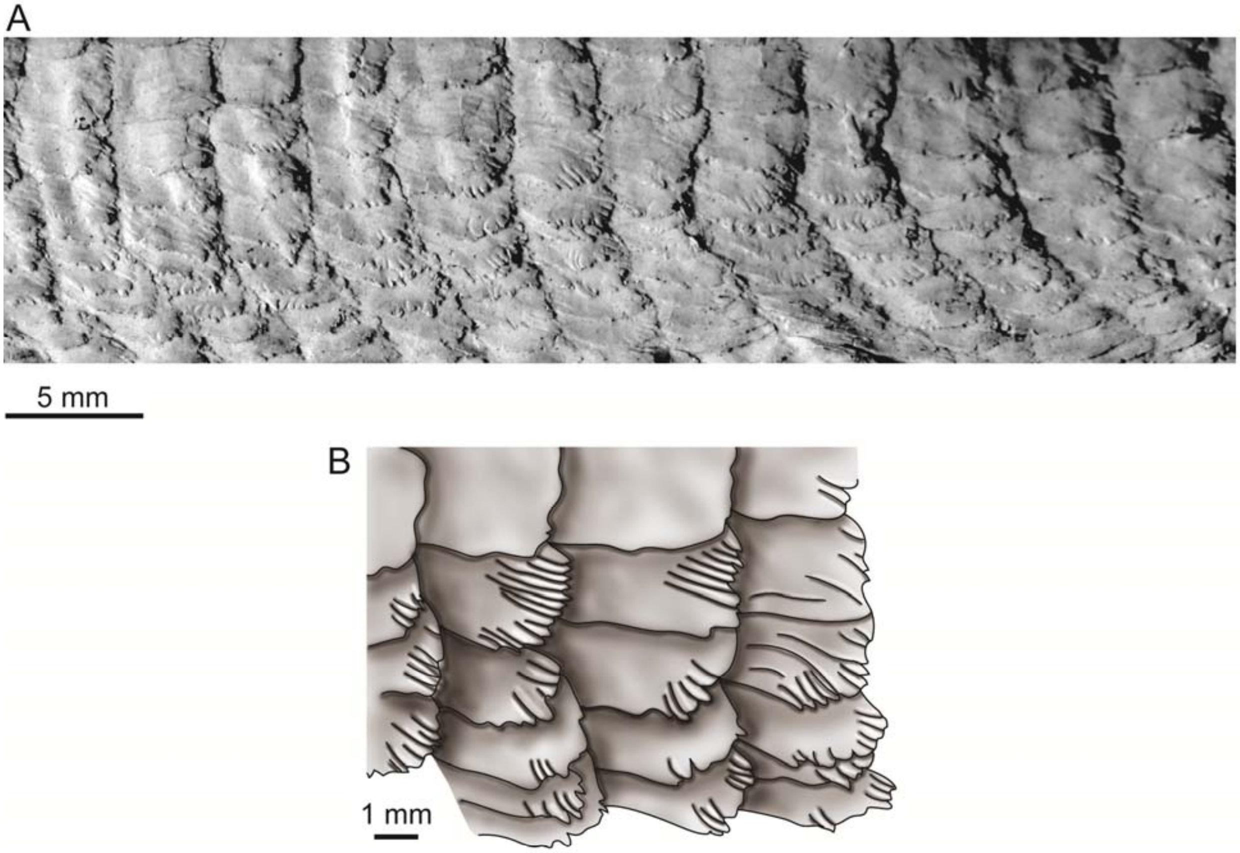


Figure 9—Scales of the type and only specimen of the New Brunswick fish YPM 8664. Scales are from region B3 (see Figure 8) and have pectinated posterior and ventral margins. **A**, photograph of scales from latex peel; **B**, illustration of scales.

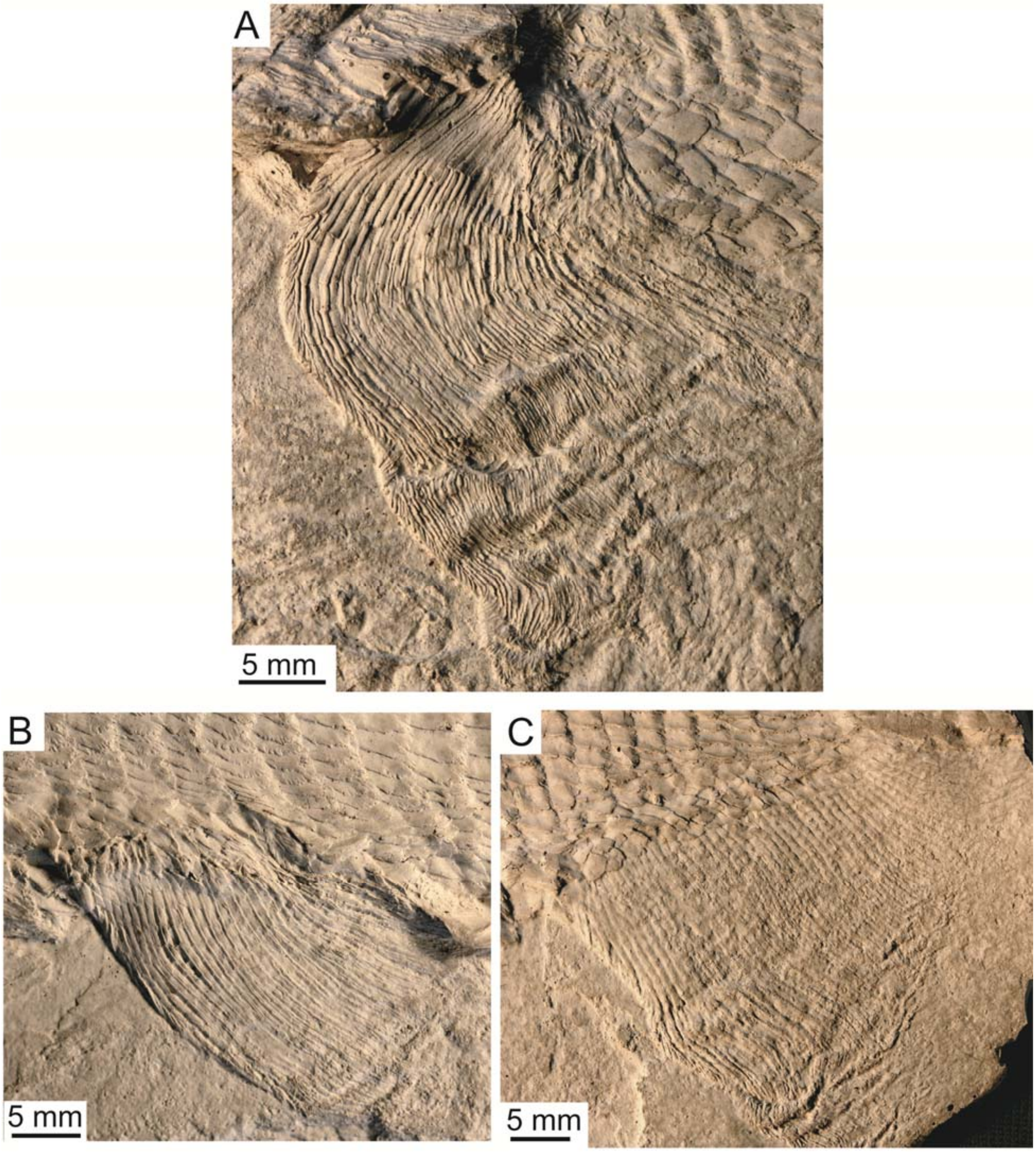


Figure 10—Photographs of the fins of the New Brunswick fish, from type and only specimen YPM 8664. **A,** pectoral fin; **B**, pelvic fin; anal fin. All photographs depict the latex peel of YPM 8664. Scale bars equal 5 mm.

CHAPTER SIX—RELATIONSHIPS OF LOWER ACTINOPTERYGIAN FISHES

INTRODUCTION

Chapters 2 and 3 detail problems with our understanding of some of the morphological characters of lower actinopterygians. Chapter 5 describes the need for redescriptions of some of the earliest described genera of 'palaeoniscoids.' With these problems, it should come as no surprise that the majority of phylogenetic analyses recover paraphyletic assemblages of fishes considered to be 'palaeoniscoids.' In general, Devonian forms are typically separated from Permocarboniferous forms. Some of the later Paleozoic forms seem to be closely related to Mesozoic and extant fishes. As a review of recent hypotheses shows, beyond these generalities there is no consensus regarding the relationships of lower actinopterygians.

Previous hypotheses of relationship

Cloutier and Arratia (2004) give a thorough review of the previous hypotheses regarding the relationships of lower actinopterygians starting with pre-cladistic hypotheses such as those from Sewertzoff (1925), Watson (1925), Gardiner (1967), to the phylogenetic hypotheses of Patterson (1982), Gardiner (1984), Gardiner and Schaeffer (1989) to Lund and Poplin (2002). This will not be repeated here, but the results of Cloutier and Arratia (2004) and subsequent publications are discussed.

Many recent analyses concentrate only on Devonian actinopterygians—Cloutier and Arratia's 2004 work is unique in that it investigates the relationships of many Devonian (13 species), Carboniferous (17 species) and Permian to Recent taxa (7 species). It also investigated the effect of different outgroups and the inclusion and exclusion of recent taxa and taxa for which there was a high percentage of characters coded as unknown (Figures 1–2).

Tested outgroups included a hypothetical ancestor, an acanthodian, sarcopterygians, and the basal actinopterygians *Cheirolepis* and *Dialipina.* Important results include how outgroup choice can drastically change the topology of the tree, though there is some consistency in the retention of certain sister group relationships and the recovery of a monophyletic Actinopterygii and of a monophyletic Palaeoniscomporpha (*Cheirolepis* and above) and Palaeonisciformes (*Moythomasia* and above) (Cloutier and Arratia, 2004). The removal of incomplete characters and/or taxa gave similar results (ibid.).

Other important results include how entire clades, specifically the deep-bodied Guildayichthyidae and the eel-shaped Tarrasiidae, were subject to large phylogenetic shifts if advanced actinopterygians were removed from the analysis (Cloutier and Arratia, 2004). When recent fishes were included in the analysis, Guildayichthidae + Tarrasiidae is recovered sister to the recent *Polypterus*. The Cladistia sensu Lund et al. (1995) and Lund (2000) was recovered. The Cladistia is sister to the remaining advanced actinopterygians (Cloutier and Arratia, fig. 10A, this chapter, Fig. 1A). When advanced actinopterygians were removed, Guildayichthyidae + Tarrasiidae was recovered sister to the fusiform Carboniferous genus *Kalops* at the top of the tree (Cloutier and Arratia, 2004, fig. 10B, this chapter Fig. 1B). The shifts also occurred when highly incomplete taxa were included and then excluded from the analysis. When highly incomplete taxa were removed, but the advanced actinopterygians retained, the Guildayichthyidae + Tarrasiidae was recovered sister to a clade containing all the advanced actinopterygians and Cladistia sensu Lund (1995) and Lund (2000) was not recovered (Cloutier and Arratia, fig. 14A, this chapter Fig. 2A). When incomplete taxa and advanced actinopterygians were removed from the analysis, Guildayichthyidae + Tarrasiidae was recovered sister to the fusiform Carboniferous genus *Kalops,* (ibid., fig. 14B, this chapter Fig. 2B). Very interesting to note is that Cloutier and

Arratia found that the inclusion of any single advanced actinopterygian would create these shifts (2004). This is important to note because Late Carboniferous, Permian, Mesozoic, and recent fishes are rarely included in analyses.

Poplin and Dutheil (2005) concentrated on investigating the relationships of the Carboniferous and Permian Aeduellidae. Their analysis consisted of 22 actinopterygian taxa, 12 of which were not aedeullids. A sarcopterygian outgroup was employed, resulting in 12 equally parsimonious trees. The Aeduellidae was recovered as monophyletic, but within the Aeduellidae, the genus *Bourbonnella* was recovered as paraphyletic (Fig. 3A). Poplin and Dutheil (2005) consider the paraphyly of *Bourbonnella* to be a product of the incompleteness of the taxa placed within this genus and therefore the amount of incomplete data in the analysis.

Friedman and Blom (2006) focused on the relationships of Devonian actinopterygians with their analyses of 13 Devonian actinopterygians. The purpose of their analysis was to investigate the relationships of articulated Devonian actinopterygians and to determine the placement of the newly described *Cuneognathus gardineri*. Four most parsimonious trees resulted from an analysis of 13 Devonian actinopterygians and 5 sarcopterygians and a consensus tree was generated (Fig. 3B). The new taxon *Cuneognathus* was recovered as the sister taxon to *Limnomis*. A novel relationship of *Tegeolepis* + *Howqualepis* was recovered (Friedman and Blom, 2006).

Friedman and Blom (2006) also called into question Schultze and Cumbaa's (2001) placement of *Dialipina* as a basal actinopterygian. Friedman and Blom (2006) attempted to investigate the effect of including and excluding *Dialipina* in their analyses. The exclusion and inclusion of *Dialipina* did not drastically change the proposed relationships of the other Devonian actinopterygians. As for the phylogenetic placement of *Dialipina*, Friedman and Blom

(2006) concluded that they could not comment on this because an analysis employing a non-osteichthyan outgroup would be necessary to do so. Friedman and Blom (2006) used their resulting trees to comment on the monophyly of certain Devonian families, but note that this is preliminary because the addition of non-Devonian taxa may change the topology of the trees.

Hurley et al. (2006) used morphological and molecular analyses to propose hypotheses regarding the timing of the early evolution of actinopterygians. Molecular analyses (Inoue et al., 2003; Yamanoue et al., 2006) present older divergence dates for clades than those supported by fossil data (Hurley et al, 2006). Hurley et al. (2006) performed morphological analysis of fossil and recent fishes on a range of fossil fishes from the Devonian (one genus), Carboniferous (three genera), Permian (two genera), the Mesozoic (17 genera), and recent (six genera). One hundred sixteen trees were recovered and a consensus tree was presented (Fig. 4). Results of this analysis supported the findings of the molecular analyses that the divergence dates of the crown group Neopterygii is too young. Based on there results, Hurley et al. (2006) proposed that the neopterygian crown radiation occurred in the Paleozoic. The younger dates for the teleost radiation, supported by molecular evidence, are not supported by morphological evidence (ibid.).

Specifically important to the understanding of the relationships of Paleozoic lower actinopterygians is the placement of the Carboniferous *Discoserra* in this analysis. *Discoserra* is one of two genera within the family Guildayichthyidae. Guildayichthyidae has been recovered sister to *Polypterus,* and part of the Cladistia (Lund et al., 1995; Lund, 2000; Cloutier and Arratia, fig. 10A; Mickle et al., 2009, discussed below). The Cladistia including the guildayichthyids, has been recovered sister to all other actinopterygians (Lund et al., 1995), or embedded in the topology of advanced actinopterygians (Lund, 2000). The Guildayichthyidae has also been recovered in a basal position, or well embedded in the topology of the tree (Cloutier and Arratia, 2004). In Hurley et al. (2006, fig. 2), *Discoserra* was recovered as a stem neopterygian, sister to all crown group neopterygians; a very different and important hypothesis. The recovery of *Discoserra* as a stem neopterygian was used to support the hypothesis of a Paleozoic divergence date for the Neopterygii (Hurley et al., 2006). This analysis included many advanced forms, specifically Mesozoic and Recent forms, which Cloutier and Arratia (2004) showed are influential in the placement of the Guildayichthyidae, but is low on the number of Paleozoic taxa.

Long et al. (2008) investigated the relationships of 16 Devonian actinopterygians, including the newly described *Donnrosenia schaefferi* by employing characters from Friedman and Blom (2006) as well as 17 additional characters. This analysis included a still undescribed species of the genus *Mimipiscis. Moythomasia durgaringa* was coded using new information from an unpublished redescription of this species (Long et al., 2008). Two most parsimonious trees were recovered and a consensus tree presented (Fig. 5A). The novel sister relationship between *Tegeolepis* and *Howqualepis* recovered by Friedman and Blom (2006) was not recovered by Long et al. (2008), rather the new taxon *Donnrosenia* was recovered sister to *Howqualepis*. As in Friedman and Blom (2006), *Cuneognathus* was recovered sister to *Limnomis.* The genus *Moythomasia* was not recovered as monophyletic (Long et al., 2008).

Swartz (2009) investigated the relationships of 15 Devonian and 3 Carboniferous taxa with 4 sarcopterygian taxa employed as the outgroup. A single tree was recovered (Fig. 5B). Like in Friedman and Blom (2006) but unlike in Long et al. (2008), *Tegeolepis* was recovered sister to *Howqualepis.* Also like Friedman and Blom (2006), Swartz (2009) recovered *Cuneognathus* sister to *Limnomis. Stegotrachelus*, which was redescribed in the same publication, was recovered sister to *Moythomasia durgaringa* and *M. nitida* (Swartz, 2009).

Mickle et al. (2009) investigated the relationships of 37 actinopterygians from the Devonian to the Recent. A theoretical ancestor and three sarcopterygian taxa were employed as the outgroup;and the analysis of 111 characters resulted in two equally parsimonious trees (Fig. 6). Like Lund (2000), but unlike the majority of other analyses, this study included a large diversity of deep-bodied Paleozoic forms. All the Paleozoic deep-bodied forms except the Guildayichthyidae form a clade. Like Lund et al. (1995), Lund (2000), Cloutier and Arratia (2004, fig. 10A), Mickle et al. (2009) recovered the Guildayichthyidae as part of the Cladistia. Cladistia was recovered as sister to the rest of the advanced actinopterygians, but unlike Lund et al. (1995) and Cloutier and Arratia (2004), the clade formed by the Cladistia and the advanced actinopterygians is well embedded in the topology of the tree. Unlike Cloutier and Arratia (2004), the sister relationships between the Guildayichthyidae and the Tarrasiidae was not recovered. The tarrasiids were recovered in a basal position, sister to *Cheirolepis* (Mickle et al., 2009).

This short review shows that there is neither a stable classification system nor hypothesis of relationship for lower actinopterygians in general and the fishes considered to be ‘palaeoniscoids’ specifically. As described in Chapter 1, this is attributed to several causes, including the need for more Paleozoic fishes to be described, more taxa included in phylogenetic analyses, and a better understanding of characters among lower actinopterygians (Cloutier and Arratia, 2004). Two specific problems dealing with taxon sampling and the identification and coding of characters are discussed below.

Problems

Problems that may lead to conflicting hypotheses of relationships and difficulty when comparing phylogenetic trees from different analyses fall into two categories—those involving differences in taxon sampling and those involving the identification and subsequent coding of morphological characters.

Taxon sampling—Comparing various hypotheses is difficult because they can differ drastically in terms of the number of taxa analyzed, temporal selection of the ingroup taxa, choice of outgroups, and the specific goals of the analyses. The number of actinopterygian taxa included in analyses varies from a little over a dozen (e.g. Lund, 2000; Schultze and Cumbaa, 2001; Friedman and Blom, 2006) to over three dozen (Dietze, 2000; Cloutier and Arratia, 2004; Mickle et al., 2009). Along with the difference in the number of taxa analyzed come differences in the type of fishes investigated.

Within the last few years, the majority of analyses have concentrated solely on the relationships of Devonian fishes (Friedman and Blom, 2006; Long et al., 2008), or include only a handful of non-Devonian fishes (Swartz, 2009). Though it is important to understand the relationships of the Devonian taxa, emphasis on certain taxa or time periods undoubtedly affects resulting hypotheses of relationship. As Friedman and Blom (2006, p. 1198) pointed out, their tree is “artificially truncated at the end of the Devonian” and so their subsequent review on the clades should be considered preliminary.

Hypotheses can also be affected if there is a specific goal in mind. Some analyses concentrated on investigating the relationships of specific groups of fishes. For example, Taverne (1996, 1997) and Lund and Poplin (2002) were specifically interested in the relationships of the tarrasiids, Dietze (2000) of the paramblypterids, Lund (2000) of the guildayichthyids, and Poplin and Dutheil (2005) of the aeduellids. Concentrating on subsets of fishes undoubtedly affects taxon choice, character choice, and resulting hypotheses.

Along those same lines, many recent analyses do not include extant actinopterygians such as *Polypterus*, *Lepisosteus*, and *Amia* (Friedman and Blom, 2006; Long et al., 2008; Swartz, 2009). This is problematic because Cloutier and Arratia (2004) showed that the inclusion of these fishes can greatly change the topology of the tree. On the other end of the spectrum, *Dialipina,* which is considered to be the basal-most actinopterygian (Schultze and Cumbaa, 2001; Zhu and Schultze, 2001; Cloutier and Arratia, 2004), has recently been excluded from analyses because of uncertainty of its phylogenetic position (Friedman and Blom, 2006; Long et al., 2008; Swartz, 2009).

Characters—Before phylogenetic analyses were performed here, some characters were scrutinized and reevaluated. As pointed out in earlier chapters, there are discrepancies on how bones are identified within actinopterygians among different workers. Chapter 2 presents how the bones of the snout have been identified differently by various researchers. This discrepancy is clearly a problem if taxa are coded from the literature. Also, a great deal of morphological diversity is missed if the old terminology and identifications are used. The identification of snout bones proposed in Chapter 2 is utilized here.

The bones of the snout are not the only series that requires reevaluation and recoding. The identification of the bones on the lateral side of the skull roof that bear the otic canal also require reevaluation before characters involving these bones are coded and analyzed. As Schultze (2008) and Wiley (2008) point out, attention to the homoligization of structures and terminology is necessary and important when attempting to construct hypotheses of relationships. Though actinopterygians are the focus of this chapter, sarcopterygians are used as the outgroup and so, it is important to consider the condition of sarcopterygians fishes as well. The identification of the dermopterotic, supratemporal, intertemporal, tabular, and dermosphenotic bones must be clarified.

Dermopterotic and supratemporotabular—The homology of the actinopterygian dermopterotic is problematic. In actinopterygian nomenclature, the term dermopterotic is commonly used to refer to the otic canal bearing bone that is located lateral to the postparietal (parietal of actinopterygian nomenclature), with its anterior portion sometimes lateral to the posterior portion of the parietal (frontal of actinopterygian nomenclature) bone (as in Lund and Poplin, 1997; Coates, 1999; Poplin and Lund, 2002; Mickle et al., 2009). This bone has also been referred to as a supratemporotabular bone, using sarcopterygian nomenclature (Jollie, 1962). Using this term suggests that the bone is the result of the fusion of the supratemporal and tabular, or take the place of the bones that are separate in the majority of sarcopterygians (ibid.). Jollie (1986) refers to the bone identified here as a dermopterotic as an intertemporo-supratemporotabular bone; suggesting a fusion of the intertemporal, supratemporal, and tabular bones that are separate in some sarcopterygians. Gardiner and Schaeffer (1989) said that developmental work by Pehrson (1922, 1944, 1947) and Jollie (1980) support the assertion that two bone primordial form the single dermopterotic bone in actinopterygians and that this single bone represents a fusion of the supratemporal and tabular bones. Gardiner and Schaeffer (1989) and Coates (1999) considered the dermopterotic to have evolved independently numerous times within actinopterygians. Character 5 in Coates (1999) dealing with the supratemporal bone describes a fusion of the supratemporal and tabular bones as resulting in the presence of a dermopterotic bone. The supratemporal bone of Arratia and Cloutier (1996, 2004) is equivalent to the dermopterotic of actinopterygian nomenclature.

These previous identifications are based on the hypothesis that the otic canal passes through two bones in actinopterygians and three bones in sarcopterygians. The posterior-most bone in actinopterygians is the bone in question here, whereas the two bones in sarcopterygians are termed the supratemporal and the tabular (Schultze, 2008). As the previously used names suggest, the single bone in actinopterygians was considered to take the place of, or be the result of a fusion of the supratemporal and tabular (and the intertemporal in the case of Jollie, 1986), or a loss of one or more of these bones.

These hypotheses were made prior to the discovery and description of *Meemannia eos* (Zhu et al., 2006), an early sarcopterygian with two bones bearing the otic canal (Fig. 6B). The posterior-most bone in this series was identified by Zhu et al. (2006) as a supratemporotabular bone. The presence of two bones bearing the otic canal in the early sarcopterygian *Meemannia* and early actinopterygians such as *Dialipina* and *Cheirolepis canadensis* suggests that the arrangement of a two bones bearing the otic canal is primitive for osteichthyans (Schultze, 2008). Since the posterior-most otic canal bearing bone in *Meemannia* occupies the space of the supratemporal and tabular bones in later sarcopterygians, the single bone in *Meemannia* can be considered homologous to these bones and can be referred to as a supratemporotabular following the sarcopterygian nomenclature (Schultze, 2008). This single supratemporotabular bone can divide to form two bones—the supratemporal and the tabular in advanced sarcopterygians (Schultze, 2008).

In terms of actinopterygians, the posterior-most bone bearing the otic canal lateral to the parietal/postparietal bone must be reconsidered in light of the description of *Meemannia.* Instead of the primitive condition being shown by sarcopterygians with three otic canal bearing bones, the condition of *Meemannia* and the basal actinopterygians *Dialipina salgueiroensis and*

Cheirolepis canadensis (Fig. 6) suggests that the osteichthyan condition is to have two bones bearing the otic canal (Schultze, 2008). The posterior-most bone could divide independently in sarcopterygians and actinopterygians (Schultze, 2008). Naming this bone an intertemporo-supratemporotabular, supratemporotabular, or supratemporal in actinopterygians is based on the presence of three bones in higher sarcopterygians, and that two bones fuse to form a single bone in actinopterygians. *Meemannia* contradicts this and brings to light a problem with the present terminology.

Sarcopterygians with more than two bones bearing the otic canal were described prior to *Meemannia.* Bones in the temporal region were termed the intertemporal, supratemporal, and tabular in sarcopterygians. These terms were then applied to actinopterygians and hypotheses of fusions or losses explained how there can be fewer bones in some actinopterygians than sarcopterygians. The description of *Meemannia* suggests that the osteichthyan condition is two bones bearing the otic canal. The posterior-most bone in this series may divide independently in sarcopterygians and actinopterygians. While the use of the term supratemporotabular for *Meemannia* is supported by the fact that this single bone is situated in the location of these bones in other sarcopterygians, the usage of sarcopterygian terminology for actinopterygians can be misleading. The term supratemporotabular has been used previously to suggest that this bone in actinopterygians represents a fusion of these two bones. This is not necessarily the case.

To resolve this, the term dermopterotic/supratemporotabular is used to refer to the posterior-most bone bearing the otic canal in actinopterygians. The term supratemporotabular is still used for the sarcopterygian *Meemannia* because of the information this name holds in regard to comparisons to other sarcopterygians. If there are more than one bone in the place of the dermopterotic/supratemporotabular, these bones are referred to as the supratemporal and tabular bones. Characters dealing with the single bone will refer to a dermopterotic/supratemporotabular. The only sarcopterygian with a single supratemporotabular bone is *Meemannia.* There are separate characters to deal with the bones in sarcopterygians that have resulted from a fragmentation of the supratemporotabular bone.

In sarcopterygians, the supratemporotabular bones can be fragmented to form the supratemporal and tabular bones. These terms are only used to describe bones in sarcopterygians fishes because a fragmentation of the single bone in sarcopterygians is independent from any fragmentation that may have occurred in actinopterygians. Figure 7 details examples of how these bones are identified in actinopterygians and sarcopterygians.

Dermosphenotic and intertemporal bones—As mentioned before, *Meemannia, Dialipina,* and *Cheirolepis canadensis* have two bones that bear the otic canal. The posteriorly placed bone and its subsequent fragmentations have been detailed above, here the anteriorly placed bone that bears the junction of the otic and infraorbital canals, and which is located near the posterodorsal corner of the orbit is discussed. Zhu et al. (2006) identified this bone in *Meemannia* and *Cheirolepis canadensis* as a dermosphenotic, using the actinopterygian nomenclature (Fig. 7B–C). Based on *Meemannia, Dialipina,* and *Cheirolepis canadensis*, it seems that the osteichthyan condition is to have a single bone bearing the junction of infraorbital and otic canals, as well as the horizontal extension of the otic canal in the temporal region (Fig. 7B–D). Like the dermopterotic/supratemporotabular, this bone fragments independently in sarcopterygians and actinopterygians. In sarcopterygians, this bone and its fragmentations are not termed dermosphenotics. In sarcopterygians, this single bone and its fragmentations, is commonly identified as the intertemporal(s) (i.e. Fig. 7A, multiple intertemporal bones in *Powichthys thorsteinssoni*, Jessen (1980)).

Actinopterygian nomenclature is a little more confusing. If two bones bear the junction of the infraorbital and otic canal, and the beginning of the horizontally oriented otic canal, sarcopterygian nomenclature is commonly used. The ventral-most bone is identified as a dermosphenotic and the dorsal bone an intertemporal (see *Limnomis,* Daeschler, 2000; *Cuneognathus gardineri,* Friedman and Blom (2006)). Alternatively, actinopterygian nomenclatural schemes have been applied to other actinopterygians. One actinopterygian nomenclatural scheme identifies the bone in the posterodorsal corner of the orbit as an infraorbital bone and the typically smaller bone (identified as an intertemporal using sarcopterygians nomenclature) as the dermosphenotic (see *Wendyichthys* and *Cyranorhis,* Lund and Poplin (1997); *Aesopichthys,* Poplin and Lund (2000); *Lineagruan* and *Beagiascus*, Mickle et al., 2009). Poplin (2004) proposed that instead of identifying these bones as an infraorbital and dermosphenotic, or a dermosphenotic and intertemporal, these bones should both be identified as dermosphenotic bones—ventral and dorsal dermosphenotic bones. Ventral and dorsal dermosphenotic bones are identified by the presence of the junction of the infraorbital and otic canal, as well as the beginning of a horizontally oriented otic canal.

Here, the actinopterygian nomenclature of a dermosphenotic is used for actinopterygians and sarcopterygians for the homologous intertemporal. The nomenclature scheme proposed by Poplin (2004) of a dorsal and ventral dermopterotic is utilized for actinopterygians. Examples of single dermosphenotic bones and dorsal and ventral dermosphenotic bones in actinopterygians are illustrated in Figure 8.

Frontal/parietal and parietal/postparietal bones

The discrepancies between actinopterygian and sarcopterygians nomenclature schemes regarding the identification of the frontal or parietal and parietal or postparietal bones of the skull roof have been discussed in Chapter 4. In that chapter, both names were given in an attempt to make comparing the newly described fish to previously described actinopterygians easier. Because sarcopterygians and actinopterygians are investigated, there is no reason to be using the actinopterygian terminology of ‘frontal’ and ‘parietal’ bones. Here, terminology based on homology is used so the skull roofing bones are referred to as parietal and postparietal (Schultze, 2008; Wiley, 2008). It should be noted that here, the term ‘parietal’ refers to the bone identified as ‘frontal’ by many researchers working on actinopterygians, and the term ‘postparietal’ is used to refer to the ‘parietal’ bone of many actinopterygian workers. An attempt has been made to clarify in the character descriptions what the traditional actinopterygian names would be as well.

Goals

The goal of this chapter is to address some of the problems that may have lead to different hypotheses of relationships for lower actinopterygian fishes. Here, results from phylogenetic analyses performed on the largest pool of actinopterygian taxa to date, are presented. In these analyses, the ingroup contains actinopterygian taxa that range from the Devonian to the Recent. The ingroup contains a high percentage of Carboniferous fishes because the Carboniferous is the time when the first radiation of ‘palaeoniscoid’ fishes occurred (Janvier, 1996). The character matrix is a compilation of previously published matrices, with the addition of new characters. Characters involving the bones of the snout and bones carrying the otic canal are coded following the new terminology presented in Chapter 2 and this chapter. For the first time, Bayesian methodologies are used to investigate the relationships of Paleozoic lower actinopterygians. Results from Parsimony and Bayesian analyses are compared to each other, as well as to previously published hypotheses. When possible, comments regarding the classification of lower actinopterygians are made.

MATERIALS AND METHODS

Taxon sampling

Eighty-one taxa, consisting of 77 actinopterygians and 4 sarcopterygian outgroup taxa, were included in the analyses presented here. This is the highest number of actinopterygian taxa included in any analysis to date. The actinopterygian fishes range from the Devonian to the recent, with a temporal breakdown of 15 Devonian, 45 Carboniferous, 4 Permian, 9 Mesozoic, and 4 extant fishes. Citations for the coding of these taxa, as well as the sarcopterygians outgroups, are provided in Table 1. A high percentage of the ingroup, approximately 58%, is made up of Carboniferous fishes. This is purposely done because the Carboniferous was the time when the first explosion of actinopterygian diversity, both in terms of the number of species and morphology, occurred (Janvier, 1996). Extant fishes and their fossil allies were included in analyses because of the effect these fishes have on the topology of the tree (Cloutier and Arratia, 2004). These fishes were removed and analyses rerun to determine the effect of these taxa.

Character Descriptions

The character matrix is primarily a revision of and an addition to Cloutier and Arratia's (2004) matrix. Some characters, specifically those that deal with the bones that make up the snout and those that carry the otic canal, have been changed from Cloutier and Arratia (2004) to reflect the newly proposed terminology in Chapter 2 and this chapter. Consequently, some taxa are coded differently than they have been in previous analyses. There are 209 characters that are predominantly focused on features of the dermal bones of the skull. Like Cloutier and Arratia (2004), the character descriptions have been organized and broken down into morphological complexes. For further explanation of the characters or character states, refer to the cited works and character numbers. Because Cloutier and Arratia (2004) was used as a starting point, new characters, or changes made to characters and/or character states from this 2004 matrix are highlighted with italics. Appendix 1 contains the coded matrix but characters and character states are described and discussed below.

Neurocranium

1. Intracranial Joint: (0) present; **(1)** absent. From Cloutier and Ahlberg (1996), character 81; Ahlberg and Johanson (1998), Zhu and Ahlberg (2004), character 71; Zhu and Schultze (2001), character 31; Zhu et al. (2001), Zhu and Yu (2002), character 20; Daeschler et al. (2006), character 50; Long et al. (2006), character 3; Zhu et al (2006), character 24; Friedman (2007), character 19; Zhu et al. (2009), character 21.

Mandibular arch

2. Premaxilla: (0) present; **(1)** absent. *The presence or absence of the premaxillae is regardless of whether or not the bone is separate or part of a complex bone.* From Cloutier and Ahlberg (1996) character 16; Lund et al. (1995), character 2; Poplin and Lund (2000), character 6; Schultze and Cumbaa (2001), character 26; Zhu and Schultze (2001), character 6; Lund and Poplin (2002), character 3 and 4; Cloutier and Arratia (2004), character 9.

3. *Premaxilla*: *(0)* *part of complex bone;* ***(1)*** *separate and distinct bone;* ***(2)*** *premaxilla absent.* Following the definitions detailed in Chapter 2, premaxillae are identified as either being complex or separate bones. A separate premaxillae is an anemestic bone, typically toothed, that is anterior to the maxilla. Modified from Coates (1999), character 13 in part; Lund (2000), character 3; Cloutier and Arratia (2004), character 9; Mickle et al. (2009), character 3 in part.

4. *Complex premaxilla: (0)* *premaxilla is part of a ventral rostro-premaxillo-lachrymal bone;* ***(1)*** *premaxilla is part of a premaxillo-lachrymal bone;* ***(2)*** *premaxilla is part of a ventral rostro-premaxilla;* ***(3)*** *premaxilla is not part of a complex bone-is separate and distinct;* ***(4)*** *premaxilla is entirely absent.* This character has been added to discuss the diversity in complex bones that involve the premaxilla. Definitions of these complex bones can be found in Chapter 2. Modified from Coates (1999), character 13 in part; Lund (2000), character 3 in part; Mickle et al. (2009), character 3 in part. *Onychodus* is coded with a '?' because though it is clear that a canal is present in the premaxilla, Andrews et al. (1997) shows a different trajectory than Long (2001). The type of complex bone cannot be determined.

5. Premaxilla, nasal process: (0) absent; **(1)** present; ***(2)*** *absent because premaxillae absent.* From Coates (1999), character 14; Zhu and Schultze (2001), character 8; Cloutier and Arratia (2004) character 10. *This character is coded regardless of whether the premaxilla is part of a complex bone or is a separate and distinct bone.*

6. Premaxilla contact: (0) abutting medially; **(1)** separated medially; ***(2)*** *premaxilla absent.* From Lund et al (1995), character 2; Lund (2000), character 2; Lund and Poplin (2002) character 3; Cloutier and Arratia (2004), character 13; Friedman and Blom (2006), character 1; Long et al. (2008), character 1; Swartz (2009), character 1. *This character is coded regardless of whether the premaxilla is part of a complex bone or is a separate and distinct bone.*

7. Position of premaxilla in regard to orbit: (0) not part of orbit; **(1)** part of orbit; ***(2)*** *premaxillae absent.* From Cloutier and Ahlberg (1996), character 18; Schultze and Cumbaa (2001), character 27; Zhu and Schultze (2001), character 7; Cloutier and Arratia (2004), character 12; Long et al. (2008), character 55; Mickle et al. (2009), character 2 in part; Swartz (2009), character 9, in part. *This character is coded regardless of whether the premaxilla is part of a complex bone or is a separate and distinct bone.*

8. Relation of premaxilla to lachrymal bone: (0) posterior margin of premaxilla contacts lachrymal bone; **(1)** premaxilla contacts ventral margin of lachrymal bone; **(2)** premaxilla not in contact with lachrymal bone; ***(3)*** *premaxilla part of complex bone with lachrymal;* ***(4)*** *premaxilla absent.* Modified from Dietze (2000), character 37; Schultze and Cumbaa (2001), character 15; Cloutier and Arratia (2004) character 13; Long et al. (2008), character 56.

9. Relation of premaxilla to nasal bone: (0) premaxilla not in contact with nasal bone; **(1)** premaxilla in contact with nasal bone; ***(2)*** *premaxilla absent.* Modified from Dietze (2000), character 34; Cloutier and Arratia (2004), character 14. *This character is coded regardless of whether the premaxilla is part of a complex bone or is a separate and distinct bone.*

10. Premaxillary teeth: (0) teeth present in midline; **(1)** teeth absent in midline; ***(2)*** *premaxillae absent.* Modified from Lund et al. (1995), character 0 in part; Schultze and Cumbaa (2001), character 29; Cloutier and Arratia (2004), character 15. *This character is coded regardless of whether the premaxilla is part of a complex bone or a separate and distinct bone.*

11. Maxilla: (0) present; **(1)** absent. Cloutier and Ahlberg (1996), character 19; Lund (2000), character 30 in part; Schultze and Cumbaa (2001), character 30; Zhu and Schultze (2001), character 53; Cloutier and Arratia (2004), character 16.

12. Anterior end of maxilla: (0) posterior to orbit; **(1)** orbital (i.e. anterior end of maxilla is ventral to the orbit); **(2)** preorbital (i.e. anterior end of the maxilla is located in front of the anterior margin of the orbit) entire maxilla limited to the postorbital region; **(3)** complete maxilla limited to the preorbital region; ***(4)*** *maxilla absent.* Modified from Cloutier and Arratia (2004), character 17. Definitions of character states from Cloutier and Arratia (2004), character 17.

13. Height of the posterior part of the maxilla: (0) low; **(1)** medium; **(2)** high; ***(3)*** *absent.* Heights are determined using the definitions and criteria of Cloutier and Arratia (2004) and Dietze (2000) of dividing the maximum height of the maxilla by its maximum length. Low is a ratio of less than 0.25, medium between 0.25 and 0.35, and high greater than 0.35. From Cloutier and Ahlberg (1996), character 20,21; Schultze and Cumbaa (2001), character 31; Zhu and Schultze (2001), character 54; Lund and Poplin (2002), character 30 in part; Cloutier and Arratia (2004), character 18.

14. Ventral margin of maxilla: (0) straight; **(1)** curved; ***(2)*** *absent.* Following the criteria of Dietze (2000) and Cloutier and Arratia (2004), a straight ventral margin is a maxilla is one where the angle enclosed by the ventral and posteroventral margin of the maxilla does not exceed 5°.

From Dietze (2000), character 26; Schultze and Cumbaa (2001), character 32; Cloutier and Arratia (2004), character 19.

15. Maxillary teeth: (0) present on complete ventral edge of the maxilla; **(1)** present only on the anterior part of the maxilla; **(2)** present only on the maxillary body, absent on the anterior articulatory region; ***(3)*** *no teeth on oral rim of the maxilla;* ***(4)*** *maxilla absent.* Modified from Cloutier and Arratia (2004), character 20.

16. Marginal teeth orientation: (0) vertical; **(1)** forward; **(2)** posteriad; ***(3)*** *marginal teeth absent.* Modified from Lund and Poplin (2002), character 35 in part; Cloutier and Arratia (2004), character 21.

17. Maxilla-preopercular ornamentation: (0) circumferential ridges of ganoine; **(1)** mainly vertical ridges of ganoine; **(2)** mainly tuberculations of ganoine; **(3)** ganoine ridges and tubercles; **(4)** absence of ornamentation on these bones; ***(5)*** *no ganoine present*. Modified from Lund (2000), character 35; Cloutier and Arratia (2004), character 22; Swartz (2009), character 25.

18. Maxilla mobility: (0) not mobile; **(1)** mobile; ***(2)*** *maxilla absent*. From Lund et al. (1995), character 50; Coates (1999), character 16; Cloutier and Arratia (2004), character 23; Hurley et al. (2006), character 37; Mickle et al. (2009), character 44.

19. Maxilla posterior plate: ***(0)*** *not differentiated;* ***(1)*** *moderate rectangular plate;* ***(2)*** *high rounded plate;* ***(3)*** *high triangular plate;* ***(4)*** *maxilla absent.* From Mickle et al. (2009), character 42.

20. Posterior end of maxilla: ***(0)*** *posterior to the orbit;* ***(1)*** *orbital;* ***(2)*** *preorbital;* ***(3)*** *maxilla absent.* From Lund (2000), character 31; Mickle et al. (2009), character 41.

21. Posteroventral process of the maxilla: ***(0)*** *absent;* ***(1)*** *slightly developed process;* ***(2)*** *strong process;* ***(3)*** *maxilla absent.* From Lund (2000), character 33; Mickle et al. (2009), character 43.

22. Maxillary teeth: ***(0)*** *marginal, acrodont;* ***(1)*** *pleurodont;* ***(2)*** *mesial surface of maxilla;* ***(3)*** *teeth absent;* ***(4)*** *small tubular teeth on bone;* ***(5)*** *maxilla absent.* From Mickle et al. (2009), character 48.

23. Maxilla: ***(0)*** *separate bone, no canal;* ***(1)*** *bearing canal, complex bone with infraorbitals;* ***(2)*** *maxilla absent.* The identification of the maxilla as a complex bone (maxillary-infraorbital) in *Polypterus* is done following the developmental data and subsequent identifications of Pehrson 1947 and 1958.

24. Supramaxilla: (0) absent; **(1)** present. From Coates (1999), character 17; Cloutier and Arratia (2004), character 24; Hurley et al. (2006), character 40; Mickle et al. (2009), character 49.

25. Adductor mandibulae fossa: (0) rear of mandible; **(1)** most of mandible. Other terms for the adductor mandibulae fossa include ‘maxilla mandibular fossa’ (Lund, 2000), ‘maxillary fossa of the mandible’ (Lund and Poplin, 2002). From Lund (2000), character 32; Lund and Poplin (2002), character 34; Cloutier and Arratia (2004), character 25.

26. Splenial: (0) present; **(1)** absent as an independent bone. From Zhu and Schultze (2001), character 85; Cloutier and Arratia (2004); character 26.

27. Surangular: (0) absent; **(1)** present. From Gardiner and Schaeffer (1989), character 7; Taverne (1997), character 4; Cloutier and Ahlberg (1996), character 93 in part; Coates (1999), character 18; Zhu and Schultze (2001), character 93; Cloutier and Arratia (2004), 27.

28. Anterior end of the prearticular: (0) far from symphysis; **(1)** near symphysis. From Schultze and Cumbaa (2001), character 38; Zhu and Schultze (2001), character 93; Cloutier and Arratia (2004), character 28.

29. Condition of the prearticular: (0) prearticular in contact with the dentary; **(1)** prearticular not in contact with the dentary. From Cloutier and Ahlberg (1996), character 96; Schultze and Cumbaa (2001), character 39; Zhu and Schultze (2001), character 94; Cloutier and Arratia (2004), character 29.

30. Dentition on coronoid bones: (0) broad tooth field; **(1)** narrow marginal tooth rows **(2)** single tooth row; ***(3)** no coronoid bones*. Modified from Cloutier and Ahlberg (1996), character 10; Zhu and Schultze (2001), character 91; Cloutier and Arratia (2004), character 30.

31. Coronoid process: (0) absent; **(1)** present. From Coates (1999), character 19; Lund (2000), character 34; Poplin and Lund (2000), character 20; Lund and Poplin (2002), character 34; Cloutier and Arratia (2004), character 31; Mickle et al. (2009), character 51.

32. Parasymphysial teeth on dentary (0) absent; **(1)** present. Friedman and Blom (2006), character 24; Long et al. (2008), character 24; Swartz (2009), character 22

33. Acrodin caps on teeth: (0) absent; **(1)** present. From Patterson (1982), character 12; Maisey (1986), character N6; Gardiner and Schaeffer (1989), character 2, B1; Cloutier and Ahlberg (1996), character 7; Taverne (1997), character 7; Coates (1999), character 1; Poplin and Lund (2000), character 21; Schultze and Cumbaa (2001), character 35; Zhu and Schultze (2001), character 210; Cloutier and Arratia (2004), character 32; Friedman and Blom (2006), character 25; Long et al. (2008), character 25.

34. Dentary and maxillary teeth: (0) dentary and maxillary teeth organized in two series; **(1)** dentary and maxillary teeth not organized in two series; ***(2)** teeth absent on oral rim.* From Dietze (2000), character 27; Schultze and Cumbaa (2001), character 36; Zhu and Schultze (2001), character 77 in part; Cloutier and Arratia (2004), character 33.

***35. Phyllodont tooth plates: (0)** absent; **(1)** present.* Modified from Lund (2000), character 37; Mickle et al. (2009), character 54.

Skull Roof

36. Ganoine ornamentation of skull roofing bones: (0) dense; **(1)** moderate; **(2)** little or absent; ***(3)** no ganoine present*. Criteria taken from Cloutier and Arratia (2004); dense is if more than 80% of the total surface of the skull roofing bones are covered by ridges and tubercles of ganoine; moderate is if 80-50% is covered; little or absent if less than 50% is covered. From Cloutier and Arratia (2004), character 34.

37. Preparietal relative length: (0) short; **(1)** elongated. Schultze and Cumbaa (2001), Zhu and Schultze (2001), and Cloutier and Arratia (2004) define the preparietal portion of the skull roof as the bones anterior to the anterior margin of the parietal (frontal of actinopterygian nomenclature). The postparietal region is short if is less than 20% the distance between the anterior part of the snout and the posterior margin of the extrascapulars (Cloutier and Arratia, 2004). From Schultze and Cumbaa (2001), character 67, Zhu and Schultze (2001), character 4; and Cloutier and Arratia (2004), character 35.

38. Snout shape: (0) blunt rounded; **(1)** sharp bump; ***(2)** elongated*; **(3)** notch; **(4)** sharp; **(5)** beak. From Lund (2000), character 8 in part; Cloutier and Arratia (2004), character 36 in part; Long et al. (2008), character 57 in part; Mickle et al. (2009), character 1 in part.

39. Rostral: (0) present as a distinct bone; **(1)** absent as a distinct bone. From Lund et al. (1995), character 3; Poplin and Lund (2000), character 4; Lund and Poplin (2002), character 5; Cloutier and Arratia (2004), character 37; Mickle et al. (2009), character 4.

40. Rostral condition: (0) *one distinct median bone;* ***(1)*** *part of a complex bone;* ***(2)*** *median and complex bone;* ***(3)*** *two separate and distinct median bones;* ***(4)*** *absent;* ***(5)*** *paired and median bones. See Chapter 2 for a clarification on complex bones involving the rostral bone. Modified from Lund (2000), character 4; Mickle et al. (2009), character 4.*

41. Rostral condition: (0) *single bone;* ***(1)*** *two bones=dorsal and ventral rostrals, ventral rostral is part of a complex bone;* ***(2)*** *two bones=dorsal and ventral rostrals, both are separate and distinct bones;* ***(3)*** *rostral(s) absent;* ***(4)*** *paired and median bones. See Chapter 2 for a clarification on complex bones involving the rostral bone.*

42. Position of median rostral: (0) median rostral does not contribute to the jaw margin; **(1)** median rostral does contribute to the jaw margin; ***(2)*** *median rostral absent.* Modified from Cloutier and Ahlberg (1996), character 22; Schultze and Cumbaa (2001), character 28; Zhu and Schultze (2001), character 9; Cloutier and Arratia (2004), character 38; Mickle et al. (2009), character 6 in part. *This character is coded regardless of whether the rostral bone is part of a complex bone or not.*

43. Shape of median rostral: (0) median rostral widens anteriorly; **(1)** equal lengths anteriorly and posteriorly; **(2)** median rostral narrows anteriorly; ***(3)*** *median rostral absent.* Modified from

Dietze (2000), character 32; Schultze and Cumbaa (2001), character 7; Cloutier and Arratia (2004), character 39; Long et al. (2008), character 58.

44. Teeth on rostral: (0) absent; **(1)** present; ***(2)*** *rostral(s) absent*. From Lund et al. (1995), character 4; Lund and Poplin (1997), character 4; Schultze and Cumbaa (2001), character 8; Cloutier and Arratia (2004), character 40.

45. Rostral notch: (0) absent; **(1)** present. From Lund et al. (1995), character 9 in part; Lund (2000), character 9 in part; Poplin and Lund (2000), character 7; Lund and Poplin (2002), character 10 in part; Cloutier and Arratia (2004), character 41; Mickle et al. (2009), character 7 in part.

46. Tuberculated snout: (0) *absent;* ***(1)*** *present. This character specifically refers to the heavy tuberculations seen in some redfieldiids (Schaeffer and McDonald, 1978).*

47. Nasal bone: (0) present; **(1)** absent. From Dietze (2000), character 33 in part; Cloutier and Arratia (2004), character 42.

48. Number of nasal bones: (0) numerous per side; **(1)** two on each side; **(2)** single on each side; ***(3)*** *1 bone + variable tubular bones;* ***(4)*** *nasal bones absent.* Lund et al. (1995), character 10; Taverne (1997), character 11; Lund (2000), character 10; Poplin and Lund (2000), character 8; Schultze and Cumbaa (2001), character 12; Lund and Poplin (2002), character 11; Cloutier and Arratia (2004), character 43; Mickle et al. (2009), character 14. *Paratarrasius hibbardi* and

Tarrasius problematicus has been described as having three nasal bones per side (Taverne, 1996; Lund and Poplin, 2002), two nasal bones per side, two parietal bones per side (Cloutier and Arratia, 2004, character 43), or two nasals per side and a frontal, parietal, postparietal bone (Lund and Melton, 1982). The identification of Lund and Melton (1982) is not used here, but it is difficult to determine if there are two nasal bones and two parietal bones or three nasals bones, one parietal bones. Because of this, *Paratarrasius* and *Tarrasius* are coded as 0/1.

49. Nasal bone notches: (0) nasal bones are not notched for the formation of the medial and lateral nasal openings; **(1)** nasal bones are notched for the formation of the medial and lateral nasal openings; ***(2)** nasal bones absent*. The terminology medial and lateral nasal openings is preferred over the more common names anterior and posterior nasal openings. From Coates (1998), character A5; Poplin and Lund (2000), character 9; Schultze and Cumbaa (2001), character 11; Cloutier and Arratia (2004), character 44; Mickle et al. (2009), character 15.

***50. Nasals notched: (0)** notched on medial and/or lateral borders; **(1)** notched on ventral border; **(2)** nasals not notched; **(3)** nasal bones absent.*

51. Rear of nasal bones: (0) preorbital; **(1)** midorbital; ***(2)** nasal bones absent.* From Lund et al. (1995), character 11; Cloutier and Arratia (2004), character 45. Because of the uncertainty of the number of nasal bones in *Paratarrasius* and *Tarrasius,* this character is coded as 0/1 for these taxa.

52. Postrostral bones: (0) present; **(1)** absent. From Cloutier and Ahlberg (1996), character 23 in part; Lund (2000), character 6 in part; Schultze and Cumbaa (2001), character 9; Zhu and Schultze (2001), character 10; Lund and Poplin (2002), character 7 in part; Cloutier and Arratia (2004), character 47; Friedman and Blom (2006), character 2; Long et al. (2008), character 2; Swartz (2009), character 2. *Identification of postrostral bones is done following the criteria listed in Chapter 2.*

53. Number of postrostral bones: (0) postrostrals are a mosaic of small variable bones; **(1)** two postrostral bones; **(2)** one bone; **(3)** three bones; ***(4)*** *four bones;* ***(5)*** *postrostrals absent.* From Lund et al. (1995), character 7 in part; Cloutier and Ahlberg (1996), character 23 in part; Lund (2000), character 6 in part; Schultze and Cumbaa (2001), character 9; Zhu and Schultze (2001), character 11; Lund and Poplin (2002), character 7 in part; Cloutier and Arratia (2004), character 48; Mickle et al. (2009), character 9 in part. *Identification of postrostral bones is done following the criteria listed in Chapter 2.*

54. Number of postrostral bones: (0) median postrostral; **(1)** paired postrostrals; ***(2)*** *more than 2 bones;* ***(3)*** *postrostral bones absent*. From Lund et al. 1995, characters 6–7 in part; Lund (2000), character 6 in part; Lund and Poplin (2002), character 7 in part; Cloutier and Arratia (2004), character 49; Mickle et al. (2009), character 9 in part.

55. Position of pineal opening: (0) in postrostral area; **(1)** in parietal area (frontal of actinopterygian nomenclature); ***(2)*** *pineal opening absent.* From Lund et al. (1995), character 20; Cloutier and Arratia (2004), character 51; Mickle et al. (2009), character 21.

56. Pineal plate: (0) present; **(1)** absent. From Taverne (1997), character 9; Cloutier and Arratia (2004), character 52.

57. Number of parietal bones: (0) one pair of parietal bones; **(1)** two pair of parietal bones; ***(2)** absent; **(3)** part of a parietal shield*. From Lund and Poplin (2002), character 14; Cloutier and Arratia (2004), character 53; Mickle et al. (2009), character 20. (note-this is the frontal bone of actinopterygian nomenclature) Because of the uncertainty in the identification of the nasal and parietal bones in *Paratarrasius* and *Tarrasius,* this character is coded as 0/1.

58. Contact of parietal bones: (0) parietal contacts the supraorbital; **(1)** parietal does not contact the supraorbital; ***(2)** no supraorbital bones present; **(3)** parietal bone absent.* Modified from Cloutier and Ahlberg (1996), character 34; Schultze and Cumbaa (2001), character 63; Zhu and Schultze (2001), character 23; Cloutier and Arratia (2004), character 54. (Note-this is the frontal bone of actinopterygian nomenclature)For *Paratarrasius hibbardi,* the identification of the parietal bone follows Lund and Poplin (2002) and not Lund and Melton (1982). Regardless of the number of nasal and parietal bones present in *Paratarrasius* and *Tarrasius,* the parietal bone contacts the supraorbital bones and is coded accordingly.

59. Postparietal: (0) without pointed anterolateral process; **(1)** with pointed anterolateral process. From Taverne (1997), character 1; Cloutier and Arratia (2004), character 55. For *Paratarrasius hibbardi*, the identification of the parietal/postparietal bone of Lund and Poplin

(2002) is used rather than the identification of Lund and Melton (1982), this character and subsequent. (Note this bone refers to the parietal bone of actinopterygian nomenclature)

60. Shape of postparietal: (0) long and rectangular; **(1)** squared; **(2)** short and rectangular; ***(3)*** *rounded*. Following the criteria of Cloutier and Arratia (2004), a long and rectangular postparietal is one where the anteroposterior axis is longer than the mediolateral axis; squared is when both axes are equal, and a short rectangular bone is where the mediolateral axis is longer than the anteroposterior axis. From Dietze (2000), character 6; Schultze and Cumbaa (2001), character 69; Cloutier and Arratia (2004), character 56; Friedman and Blom (2006), character 10; Long et al. (2008), character 10 in part; Swartz (2009), character 12. For *Paratarrasius hibbardi,* the identification of the parietal/postparietal bone follows Lund and Poplin (2002). (Note this bone refers to the parietal bone of actinopterygian nomenclature)

61. Relative size of postparietal: (0) postparietal longer than parietal; **(1)** postparietal almost equal to parietal; **(2)** postparietal shorter than parietal (parietal is over two times the length of the postparietal); **(3)** postparietal shorter than parietal (parietal over two times the length of the postparietal). (Note this is the parietal bone of actinopterygian nomenclature, postparietal is the parietal of actinopterygian nomenclature). From Taverne (1997), character 3; Poplin and Lund (2000), character 10; Schultze and Cumbaa (2001), character 70; Lund and Poplin (2002), character 15; Cloutier and Arratia (2004), character 57; Friedman and Blom (2006), character 11; Long et al. (2008), character 11; Swartz (2009), character 13. For *Paratarrasius hibbardi,* the identification of the parietal and postparietal bones follows Lund and Poplin (2002).

62. Contact of postparietal bones: (0) postparietal bones contact lateral extrascapulars; **(1)** postparietal bones do not contact lateral extrascapulars; ***(2)** extrascapulars absent*. From Dietze (2000), character 5; Schultze and Cumbaa (2001), character 71; Cloutier and Arratia (2004), character 59. (Note-this is parietal bone of actinopterygian nomenclature). For *Paratarrasius hibbardi,* the identification of the postparietal bone follows Lund and Poplin (2002) rather than Lund and Melton (1982).

***63. Postparietal: (0)** pair, one bone per side; **(1)** three bones, one bone per side and median; **(2)** postparietal fused to dermopterotic/supratemporotabular; **(3)** present as parietal shield.* (Note this bone refers to the parietal bone of actinopterygian nomenclature)

***64. B bone: (0)** present; **(1)** absent.* From Schultze and Cumbaa (2001), character 72; Zhu and Schultze (2001), character 19.

***65. Extrascapular rows: (0)** one row; **(1)** two separate rows; **(2)** two rows, shared median bone; **(3)** extrascapulars absent.* From Mickle et al. (2009), character 33.

66. Total number of extrascapulars (principal row): (0) three; **(1)** two; **(2)** four; ***(3)** more than four; **(4)** variable; **(5)** absent*. From Lund (2000), character 20 in part; Lund and Poplin (2002), character 21; Cloutier and Arratia (2004), character 60; Friedman and Blom (2006), character 15, in part; Long et al. (2008), character 15 in part; Swartz (2009), character 28 in part.

67. Dermal supraoccipital: (0) absent; **(1)** present. From Lund et al. (1995), character 27; Lund (2000), character 18; Cloutier and Arratia (2004), character 61; Mickle et al. (2009), character 30.

68. Supraorbital bones: (0) present with a supraorbital canal. **(1)** present without supraorbital canal; **(2)** supraorbital bones absent. From Gardiner and Schaeffer (1989), character 14; Coates (1999), character 7; Lund et al. (1995), characters 13, 17; Dietze (2000), character 33 in part; Zhu and Schultze (2001), character 17; Lund and Poplin (2002), character 12 in part; Cloutier and Arratia (2004), character 62; Hurley et al. (2006), character 28.

69. Supraorbital bones: (0) single series; **(1)** double series; ***(2)*** *single bone;* ***(3)*** *supraorbitals absent*. Modified from Lund et al. (1995), character 13 in part; Lund (2000), character 11 in part; Lund and Poplin (2002), character 12 in part; Cloutier and Arratia (2004), character 63; Mickle et al. (2009), character 17. In *Paratarrasius hibbardi,* the bones identified by Lund and Poplin (2002) as sclerotic plates are reidentified here as a second row of supraorbital bones.

70. Dermosphenotic/Intertemporal: (0) absent; **(1)** present. From Cloutier and Arratia (2004), character 64.

71. Dermosphenotic/Intertemporal shape: (0) absent as a distinct bone; **(1)** T-shaped; **(2)** rectangular; **(3)** elongate. *This character takes into account the shape of the single dermosphenotic bone, or the ventral dermosphenotic if there are two dermosphenotics present.* Modified from Gardiner and Schaeffer (1989), character 65; Lund (2000), character 23 in part, Schultze and Cumbaa (2001), character 77; Cloutier and Arratia (2004), character 65; Friedman and Blom (2006), character 54 in part; Long et al. (2008), character 54; Swartz (2009), character 14 in part.

72. Dermosphenotic/Intertemporal contact: ***(0)*** *dermosphenotic absent;* **(1)** contacts nasal bone; **(2)** not in contact with the nasal bone. *This character takes into account the single dermosphenotic bone, or the ventral dermosphenotic if there are two dermosphenotics present.* From Gardiner and Schaeffer (1989), character 19; Coates (1999), character 6; Lund et al. (1995), character 25; Lund (2000), character 17; Dietze (2000), character 14;: Cloutier and Arratia (2004), character 66..

73. Relative size of dermosphenotic/intertemporal: ***(0)*** *dermosphenotic/intertemporal absent;* **(1)** length of dermosphenotic/intertemporal almost equal to the *dermopterotic/supratemporotabular;* **(2)** *dermopterotic/supratemporotabular* longer than the dermosphenotic; **(3)** supratemporotabular more than two times longer than the dermosphenotic; ***(4)*** *dermosphenotic/intertemporal longer than dermopterotic/supratemporotabular. This character takes into account the single dermosphenotic/intertemporal bone, or the ventral dermosphenotic/intertemporal if there are two dermosphenotics present.* From Cloutier and Arratia (2004), character 67.

74. Dermosphenotic/Intertemporal contact: ***(0)*** *dermosphenotic absent*; **(1)** dermosphenotic in contact with the dermohyal; **(2)** dermosphenotic not in contact with the dermohyal ***(3)*** *no dermohyal present.* From Cloutier and Arratia (2004), character 68.

75. Dermosphenotic/Intertemporal number: *(0) no dermosphenotic present*; **(1)** one bone; *(2) two bones-a dorsal and ventral dermosphenotic. Dorsal and ventral dermosphenotic bones are identified following Poplin (2004).* From Dietze (2000), character 13; Schultze and Cumbaa (2001), character 76; Cloutier and Arratia (2004), character 69.

76. Dermopterotic/supratemporotabular: (0) present; **(1)** absent ***(2)*** *present as complex bone with postparietal*. From Gardiner and Schaeffer (1989), character 1; Coates (1999), character 5 in part; Cloutier and Arratia (2004), character 70; Hurley et al. (2006), character 26. (Note here the postparietal bone refers to the parietal bone of actinopterygian nomenclature)

77. Dermopterotic/supratemporotabular contact: (0) not in contact with parietal bone; **(1)** anterior one third of dermopterotic/supratemporotabular bone contacts the parietal bone*;* ***(2)*** *more than 1/3 of dermopterotic/supratemporotabular contacts parietal bone;* ***(3)*** *not applicable, dermopterotic/supratemporotabular absent.* (Note-the parietal bone of this character is homologous to the frontal in actinopterygian nomenclature). For *Paratarrasius hibbardi*, the identification of the parietal bone follows Lund and Poplin (2002) rather than Lund and Melton (1982). Modified from Coates (1999), character 5 in part; Dietze (2000), character 12; Schultze and Cumbaa (2001), character 79; Cloutier and Arratia (2004), character 72.

78. Dermopterotic/supratemporotabular contact: (0) dermopterotic/supratemporotabular not in contact with the operculum; **(1)** dermopterotic/supratemporotabular ventrally in contact with operculum; **(2)** dermopterotic/supratemporotabular ventroposteriorly in contact with operculum;

***(3)** operculum absent; **(4)** not applicable, dermopterotic/supratemporotabular absent.* Modified from Dietze (2000), character 43; Schultze and Cumbaa (2001), character 80; Cloutier and Arratia (2004), character 73.

79. Ventral protuberance off dermopterotic/supratemporotabular: (0) present; **(1)** absent; ***(2)** not applicable, dermopterotic/supratemporotabular absent as a distinct bone.* Modified from Dietze (2000), character 11; Cloutier and Arratia (2004), character 74.

***80. Dermopterotic/supratemporotabular: (0)** separate bones; **(1)** fused to postparietal bone; **(2)** not applicable, dermopterotic/supratemporotabular absent as distinct bone.* (Note here the postparietal bone refers to the parietal bone of actinopterygian nomenclature)

81. Tabular: (0) present; **(1)** absent. From Gardiner and Schaeffer (1989); Lund et al. (1995), character 21; Cloutier and Ahlberg (1996), character 37 in part; Schultze and Cumbaa (2001), character 74; Zhu and Schultze (2001), character 27; Cloutier and Arratia (2004), character 75; Long et al. (2008), character 70; Swartz (2009), character 17.

82. Spiracle shape: (0) angular shape; **(1)** round; **(2)** absent. From Cloutier and Ahlberg (1996), character 38 in part; Schultze and Cumbaa (2001), character 78; Cloutier and Arratia (2004), character 76.

Cheek

83. Cheek fit: (0) tight, abutting; **(1)** thin, overlapping; **(2)** thick, peripheral gaps. From Lund et al. (1995), character 38; Cloutier and Arratia (2004), character 77.

84. Lachrymal/antorbital bone: (0) absent; **(1)** present. From Lund et al. (1995), character 16 in part; Dietze (2000), character 33 in part; Lund (2000), characters 24, 25 in part; Cloutier and Arratia (2004), character 78; Mickle et al. (2009), character 12.

85. Lachrymal/antorbital bone: (0) *part of a complex bone;* ***(1)*** *separate and distinct bone;* ***(2)*** *absent.* Modified from Gardiner and Schaeffer (1989), character 11 A10; Coates (1999), character 13 in part; Lund (2000), characters 24 and 25 in part; Lund and Poplin (2002), character 8 in part; Cloutier and Arratia (2004), character 78 in part; Mickle et al. (2009), character 11 in part.

86. *Lachrymal*/antorbital shape: (0) absent; **(1)** rhombic; **(2)** inverted L; **(3)** vertical pillar; **(4)** triangular; ***(5)*** *rectangular.* From Lund et al. (1995), character 15; Lund (2000), character 25; Poplin and Lund (2000), character 4; Lund and Poplin (2002), character 9; Cloutier and Arratia (2004), character 79; Mickle et al. (2009), character 12.

87. Tectal: (0) present; **(1)** absent. From Lund et al. (1995), character 12 in part; Cloutier and Ahlberg (1996), character 42; Lund (2000), character 12; Zhu and Schultze (2001), character 15; Lund and Poplin (2002), character 13; Cloutier and Arratia (2004), character 80; Mickle et al. (2009), character 18; Swartz (2009), character 8.

88. Postorbital notch in jugal/IO3: (0) absent; **(1)** present. From Cloutier and Arratia (2004), character 81; Friedman and Blom (2006), character 17; Long et al. (2008), character 17; Swartz (2008), character 19. The term jugal is used for sarcopterygians and actinopterygians to refer to the infraorbital bone in the posteroventral corner of the orbit.

89. Jugal/infraorbital 3/posteroventral infraorbital, contact of: (0) contacts suborbital bone(s) posteriorly; **(1)** contacts suborbital bone(s) posterodorsally; **(2)** not in contact with suborbital; ***(3)*** *suborbital bones absent;* ***(4)*** *contacts suborbital ventrally.* From Dietze (2000), character 21 in part; Cloutier and Arratia (2004), character 82. The identification of suborbital bones by Lund and Poplin (2002) in *Paratarrasius hibbardi* is accepted here.

90. Number of infraorbital bones, including lachrymal: (0) two; **(1)** three; **(2)** more than three. Modified from Coates 1998, character A9; Poplin and Lund (2000), character 14; Schultze and Cumbaa (2001), character 25; Cloutier and Arratia (2004), character 83.

91. Number of infraorbital bones ventral to the orbit: (0) *one;* ***(1)*** *two;* ***(2)*** *more than two;* ***(3)*** *just jugal/infraorbital 3/posteroventral infraorbital.*

92. Suborbital bones: (0) absent; **(1)** present. From Gardiner and Schaeffer (1989), character 9; Coates (1999), character 8; Lund et al. (1995), character 37, 39 in part; Lund (2000), characters 26–28 in part; Poplin and Lund (2000), characters 15–17; Schultze and Cumbaa (2001), character 54; Lund and Poplin (1997), character 37; Dietze (2000), character 19; Lund and

Poplin (2002), characters 26–28 in part; Cloutier and Arratia (2004), character 84. The identification of suborbital bones by Lund and Poplin (2002) in *Paratarrasius hibbardi* is accepted here and in subsequent characters.

93. Number of suborbital bones: ***(0)*** *absent;* **(1)** one to three; **(2)** four to six; **(3)** more than 6. Modified from Lund et al. (1995), character 37 in part; Dietze (2000), character 19; Poplin and Lund (2000), character 17; Cloutier and Arratia (2004), character 85; Mickle et al. (2009), character 37 in part.

94. Arrangement of suborbital bones: ***(0)*** *absent;* **(1)** one row; **(2)** two rows; **(3)** many. Modified from Lund (2000), character 26 in part; Lund and Poplin (2002), character 26 in part; Cloutier and Arratia (2004), character 86 in part; Mickle et al. (2009), character 37 in part.

95. Suborbital fit: ***(0)*** *absent;* **(1)** sutured; **(2)** loose with gaps. From Lund (2000), character 27; Lund and Poplin (2000), character 16; Lund and Poplin (2002), character 27; Cloutier and Arratia (2004), character 87; Mickle et al. (2009), character 38.

96. Suborbital contact: ***(0)*** *suborbital bone(s) absent;* **(1)** maxilla not in contact with suborbital bones; **(1)** maxilla contacts suborbital bones. From Lund et al. (1995), character 40; Dietze (2000), character 24; Lund (2000), character 29; Cloutier and Arratia (2004), character 88; Friedman and Blom (2006), character 18; Mickle et al. (2009), character 40 in part.

97. Sclerotic ring: (0) present; **(1)** absent. From Dietze (2000), character 55; Lund and Poplin (2002), character 52 in part; Cloutier and Arratia (2004), character 89.

98. Sclerotic plate number: (0) many; **(1)** four; **(2)** two; ***(3)** three; **(4)** sclerotic ring absent.* Modified from Lund et al. (1995), character 70; Cloutier and Ahlberg (1996), character 49; Lund (2000), character 55; Zhu and Schultze (2001), character 41; Lund and Poplin (2002), character 52; Mickle et al. (2009), character 83; Swartz (2009), character 10 in part.

99. Squamosal: (0) present; **(1)** absent. From Patterson (1982), character 6; Gardiner and Schaeffer (1989), character A11; Coates (1998) character A11; Cloutier and Ahlberg (1996); Schultze and Cumbaa (2001), character 82; Zhu and Schultze (2001), character 63; Lund and Poplin (2002), character 37 in part; Cloutier and Arratia (2004), character 91; Swartz (2009), character 27.

100. Quadratojugal: (0) present; **(1)** absent. From Lund et al (1995), character 47 in part; Cloutier and Ahlberg (1996), character 57 in part; Dietze (2000), character 31; Schultze and Cumbaa (2001), character 83; Zhu and Schultze (2001), character 65 in part; Cloutier and Arratia (2004), character 92; Hurley et al. (2006), character 43 in part; Long et al. (2008), character 61; Swartz (2009), character 26.

101. Quadratojugal size: (0) small; **(1)** large; ***(2)** absent*. From Lund et al. (1995), character 47 in part; Cloutier and Ahlberg (1996), character 57 in part; Schultze and Cumbaa (2001), character 83; Zhu and Schultze (2001), character 65 in part; Cloutier and Arratia (2004), character 93.

102. Platysomid ventral suborbital/quadratojugal: (0) *absent;* ***(1)*** *one large bone, no canal;* ***(2)*** *one large bone with canal.* For descriptions of the platysomid ventral suborbital/quadratojugal, see Mickle and Bader (2009).

103. Postspiracular: (0) present; **(1)** absent. From Cloutier and Ahlberg (1996), character 53; Dietze (2000), character 48; Lund (2000), character 53; Zhu and Schultze (2001), character 61; Lund and Poplin (2002), character 50; Cloutier and Arratia (2004), character 94; Mickle et al. (2009), character 81 in part.

104. Dermohyal *(0)* *absent*; **(1)** single; **(2)** series. From Lund et al. (1995), character 48 in part; Cloutier and Ahlberg (1996), character 52 in part; Dietze (2000), character 41 in part; Lund (2000), character 44 in part; Schultze and Cumbaa (2001), character 2; Zhu and Schultze (2001), character 60; Lund and Poplin (2002), character 41 in part; Cloutier and Arratia (2004), characters 95, 96; Friedman and Blom (2006), character 53; Long et al. (2008), character 53; Mickle et al. (2009), character 62 in part; and Swartz (2009), character 34. The ovoid bone identified by Westoll (1944) as a possible antopercular bone in *Haplolepis ovoidea* is interpreted here as a dermohyal.

105. Supraopercular bone: (0) absent; **(2)** present. From Lund et al. (1995), character 58; Cloutier and Arratia (2004), character 97.

106. Preoperculum: (0) preoperculum without distinct regions; **(1)** preoperculum with distinct anterodorsal and ventral regions; ***(2)*** *absent*. From Gardiner and Schaeffer (1989), character A11; Coates (1998), character A11; Lund et al. (1995), character 42 in part; Lund (2000), character 39 in part; Dietze (2000), character 35; Cloutier and Arratia (2004), character 98; Swartz (2009), character 35.

107. Preoperculum anterodorsal region: (0) subhorizontal; **(1)** subvertical or vertical; ***(2)*** *not applicable, no distinction between anterodorsal and ventral regions;* ***(3)*** *preoperculum absent.* From Cloutier and Arratia (2004), character 99.

108. Angle of the preoperculum: (0) angle between the anterior and ventral portions of the preopercular bone is wider than 90°; **(1)** angle between the anterior and ventral portions of the preopercular bone narrower than 90°; ***(2)*** *not applicable, no distinction between anterodorsal and ventral regions* ***(3)*** *preoperculum absent*. From Dietze (2000), character 40; Cloutier and Arratia (2004), character 100.

109. Number of preopercular bones: (0) one; **(1)** two; ***(2)*** *preoperculum absent*. From Lund and Poplin (2002), character 15; Zhu and Schultze (2001), character 66; Cloutier and Arratia (2004), character 101; Mickle et al. (2009), character 55.

110. Contact of the preoperculum: ***(0)*** *preoperculum contacts dorsal and posterior margins of the maxilla;* ***(1)*** *preoperculum contacts posterior margin of the maxilla;* **(2)** preoperculum not in contact with maxilla; ***(3)*** *preoperculum contacts dorsal margin of maxilla;* ***(4)*** *no maxilla present;* ***(5)*** *preoperculum absent*. Modified from Coates (1999), character 15; Zhu and Schultze (2001), character 66; Cloutier and Arratia (2004), character 102.

111. Anterior contact of the preoperculum: (0) *squamosal;* ***(1)*** *preoperculum contacts suborbitals;* ***(2)*** *preoperculum contacts infraorbitals extensively;* ***(3)*** *no anterior contact;* ***(4)*** *preoperculum absent* ***(5)*** *preoperculum contacts platysomid quadratojugal/suborbital bone. From Mickle et al. (2009), character 59.* The identification of suborbital bones by Lund and Poplin (2002) in *Paratarrasius hibbardi* is accepted here.

112. Preopercular width: (0) *widest anterodorsally;* ***(1)*** *widest midbone;* ***(2)*** *even;* ***(3)*** *cinched in middle;* ***(4)*** *widest anteroventrally;* ***(5)*** *preoperculum absent.*

Opercular Region

113. Gap between operculum and skull roof bones: (0) present; **(1)** absent; ***(2)*** *operculum absent*. From Dietze (2000), character 45; Cloutier and Arratia (2004), character 103.

114. Extent of antopercular bones: (0) *antopercular bones absent;* ***(1)*** *antopercular bones do not extend down to the bottom of the operculum;* ***(2)*** *antopercular bones extend to the bottom of the operculum;* ***(3)*** *antopercular bones extend down to the bottom of the suboperculum;* ***(4)*** *antopercular bones are ventrally placed, are only along the anterior border of the suboperculum;* ***(5)*** *antopercular bones are located on the ventral half of the operculum.* Modified from Dietze (2000), character 56; Schultze and Cumbaa (2001), character 3; Cloutier and Arratia (2004), character 104; Friedman and Blom (2006), character 19; Long et al. (2008), character 19; Mickle et al. (2009), characters 63, 64; Swartz (2009), characters 32, 39 in part.

115. Width of antopercular bones: (0) *antopercular bones absent;* ***(1)*** *antopercular bones have uniform width;* ***(2)*** *antopercular bones widen ventrally;* ***(3)*** *antopercular bones taper ventrally. From Mickle et al. (2009), character 65.*

116. Thickness of antopercular bones: (0) *antopercular bones absent;* ***(1)*** *thickness of antopercular bones same as adjacent bones;* ***(2)*** *antopercular bones extremely thin.* From Mickle et al. (2009), character 66.

117. Interoperculum: (0) absent; **(1)** present. From Gardiner and Schaeffer (1989), character 18; Lund et al. (1995), character 43 in part; Coates (1999), character 10; Cloutier and Arratia (2004), character 105; Hurley et al. (2006), character 47; Mickle et al. (2009), character 71.

118. Operculum: (0) present; **(1)** absent. From Zhu and Schultze (2001), character 103; Cloutier and Arratia (2004), character 106. The operculum is coded as absent in *Acipenser brevirostrum* and *Polydon spathula* following Bemis et al. (1997), Findeis (1997), and Hilton et al. (2011).

119. Shape of operculum: (0) first axis longer than second axis; **(1)** both axes approximately equal; **(2)** second axis longer than first axis; ***(3)*** *operculum absent.* The shape is determined using the criteria of Cloutier and Arratia (2004); the first axis (depth) is determined by the distance between the dorsal part of the operculum and the ventral margin of the operculum; the second axis (width, or length) is defined by the distance between the anterior and posterior margins of the operculum taken perpendicular and at mid-distance from the first axis. From Lund et al. (1995), character 59 in part; Cloutier and Arratia (2004), character 107; Long et al. (2008), character 62.

120. Position of the operculum: (0) operculum located dorsally to preoperculum; **(1)** operculum located posterior to the preoperculum; ***(2)*** *operculum absent.* From Cloutier and Arratia (2004), character 108; Long et al. (2008), character 63; Swartz (2009), character 36.

121. Size of operculum: (0): operculum three times deeper than the suboperculum; **(1)** operculum two times deeper than the suboperculum; **(2)** operculum approximately the same height of the suboperculum; ***(3)*** *suboperculum deeperr than operculum;* ***(4)*** *operculum absent;* ***(5)*** *suboperculum absent.* From Lund et al. (1995), character 60; Lund (2000), character 45; Lund and Poplin (2002), character 43; Cloutier and Arratia (2004), character 109; Long et al. (2008), character 64 in part; Swartz (2009), character 37 in part.

122. Contact of the operculum: (0) not in contact with the lateral extrascapular; **(1)** in contact with the lateral extrascapular; ***(2)*** *operculum absent;* ***(3)*** *extrascapulars absent.* From Dietze (2000), character 4 in part; Cloutier and Arratia (2004), character 110; Long et al. (2008), character 65 in part; Swartz (2009), character 38 in part.

***123. Subopercular upper suture: (0)** horizontal; **(1)** diagonal; **(2)** concave; **(3)** sigmoidal; **(4)** convex; **(5)** suboperculum absent. From Mickle et al. (2009), character 67.*

***124. Subopercular lower suture: (0)** horizontal; **(1)** diagonal; **(2)** concave; **(3)** sigmoidal; **(4)** convex; **(5)** suboperculum absent. From Mickle et al. (2009), character 68.*

125. Branchiostegal rays: (0) present; **(1)** absent; ***(2)** present as a branchiostegal plate*. From Lund et al. (1995), character 62 in part; Cloutier and Ahlberg (1996), character 62; Dietze (2000), character 39; Schultze and Cumbaa (2001), character 87; Zhu and Schultze (2001), character 105; Cloutier and Arratia (2004), character 111; Long et al. (2008), character 71; Swartz (2009), character 41.

126. Branchiostegal rays: (0) between the mandibles; **(1)** not between the mandibles; ***(2)** branchiostegal rays absent.* Modified from Lund et al. (1995), character 61; Lund (2000), character 25; Poplin and Lund (2000), character 25; Lund and Poplin (2002), character 44; Cloutier and Arratia (2004), character 112; Mickle et al. (2009), character 73 in part.

127. Relative size of first branchiostegal ray (branchiostegal ventral to suboperculum): (0) as deep as the second branchiostegal ray; **(1)** deeper than the second branchiostegal ray; ***(2)** branchiostegal rays absent; **(3)** not applicable, only one branchiostegal ray present.* From Lund et al. (1995), character 59; Cloutier and Arratia (2004), character 113; Mickle et al. (2009), character 72.

128. Number of branchiostegal rays, per side: (0) 12 branchiostegal rays of more; **(1)** less than 12 branchiostegal rays; ***(2)** branchiostegal rays absent.* From Coates (1999), character 12; Dietze (2000), character 39; Lund et al. (1995), character 61; Cloutier and Ahlberg (1996), character 63; Zhu and Schultze (2001), character 106; Cloutier and Arratia (2004), character 114; Mickle et al. (2009), characters 73–74 in part.

Gular series

129. Median gular: (0) present; **(1)** absent. From Lund et al. (1995), character 64; Cloutier and Ahlberg (1996), character 66; Coates (1999), character 11; Lund (2000), character 49; Schultze and Cumbaa (2001), character 84; Zhu and Schultze (2001), character 109; Lund and Poplin (2002), character 47; Cloutier and Arratia (2004), character 115.

130. Extralateral gular/submadibula: (0) absent; **(1)** present. From Lund et al. (1995), character 63; Lund (2000), character 48; Poplin and Lund (2000), character 26; Lund and Poplin (2002), character 46; Cloutier and Arratia (2004), character 116; Mickle et al. (2009), character 75.

***131. Placement of extralateral gulars/submandibulae: (0)** extralateral gulars/submandibulae absent; **(1)** extralateral gular/submandibula begins at the anterior most tip of the median gular; **(2)** extralateral gular/submandibula begins at the midpoint of the median gular.*

132. Lateral gular: (0) present; **(1)** absent. From Cloutier and Ahlberg (1996), character 68; Lund and Poplin (1997); Coates (1999), character 11; Lund (2000), character 50; Schultze and

Cumbaa (2001), character 85; Zhu and Schultze (2001), character 111; Lund and Poplin (2002), character 48; Cloutier and Arratia (2004), character 117; Friedman and Blom (2006), character 20 in part.

133. Shape of lateral gular: (0) rounded posterolateral profile; **(1)** posterior and anterior margins angled; ***(2)** lateral gulars absent.* From Coates (1999), character 11; Cloutier and Arratia (2004), character 118; Friedman and Blom (2006), character 20 in part; Long et al. (2008), character 20 in part; Swartz (2009), character 33 in part.

134. Size of lateral gular: (0) lateral gular and branchiostegal rays similarly sized; **(1)** lateral gular larger than branchiostegal rays; ***(2)** lateral gular absent; **(3)** not applicable, branchiostegal rays absent.* From Cloutier and Ahlberg (1996), character 64; Lund (2000), character 50; Schultze and Cumbaa (2001), character 86; Zhu and Schultze (2001), character 107; Cloutier and Arratia (2004), character 119; Mickle et al. (2009), character 77 in part.

Palate

135. Size of parasphenoid: (0) short; **(1)** long. From Lund et al. (1995), character 71; Schultze and Cumbaa (2001), character 51; Zhu and Schultze (2001), character 124; Lund and Poplin (2002), character 53; Cloutier and Arratia (2004), character 121; Mickle et al. (2009), character 84 in part.

136. Buccohypophysial foramen: (0) present; **(1)** absent. From Cloutier and Ahlberg (1996), character 75; Schultze and Cumbaa (2001), character 50; Zhu and Schultze (2001), character 122; Cloutier and Arratia (2004), character 122.

137. Posterior ascending process of parasphenoid: (0) present; **(1)** absent. From Patterson (1982), character 9; Dietze (2000), character 54; Schultze and Cumbaa (2001), character 52; Zhu and Schultze (2001), character 125; Cloutier and Arratia (2004), character 123.

138. Parasphenoid: (0) not sutured to vomer; **(1)** sutured to vomer. From Cloutier and Ahlberg (1996), character 73; Schultze and Cumbaa (2001), character 49; Zhu and Schultze (2001), character 120; Cloutier and Arratia (2004), character 124; Hurley et al. (2006), character 23.

Canals

139. Ethmoid commissure: (0) present; **(1)** absent. From Gardiner and Schaeffer (1989), character A4; Coates (1998), character A4; Lund (2000), character 5; Schultze and Cumbaa (2001), character 5; Zhu and Schultze (2001), character 42; Lund and Poplin (2002), character 6; Cloutier and Arratia (2004), character 125; Mickle et al. (2009), character 8 in part.

140. Trajectory of the ethmoid commissure: (0) through the median rostral; ***(1)** through median ventral rostral;* ***(2)*** sutural course; ***(3)** through bone center of a complex premaxillary bone;* ***(4)** through paired complex bone;* ***(5)** ethmoid commissure absent.* Modified from Lund et al. (1995), character 5; Cloutier and Ahlberg (1996), character 100; Schultze and Cumbaa (2001), character 6; Zhu and Schultze (2001), character 43; Cloutier and Arratia (2004), character 126.

For definitions of ventral rostral bones and complex bones with the premaxilla as a component, see Chapter 2.

141. Trajectory of the ethmoid commissure: (0) across midline; **(1)** not across midline; ***(2)*** *absent*. From Lund et al. (1995), character 5; Lund (2000), character 5; Lund and Poplin (2002), character 6; Cloutier and Arratia (2004), character 127; Mickle et al. (2009), character 8 in part.

142. Trajectory of the supraorbital canal: (0) canal runs anterior to the nasal openings; **(1)** *canal runs between the medial and lateral nasal openings.* From Lund et al. (1995), character 14; Zhu and Schultze (2001), character 44; Cloutier and Arratia (2004), character 128. The terminology has been changed from anterior and posterior nasal openings to medial and lateral nasal openings to better describe the placement of these nasal openings.

143. Trajectory of the supraorbital canal: (0) posterior part of canal is in postparietal bone; **(1)** posterior part of the canal is in the parietal bone; **(2)** posterior part of the canal is in the intertemporal; ***(3)*** *posterior part of canal in dermopterotic/supratemporotabular*. From Lund and Poplin (2002), character 17; Cloutier and Arratia (2004), character 129; Mickle et al. (2009), character 23. (Note here the parietal bone is homologous to the frontal in actinopterygian nomenclature, postparietal the parietal). For *Paratarrasius hibbardi,* the identification of the parietal and postparietal bones follows Lund and Poplin (2002).

144. Supraorbital canal trajectory: (0) not in contact with otic canal; **(1)** in contact with the otic canal. From Cloutier and Ahlberg (1996), character 102; Schultze and Cumbaa (2001), character 65; Zhu and Schultze (2001), character 49; Cloutier and Arratia (2004), character 130.

145. Supraorbital and infraorbital canals: (0) supraorbital and infraorbital canals contact rostrally; **(1)** supraorbital and infraorbital canals do not contact rostrally. From Cloutier and Ahlberg (1996), character 99; Schultze and Cumbaa (2001), character 66; Zhu and Schultze (2001), character 45; Cloutier and Arratia (2004), character 131; Mickle et al. (2009), character 10 in part.

146. Trajectory of the otic canal: (0) three bones; **(1)** two bones; **(2)** one bone. From Lund (2000), character 15; Lund and Poplin (2002), character 16; Cloutier and Arratia (2004), character 132; Mickle et al. (2009), character 25.

147. Profundus canal: (0) absent; **(1)** present. From Lund et al. (1995), character 31; Cloutier and Arratia (2004), character 133.

148. Trajectory of the supratemporal commissure: (0) across midline; **(1)** not across midline. From Lund et al. (1995), character 29; Lund (2000), character 10; Poplin and Lund (2000), character 13; Lund and Poplin (2002), character 20; Cloutier and Arratia (2004), character 134; Mickle et al. (2009), character 31.

149. Trajectory of the supratemporal commissure: (0) only through the extrascapular bones; **(1)** on the skull roof (dermal supraoccipital); ***(2)*** *extrascapulars absent;* ***(3)*** *through extrascapular and postparietal bones.* From Zhu and Schultze (2001), character 52; Lund and Poplin (2002), character 20; Cloutier and Arratia (2004), character 135. (Note here the postparietal bone refers to the parietal bone of actinopterygian nomenclature)

150. Jugal canal: (0) present; **(1)** absent. From Maisey (1986), character N4; Gardiner and Schaeffer (1989), character A12; Lund et al. (1995), character 46; Cloutier and Ahlberg (1996), character 106; Schultze and Cumbaa (2001), character 55; Zhu and Schultze (2001), character 75; Cloutier and Arratia (2004), character 136; Mickle et al. (2009), character 61 in part.

151. Horizontal pit line of preoperculum: (0) absent; **(1)** present. From Gardiner and Schaeffer (1989), character A12; Lund et al. (1995), character 46; Zhu and Schultze (2001), character 72; Lund and Poplin (2002), character 40; Cloutier and Arratia (2004), character 137.

152. Vertical preopercular pit line: (0) present; **(1)** absent. From Lund (2000), character 42; Lund and Poplin (2002), character 39; Cloutier and Arratia (2004), character 138.

153. Preopercular canal: (0) to mid-otic region; **(1)** to postorbital corner; **(2)** to postotic region. From Lund (2000), character 40; Lund and Poplin (2002), character 38; Cloutier and Arratia (2004), character 139; Mickle et al. (2009), character 57.

154. Trajectory of the preopercular canal: (0) preopercular canal ends blindly in half the length of the preoperculum; **(1)** preopercular canal extends from the dorsal part of the cheek to the mandible. From Cloutier and Ahlberg (1996), character 105; Lund (2000), character 41; Schultze and Cumbaa (2001), character 81; Zhu and Schultze (2001), character 74; Cloutier and Arratia (2004), character 140; Mickle et al. (2009), character 58.

155. Mandibular canal trajectory: (0) mandibular canal through dentary; **(1)** mandibular canal not through dentary. From Gardiner and Schaeffer (1989), character A14; Cloutier and Ahlberg (1996), character 110; Coates (1998), character A14; Schultze and Cumbaa (2001), character 43; Zhu and Schultze (2001), character 101; Cloutier and Arratia (2004), character 141.

156. Mandibular canal trajectory: (0) mandibular canal through the posterior infradentary; **(1)** mandibular canal not through the posterior infradentary (surangular). From Cloutier and Ahlberg (1996), character 111; Schultze and Cumbaa (2001), character 44; Zhu and Schultze (2001), character 102; Cloutier and Arratia (2004), character 142.

Pectoral girdle

157. Pectoral fin: (0) lobe based; **(1)** not lobed. From Coates (1999), character 58; Lund (2000), character 61; Cloutier and Arratia (2004), character 143; Friedman and Blom (2006), character 43; Long et al. (2008), character 43; Mickle et al. (2009), character 94 and 95 in part; Swartz (2009), character 51

158. Pectoral fin rays: (0) anteriormost pectoral lepidotrichia segmented proximally; **(1)** anteriormost pectoral lepidotrichia segmented only distally. From Coates (1999), character 60; Cloutier and Arratia (2004), character 144; Friedman and Blom (2006), character 44; Long et al. (2008), character 44 in part.

159. Presupracleithrum: (0) absent; **(1)** present. From Patterson (1982), character 13; Gardiner and Schaeffer (1989), character A13; Lund (2000), character 54; Lund and Poplin (2002), character 51; Schultze and Cumbaa (2001), character 96; Zhu and Schultze (2001), character 160; Cloutier and Arratia (2004), character 145; Friedman and Blom (2006), character 39; Long et al. (2008), character 39; Mickle et al. (2009), character 82; Swartz (2009), character 29.

160. Postcleithrum: (0) present; **(1)** absent. From Gardiner and Schaeffer (1989), character B2; Lund et al. (1995), character 69; Cloutier and Ahlberg (1996), character 112; Dietze (2000), character 46; Poplin and Lund (2000), character 28; Schultze and Cumbaa (2001), character 92; Zhu and Schultze (2001), character 153; Cloutier and Arratia (2004), character 146.

161. Cleithrum number: (0) one; **(1)** two. From Cloutier and Arratia (2004), character 147.

162. Dorsal end of cleithrum: (0) pointed; **(1)** broad and rounded. From Cloutier and Ahlberg (1996), character 115; Schultze and Cumbaa (2001), character 94; Zhu and Schultze (2001), character 164; Cloutier and Arratia (2004), character 148.

163. Posterior process of cleithrum: (0) present; **(1)** absent. From Schultze and Cumbaa (2001), character 95; Zhu and Schultze (2001), character 165; Cloutier and Arratia (2004), character 149.

164. Cleithrum dorsal arm: (0) *narrow;* ***(1)*** *stout and wide.* This character has been added to describe the dorsal arm of the cleithrum in haplolepids.

165. Clavicle: (0) present; **(1)** absent. From Lund et al. (1995), character 66; Coates (1999), character 53; Lund (2000), character 51, 52; Zhu and Schultze (2001), character 167; Lund and Poplin (2002), character 49; Cloutier and Arratia (2004), character 150; Mickle et al. (2009), character 79 in part.

166. Length of clavicle: (0) short; **(1)** elongated; ***(2)*** *clavicle absent.* From Lund (2000), character 52; Cloutier and Arratia (2004), character 151; Mickle et al. (2009), character 79.

167. Clavicle contact: (0) absent; **(1)** short; **(2)** elongate; ***(3)*** *clavicles absent.* From Lund et al. (1995), character 67; Cloutier and Arratia (2004), character 152.

168. Interclavicle: (0) present; **(1)** absent. From Cloutier and Ahlberg (1996), character 118; Dietze (2000), character 47; Schultze and Cumbaa (2001), character 91; Zhu and Schultze (2001), character 170; Cloutier and Arratia (2004), character 153; Mickle et al. (2009), character 80.

Postcranial skeleton

169. Body form: (0) fusiform/elongate; **(1)** deep; **(2)** round; ***(3)** angulated; **(4)** blade-like.* From Lund (2000), character 0; Poplin and Lund (2000), character 1; Lund and Poplin (2002), character 0; Cloutier and Arratia (2004), character 154; Long et al. (2008), character 68 in part; Mickle et al. (2009), character 109; Swartz (2009), character 59 in part.

170. Basal fulcra between dorsal and caudal fins: (0) absent; **(1)** present. From Cloutier and Arratia (2004), character 155; Friedman and Blom (2006), character 47 in part; Long et al. (2008), character 47 in part; Mickle et al. (2009), character 100, in part.

171. Fringing fulcra: (0) absent; **(1)** present. From Dietze (2000), character 51; Coates (1999), character 61; Schultze and Cumbaa (2001), character 90; Cloutier and Arratia (2004), character 156; Friedman and Blom (2006), character 37; Long et al. (2008), character 37; Swartz (2009), character 47.

172. Fringing fulcra: ***(0)** absent*; **(1)** formed by terminal lepidotrichial segments expanded in leading edge of fin; **(2)** formed by terminal expansion and multiple branching of a distal lepidotrichial segment. From Coates (1999), character 61; Cloutier and Arratia (2004), character 157.

173. Basal fulcra anterior to the dorsal fin: (0) absent; **(1)** present. From Patterson (1982), character 19; Cloutier and Arratia (2004), character 158. The definition of basal fulcra sensu Arratia (2008) is used here. Basal fulcra are “large, laterally expanded, paired or unpaired scale-like structures that precede the bases of the median fins or of both paired and median fins… may be lanceolate, leaf-like, or arrow-like in shape. Each fulcrum broadly overlaps the following one" (Arratia, 2008, pg 71)

174. Predorsal scutes/predorsal ridge scales: (0) few; **(1)** many; **(2)** complete to occiput; ***(3)*** *absent.* From Lund (2000), character 65; Poplin and Lund (2000), character 33; Cloutier and Arratia (2004), character 159; Friedman and Blom (2006), character 48; Long et al. (2008), character 48; Mickle et al. (2009), character 99; Swartz (2009), character 54. A scute, also referred to in the literature as a dorsal ridge scale, is identified using the criteria of Arratia (2008) as an "unpaired, elongated structure" that lies "almost horizontally in front of the most anterior rays forming the unpaired fins" (Arratia, 2008, p. 85)

175. Body scale rows to predorsal scutes/dorsal ridge scales: (0) *not applicable, dorsal ridge scales/predorsal scutes absent;* ***(1)*** *one to one;* ***(2)*** *more than one body scale row per predorsal scute/dorsal ridge scale;* ***(3)*** *more than one ridge scale per scale.*

176. Dorsal ridge scales: (0) *no spine/spike;* ***(1)*** *spine shaped;* ***(2)*** *peg-like;* ***(3)*** *absent.*

177. Base of dorsal fin: (0) no specialization; **(1)** scaled lobe; **(2)** guard scales; ***(3)*** *smaller scales*. From Lund (2000), character 60; Poplin and Lund (2000), character 33; Cloutier and Arratia (2004), character 160; Mickle et al. (2009), character 93.

178. Length of dorsal fin: (0) rear of dorsal fin far from caudal fin; **(1)** rear of dorsal fin close to caudal fin; **(2)** rear of dorsal fin merged with caudal fin. From Lund (2000), character 38; Cloutier and Arratia (2004), character 161; Mickle et al. (2009), character 90.

179. Dorsal fin origin: (0) dorsal fin originates behind anal fin; ***(1)** dorsal fin originates at the same level as the anal fin;* ***(2)** dorsal fin originates anterior to anal fin*. From Poplin and Lund (2000), character 36; Cloutier and Arratia (2004), character 162; Friedman and Blom (2006), character 51; Long et al. (2008), character 51 in part; Mickle et al. (2009), character 88; Swartz (2009), character 57 in part.

180. Dorsal fin shape: (0) triangular; **(1)** sigmoidal; **(2)** long, acuminate; **(3)** very high and long; **(4)** long and low; **(5)** short, rounded. From Lund (2000), character 59; Poplin and Lund (2000), character 37; Cloutier and Arratia (2004), character 163; Mickle et al. (2009), 91, 92 in part.

181. Dorsal fin number: (0) two dorsal fins; **(1)** one dorsal fin. From Gardiner and Schaeffer (1989), character A17; Schultze and Cumbaa (2001), character 98; Zhu and Schultze (2001), character 184; Cloutier and Arratia (2004), character 164; Friedman and Blom (2006), character 52; Long et al. (2008), character 52; Mickle et al. (2009), character 86; Swartz (2009), character 58.

***182. Number of dorsal fin rays: (0)** more than 10;* ***(1)** 10 or less;* ***(2)** dorsal finlets.*

183. Pelvic fin: (0) present; **(1)** absent. Cloutier and Arratia (2004), character 165; Friedman and Blom (2006), character 38; Long et al. (2008), character 38 in part; Mickle et al. (2009), character 96 in part; Swartz (2009), character 48 in part.

184. Insertion of pelvic fin: (0) long base; **(1)** short base; **(2)** reduced base; ***(3)*** *pelvic fin absent.* From Gardiner and Schaeffer (1989), character A16; Coates (1998), character A16; (1999), character 64; Lund (2000), character 62; Schultze and Cumbaa (2001), character 99; Cloutier and Arratia (2004), character 166; Friedman and Blom (2006), character 45; Long et al. (2008), character 45; Mickle et al. (2009), character 96 in part; Swartz (2009), character 52.

185. Basal fulcra *and/or scutes* between pelvic and anal fins: (0) absent; **(1)** present. From Cloutier and Arratia (2004), character 167. Friedman and Blom (2006), character 50 in part; Long et al. (2008), character 50 in part; Swartz (2009), character 56 in part. This character has been modified to include both basal fulcra and scutes because of the difficulty in determining if structures are basal fulcra or scute anterior to fins in specimens preserved in lateral view.

186. Anal fin base: (0) anal fin ends far from caudal fin; **(1)** anal fin ends close to caudal fin; **(2)** anal fin merged with caudal fin. From Lund (2000), character 66; Poplin and Lund (2000), character 39; Cloutier and Arratia (2004), character 168; Mickle et al. (2009), character 103.

187. Basal fulcra *and/or scutes* between anal and caudal fin: (0) absent; **(1)** present. From Cloutier and Arratia (2004), character 169; Friedman and Blom (2006), character 49 in part; Long et al. (2008), character 49 in part; Swartz (2009), character 55 in part. See character 185 for a definition of basal fulcra and scutes. This character has been modified to include both basal fulcra and scutes because of the difficulty in determining if structures are basal fulcra or scute anterior to fins in specimens preserved in lateral view.

188. Median neural spines: (0) absent in caudal region; **(1)** present in caudal region. From Coates (1999), character 56; Cloutier and Arratia (2004), character 170; Hurley et al. (2006), character 59.

189. Caudal fin: (0) without hinge line/scale row inversion; **(1)** with hinge line/scale row inversion. From Gardiner and Schaeffer (1989), character A18; Poplin and Lund (2000), character 35; Cloutier and Arratia (2004), character 171; Mickle et al. (2009), character 106 in part. .

190. Shape of caudal fin: (0) heterocercal; **(1)** triphycercal; **(2)** diphycercal; **(3)** hypocercal; ***(4)*** *abbreviated heterocercal*. From Lund (2000), character 63, 64; Schultze and Cumbaa (2001), character 100; Cloutier and Arratia (2004), character 172; Mickle et al. (2009), character 97.

191. Caudal fin rays: (0) *not webbed;* ***(1)*** *webbed. From Lund (2000), character 67; Mickle et al. (2009), character 104.*

192. Caudal outline (0) *cleft equilobate;* ***(1)*** *strongly inequilobate;* ***(2)*** *rounded;* ***(3)*** *pointed;* ***(4)*** *not cleft. From Lund (2000), character 64, Long et al. (2008), character 66 in part; Mickle et al. (2009), character 98.*

193. Epichordal fin rays of caudal fin: (0) present; **(1)** absent. From Cloutier and Ahlberg (1996), character 134; Schultze and Cumbaa (2001), character 101; Zhu and Schultze (2001), character 191; Cloutier and Arratia (2004), character 173.

194. Epichordal fin rays of the caudal fin: (0) short; **(1)** elongated; **(2)** absent. From Coates (1999), character 57; Cloutier and Arratia (2004), character 174.

Scales

195. Scale size: (0) macromeric; **(1)** micromeric. From Long (1988), character 34; Taverne (1997), character 6; Cloutier and Arratia (2004), character 175; Friedman and Blom (2006), character 34; Long et al. (2008), character 34; Swartz (2009), character 44.

196. Shape of scales: (0) “acanthodian” shape; **(1)** rhombic; **(2)** rounded; ***(3)*** *round and rhombic scales present;* ***(4)*** *round base and rhombic.* From Cloutier and Ahlberg (1996), character 3; Zhu and Schultze (2001), character 198; Cloutier and Arratia (2004), character 176; Mickle et al. (2009), character 105 in part.

197. Peg and socket articulation of scales: (0) absent; **(1)** present. From Maisey (1986), character N7; Gardiner and Schaeffer (1989), character 3, A20; Cloutier and Ahlberg (1996), character 4; Coates (1999), character 3; Dietze (2000), character 57; Poplin and Lund (2000), character 30; Schultze and Cumbaa (2001), character 88; Cloutier and Arratia (2004), character 177; Long et al. (2008), character 32; Swartz (2009), character 42.

198. Peg and socket articulation of scales: (0) broad; **(1)** narrow; ***(2)** not applicable, no peg and socket articulation.* From Patterson (1982), character 5; Cloutier and Ahlberg (1996), character 4; Dietze (2000), character 57; Schultze and Cumbaa (2001), character 88; Zhu and Schultze (2001), character 199; Cloutier and Arratia (2004), character 178; Friedman and Blom (2006), character 32.

199. Anterodorsal extension of scale: (0) absent; **(1)** present. From Patterson (1982), character 4; Gardiner (1984), character 1; Gardiner and Schaeffer (1989) character A20; Schultze and Cumbaa (2001), character 89; Zhu and Schultze (2001), character 201; Cloutier and Arratia (2004), character 179; Friedman and Blom (2006), character 33; Long et al. (2008), character 33; Swartz (2009), character 43.

200. Posterior edges of rhombic scales: (0) serrated; **(1)** straight; **(2)** not applicable. From Dietze (2000), character 49; Cloutier and Arratia (2004), character 180.

***201. Ventral edges of scales: (0)** unserrated; **(1)** serrated; **(2)** not applicable serrated.* This character has been added to describe the condition of the new taxon from New Brunswick, Canada.

202. Ganoine: (0) absent; **(1)** present. From Patterson (1982), character 3; Maisey (1986), character N5; Gardiner and Schaeffer (1989), character A3; Cloutier and Ahlberg (1996), character 6; Taverne (1997), character 5; Coates (1998), character A3; Schultze and Cumbaa

(2001), character 4; Zhu and Schultze (2001), character 211; Cloutier and Arratia (2004), character 181; Friedman and Blom (2006), character 30; Long et al. (2008), character 30 in part.

203. Cosmine: (0) *present;* ***(1)*** *absent.* From Cloutier and Ahlberg (1996), character 1; Schultze and Cumbaa (2001), character 105; Zhu and Schultze (2001), character 203.

204. Occipital scale row: (0) absent; **(1)** present. From Lund et al. (1995), character 28; Cloutier and Arratia (2004), character 182.

205. Enlarged postcleithral scales: (0) absent; **(1)** present. From Dietze (2000), character 44; Poplin and Lund (2000), character 29; Cloutier and Arratia (2004), character 183.

206. Flank scales: (0) same size as others; **(1)** deep; ***(2)*** *not applicable, flank scales absent.* From Lund (2000), character 70; Poplin and Lund (2000), character 31; Cloutier and Arratia (2004), character 184; Mickle et al. (2009), character 107.

207. Ventrolateral flank scales: (0) same proportions as others; **(1)** narrow; ***(2)*** *micromeric;* ***(3)*** *shorter;* ***(4)*** *not applicable, flank scales absent.* From Lund (2000), character 71; Poplin and Lund (2000), character 32; Cloutier and Arratia (2004), character 185; Mickle et al. (2009), character 108.

208. Stellate bones in snout: (0) *absent;* ***(1)*** *present.* This character has been added to describe the condition of *Polydon*. From Hilton et al. (2011), character 4;

209. Rhombic scales limit: (0) *extend beyond caudal region;* ***(1)*** *limited to caudal region;* ***(2)*** *rhombic scales absent.* This character has been added to describe the condition in *Acipenser, Chondrosteus, Polydon,* and *Priscosturion.*

Analyses

The character matrix was constructed in Mesquite (Maddison and Maddison, 2010). Parsimony analyses were performed using the Willi Hennig Society edition of the phylogenetic software TNT (Goloboff et al., 2008). *Onychodus* was specified as the outgroup taxon—TNT only allows for one taxon to be designated as the outgroup rather than a suite of taxa. All characters were run unordered and unweighted. Two parsimony analyses were carried out—one with the recent fishes and their fossil allies included, one with these fishes excluded. In both cases, tree searches were performed using the traditional search option with the settings of 1000 replications and the swapping algorithm set to tree bisection reconnection (TBR). Strict/Nelsen consensus trees were generated in TNT. Absolute bootstrap values were generated in TNT for the resulting consensus trees and 10,000 replicates. Trees were rerooted in Mesquite to have all sarcopterygians taxa as the outgroup. Trees and characters supporting the nodes were viewed in Mesquite and Winclada (Nixon, 2002; Maddison and Maddison, 2010).

For the first time, ‘palaeoniscoid’ lower actinopterygian fishes are investigated using Bayesian methodology. Bayesian analyses were performed using MrBayes (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Again, two sets of analyses were performed—one with recent fishes and their fossil allies, one without these fishes. The default settings for standard morphological analyses were employed and analyses were run for

10,000,000 generations. Samples were taken every 1000 generations. FigTree version 1.3.1 (Rambaut, 2009) was used to visualize trees and posterior probabilities of clades. Trees were rooted in FigTree with the sarcopterygians as the outgroup. Fifty percent majority consensus trees are presented here. In order to determine the characters supporting the nodes of the Bayesian tree with all taxa included, all characters were traced across the 50 percent consensus tree by utilizing ancestral state reconstruction methods in Mesquite. Because of the high amount of characters coded as a question mark, the likelihood ancestral state reconstruction method could not be used. The parsimony ancestral state reconstruction method could be used and these results are presented here.

RESULTS

Parsimony analysis, extinct and extant taxa included

When all actinopterygian taxa are included and analyzed, 4 equally parsimonious trees are recovered. A strict consensus tree was generated and discussed here (Figure 9). First, a monophyletic Actinopterygii is recovered (Figure 9, Node 1, Appendix 2) and supported by characters that have previously been considered actinopterygian synapomorphies. Among others, these include the absence of splenial and separate tabular bones, a mandibular canal that passes through the dentary, and the presence of ganoine (Cloutier and Arratia, 2004). The Actinopterygii has a bootstrap value of 52 (Appendix 2). Figure 9 shows that the recent forms and their fossil relatives (Node 2) are separated from the remaining Paleozoic and Mesozoic fossil fishes (Node 9).

Recent fishes and fossil relatives—Extant forms and their fossil allies (Figure 9, Node 2) are recovered sister to the remaining Paleozoic and Mesozoic fishes (Node 10). *Polypterus* is recovered sister to [Chondrostei + Holostei]. This "Recent" fish clade is defined by the characters listed in Appendix 2, which include characters dealing with the premaxilla, surangular, and sclerotic ring. This clade is not supported in terms of characters or support values—the bootstrap value for *Polypterus* + [Chondrostei + Holostei] is zero. Node 3 is the Chondrostei + Holostei, supported by characters dealing with the lateral gulars, branchiostegal rays, supraorbital canal, and a cheek with peripheral gaps (Appendix 2). Again, this clade is not highly supported with a bootstrap value of 8 (Appendix 2). A monophyletic Chondrostei (Node 4) is recovered, supported by characters dealing with the absence of the premaxillary and maxillary bones and incomplete squamation (Appendix 2). The Chondrostei consists of the fossil taxon †*Chondrosteus* + Acipenseriformes. Paleozoic and Mesozoic fossils fishes do not fall within the Chondrostei as classically described (Gardiner, 1967a; Moy-Thomas and Miles, 1971; Carroll, 1988; Nelson, 1994, 2006, Helfman et al., 1997). The Chondrostei is well supported, with a bootstrap value of 99 (Appendix 2)

The Acipenseriformes (Node 5), formed by *Polydon spathula* + *Acipenser brevirostrum*, is recovered and supported by characters dealing with the absence of the operculum, and scale shape (Bootstrap of 55; Appendix 2).

As in Grande (2010), Olsen and McCune (1991), Normark et al. (1991), Kikugawaa et al. (2004), and Chenhong et al., (2008), but contrary to Patterson (1973) and Hurley et al. (2006), the Holostei (i.e. Amiiformes + Lepisosteiformes) is recovered (Node 6). The Holostei is supported by characters dealing with the supramaxillae, infraorbital bones, and the caudal fin shape, but not well supported with a bootstrap value of 26 (Appendix 2). The Amiiformes (Node

7), formed by *Amia calva* + †*Solnhofenamia elongata*, is supported by characters dealing with the postparietal bones, preoperculum, interoperculum, and the absence of the quadratojugal, ganoine, and rhombic scales (Bootstrap of 41; Appendix 2). The Lepisosteiformes (Node 8), *Lepisosteus osseous* + †*Obaichthys decoratus*, is supported by characters dealing with the maxilla, coronoids, dorsal fin, and postcleithral scales (Bootstrap of 48; Appendix 2).

Paleozoic and Mesozoic fossil fishes—Node 9 (Figure 9) includes all Paleozoic and Mesozoic fossil fishes included in the analysis. This node has been named Palaeonisci sensu Berg et al. (1964). The Palaeonisci includes fishes that are traditionally considered advanced Carboniferous forms—the Tarrasiiformes (Node 10) and Guildayichthyiformes (Node 12), as well as the Palaeoniscomorpha (Node 13). The identification of the Palaeonisci should be considered tentative because the character support—dense ganoine ornamentation on the skull roof, branchiostegal rays between the mandible, rectangular shaped lachrymal bone, and a broad and round dorsal end of the cleithrum, is not very strong. This clade is also not strongly supported with a bootstrap value of two (Appendix 2).

The Tarrasiiformes (Node 10) is supported by characters involving the rostral bones, body form, fins, and scales (Bootstrap of 48; Appendix 2). Node 11 is the Palaeonisci minus the Tarrasiiformes. This clade is defined by characters dealing with the presence of postrostral bones and scutes and/or basal fulcra, but no bootstrap support (Appendix 2). Node 12, the Guildayichthyiformes, is defined by numerous characters dealing with the snout, preoperculum, suboperculum, suborbitals, dermal supraoccipital, body form, fins, and more (Appendix 2). This clade is strongly supported in terms of character support and a bootstrap value of 99. Guildayichthyiformes (Node 12) are separated from the Palaeoniscomorpha (Node 13). The placement of Tarrasiiformes and Guildayichthyiformes are discussed more in the discussion section.

A monophyletic Palaeoniscomorpha is recovered (Figure 9, Node 13). Characters supporting this clade are a maxilla with a curved ventral margin, a single nasal bone on each side of the head, the presence of fringing fulcra, and a triangular dorsal fin (Appendix 2). There is no bootstrap support for this node, nor any of the subsequent internal nodes. The Palaeonisciformes contains Devonian, Carboniferous, Permian, and Mesozoic fishes. *Dialipina* is recovered as the basal-most member (Figure 9). The majority of Devonian forms (*Dialipina,* Clades 14–29) are recovered in step-wise branching pattern above the Permocarboniferous and Mesozoic forms (Nodes 30–74). Not all of the clades within the Palaeoniscomorpha are resolved.

The Palaeoniscomorpha minus *Dialipina* (Node 14) could be referred to as the Palaeonisciformes. Palaeonisciformes is defined by the presence of a complex premaxilla, a maxilla with a moderate rectangular posterior plate and a strong posteroventral process, a long and rectangular postparietal bone; a ventral protuberance off the dermopterotic/supratemporotabular, a preoperculum that is widest anterodorsally, a median gular, a cleithrum with a pointed dorsal end, and a caudal fin with a hinge line/scale row inversion (Appendix 2). Many of these characters—specifically dealing with the maxilla and preoperculum, have been used as characters to define palaeoniscoids.

The Cheirolepididae (Figure 9, Node 15) is defined by features of the maxilla, dermosphenotic, preoperculum and maxilla contact, lack of peg and socket articulation, micromeric scales, placement of the dorsal fin, and more (Appendix 2). The Cheirolepididae has a strong bootstrap value of 96. Within the Cheirolepididae, *Cheirolepis trailli* is recovered sister to [*Cheirolepis canadensis + C. schultzei*]. The sister relationship between *Cheirolepis* *canadensis* + *C. schultzei* (Node 16) is supported by characters dealing with the nasal bones, supraorbital bones, and bones bearing the otic canal and a bootstrap value of 16 (Appendix 2). *Cheirolepis schultzei* was recently described (Arratia and Cloutier, 2004) so it has not been included in many analyses. Of the recent analyses that have included *C. schultzei,* only Swartz (2009) has recovered this taxon sister to *Cheirolepis canadensis*. This relationship was not recovered by Cloutier and Arratia (2004, *Cheirolepis* n. sp.) or Long et al. (2008).

The Palaeonisciformes minus the Cheirolepididae (Figure 9, Node 17) is defined by the presence of acrodin caps on teeth, the absence of postrostral and supraorbital bones, contact between the dermosphenotic and nasal bone and the operculum and dermopterotic/supratemporotabular, and unlobed pectoral fins (Appendix 2). One Carboniferous taxon, *Woodichthys bearsdeni* is recovered among the other Devonian fishes, above *Kentuckia.* A monophyletic clade formed by Devonian taxa is not recovered. Some clades that should be discussed in detail include the one uniting *Gogosardinia* and *Mimipiscis* (Node 21). *Gogosardinia* is a recently described fish that has not been included in any published analyses, but the original description notes that it seems most similar to *Mimipiscis* (Choo et al., 2009). This sister relationship is supported here with a bootstrap value of 66.

Donnrosenia schaefferi is recovered sister to *Howqualepis rostridens* (Figure 9, Node 23), a result recovered by Long et al. (2008) but at odds with Friedman and Blom (2006) and Swartz (2009) who recovered a clade of *Howqualepis* + *Tegeolepis.* Swartz (2009) did recover *Donnrosenia schaefferi* sister to *Howqualepis* + *Tegeolepis. Donnrosenia,* described in 2008, was not included in Friedman and Blom's 2006 analysis. Here, the bootstrap value for *Donnrosenia schaefferi* + *Howqualepis rostridens* is 13.

Also at odds with Friedman and Blom (2006) and Swartz (2009) is the recovery of the clade *Stegotrachelus* + *Limnomis* + [*Cuneognathus* + *Melanecta*] (Figure 9, Node 25). Again, *Cuneognathus* is a recently described fish (Friedman and Blom, 2006) that has not been included in many analyses. In the analyses that have included *Cuneognathus*, it is recovered sister to *Limnomis* (Friedman and Blom, 2006; Long, 2008; Swartz, 2009). *Cuneognathus* + *Limnomis* is recovered sister to *Kentuckia* and part of an unresolved polytomy with *Moythomasia* and *Krasnoyarichthys* (Friedman and Blom, 2006), sister to *Limnomis* and not closely related to *Kentuckia* (Long et al., 2008), and above a clade of *Stegotrachelus finlayi* + [*Moythomasia durgaringa* + *M. nitida*] by Swartz (2009). *Krasnoyarichthys* has not been included in the analyses presented here because of the lack of information on the morphology of the head. *Moythomasia durgaringa* has also not been included because the original description is known to be wrong and a redescription by Choo is forthcoming (Choo, 2009; Long et al., 2008). Here, *Stegotrachelus* + [*Limnomis* + [*Cuneognathus* + *Melanecta*]] is basal to *Moythomasia nitida*. *Melanecta* is a Carboniferous fish. There is no bootstrap support for *Stegotrachelus* + *Limnomis* + [*Cuneognathus* + *Melanecta*], but it is supported by characters dealing with the shape of the median rostral and postparietal bones, the lack of a ventral protuberance off the dermopterotic/supratemporotabular, and the absence of a postcleithrum (Appendix 2). Node 26, is supported by characters dealing with the premaxillae and the rostral bone while Node 27, *Cuneognathus* + *Melanecta*, is supported by characters dealing with the maxillary posteroventral process and the preparietal length (Appendix 2). It should be noted that *Melanecta* is a Carboniferous palaeonisciform from Scotland (Coates, 1998). Like the Devonian fish it is recovered with, *Melanecta* lacks suborbital bones (ibid.). In the original description of this taxon, similarities to Devonian fishes are pointed out (Coates, 1998).

Moythomasia nitida and *Osorioichthys* are recovered above all of the other Devonian fishes and below a clade of Permocarboniferous and Mesozoic fishes (Figure 9). This is different from many previous hypotheses that recover *Moythomasia* and *Osorioichthys* in more basal positions below many Devonian genera. *Moythomasia nitida* is recovered in a more basal position by Cloutier and Arratia (2004, fig. 10A, 13B, 14A), and to a lesser extent, Long et al. (2008). *Osorioichthys* has been recovered in a rather basal position, above only the Cheirolepididae, by Friedman and Blom (2006), Long et al. (2008) and Swartz (2009). Taverne (1997) and Coates (1999) have also recovered *Osorioichthys* in a rather basal position in comparison to the other Devonian fishes. It is not at odds with Cloutier and Arratia (2004, figs. 10A, 13A) who recover *Osorioichthys* higher in the tree and above the majority of Devonian forms.

Node 28, *Moythomasia nitida* + [*Osorioichthys marginis* + [all other Palaeonisciformes]], is supported by, among others, characters dealing with the presence of suborbital bones (Appendix 2). *Moythomasia nitida* and *Osorioichthys marginis* are the only Devonian taxa with suborbital bones. The shared presence of these bones between these two Devonian taxa and the remaining Palaeonisciformes is responsible for the higher position of *Moythomasia* and *Osorioichthys* in this analysis.

A clade of Permocarboniferous and Mesozoic fishes, here named Carbopermoichtyidae is recovered at Node 30 (Figure 9). This clade is supported by characters including a square shaped postparietal, absence of a surangular, and more than 1/3 of the dermopterotic/supratemporotabular bone in contact with the parietal bone (Appendix 2). Node 31 includes the Mesozoic *Pteronisculus* recovered sister to a clade of Carboniferous fishes. This node is supported by characters dealing with the premaxillary and lachrymal bones, and the cleithrum (Appendix 2).

Important to note in the clade of Carboniferous forms is the recovery of the Aesopichthyidae (Figure 9, Node 35), supported by characters dealing with the rostral, infraorbital, suborbital, preopercular, and opercular bones, the fins, and scales, and a bootstrap value of 29 (Appendix 2). Node 34 is the Aesopichthyidae + [*'Elonichthys'* + *Mansfieldiscus*]. Node 34 is recovered sister to Node 37, containing a majority of the Bear Gulch Carboniferous fishes.

Node 39 is an unresolved polytomy formed by *Beagisascus, Lineagruan judithi,* and *Lineagruan snowyi* (Figure 9). This is recovered sister to *Coccocephalus* + the newly described *Spinofacia.* Node 40, *Coccocephalus* + *Spinofacia* is supported by characters dealing with features of the dermosphenotic and dermopterotic/supratemporotabular bones and ganoine ornamentation on the skull roofing bones and a bootstrap of 16 (Appendix 2). *Beagisascus, Lineagruan judithi, Lineagruan snowyi* + [*Coccocephalus* + *Spinofacia*] is recovered sister to Node 41, *Cyranhoris* + [*Wendyichthys dicksoni* + *W. lautreci*]. Node 41 is supported by characters dealing with the absence of premaxillary bones, the presence of a rostral notch, and a bootstrap of 26. It should be noted that *Cyranorhis* and *Wendyichthys,* regarded as rhadinichthyids by Lund and Poplin (1997) and Poplin and Lund (2000), are not recovered in the same clade as *Rhadinichthys canobiensis.* This said, the genus *Rhadinichthys* is in need of revision and it cannot be determined if the species included in this analysis will remain within the genus *Rhadinichthys* after a redescription is finished.

Node 43 is composed of other Permocarboniferous and Mesozoic forms (Figure 9). This node is defined by characters dealing with the number of branchiostegal rays, the otic canal trajectory, and the absence of a presupracleithrum (Appendix 2). The Amblypteridae is recovered at Node 44, defined by features of the maxilla, a gap between the operculum and skull roof bones, and a bootstrap of 11 (Appendix 2).

Node 46 is composed of the remaining Permocarboniferous fishes (Figure 9). This node is supported by characters dealing with the premaxilla, dentition, rostral bone, trajectory of the ethmoid commissure, and the size of the pelvic fin (Appendix 2). *Rhadinichthys canobiensis* is recovered sister to *Cycloptychius concentricus* + *Novogonatodus kasantsevae* at Node 47. These taxa are united by characters dealing with the shape of the snout, lachrymal bone, and the upper suture of the suboperculum. It is not highly supported with a bootstrap of 4. Node 48, *Cycloptychius concentricus* + *Novogonatodus kasantsevae,* is also not well supported, with only one character dealing with the height of the posterior portion of the maxilla and a bootstrap value of 2.

Palaeoniscum freieslebeni is recovered sister to the New Brunswick fish + *Gonatodus* + [*Kalops diophrys* + *Kalops monphrys*] at node 49 (Figure 9). This node is supported by characters dealing with features of the supraorbital and dermosphenotic bones (Appendix 2). Node 50, New Brunswick fish + *Gonatodus* + [*Kalops diophrys* + *Kalops monphrys*], is supported by features of the premaxillary bones (Appendix 2). Node 51, *Gonatodus* + [*Kalops diophrys* + *Kalops monphrys*], is supported by features of the premaxillary bones, the shape of the postparietal bones, branchiostegal rays, and a scaled pectoral fin (Appendix 2). Node 52, *Kalops diophrys + K. monophrys* is strongly supported with a bootstrap value of 85 and characters dealing with features of the premaxillary, rostral, nasal, suborbital, and opercular bones, the number of sclerotic plates, and the trajectory of the ethmoid, supraorbital, and supratemporal canals (Appendix 2).

Node 54 recovers the Carboinferous *Mesopoma* with the Triassic [*Boreosomus pivetaeau* +Redfieldiidae] (Figure 9). The two species of *Mesopoma* are unresolved, but *Boreosomus* is recovered sister to the Redfieldiidae (Node 55). *Boreosomus pivetaeau* +Redfieldiidae is defined by features of the nasal bones and the presence of a caudal fin with a cleft equilobate outline. The bootstrap support for this node is not strong with a value of 2. Node 56, the Redfieldiidae, is supported by features of the maxilla and branchiostegal rays, a preoperculum contacting the infraorbital bones, a tuberculated snout, and the trajectory of the supraorbital canal (Appendix 2). The Redfieldiidae is supported with a bootstrap value of 53 (Appendix 2).

The Aeduellidae is recovered as paraphyletic. *Aeduella blainvillei* is recovered sister to *Bourbonnella guilloti* at Node 61 with a bootstrap support of 63 (Figure 9). This node is supported by characters dealing with the shape of the postparietal bones, the absence of a dermohyal and postcleithrum, a lobed based pectoral fin, and the size of the operculum in relation to the suboperculum (Appendix 2). *Aeduella blainvillei* + *Bourbonnella guilloti* is recovered sister to the Haplolepidae (Node 62), supported by characters dealing with the preparietal length, contact between infraorbital and suborbital bones, and branchiostegal rays being absent below the mandible (Appendix 2). The bootstrap support though is low at 6 (Appendix 2).

A monophyletic Haplolepidae (Figure 9, Node 62) is recovered, defined by, among other characters, (Appendix 2) the presence of the pineal opening in the parietal area, features of the preoperculum, number of dorsal fin rays, and the shape of the cleithrum (Appendix 2). Haplolepidae has a high bootstrap value of 85. Node 63, *Parahaplolepis* + *Microhalolepis* also has strong bootstrap support of 69 and is united by characters dealing with features of the maxilla and the fusion of the dermopterotic/supratemporotabular and postparietal bones (Appendix 2).

Bourbonnella jocelynae is recovered sister to the scanilepid *Beishanichthys brevicaudalis* at Node 64 (Figure 9). *Bourbonnella jocelynae* + *Beishanichthys brevicaudalis* is recovered sister to the remaining Aeduellids + Haplolepidae at Node 59. *Bourbonnella jocelynae* and *Beishanichthys brevicaudalis* are united by two characters—a straight ventral margin of the maxilla and the absence of fringing fulcra (Appendix 2). This node has a low bootstrap support of 2. Though not shown here, if *Beishanichthys* is removed from the analysis, *Bourbonnella jocelynae* is recovered sister to *Aeduella blainvillei* + *Bourbonnella guilloti* and a monophyletic Aeduellidae is recovered.

The deep-bodied forms, referred to here as the Platysomidae, are recovered at Node 65, though not strongly supported with bootstrap values (see Appendix 2). Along with a deep body form, this clade is defined by characters dealing with features of the maxilla, preoperculum, dorsal and anal fins, and a lack of suborbital bones (Appendix 2). Important to note is how the genus *Platysomus* is not monophyletic, as suggested by Zidek (1992), Mickle and Bader (2009), and Mickle et al. (2009).

Parsimony analysis, extant and fossil allies excluded

A second parsimony analysis was run with *Acipenser*, †*Chondrosteus*, *Lepisosteus*, †*Obaichthys, Polydon*, *Polypterus,* and †*Solnhofenamia* excluded. Nine parsimonious trees were recovered and a strict consensus tree was generated (Figure 10). Some of the resulting relationships do not change with the exclusion of the recent fishes. Not all character and bootstrap support is not detailed as it was above, refer to Appendix 3 to see these.

As in the first analysis, a monophyletic Palaeonisci is recovered (Figure 10, Node 1). Node 2 consists of *Tarrasius problematicus* + [*Paratarrasius hibbardi* + [Guildayichthyiformes]]. Unlike the first parsimony analysis, a monophyletic Tarrasiiformes is not recovered here. Node 2 is recovered sister to the remaining Permocarboniferous and Mesozoic fishes at node 5. Node 5 is the Palaeoniscomorpha. *Dialipina* is again recovered as the basal most member of the Palaeoniscomorpha. The Cheirolepididae (Node 7) is recovered, with *Cheirolepis canadensis* again being recovered sister to *C. schultzei* (Node 8). Like the previously discussed analysis, the Devonian forms are recovered in a step-wise pattern. Also as in the first parsimony analysis, *Donnrosenia* is recovered sister to *Howqualepis* (Node 12) and *Gogosardinia* is recovered in a clade with *Mimipiscis toombsi* (Node 14).

One difference between this analysis and the previous analysis deals with the relationships of the Devonian *Cuneognathus, Limnomis,* and *Stegotrachelus* and the Carboniferous *Melanecta.* When recent fishes are excluded, *Cuneognathus* is recovered sister to [*Limnomis* + *Stegotrachelus*] (Figure 10, Node 16). The sister relationship of [*Cuneognathus* + *Melanecta*] is not recovered. Instead, when recent taxa are excluded, *Melanecta* is recovered sister to the Devonian [*Moythomasia* + *Osorioichthys*] at Node 25.

A monophyletic Redfieldiidae is recovered here as well at Node 23 (Figure 10). As in the previous analysis, the Redfieldiidae is part of a clade of *Mesopoma* + [*Boreosomus* + *Redfieldiidae*]. Unlike the previous analysis, the relationships of the two *Mesopoma* species are resolved. *Mesopoma planti* is recovered sister to [*Mesopoma carracki* + [*Boreosomus* + Redfieldiidae]] (Node 20).

Node 28 (Figure 10) includes the same taxa as Node 31 (Figure 9) in the first parsimony analysis, but the interrelationships of these taxa differ between the two analyses. There is a lack of resolution in the tree when recent fishes are excluded. Like the first analysis, *Beagiascus, Lineagruan judithi,* and *Lineagruan snowyi* are recovered in a polytomy at Node 30. Unlike the first analysis, *Cyranorhis, Wendyichthys dicksoni,* and *W. lautreci* also form a polytomy (Figure

10). Also different is the placement of *Pteronisculus.* Here, *Pteronisculus* is recovered sister to *'Elonichthys' palatinus* (FIugre 10, Node 37).

There is a loss of resolution at Node 41 as well. The relationships between *Rhadinichthys, Novogonatodus,* and *Cycloptychius* were resolved in the first parsimony tree (Figure 9), but are unresolved in this tree (Figure 10).

Another difference between this tree and the tree recovered when all taxa were analyzed revolves around *Beishanichthys. Beishanichthys* was recovered sister to *Bourbonnella joceylnae* when all taxa were included. Here, *Beishanichthys* is recovered sister to *Palaeoniscum* (Figure 10, Node 37).

A monophyletic Amblypteridae is recovered again (Figure 10, Node 43). Unlike the analysis that included the recent fishes, a monophyletic Aeduellidae is recovered here at Node 47. *Bourbonnella jocelynae* is recovered sister to *Aeduella blainvillei* + *Bourbonnella guilloti.* As in Poplin and Dutheil (2005), the genus *Bourbonnella* is paraphyletic. The Aeduellidae is recovered sister to a monophyletic Haplolepidae (Node 46).

As in the parsimony analysis that includes recent fishes (Figure 9), the deep bodied fishes are recovered in a clade (Figure 10, Node 51). The genera *Platysomus* and *Amphicentrum* are again recovered as paraphyletic. *Ebenaqua* is again recovered sister to *Platysomus gibbosus* and *Platysomus schultzei* again sister to *P. swaffordae.*

Bayesian analysis, extinct and extant taxa included

As in the parsimony analyses, two sets of Bayesian analyses were performed. Both sets of Bayesian recover the majority of the Permocarboniferous and Mesozoic fishes in a large polytomy. This polytomy is similar to what is recovered in the parsimony trees if nodes with no bootstrap support are collapsed. The differences between the trees from the two types of analyses are discussed, as are some important similarities.

Recent fishes and fossil relatives—The resulting hypothesis of relationship recovered from Bayesian analysis with all taxa included is presented in Figure 11. Posterior probabilities are also presented on this tree. . Appendix 4 has the characters supporting the nodes recovered through ancestral state reconstruction. The Actinopterygii is recovered with a posterior probability of 81%. Characters recovered supporting this node include the absence of splenial bones and the presence of acrodin caps on teeth, the mandibular canal through the dentary, and ganoine (Appendix 4). Unlike the parsimony tree, the Actinopteri, or actinopterygians minus *Polypterus,* is recovered with a posterior probability of 57%. Characters supporting the Actinopteri include characters dealing with the branchiostegal rays, presence of a single nasal bone, and an unlobed pectoral fin (Appendix 4). The Actinopteri is a polytomy formed by a strongly supported Chondrostei (posterior probability of 100%), Holostei (posterior probability of 75%) and the Palaeonisci (posterior probability 72%). The relationships between the Palaeonisci and the Holostei and Chondrostei are not resolved.

Paleozoic and various Mesozoic fossil fishes—Among others, the Palaeonisci shares characters dealing with features of the maxilla, nasal bones, branchiostegal rays, suborbital bones, fringing fulcra, scutes/ridges scales, and the caudal fin (Appendix 4). Within the Palaeonisci, there are strongly supported clades. The relationships among these clades are not resolved and the Palaeonisci is a large polytomy. One big difference between the results of the parsimony analyses and the Bayesian analysis that includes all of the taxa, is the recovery of a clade of all the Devonian genera, minus *Dialipina* (Figure 11). This clade is supported with a posterior probability of 83%. This clade is supported by characters dealing with the presence of a premaxillo-lachrymal bone, a T-shaped dermosphenotic, a preoperculum with a subhorizontal anterodorsal region, and other characters presented in Appendix 4. One Carboniferous taxon, *Woodichthys bearsdeni,* is recovered in this clade of Devonian taxa. *Woodichthys* was also recovered among the Devonian taxa in the parsimony analyses (Figures 9–10).

There are similarities regarding the hypothesized relationships of the Devonian taxa between this analysis and the parsimony analyses. Again, the Cheirolepididae is recovered and strongly supported with a posterior probability of 100%. Like the parsimony analyses, *Cheirolepis canadensis* is recovered sister to *C. schultzei* (Figures 9–11). The Cheirolepididae is recovered sister to *Kentuckia.* Again, *Donnrosenia schaefferi* is recovered sister to *Howqualepis rostridens* (Figures 9–11). Here though, *Donnrosenia schaefferi* + *Howqualepis rostridens* is recovered sister to Cheirolepididae + *Kentuckia* (Figure 11). The Bayesian tree presents *Cuneognathus gardineri* sister to a clade of *Limnomis delaneyi +Stegotrachelus finlayi,* a result recovered in the parsimony analysis with recent fishes excluded (Figures 10–11). As in both sets of parsimony analyses, *Gogosardinia coatesi* is recovered sister to *Mimipiscis toombsi* (Figures 9–11). Characters recovered at these nodes are presented in Appendix 4.

Within the Palaeonisci clade, there is a clade that consists of the Aeduellidae + Haplolepidae. As in the parsimony analysis with recent fishes excluded, the Aeduellidae is monophyletic but the genus *Bourbonnella* is paraphyletic (Figures 10–11). Both Bayesian and parsimony analyses have recovered *Microhaplolepis* sister to *Parahaplolepis,* and [*Haplolepis* + [*Microhaplolepis* + *Parahaplolepis*]] (Figures 9–11). The Aeduellidae, Haplolepidae, and [Aeduellidae + Haplolepidae] are all strongly supported with posterior probabilities of 85, 100, and 99, respectively.

Not all of the deep bodied fish are recovered in one clade as in the parsimony analyses. The relationships of many deep-bodied taxa such as *Paramesolepis, Cheirodopsis, Platysomus superbus,* and *P. striatus* to the other taxa are unresolved (Figure 11). The remaining deep-bodied fishes are recovered in a clade where *Platysomus* is again recovered as paraphyletic, and [*Ebenaqua* + *Platysomus gibbosus*] is recovered sister to [*Platysomus schultzei* + *Platysomus swaffordae*]. *Amphicentrum* is also recovered as paraphyletic.

A clade of [*Palaeoniscum* + [*Beishanichthys* + [*Gonatodus* + New Brunswick fish]]] + [*Rhadinichthys* + [*Cycloptychius* + *Novogonatodus*]] is recovered with a posterior probability of 92%. Characters recovered supporting this clade include characters dealing with features of the premaxilla, rostral bones, and the ethmoid commissure (Appendix 4). *Rhadinichthys* + [*Cycloptychius* + *Novogonatodus*] was recovered by the parsimony analysis with recent taxa included (Figure 9). Here, this clade is supported with a posterior probability of 94% (Figure 11).

A clade that includes a majority of the Bear Gulch fishes is recovered. This clade, [*Beagiascus* + [*Lineagruan judithi* + *L. snowyi*]] + [*Coccocephalus* + *Spinofacia*] + [*Cyranorhis* + [*Wendyichthys dicksoni* + *W. lautreci*]] is well supported with a posterior probability of 99% (Figure 11). Recovered character supporting this clade include charaters dealing with features of a separate lachrymal bone, presence of extralateral gulars, and the margins of the suboperculum (Appendix 4). Many of these taxa were unresolved in the parsimony analyses (Figures 9–10).

The tarrasiids *Paratarrasius* and *Tarrasius* are recovered in a clade, the Tarrasiidae, sister to *Kalops monophrys* and *Kalops diophrys* (Figure 11). *Kalops* and the Tarrasiidae are united by characters dealing with separate and distinct premaxillary bones, features of the rostral, supraorbital, lachrymal, and suborbital bones, and the presence of lobed pectoral fins (Appendix 4). In parsimony analysis with all taxa included, the tarrasiids were recovered as part of the

Palaeonisci but separate from the Palaeonisciformes (Figure 9). In the parsimony analysis with the recent fishes excluded, the tarrasiids were paraphyletic with *Tarrasius problematicus* + [*Paratarrasius hibbardi* +[Guildayichthyiformes]] (Node 2, Figure 10). *Kalops* was not recovered as sister to the tarrasiids in any other analysis here, but *Kalops* was recovered sister to [Tarrasiidae + Guildayichthyidae] by Cloutier and Arratia (2004, figures 10B, 11B, 12B, 13A–C, 14B).

The Guildayichthyidae is recovered as monophyletic and strongly supported with a posterior probability of 100%. The relationships of the guildayichthyids to the other fishes are not resolved. The Aesopichthyidae are also recovered as monophyletic, but the relationships of these fishes to the others in the ingroup are not resolved as well. The Aesopichthyidae is strongly supported with a posterior probability of 99% (Figure 11). Characters supporting both of these clades are presented in Appendix 4.

The Redfieldiidae has been recovered in both Bayesian and parsimony analyses. Like both parsimony analyses, the Bayesian analysis with recent fishes included recovered Redfieldiidae sister to *Boreosomus* (Figures 9–11). This association is supported by characters dealing with the nasal bones and the caudal fin (Appendix 4). As in the parsimony analysis with recent fishes excluded (Figure 10), the Bayesian analysis with all taxa included recovers [*Boreosomus* + Redfieldiidae] in a clade of [*Mesopoma planti* + [*Mesopoma carracki* + [*Boreosomus* + Redfieldiidae]]]. This is supported by characters dealing with features of the premaxilla, maxilla, and suborbital bones (Appendix 4). The relationships among the species of *Mesopoma* were unresolved in the parsimony analysis with the recent taxa (Figure 9). Here, the Redfieldiidae, [*Boreosomus* + Redfieldiidae], and *Mesopoma planti* + [*Mesopoma carricki*] +

[*Boreosomus* + Redfieldiidae] all have high posterior probabilities of 100, 96, and 100, respectively.

The Amblypteridae is recovered in the Bayesian analysis, but here *Guntherichthys* is recovered as an amblypterid (Figure 11). The Amblypteridae including *Guntherichthys* is supported by characters dealing with the premaxilla forming part of the orbit, a maxilla with a slightly developed posteroventral process, a short preparietal length, two dermosphenotic bones and a small quadratojugal (Appendix 4). This was not recovered in either of the parsimony analyses. The posterior probabilities of *Amblypterus* + *Guntherichthys* and *Paramblypterus* + [*Amblypterus* + *Guntherichthys*] are not very high at 58 and 53, respectively. [*Amblypterus* + *Guntherichthys*] is supported by the presence of moderate ganoine ornamentation on the skull roof, absence of a postcleithrum, rhombic scales with straight posterior edges, and a concave suboperculuar upper suture (Appendix 4).

'Elonichthys' palatinus, Mansfieldiscus sweeti, and Pteronisculus stensioei are recovered in an unresolved polytomy. Parsimony analysis without the recent taxa included resulted in *Mansfieldiscus* + [*'Elonichthys'* + *Pteronisculus*] (Figure 10), whereas when all taxa were included in the parsimony analysis, '*Elonichthys'* was recovered sister to *Mansfieldiscus* (Figure 9)

Canobius elegantulus, *Cheirodopsis geikiei*, *Dialipina salgueiroensis*, *Paramesolepis tuberculata*, *Platysomus striatus*, and *Platysomus superbus* are part of the Palaeonisci, but the relationships between these fishes and the other members of the Palaeonisci are not resolved in this tree (Figure 11).

Bayesian analysis, extant and fossil allies excluded

There are differences between the Bayesian tree that has all the taxa included and the Bayesian tree recovered when the recent fishes are excluded. Because the results of the Bayesian analysis with all taxa included were discussed in depth above, only the differences between the two analyses will be covered here. Figure 12 is the tree investigating the relationships of fossil lower actinopterygian fishes with recent fishes excluded. Posterior probabilities are presented on the tree in Figure 12 as well

A big difference between the two Bayesian trees is the loss of resolution regarding the Devonian taxa in the tree with recent fishes excluded. Unlike the Bayesian tree with all taxa included (Figure 11), the Bayesian tree without the recent forms does not recover a monophyletic clade of Devonian fishes (Figure 12). There are numerous clades of Devonian fishes, but how these clades are related to each other or other fishes included in the analysis is not resolved. Like the other analyses, the Cheirolepididae is recovered and *Cheirolepis canadensis* is recovered sister to *C. schultzei* (Figures 9–12). Like the previously discussed Bayesian analysis, the Cheirolepididae is recovered sister to *Kentuckia* (Figures 11–12). Also similar to the first Bayesian analysis is the recovery of [*Cuneognathus* + [*Limnomis* + *Stegotrachelus*]] + [*Gogosardinia* + *Mimipiscis*] (Figures 11–12). Unlike all of the previously discussed analyses, the relationship between *Donnrosenia* and *Howqualepis* is not recovered in this tree (Figures 9–12). The relationships of these fishes to each other and the other members of the Palaeonisci are unresolved.

Though there is a loss of resolution regarding the Devonian fishes, there is more resolution for the deep-bodied fishes. A clade of all the deep-bodied fishes is recovered (Figure 12). Many of these taxa were unresolved in the other Bayesian tree (Figure 11). Another difference is that the clade of deep-bodied fishes is recovered sister to [Aeduellidae + Haplolepidae] (Figure 12). This is similar to what was recovered in both parsimony analyses (Figures 9–10).

The relationships of *Dialipina, Donnrosenia, Howqualepis, Melanecta, Moythomasia, Osorioichthys, Paramblypterus, Tegeolepis,* and *Woodichthys* to each other and all other taxa within the Palaeonisci are unresolved (Figure 12). This is more than the previously discussed Bayesian tree (Figure 11).

DISCUSSION

Devonian taxa

There are some conflicting results regarding the recovery of the Devonian taxa in the Parsimony and Bayesian analyses. The results of both parsimony analyses and the Bayesian analysis with all taxa included suggest that there is no monophyletic clade containing only Devonian fishes. The parsimony analysis with all taxa included has a step ladder of Devonian forms and the Devonian *Moythomasia nitida* and *Osorioichthys marginis* recovered in a clade with Permocarboniferous and Mesozoic fishes (Node 28, Figure 9). The parsimony analysis with recent fish excluded recovers a step ladder of Devonian forms and *Moythomasia + Osorioichthys* sister to the Carboniferous *Melanecta* and part of a clade of Permocarboniferous and Mesozoic fishes (Node 22, Figure 10).

In the Bayesian analysis excluding recent fishes, there is a lack of resolution regarding the relationships of the Devonian fishes (Figure 12), but in the Bayesian analysis including recent fishes, a clade of Devonian fish (plus one Carboniferous taxon, *Woodichthys)* is recovered (Figure 11).

These results bring into question the worth of analyses that exclude Carboniferous and younger forms and only analyze Devonian fishes. This has recently become a trend—many publications over the last five years have concentrated on Devonian fish only, or have only included a few token Carboniferous taxa (Friedman and Blom, 2006; Long et al. 2008, Swartz, 2009). The justification for this has been that the authors are interested in determining the placement of newly described Devonian fishes amongst previously described Devonian forms (Friedman and Blom, 2006), but it seems that by doing so, more advanced Devonian forms such as *Osorioichthys* are recovered in a basal position above the Cheirolepididae (Friedman and Blom, 2006 figure 8; Long et al., 2008 figure 11A, Swartz, 2009 figure 34). When Carboniferous and younger fishes are included, *Osorioichthys* is recovered higher in the tree (see also Cloutier and Arratia, 2004 figures 10A and B, 14A).

Permocarboniferous forms

There are some clades that are consistently recovered regardless of whether parsimony or Bayesian methodologies are employed, recent taxa and fossil allies are included or excluded, and, not presented here, but when different outgroups are used. Many of these clades have strong bootstrap support and/or high posterior probabilities. These include the recovery of a monophyletic Aeduellidae, Aesopichthyidae, Cheirolepididae, Guildayichthyidae, Haplolepidae, Tarrasiidae, and Redfieldiidae. Some taxa are consistently recovered sister to each other, such as [*Gogosardinia coatesi* + *Mimipiscis toombsi*], [*Donnrosenia* + *Howqualepis*], and [*Ebenaqua ritchiei* + *Platysomus gibbosus*] + [*Platysomus schultzei* + *P. swaffordae*], among others. Consistently recovered clades and their bootstrap support or posterior probabilities are given in Table 2. Important to note is that a supported clade recovered by parsimony analysis is typically recovered by Bayesian analysis as well. The two different methodologies gave similar results in some regards.

The recovery of many of the same clades regardless of methodology and whether or not recent fishes are included in analyses suggests that they should be viewed with some confidence. What are lacking, are strong hypotheses as to how these clades are related to each other. There are no internal nodes with strong support values, and at times, no strong character support. This may be resolved with the addition of more Permocarboniferous taxa. Though this analysis includes the most taxa analyzed to date, there are many genera that have not been included. This point cannot be stressed enough. There are estimated to be over 250 described genera of palaeoniscoid fishes. The analyses presented here include the highest number of fossil lower actinopterygian fishes analyzed to date, nevertheless, ingroup represents less than a quarter of the described genera of palaeoniscoid fishes. It should not be surprising that there is a lack of resolution regarding the interrelationships of these fishes.

On top of that, the analyses presented here typically include one representative species for many genera with multiple species. For instance, there are many species within the genera *Rhadinichthys, Palaeoniscum,* and *Elonichthys.* As pointed out in Chapter 5, these genera are in need of redescription. Such redescriptions may result in the erection of new genera, better described species, and discovery of new characters. All of these improvements may help to resolve the interrelationships of the Permocarboniferous fishes.

Redescriptions of taxa may also lead to improved resolution in another way. Many of the described genera do not have detailed illustrations, photographs, or descriptions. If taxa are coded from the literature, it is impossible to determine if certain features are present or absent and so characters must be coded as unknown with a question mark. Redescriptions of genera could lead to more complete coding of taxa and further resolution, character support, and support values.

The recovery of paraphyletic genera in the analyses presented here also highlights the need for revisionary work. In all the parsimony and Bayesian analyses, the deep bodied genera *Platysomus* and *Amphicentrum* are recovered as paraphyletic (Figures 9–12). The genera *Bourbonnella* and *Wendyichthys* have also been recovered as paraphyletic (Figures 9–12). The recovery of multiple paraphyletic genera brings up the fact that the inclusion of more than one representative species from a genus may be important in recognizing areas in need of reinvestigation.

Guildayichthyiformes and Tarrasiiformes

The Guildayichthyiformes have not been included in many analyses, but the resulting hypotheses of their relationships to other actinopterygians have been drastically different. Likewise, the Tarrasiiformes have been recovered in drastically different positions. To review the previously published analyses, the Guildayichthyiformes have been recovered: sister to the extant *Polypterus* as part of the Cladistia in either a basal position (Lund et al., 1995;) or in the upper part of the tree (Lund, 2000; Mickle et al., 2009); sister to the Tarrasiiformes in the upper part of the tree (Cloutier and Arratia, 2004, fig. 14B, this chapter Fig. 2B), in a clade with the Tarrasiiformes and sister to the recent actinopterygians (Cloutier and Arratia, 2004, fig. 14A, this chapter Fig. 2A); and as a stem neopterygian (Hurley et al., 2006, this chapter Fig. 4). The Tarrasiiformes have also been recovered sister to the Mesozoic *Birgeria* (Lund et al., 1995), closely related to the Polypteriformes (Taverne, 1996, 1997), sister to a clade of the [Cladista + Platysomidae] (Lund, 2000), sister to Cheirolepis + all other investigated palaeoniscoids (Lund and Poplin, 2002), and closely related to the Carboniferous genus *Kalops* (Cloutier and Arratia, 2004, figures 9B, 10B, 11B, 13 BC, 14B, 15B).

Here, when recent fishes are included in parsimony analyses, the Tarrasiiformes and Guildayichthyiformes have been recovered as part of the Palaeonisci, sister to the remaining fossil fishes. The Tarrasiiformes are recovered above the Guildayichthyiformes. When recent fishes are excluded, the Guildayichthyiformes and tarrasiids are again recovered sister to the remaining fossil fishes. In both sets of Bayesian analyses *Discoserra* + *Guildayichthys* is recovered, but the relationships between this clade and the other fishes in the analysis is not resolved (Figures 11–12). The trees presented here give two very different hypotheses to be added to the list of drastically different results regarding the relationships of the guildayichthyiform fishes. It can be said that here, there is no support for the inclusion of the Guildayichthyiformes in the Cladistia, or a close relationship between these fishes and any of the extant fishes. The tarrasiids are recovered sister to *Kalops* in the Bayesian analyses, but the relationships of the Tarrasiidae + *Kalops* to other fishes are not resolved (Figures 11–12).

It should be noted that though guildayichthyids have been included in multiple analyses, the interpretations and coding of these taxa is not consistent across all of these analyses. Hurley et al. (2006) has reinterpreted features of *Discoserra,* including the interpretation of the bones in the snout, skull roof, and otic region. Some of these reinterpretations have been utilized here to code this taxon. Some of Lund (2000) original identifications of some snout and skull roofing bones have been changed here based on the reidentifications of Hurley et al. (2006), as well as personal examination of specimens. On top of this, identification of bones in *Polypterus* also differs from Lund (2000), Mickle et al. (2009), Cloutier and Arratia (2004), and others. Though all of this could explain the differences in the hypothesized relationships of

Guildayichthyiformes to other actinopterygians, it is most likely not a case of simple coding differences. As Cloutier and Arratia noted in their 2004 paper, these fishes drastically change position depending on whether they excluded or included recent fishes and/or taxa and character for which there are large amounts of unknown data. Differences across analyses regarding how characters were coded would not lead to this situation.

Cloutier and Arratia (2004) warned that the recovery of these taxa in a basal position is most likely due to poor taxon sampling. They specifically warned that the lack of advanced and intermediate actinopterygian taxa, specifically Late Paleozoic and Mesozoic forms, was responsible for recovering advanced actinopterygians such as the Guildayichthyiformes and the Tarrasiiformes in a basal position (ibid.). Here, as in Cloutier and Arratia (2004), the Tarrasiiformes and the Guildayichthyiformes are supported by numerous synapomorphies, and have either strong bootstrap support or posterior probabilities. Unfortunately, with the lack of shared characters with the other taxa in the analyses, these advanced fossil fishes are not embedded in the tree (ibid.). This may also explain why some analyses recover these fishes closely related to the polypterids. There may not be a true phylogenetic signal in this recovered relationship, instead these taxa fall out together because they are so different from the other fishes included in the analysis.

In order to better understand the relationships of the Guildayichthyiformes and the Tarrasiiformes to other actinopterygians, analyses that have more Late Paleozoic and Mesozoic taxa in the ingroup are necessary. This will be a large undertaking because it is not as simple as coding additional taxa. Character and character states will need to be revised to be able to adequately handle the changes in morphology that are seen between the Paleozoic and the Mesozoic and questions of homology will also have to be tackled. As for what fishes should be included in the future, more neopterygian fishes need to be included. A vast array of pycnodontiform, halecomorph, macrosemiiform, semionotiform, and basal teleost fishes should be added to analyses. So called ‘subholostean’ fishes must also be considered. This said, the addition of these fishes may not help resolve the relationships of the Paleozoic ‘palaeoniscoid’ fishes.

Palaeonisci

In Chapter 1, the classic definitions and usage of the Chondrostei, Holostei, and Teleostei are discussed. Specifically important here is the Chondrostei. The term Chondrostei originally included the “ganoid” fishes (Müller, 1845). Though this traditional definition was found to be paraphyletic (Patterson, 1982; Lauder and Liem, 1983) and the usage of Chondrostei was restricted to describe the Acipenseridae + Polyodontidae + closely related fossil groups by some scientists, not all workers have let go of the traditional terminology. The Chondrostei defined as Acipenseridae + Polyodontidae + closely related fossil taxa + Paleozoic fossils including ‘palaeoniscoids’ is still commonly used today. This definition was used by Carroll (1988), Nelson (1994, 2006), and Helfman et al. (1997).

Here, there is no support for a Chondrostei in its traditional usage. The Chondrostei sensu Patterson (1982) and Lauder and Liem (1983) is recovered, and strongly supported in both Parsimony and Bayesian analyses. The Chondrostei contains the Acipenseridae, Polyodontidae and closely related fossil taxa, including the genus, which gives the Chondrostei its name, †*Chondrosteus.*

Though it is not a novel result, it is one that should be repeated, especially since the term Chondrostei is still currently used in the traditional sense and in common ichthyology texts (Nelson, 2006; Helfman, 1997). There is no support for the inclusion of Paleozoic fishes within the Chondrostei. The results of the parsimony analysis suggest that the Paleozoic and Mesozoic fossil fishes included in this analysis form a clade, as presented by Cloutier and Arratia (2004, figures 9B, 10B). This clade is referred to here as the Palaeonisci, using the term Berg et al. (1964) coined for many of the families of fossil fishes once lumped into the Chondrostei. The results from the Bayesian analysis also include a clade of Paleozoic and Mesozoic fossil fishes, though the relationship of this clade to the recent fishes is unresolved. The major divisions of actinopterygian fishes seem to include the Cladistia, Chondrostei, Holostei, Teleostei, and Palaeonisci.

Palaeoniscomorpha

A monophyletic Palaeoniscomorpha and Palaeonisciformes have been recovered here by parsimony analyses. This is in agreement with Cloutier and Arratia (2004 figure 10A, 14A). The Palaeoniscomorpha includes *Dialipina,* whereas Palaeonisciformes excludes *Dialipina.* Though there is either no or low bootstrap support, there are characters supporting both the Palaeoniscomorpha and Palaeonisciformes. In the parsimony analysis with recent fishes included, the characters supporting Palaeoniscomorpha deal with the presence of a maxilla with a curved ventral margin, the presence of a single nasal bone on each side of the head, the presence of fringing fulcra, and a triangular dorsal fin (Figure 9, Appendix 2). Some of these characters are features that have been used to describe ‘palaeoniscoids’ (Moy-Thomas and Miles, 1971; Janvier, 1996). The Palaeonisciformes is supported by characters including, among others, the presence of a complex premaxillary bone, a maxilla with a moderate rectangular plate and a strong posteroventral process, a preoperculum that is widest anterodorsally, and a caudal fin with a hinge line (Figure 9, Appendix 2). Again, some of these characters are features that have been traditionally discussed as defining ‘palaeoniscoids’ (Moy-Thomas and Miles; Janvier, 1996).

These results are tentative, but it is interesting that these clades have been recovered as monophyletic. Though support values are not high, there are characters supporting these clades, suggesting that there is phylogenetic signal. Much more work must be done to determine if there is further support for the Palaeonisciformes, Palaeoniscomorpha, and the Palaeonisci. Some of the necessary work is detailed below.

Future Directions

Many genera of Carboniferous fishes must be redescribed. For instance, there are many taxa described, or redescribed, by Agassiz (1833–44), Traquair (1877–1914; 1881), Moy-Thomas and Bradley Dyne (1938), Gardiner (1967). The majority of these descriptions do not include photographs, detailed illustrations, or descriptions of features that have subsequently been found to be important morphological characters. Accordingly, these taxa are either not included in analyses, or if they are, the taxa have many characters coded as unknown regardless of whether or not the information is actually preserved or not. A concerted effort must be made to describe many of the "classic" genera of lower actinopterygian fishes. Redescriptions of these fishes could potentially allow for the addition of further taxa and more confidence in the coding of taxa.

Summary

Elucidating the relationships of lower actinopterygian fishes in general, and the palaeoniscoid fishes specifically, is not an easy task. These fishes are diverse in terms of number of genera and species, as well as morphology. This diversity can be compared to the scale of which is seen for living teleosts today. With this comparison in mind, it is not surprising that strong hypotheses for these fossil lower actinopterygians do not exist.

Here, an attempt was made to include the largest amount of lower actinopterygians in phylogenetic analyses using both parsimony and Bayesian methodologies. While fully resolved and strongly supported trees are not recovered, it is important to note what has been recovered. There are areas of stability across the trees regardless of methodologies used or if recent fishes are included or excluded. This stability suggests that these clades can be viewed with some confidence. The areas of instability are also because important because they signify areas in need of attention in terms of redescriptions, reevaluation of characters, reevaluation of the coding presented here, or taxon sampling. Future work must be concerned with these areas of instability, and in that regard, the unresolved portions of the trees and the areas of conflict among the trees are valuable.

Though not a new result, these trees support the hypothesis that the majority of fossil Paleozoic and Mesozoic fishes cannot be lumped within the Chondrostei. While this commonly accepted amongst fossil fish workers, this has not carried over into the general ichthyology community. It is suggested that the Palaeonisci sensu Berg et al. (1964) may better describe these Paleozoic and Mesozoic fossil forms.

Lastly, a monophyletic Palaeoniscomorpha and Palaeonisciformes are recovered by the parsimony analyses presented here. The Palaeoniscomorpha and Palaeonisciformes are supported by some characters traditionally associated with ‘palaeoniscoid’ fishes. This is an exciting development because it suggests that there is phylogenetic signal within the “wastebasket” of lower actinopterygian ‘palaeoniscoid’ fishes. The recovery of the Palaeoniscomorpha and the Palaeonisciformes is a call for action and future work.

Larger analyses that include a more comprehensive array of Paleozoic, Mesozoic, and recent fishes are necessary. Classic genera must be redescribed and multiple species from these genera need to be included in analyses for the first time. The addition of more taxa is not the magic bullet though. Characters and homology statements must be scrutinized and matrices updated to reflect new information. A better understanding of the osteology and development of extant actinopterygian fishes has the potential to add to our understanding of the extinct forms, as well as our homology statements. With all of this work to be done, the data matrix and hypotheses of relationships presented here need to be looked at as a work in progress.

Table 1—Taxa included in phylogenetic analyses, detailing age and source.

Actinopterygians		
Taxon	**Age**	**Source**
Acipenser brevirostrum	Recent	Hilton et al., 2011
Aeduella blainvillei	Carboniferous	Heyler, 1969; Poplin and Dutheil, 2005
Aesopichthys erinaceus	Carboniferous	Poplin and Lund, 2000
Amblypterus latus	Permian	Dietze, 2000
Amia calva	Recent	Grande and Bemis, 1998
Amphicentrum granulosum	Carboniferous	Bradley Dyne, 1939
Amphicentrum jurgenai	Carboniferous	Zidek,1992
Beagiascus pulcherrimus	Carboniferous	Mickle et al., 2009
Beishanichthys brevicaudalis	Triassic	Xu and Gao, 2011
Boreosomus pivetaeau	Triassic	Nielsen, 1942
Bourbonnella guilloti	Carboniferous	Heyler, 1967; Poplin 2001; Poplin and Dutheil,2005
Bourbonnella jocelynae	Carboniferous	Mickle, 2011
Canobius elegantulus	Carboniferous	Moy-Thomas and Bradley Dyne, 1938
Cheirodopsis geikiei	Carboniferous	Moy-Thomas and Bradley Dyne, 1938
Cheirolepis canadensis	Devonian	Arratia and Cloutier, 1996
Cheirolepis schultzei	Devonian	Arratia and Cloutier, 2004
Cheirolepis trailli	Devonian	Pearson and Westoll, 1979; Arratia and Cloutier, 1996
Chondrosteus acipenseroides	Jurassic	Hilton and Forey, 2009
Coccocephalus wildi	Carboniferous	Poplin and Veran, 1996
Cuneognathus gardineri	Devonian	Friedman and Blom, 2006
Cycloptychius concentricus	Carboniferous	Moy-Thomas and Bradley Dyne, 1938
Cyranorhis bergeraci	Carboniferous	Lund and Poplin, 1997
Dialipina salgueiroensis	Devonian	Schultze and Cumbaa, 2001
Dictyopyge sp.	Triassic	Schaeffer and McDonald, 1978
Discoserra pectinodon	Carboniferous	Lund, 2000
Donnrosenia schaefferi	Devonian	Long et al., 2008
Ebenaqua ritchiei	Permian	Campbell and Phuoc, 1983
'Elonichthys' palatinus	Permian	Schindler, 1993
Gogosardinia coatesi	Devonian	Choo et al., 2009
Gonatodus punctatus	Carboniferous	Gardiner, 1967a
Guildayichthys carnegiei	Carboniferous	Lund, 2000, Hurley et al., 2006
Guntherichthys lehiensis	Carboniferous	Mickle, 2011
Haplolepis corrugata	Carboniferous	Westoll, 1944; Lowney, 1980
Howqualepis rostridens	Devonian	Long, 1988b
Kalops diophrys	Carboniferous	Poplin and Lund, 2002
Kalops monophrys	Carboniferous	Poplin and Lund, 2002
Kentuckia deani	Devonian	Rayner, 1951
Lepisosteus osseus	Recent	Grande, 2010
Limnomis delaneyi	Devonian	Daeschler, 2000
Lineagruan judithi	Carboniferous	Mickle et al., 2009
Lineagruan snowyi	Carboniferous	Mickle et al., 2009
Mansfieldiscus sweeti	Carboniferous	Long, 1988b
Melanecta anneae	Carboniferous	Coates, 1998

Actinopterygians (continued)

Taxon	Age	Source
Mesopoma carricki	Carboniferous	Coates, 1993
Mesopoma planti	Carboniferous	Coates, 1999
Microhaplolepis ovoidea	Carboniferous	Westoll, 1944; Lowney, 1980
Mimipiscis toombsi	Devonian	Gardiner, 1984
Moythomasia nitida	Devonian	Jessen, 1968
New Brunswick fish	Carboniferous	Mickle, Ch. 2
Novogonatodus kasantsevae	Carboniferous	Long, 1988b
Obaichthys decoratus	Cretaceous	Grande, 2010
Osorioichthys marginis	Devonian	Taverne, 1997
Palaeoniscum freieslebeni	Carboniferous	Westoll, 1934 in Aldinger, 1937
Parahaplolepis tuberculata	Carboniferous	Westoll, 1944; Lowney, 1980
Paramblypterus decorus	Carboniferous	Dietze, 2000
Paramesolepis tuberculata	Carboniferous	Moy-Thomas and Bradley Dyne, 1938
Paratarrasius hibbardi	Carboniferous	Lund and Melton, 1982; Lund and Poplin, 2002
Platysomus gibbosus	Permian	Campbell and Phuoc, 1983; Zidek, 1992
Platysomus parvulus	Carboniferous	Moy-Thomas and Miles, 1971
Platysomus schultzei	Carboniferous	Zidek,1992
Platysomus striatus	Carboniferous	Traquair, 1879; Zidek, 1992
Platysomus superbus	Carboniferous	Moy-Thomas and Bradley Dyne, 1938; Zidek, 1992
Platysomus swaffordae	Carboniferous	Mickle and Bader, 2009
Polydon spathula	Recent	Grande and Bemis, 1991
Polypterus bichir	Recent	Allis, 1922; Pehrson, 1947, 1958
Proceramala montanensis	Carboniferous	Poplin and Lund, 2000
Pteronisculus stensioei	Triassic	Nielsen, 1942
Redfieldius gracilis	Triassic	Schaeffer and McDonald, 1978
Rhadinichthys canobiensis	Carboniferous	Moy-Thomas and Bradley Dyne, 1938
Solnhofenamia elongata	Jurassic	Grande and Bemis, 1998
Spinofacia pectinatus	Carboniferous	Mickle, 2011
Stegotrachelus finlayi	Devonian	Swartz, 2009
Tarrasius problematicus	Carboniferous	Taverne, 1996; Lund and Poplin, 2002
Tegeolepis clarki	Devonian	Dunkle and Schaeffer, 1973
Wendyichthys dicksoni	Carboniferous	Lund and Poplin, 1997
Wendyichthys lautreci	Carboniferous	Lund and Poplin, 1997
Woodichthys bearsdeni	Carboniferous	Coates, 1998

Sarcopterygians (Outgroups)

Taxon	Age	Source
Onychodus jandemarrai	Devonian	Andrews et al., 2006; Long, 2001
Miguashaia bureaui	Devonian	Schultze, 1973; Cloutier 1996
Diabolepis	Devonian	Chang and Yu, 1984
Psarolepis romeri	Devonian	Yu, 1998; Zhu et al., 1999

Table 2—Clades recovered in more than one set of analyses and their support values.

Clade	Bootstrap parsimony with recent	Bootstrap parsimony w/o recent	Posterior probability with recent	Posterior probability w/o recent
Cheirolepididae	96	92	100	100
Cheirolepis canadensis + C. schultzei	16	14	99	95
Donnrosenia + Howqualepis	13	14	61	–
Cuneognathus + (Limnomis + Stegotrachelus)	–	4	84	90
Limnomis + Stegotrachelus	–	16	72	80
Gogosardinia + Mimipiscis	66	66	100	99
Chondrostei	99	n/a	100	n/a
Holostei	26	n/a	75	n/a
Amiiformes	41	n/a	93	n/a
Lepisosteiformes	48	n/a	93	n/a
Acipenseriformes	55	n/a	100	n/a
Aeduellidae	–	7	85	83
Haplolepidae	85	85	100	100
Aesopichthyidae	29	28	99	100
Aeduella blainvillei + Bourbonnella guilloti	–	67	98	98
Microhaplolepis + Parahaplolepis	69	70	100	100
Beagiascus + (Lineagruan judithi + L. snowyi)	–	–	100	100
Lineagruan judithi + L. snowyi	–	–	82	84
Coccocephalus + Spinofacia	16	16	98	97
Kalops diophrys + K. monophrys	85	86	95	95
Tarrasiidae	–	–	99	96
Tarrasiiformes	48	–	–	–
Ebenaqua + Platysomus gibbosus	16	18	73	90
Platysomus schultzei + P. swaffordae	27	27	78	86
Gonatodus + New Brunswick fish	–	–	99	98
Haplolepidae + Aeduellidae	–	7	99	99
(*Ebenaqua + Platysomus gibbosus*) + (*Platysomus schultzei + P. swaffordae*)	30	44	72	91
Cheirolepididae + *Kentuckia*	–	–	100	99
Redfieldiidae	53	54	100	100
Redfieldiidae + *Boreosomus*	2	3	96	95
Guildayichthyiformes	99	99	–	–
Guildayichthyidae	–	–	100	100
Cycloptychius + Novogonatodus	2	–	71	72
Rhadinichthys + (*Cycloptychius + Novogonatodus*)	4	–	94	95
Platysomidae	3		–	91
[*Cyranorhis + Wendyichthys dicksoni*] + *W. lautreci*	–		99	99
Cyranorhis + [*Wendyichthys dicksoni + W. lautreci*]	26		–	–

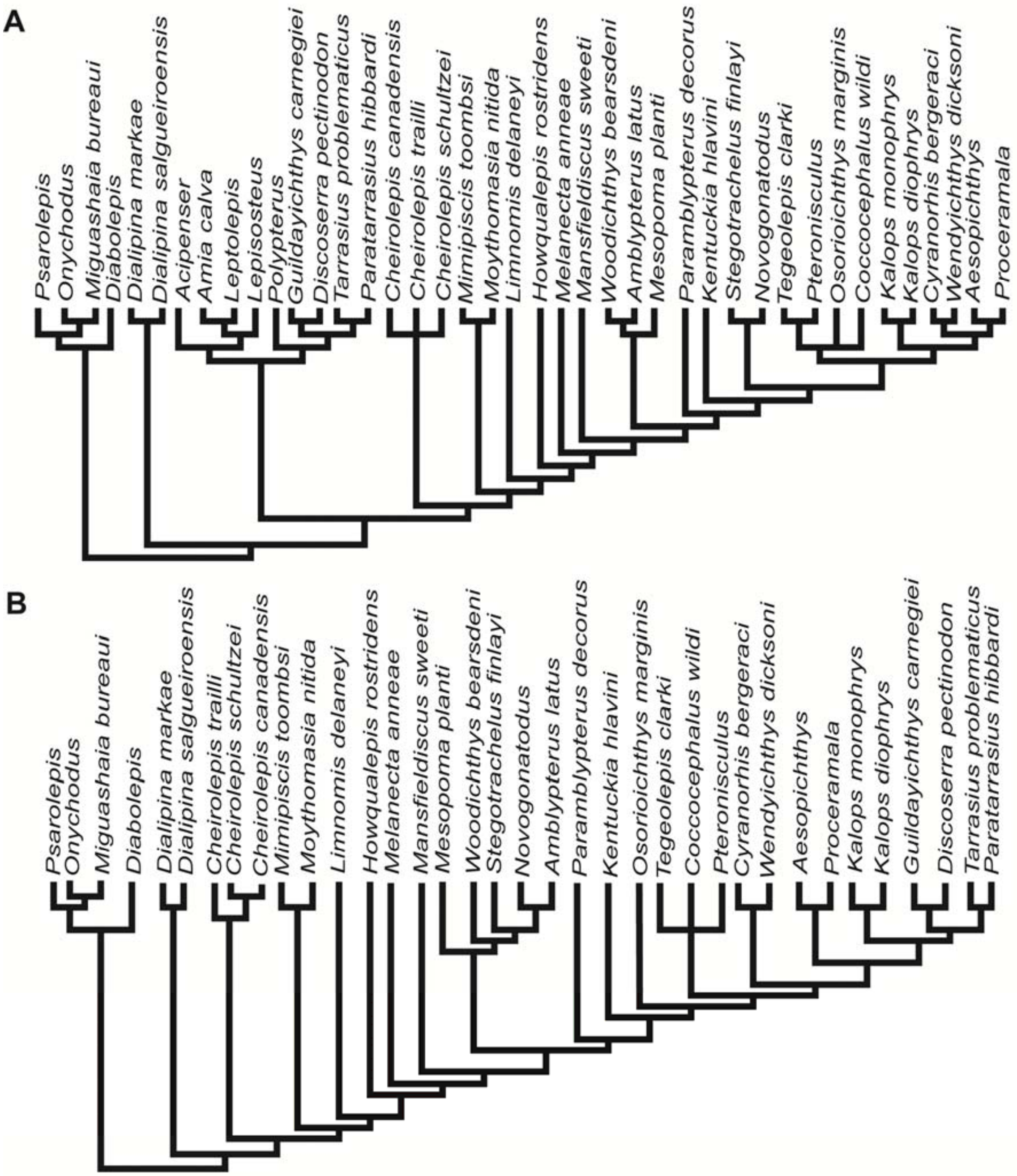


Figure 1—Cloutier and Arratia's (2004) phylogenetic hypotheses of basal actiniopterygians based on 185 characters and employment of sarcopterygians outgroups. **A,** Consensus tree of 110 most parsimonious trees that resulted from analysis of all taxa—extinct and extant (Cloutier and Arratia, 2004, figure 10A). **B,** Consensus tree of 15 most parsimonious trees that resulted after the removal of the advanced actinopterygians *Acipenser, Amia, Lepisosteus, Leptolepis*, and *Polypterus* (Cloutier and Arratia, 2004, figure 10B).

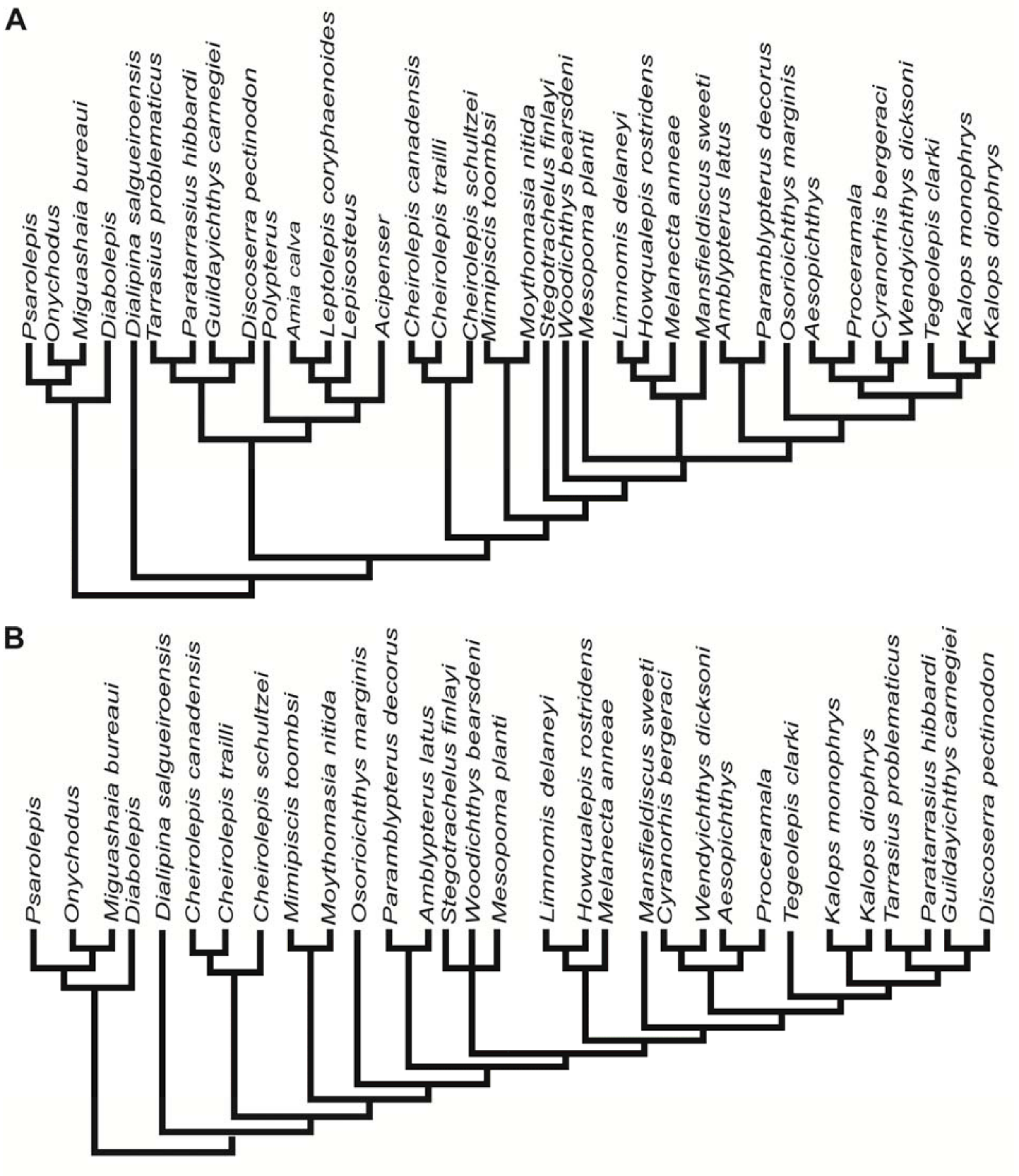


Figure 2—Cloutier and Arratia's (2004) phylogenetic hypotheses of basal actinopterygians based on 185 characters, employment of sarcopterygians outgroups, and the inclusion of only the most complete actinopterygian taxa. A, Consensus tree of the two most parsimonious trees that resulted from the analysis including extinct and extant taxa (Cloutier and Arratia, 2004, figure 14A). B, Consensus tree of the two most parsimonious trees that resulted after the removal of advanced actinopterygians *Acipenser, Amia, Lepisosteus, Leptolepis*, and *Polypterus* (Cloutier and Arratia, 2004, figure 14B).

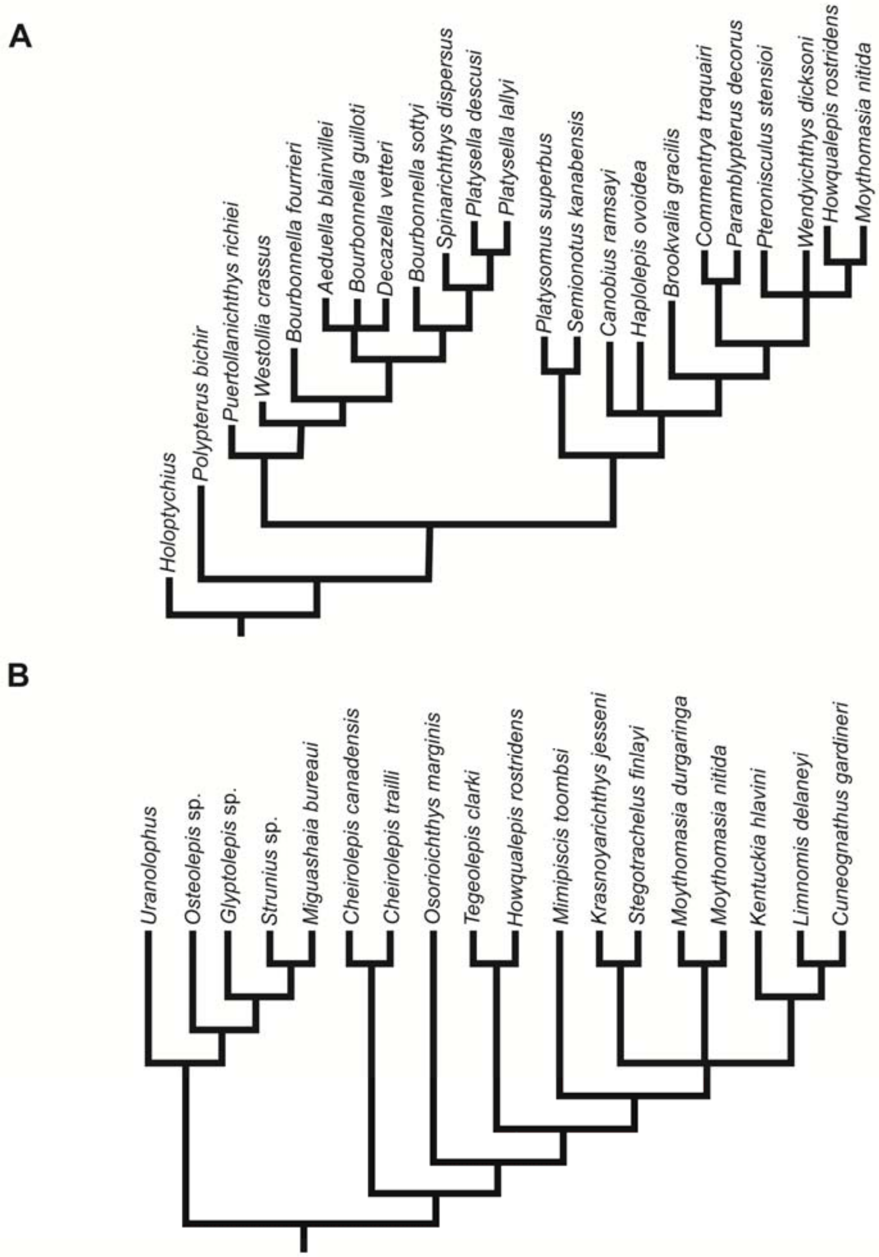


Figure 3—Phylogenetic hypotheses of lower actinopterygian fishes. **A,** Poplin and Dutheil's (2005) phylogenetic hypothesis of Aeduellid fishes based on 72 characters and the employment of a sarcopterygians outgroup, consensus tree of the 12 most parsimonious trees (Poplin and Dutheil, 2005, figure 3). **B,** Friedman and Blom's (2006) phylogenetic hypothesis regarding the relationships of Devonian actinopterygians based on 54 characters and a sarcopterygians outgroup, consensus tree of the four most parsimonious trees (Friedman and Blom, 2006, figure 8).

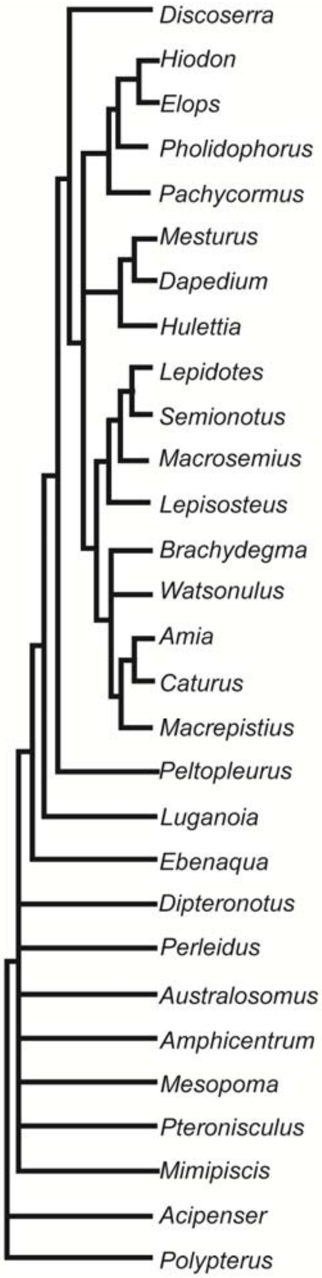


Figure 4—Hurley et al. (2006) phylogenetic hypothesis of fossil and recent actinopterygians, focusing on neopterygians and advanced Paleozoic taxa based on 70 characters, consensus tree of the 116 most parsimonious trees (Hurley et al., 2006, figure 2).

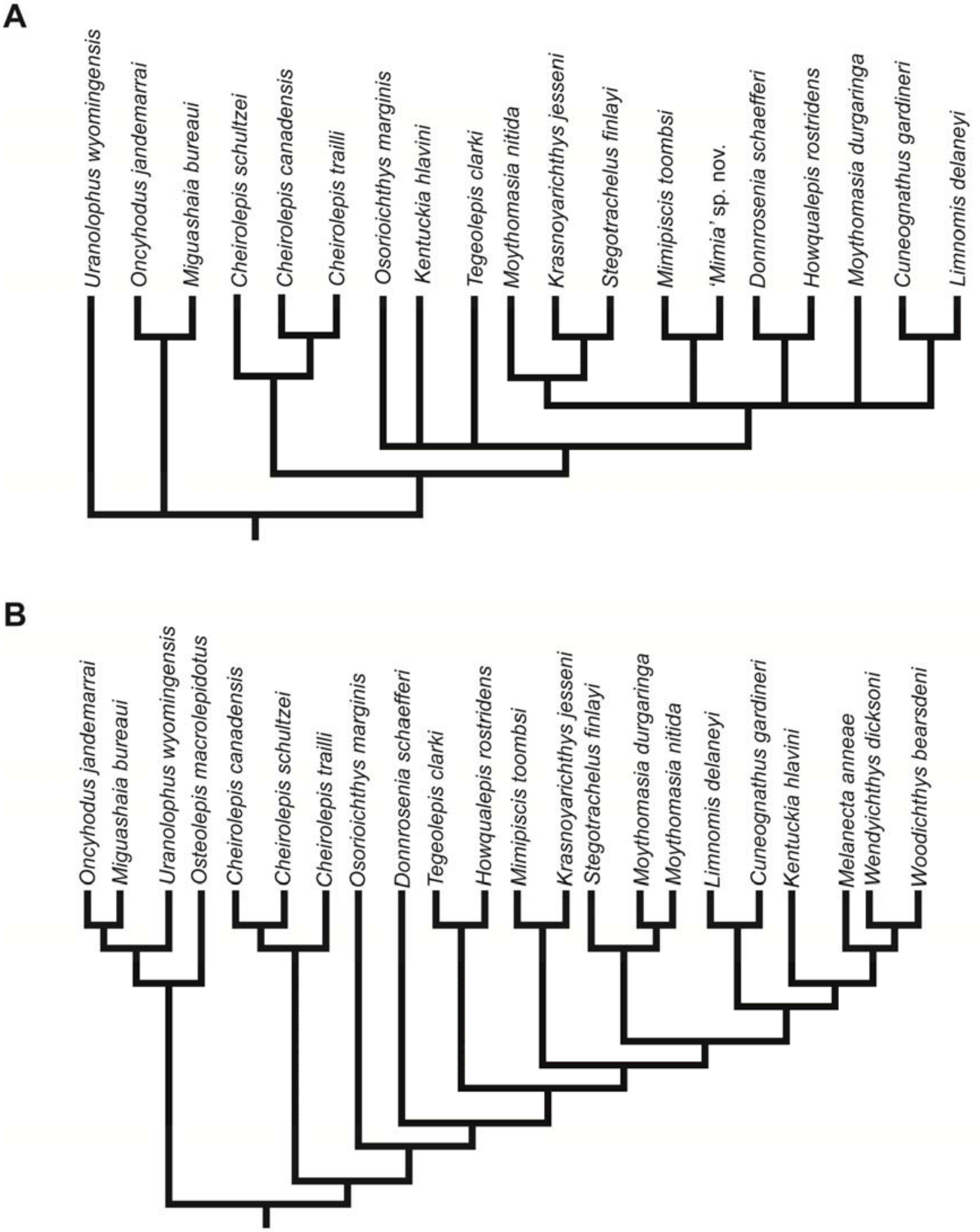


Figure 5—Phylogenetic hypotheses of relationships of Devonian actinopterygians. **A,** Long et al. (2008) tree based on 71 characters and a sarcopterygians outgroup. Consensus tree of the two most parsimonius trees (Long et al., 2008, figure 11A). **B,** Swartz's (2009) tree based on 59 characters and a sarcopterygians outgroup (Swartz, 2009, figure 34).

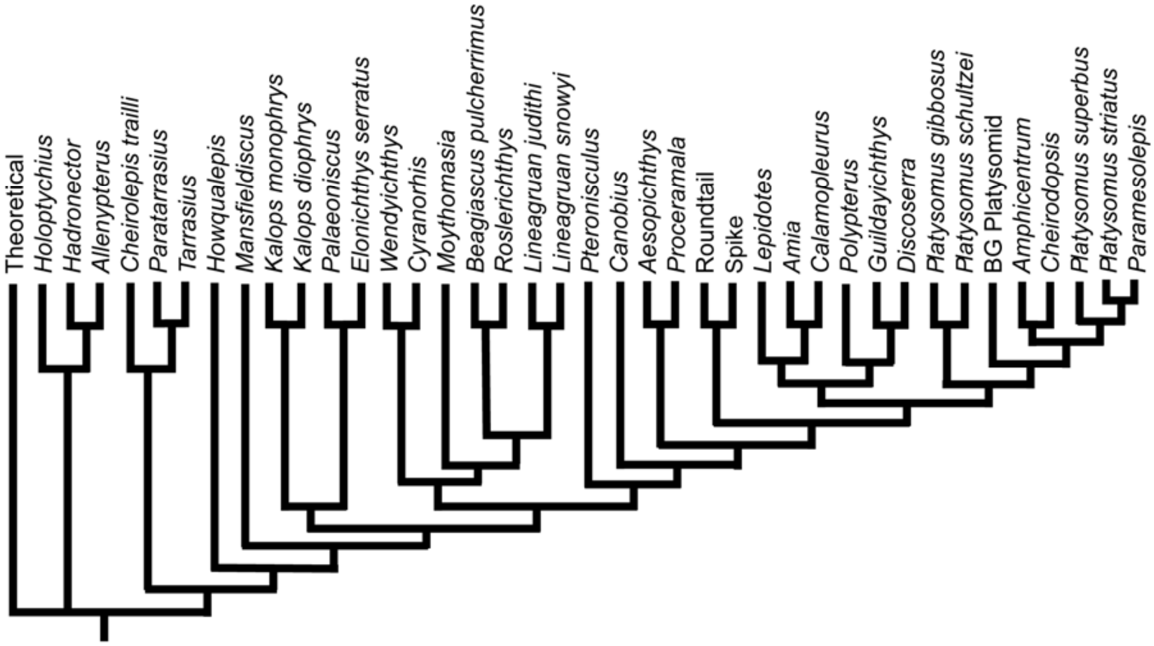


Figure 6—Mickle et al. (2009) Phylogenetic hypothesis of the relationships of lower actinopterygian fishes based on 111 characters and theoretical and sarcopterygians outgroups. Modified from figure 16 Mickle et al., 2009.

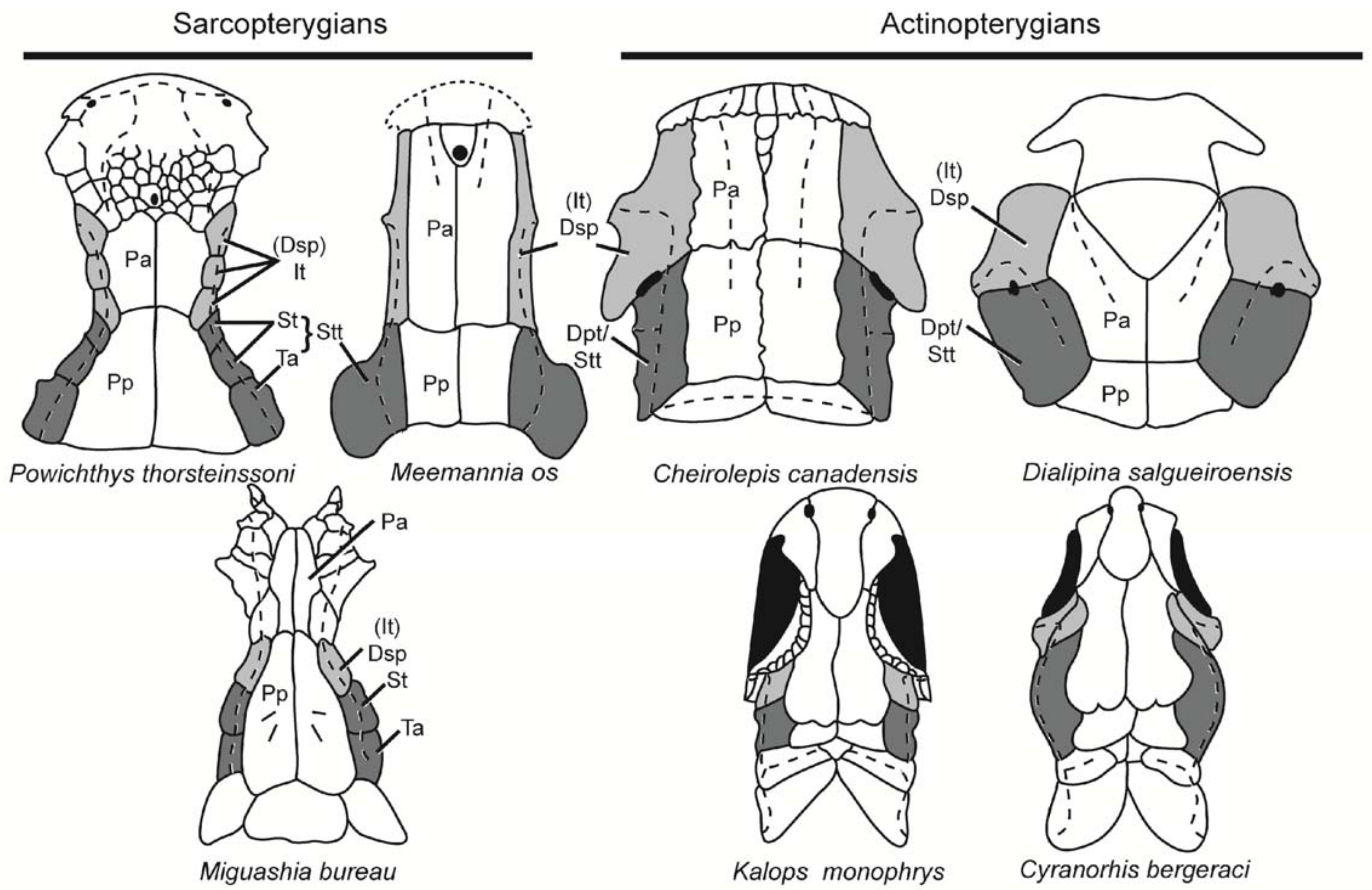
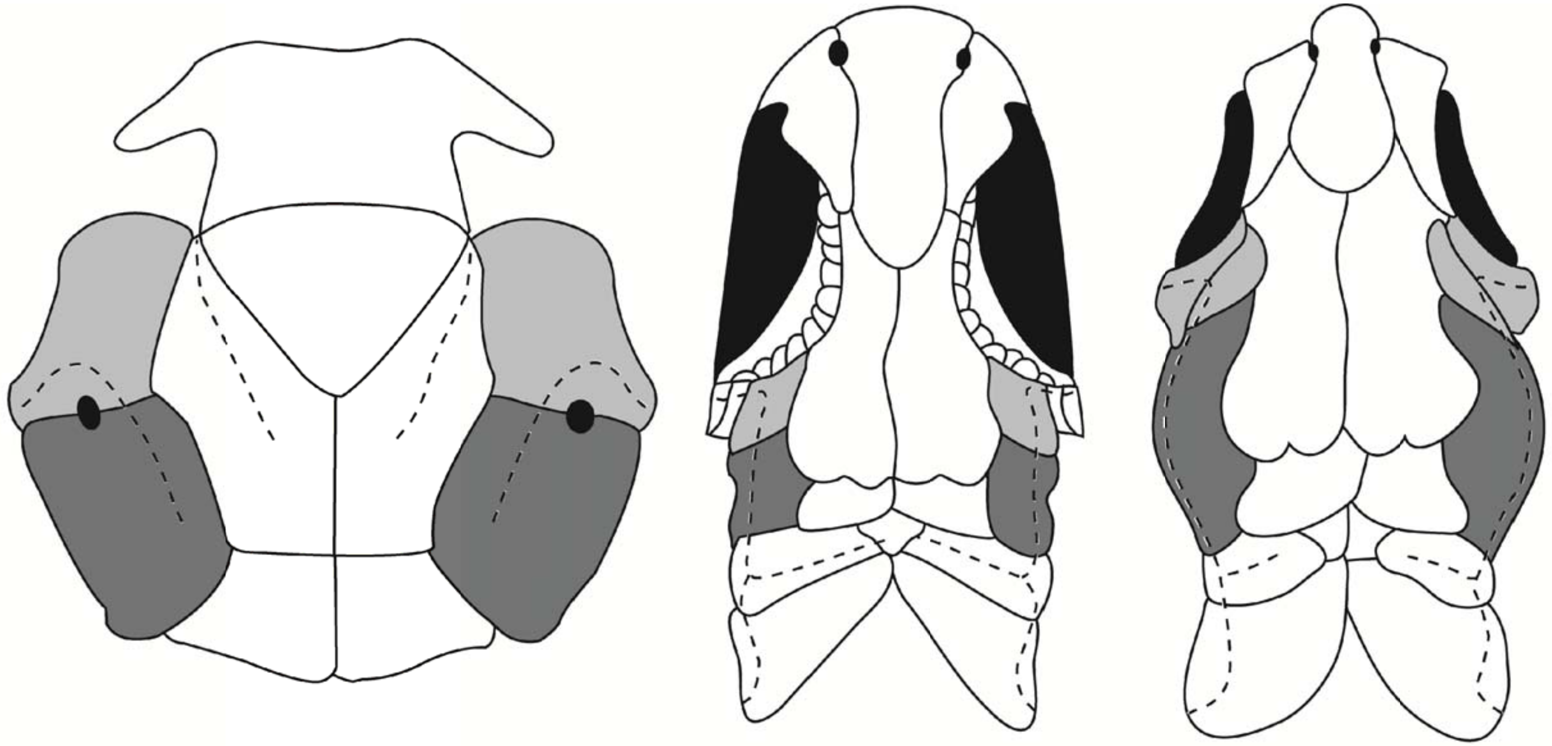
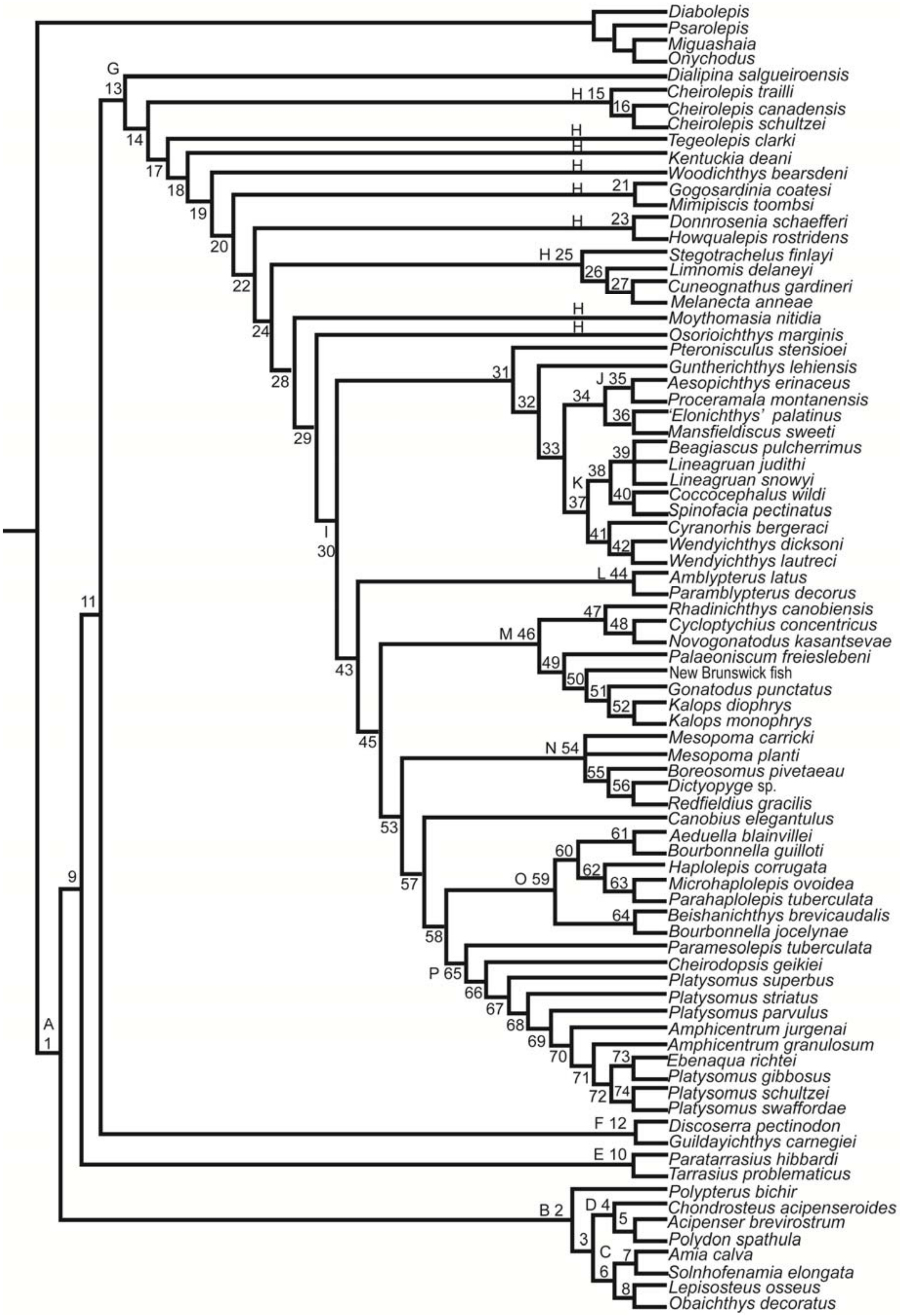


Figure 7—Skull roofing bones of basal sarcopterygians and actinopterygian fishes. Sarcopterygian fishes *Powichthys thorsteinssoni* after Jessen, 1980, *Meemannia eos* after Zhu et al., 2006, and *Miguashia bureau* after Cloutier, 1996. Actinopterygian fishes *Cheirolepis canadensis* after Arratia and Cloutier, 1996, *Dialipina salgueiroensis* after Schultze and Cumbaa, 2001, *Kalops monophrys* after Poplin and Lund, 2002, and Cyranorhis bergeraci after Lund and Poplin, 1997. Bones shaded in dark grey are the dermopterotic/supratemporotabular bones. Bones shaded in light grey are the dermosphenotic/intertemporal bone(s). Figure modified from Schultze (2008) figure 5, Schultze and Cumbaa (2001) figure 18.2.; Cloutier (1996) figure 3; Poplin and Lund (2002) figure 2.1, Lund and Poplin (1997) figure 15A. **Abbreviations: Dpt/Stt,** dermopterotic/supratemporotabular; **Dsp/It,** dermosphenotic/intertemporal; **Pa,** parietal; **Pp,** postparietal; **It,** intertemporal; **St,** supratemporal; **Stt**, supratemporotabular; **Ta**, tabular.



Dialipina salgueiroensis *Kalops monophrys* *Cyranorhis bergeraci*

Figure 8—Skull roofing bones of actinopterygians showing different patterns of dermosphenotic/intertemporal bones. Dark grey signifies the dermopterotic/supratemporotabular bone, light grey the dermosphenotic/intertemporal bone(s). *Dialipina* modified from Schultze and Cumbaa, 2001, figure 18.2, *Kalops monophrys* Poplin and Lund, 2002, figure 2.1, and *Cyranorhis bergeraci*, Lund and Poplin, 1997, figure 15A.



Diabolepis
Psarolepis
Miguashaia
Onychodus
G
13
Dialipina salgueiroensis
H 15
Cheirolepis trailli
16
Cheirolepis canadensis
Cheirolepis schultzei
14
H
Tegeolepis clarki
H
Kentuckia deani
17
H
Woodichthys bearsdeni
18
H
21
Gogosardinia coatesi
Mimipiscis toombsi
19
H
23
Donnrosenia schaefferi
Howqualepis rostridens
20
H 25
Stegotrachelus finlayi
22
26
Limnomis delaneyi
27
Cuneognathus gardineri
Melanecta anneae
24
H
Moythomasia nitidia
H
Osorioichthys marginis
Pteronisculus stensioei
28
31
Guntherichthys lehiensis
J 35
Aesopichthys erinaceus
32
34
Proceramala montanensis
36
'Elonichthys' palatinus
Mansfieldiscus sweeti
29
33
39
Beagiascus pulcherrimus
38
Lineagruan judithi
K
Lineagruan snowyi
40
Coccocephalus wildi
37
Spinofacia pectinatus
41
Cyranorhis bergeraci
I
42
Wendyichthys dicksoni
30
Wendyichthys lautreci
L 44
Amblypterus latus
Paramblypterus decorus
11
47
Rhadinichthys canobiensis
48
Cycloptychius concentricus
M 46
Novogonatodus kasantsevae
Palaeoniscum freieslebeni
43
49
New Brunswick fish
50
51
Gonatodus punctatus
52
Kalops diophrys
Kalops monophrys
45
Mesopoma carricki
N 54
Mesopoma planti
55
Boreosomus pivetaeau
56
Dictyopyge sp.
Redfieldius gracilis
53
Canobius elegantulus
61
Aeduella blainvillei
60
Bourbonnella guilloti
62
Haplolepis corrugata
9
O 59
63
Microhaplolepis ovoidea
57
Parahaplolepis tuberculata
64
Beishanichthys brevicaudalis
Bourbonnella jocelynae
58
Paramesolepis tuberculata
P 65
Cheirodopsis geikiei
66
Platysomus superbus
67
Platysomus striatus
68
Platysomus parvulus
A
69
Amphicentrum jurgenai
1
70
Amphicentrum granulosum
73
Ebenaqua richtei
71
Platysomus gibbosus
72
74
Platysomus schultzei
Platysomus swaffordae
F 12
Discoserra pectinodon
Guildayichthys carnegiei
E 10
Paratarrasius hibbardi
Tarrasius problematicus
Polypterus bichir
B 2
D 4
Chondrosteus acipenseroides
5
Acipenser brevirostrum
Polydon spathula
3
C
7
Amia calva
Solnhofenamia elongata
6
8
Lepisosteus osseus
Obaichthys decoratus

Figure 9 (Previous page)—Phylogenetic hypothesis of relationships of lower actinopterygian fishes resulting from parsimony analysis and the inclusion of recent fishes and their fossil allies. Sarcopterygian outgroups were employed. Strict/Nielsen consensus tree of the four most parsimonious trees. Numbers refer to node numbers discussed in the text and the appendix. Refer to Appendix 2 to see the characters supporting the nodes, and bootstrap values. Letters are kept consistent to identify taxa of note among all the trees presented here.

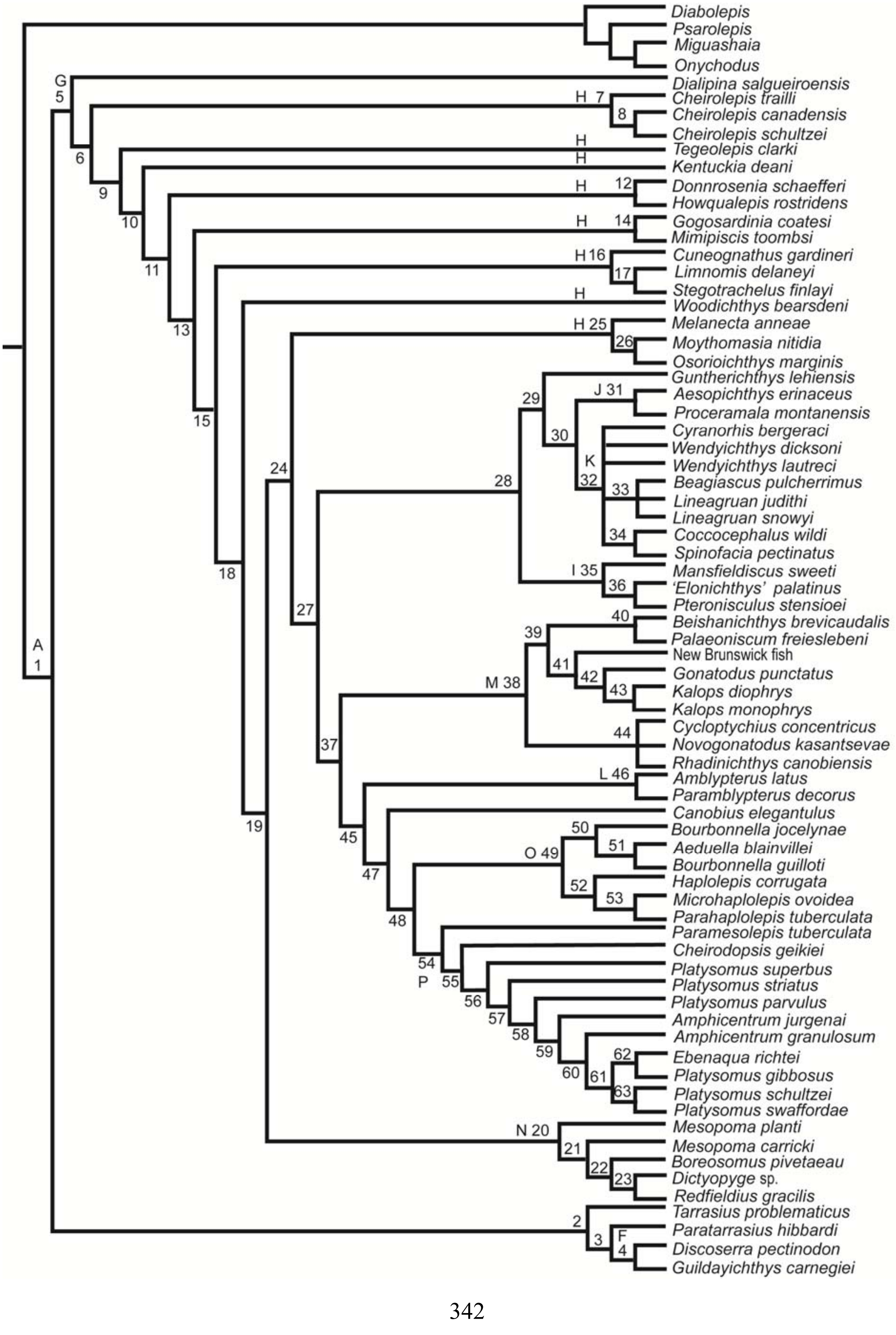

Diabolepis
Psarolepis
Miguashaia
Onychodus
G
5
Dialipina salgueiroensis
H 7
Cheirolepis trailli
8
Cheirolepis canadensis
Cheirolepis schultzei
6
H
Tegeolepis clarki
H
Kentuckia deani
9
H 12
Donnrosenia schaefferi
Howqualepis rostridens
10
H 14
Gogosardinia coatesi
Mimipiscis toombsi
11
H 16
Cuneognathus gardineri
17
Limnomis delaneyi
Stegotrachelus finlayi
H
Woodichthys bearsdeni
13
H 25
Melanecta anneae
26
Moythomasia nitidia
Osorioichthys marginis
29
Guntherichthys lehiensis
J 31
Aesopichthys erinaceus
15
Proceramala montanensis
30
Cyranorhis bergeraci
Wendyichthys dicksoni
K
Wendyichthys lautreci
24
28
32
33
Beagiascus pulcherrimus
Lineagruan judithi
Lineagruan snowyi
34
Coccocephalus wildi
Spinofacia pectinatus
18
I 35
Mansfieldiscus sweeti
36
'Elonichthys' palatinus
Pteronisculus stensioei
27
40
Beishanichthys brevicaudalis
39
Palaeoniscum freieslebeni
A
New Brunswick fish
1
41
42
Gonatodus punctatus
M 38
43
Kalops diophrys
Kalops monophrys
Cycloptychius concentricus
44
Novogonatodus kasantsevae
37
Rhadinichthys canobiensis
L 46
Amblypterus latus
Paramblypterus decorus
Canobius elegantulus
19
50
Bourbonnella jocelynae
45
51
Aeduella blainvillei
O 49
Bourbonnella guilloti
47
Haplolepis corrugata
52
53
Microhaplolepis ovoidea
48
Parahaplolepis tuberculata
Paramesolepis tuberculata
Cheirodopsis geikiei
54
55
Platysomus superbus
P
56
Platysomus striatus
57
Platysomus parvulus
58
Amphicentrum jurgenai
59
Amphicentrum granulosum
62
Ebenaqua richtei
60
61
Platysomus gibbosus
63
Platysomus schultzei
Platysomus swaffordae
N 20
Mesopoma planti
21
Mesopoma carricki
22
Boreosomus pivetaeau
23
Dictyopyge sp.
Redfieldius gracilis
2
Tarrasius problematicus
F
Paratarrasius hibbardi
3
4
Discoserra pectinodon
Guildayichthys carnegiei

Figure 10 (Previous page)—Phylogenetic hypothesis of relationships of lower actinopterygian fishes resulting from parsimony analysis and the exclusion of recent fishes and their fossil allies. Sarcopterygian outgroups were employed. Strict/Nielsen consensus tree of the nine most parsimonious trees. Numbers refer to node numbers discussed in the text and the appendix. Refer to Appendix 3 to see the characters supporting the nodes, and bootstrap values.

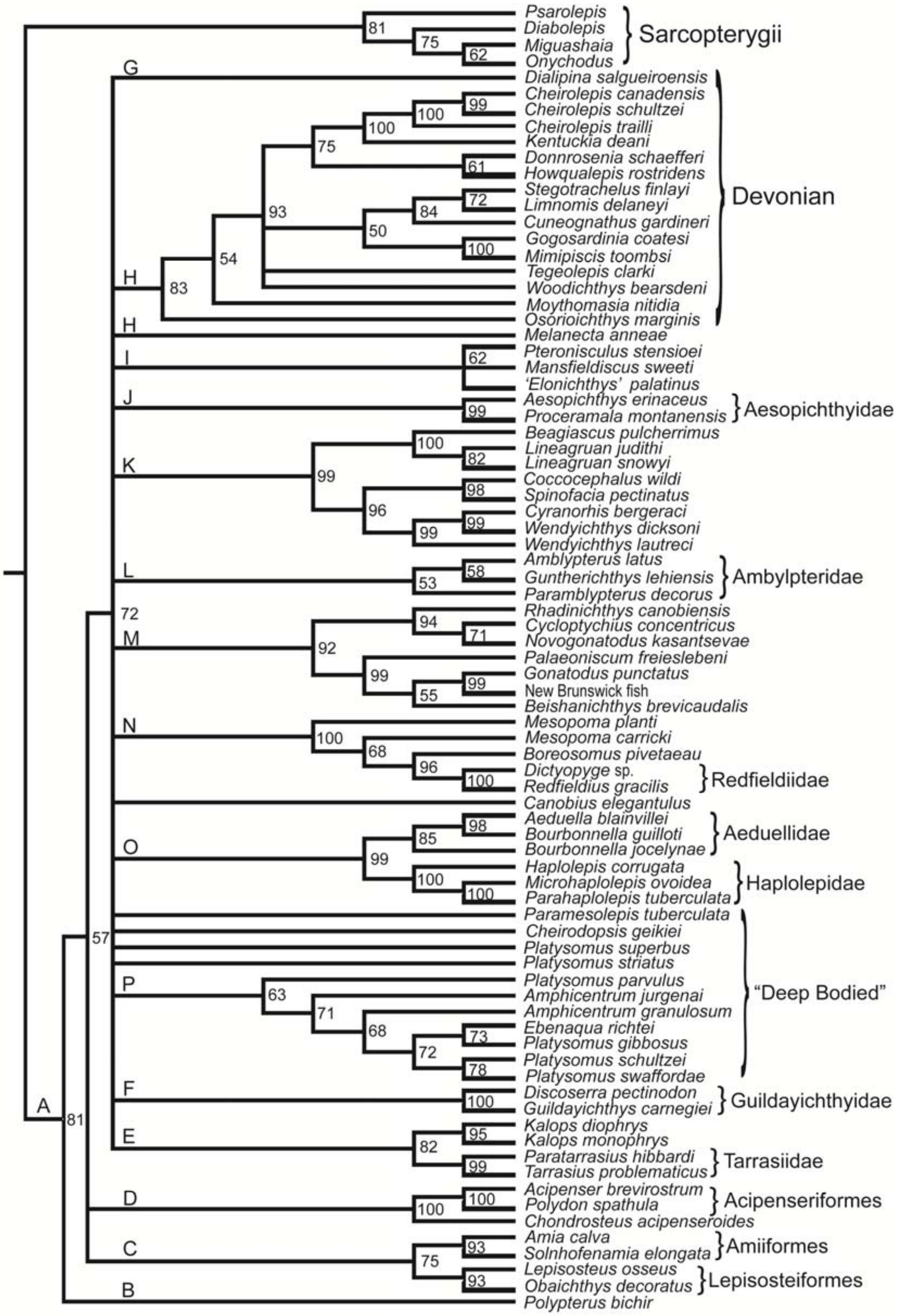

81
75
62
Psarolepis
Diabolepis
Miguashaia
Onychodus
Sarcopterygii
G
Dialipina salgueiroensis
100
99
100
75
Cheirolepis canadensis
Cheirolepis schultzei
Cheirolepis trailli
Kentuckia deani
61
Donnrosenia schaefferi
Howqualepis rostridens
93
84
72
Stegotrachelus finlayi
Limnomis delaneyi
Cuneognathus gardineri
50
100
Gogosardinia coatesi
Mimipiscis toombsi
H
83
54
Tegeolepis clarki
Woodichthys bearsdeni
Moythomasia nitidia
Osorioichthys marginis
Devonian
H
Melanecta anneae
I
62
Pteronisculus stensioei
Mansfieldiscus sweeti
'Elonichthys' palatinus
J
99
Aesopichthys erinaceus
Proceramala montanensis
Aesopichthyidae
K
99
100
82
Beagiascus pulcherrimus
Lineagruan judithi
Lineagruan snowyi
96
98
99
99
Coccocephalus wildi
Spinofacia pectinatus
Cyranorhis bergeraci
Wendyichthys dicksoni
Wendyichthys lautreci
L
53
58
Amblypterus latus
Guntherichthys lehiensis
Paramblypterus decorus
Ambylpteridae
72
M
92
94
71
Rhadinichthys canobiensis
Cycloptychius concentricus
Novogonatodus kasantsevae
99
55
99
Palaeoniscum freieslebeni
Gonatodus punctatus
New Brunswick fish
Beishanichthys brevicaudalis
N
100
68
96
100
Mesopoma planti
Mesopoma carricki
Boreosomus pivetaeau
Dictyopyge sp.
Redfieldius gracilis
Redfieldiidae
Canobius elegantulus
O
99
85
98
Aeduella blainvillei
Bourbonnella guilloti
Bourbonnella jocelynae
Aeduellidae
100
100
Haplolepis corrugata
Microhaplolepis ovoidea
Parahaplolepis tuberculata
Haplolepidae
57
Paramesolepis tuberculata
Cheirodopsis geikiei
Platysomus superbus
Platysomus striatus
P
63
71
68
72
73
78
Platysomus parvulus
Amphicentrum jurgenai
Amphicentrum granulosum
Ebenaqua richtei
Platysomus gibbosus
Platysomus schultzei
Platysomus swaffordae
"Deep Bodied"
F
100
Discoserra pectinodon
Guildayichthys carnegiei
Guildayichthyidae
A
81
E
82
95
99
Kalops diophrys
Kalops monophrys
Paratarrasius hibbardi
Tarrasius problematicus
Tarrasiidae
D
100
100
Acipenser brevirostrum
Polydon spathula
Chondrosteus acipenseroides
Acipenseriformes
C
75
93
93
Amia calva
Solnhofenamia elongata
Amiiformes
Lepisosteus osseus
Obaichthys decoratus
Lepisosteiformes
B
Polypterus bichir

Figure 11 (Previous page)—Phylogenetic hypothesis of relationships of lower actinopterygian fishes resulting from Bayesian analysis and inclusion of all taxa. Rooted on a sarcopterygian outgroup. Tree is the 50 percent majority consensus tree. Numbers are posterior probabilities of the clades, given in percentages.

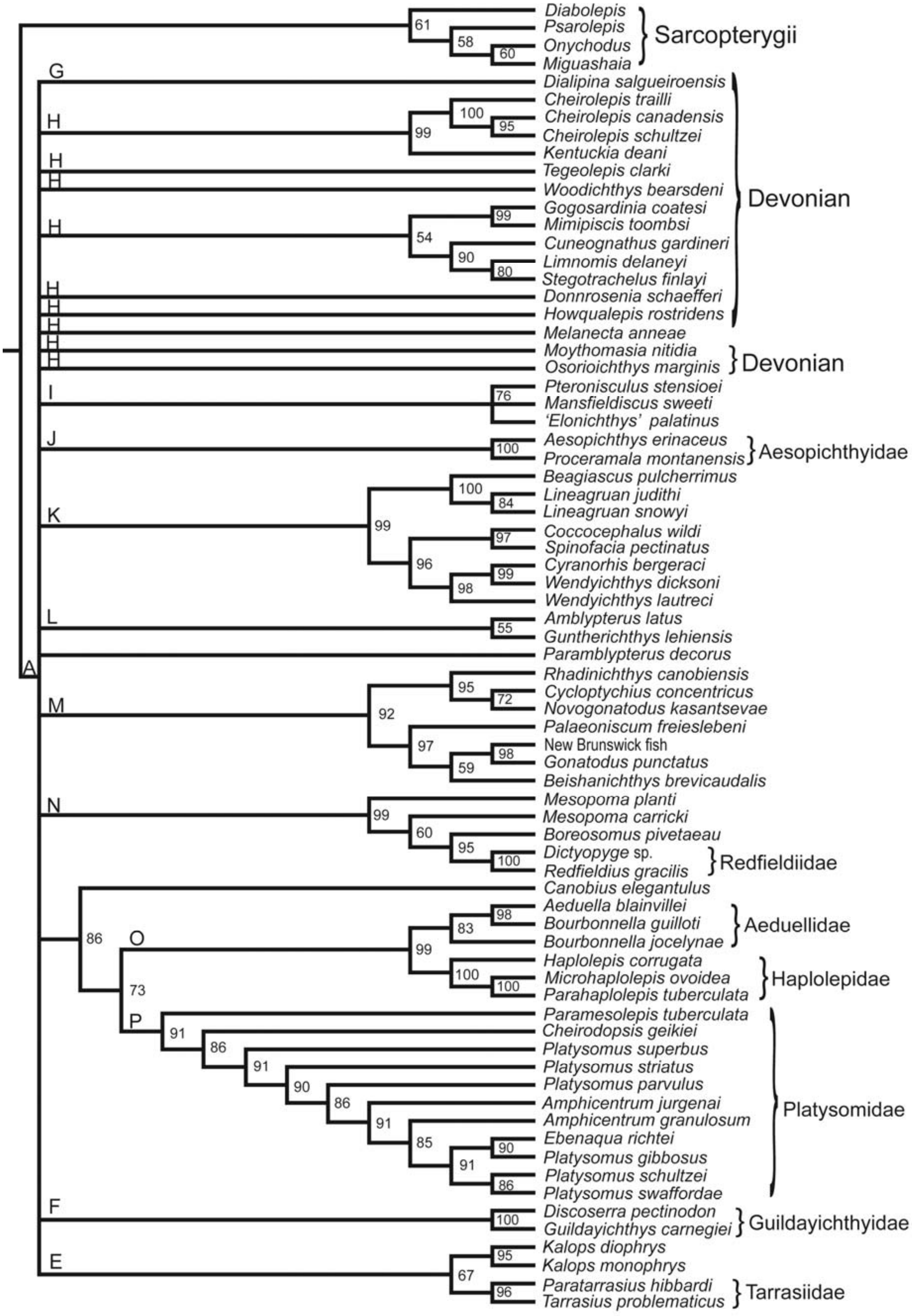

Diabolepis
61
Psarolepis
58
Onychodus
60
Miguashaia
Sarcopterygii
G
Dialipina salgueiroensis
Cheirolepis trailli
100
Cheirolepis canadensis
H
95
99
Cheirolepis schultzei
Kentuckia deani
H
Tegeolepis clarki
H
Woodichthys bearsdeni
Devonian
Gogosardinia coatesi
99
Mimipiscis toombsi
H
54
Cuneognathus gardineri
90
Limnomis delaneyi
80
Stegotrachelus finlayi
H
Donnrosenia schaefferi
H
Howqualepis rostridens
H
Melanecta anneae
H
Moythomasia nitidia
H
Osorioichthys marginis
Devonian
I
Pteronisculus stensioei
76
Mansfieldiscus sweeti
'Elonichthys' palatinus
J
Aesopichthys erinaceus
100
Proceramala montanensis
Aesopichthyidae
Beagiascus pulcherrimus
100
Lineagruan judithi
84
Lineagruan snowyi
K
99
Coccocephalus wildi
97
Spinofacia pectinatus
96
Cyranorhis bergeraci
99
Wendyichthys dicksoni
98
Wendyichthys lautreci
L
Amblypterus latus
55
Guntherichthys lehiensis
Paramblypterus decorus
A
Rhadinichthys canobiensis
95
Cycloptychius concentricus
72
M
Novogonatodus kasantsevae
92
Palaeoniscum freieslebeni
97
New Brunswick fish
98
Gonatodus punctatus
59
Beishanichthys brevicaudalis
N
Mesopoma planti
99
Mesopoma carricki
60
Boreosomus pivetaeau
95
Dictyopyge sp.
100
Redfieldius gracilis
Redfieldiidae
Canobius elegantulus
Aeduella blainvillei
98
83
Bourbonnella guilloti
86
O
Bourbonnella jocelynae
Aeduellidae
99
Haplolepis corrugata
100
Microhaplolepis ovoidea
73
100
Parahaplolepis tuberculata
Haplolepidae
P
Paramesolepis tuberculata
91
Cheirodopsis geikiei
86
Platysomus superbus
91
Platysomus striatus
90
Platysomus parvulus
86
Amphicentrum jurgenai
91
Amphicentrum granulosum
85
Ebenaqua richtei
90
Platysomus gibbosus
91
Platysomus schultzei
86
Platysomus swaffordae
Platysomidae
F
Discoserra pectinodon
100
Guildayichthys carnegiei
Guildayichthyidae
Kalops diophrys
95
E
Kalops monophrys
67
Paratarrasius hibbardi
96
Tarrasius problematicus
Tarrasiidae

Figure 12 (Previous page)—Phylogenetic hypothesis of the relationships of lower actinopterygian fishes resulting from Bayesian analysis and the exclusion of recent fishes and their fossil allies. Rooted on a sarcopterygians outgroup. Tree is the 50 percent majority consensus tree. Numbers are posterior probabilities of the clades, given in percentages.

CONCLUDING REMARKS

The ultimate goal of this work was to investigate the relationships of a group of fossil fishes, which have traditionally been considered paraphyletic, the palaeoniscoids. It was hoped that a greater understanding of these fishes and stronger hypotheses of relationships would be formed if certain problems within lower actinopterygian systematics were addressed. These problems included the need for more Carboniferous taxa to be described, investigations into suites of morphological characters amongst lower actinopterygians, and phylogenetic analyses that integrated these new findings into a character matrix that included a vast array of lower actinopterygian fishes. These problems were addressed, providing some interesting results and insight into what future work must be done.

Three new genera and one new species were described from the Carboniferous Manning Canyon Shale Formation of Utah and the Albert Formation of New Brunswick, Canada. Descriptive work is necessary to strengthen our understanding of lower actinopterygian fishes, not only because it provides new taxa that should be considered in phylogenetic analyses, but because it provides opportunities to uncover new characters and to see characters differently. For instance, the description of the New Brunswick taxon was the impetus behind a closer look at the condition of the snout in lower actinopterygians and a comparison of some morphological features of Devonian and Carboniferous fishes. Many lower actinopterygians remain to be described, especially from the Carboniferous. Along with descriptions of new taxa, Chapter Three details the need for redescriptions of large and important genera.

Probably more important than the descriptive work are the investigations into morphological suites of characters. There is no standardized nomenclatural scheme for identifying and naming many of the bones in lower actinopterygian fishes and the literature presents a confusing mixture of names and identifications. Often, the same bone name can be used to identify very different bones and non-homologous structures. This creates a nightmare situation when character matrices are built and coded. As pointed out by Schultze (2008) and Wiley (2008), this problem is only intensified when outgroup taxa are coded. Here, a new identification scheme for the bones of the snout was presented and implemented. Patterns regarding the makeup of the snout in Devonian and Carboniferous fishes were discussed.

With new insights on taxa and characters, phylogenetic analyses were performed. Palaeoniscoids have been recovered as paraphyletic by numerous studies, among them Patterson (1982), Lauder and Liem (1983), Gardiner (1984), Long (1988), Gardiner and Schaeffer (1989), and most recently, Mickle et al. (2009). Here though, a monophyletic Palaeoniscomorpha and Palaeonisciformes are recovered. This is not the first time a monophyletic Palaeoniscomorpha or Palaeonisciformes has been recovered. Palaeoniscoids have been recovered as monophyletic by Lund et al. (1995), Cloutier and Arratia (2004), and now here. What could be the reason for the different results? As pointed out in Chapters One and Six, the discrepancies between different analyses makes comparing results difficult. Analyses differ in regard to taxon selection, concentration on certain families or time periods, utilization of different outgroups, and homology statements and coding. Also, many of the analyses that recover a palaeoniscoids are paraphyletic or polyphyletic do not include that many fishes traditionally considered to be palaeoniscoids. Also, matrices from Gardiner (1984), Gardiner and Schaeffer (1989) have been used by other workers in their analyses.

The question regarding the status of palaeoniscoids is compounded by the fact that currently, there are not many analyses which are equipped to discuss the monophyly or paraphyly of these fishes. In order to do so, analyses must include more than just small subsets of fishes, and more advanced or recent forms. Since Cloutier and Arratia's 2004 study, only one study has been published with wide taxon sampling of Devonian, Carboniferous, and Mesozoic or Recent fishes (Mickle et al., 2009). In contrast, there have been at least three analyses that concentrate on Devonian forms (Friedman and Blom, 2006; Long et al., 2008; Swartz, 2009). What is needed are larger analyses with broader taxonomic scope.

The analyses presented here investigated the largest number of lower actinopterygians to date. Extant fishes and their fossil allies were included. A concerted effort was made to increase the number of Carboniferous fishes included in the analyses because the Carboniferous was when the first radiation of actinopterygians took place. Fishes not typically included in analyses—redfieldiids, platysomids, and haplolepids, were added. Characters and character states were updated to reflect new ideas regarding the homology of otic canal bearing bones. The new nomenclature scheme for identifying bones in the snout of lower actinopterygians was also used. Lastly, parsimony and Bayesian analyses were employed. This is the first time Bayesian analysis has been used to investigate the relationships of lower actinopterygian fossil fishes.

All of this resulted in the recovery of a clade of fossil fishes separate from the Chondrostei and Holostei across methodologies. Parsimony analyses recovered a monophyletic Palaeonisci, Palaeoniscomorpha, and Palaeonisciformes. Bayesian analyses recovered the Palaeonisci separate from the Chondrostei and the Holostei, but the relationships amongst these fossil fish were not resolved.

These are promising and interesting results, but as mentioned in Chapter Six, what these results call for is additional work. Interrelationships amongst palaeoniscoids are not resolved. The relationships between recent fishes and the Palaeonisci are not resolved. Many questions remain in regard to the relationships of the Guildayichthyidae and Tarrasiidae to other actinopterygians. Though this matrix represents the largest number of lower actinopterygians examined to date, it is not enough. More Paleozoic fishes must be included in analyses, as well as Mesozoic forms. The matrix and results presented here must be looked at as works in progress that will need to be expanded on and revised.

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Appendix 1—Data matrix of 209 characters, 77 actinopterygians and 4 sarcopterygian outgroups. A = 0/1, B = 0/2, C = 2/3.

	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**1**	**1**	**1**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**
Onychodus	0	0	0	?	0	1	0	?	1	0	0	2	0	1	1
Diabolepis	1	0	1	3	0	0	0	?	?	0	?	?	?	?	?
Miguashaia	?	0	0	1	0	0	0	?	0	0	1	4	3	2	4
Psarolepis	0	0	?	?	0	?	1	?	?	1	0	?	0	0	0
Acipenser	1	1	2	4	2	2	2	4	2	2	1	4	3	2	4
Aeduella blainvillei	1	1	2	4	2	2	2	4	2	2	0	2	2	1	3
Aesopichthys	1	0	1	3	0	1	0	2	0	1	0	2	2	1	0
Amblypterus latus	1	0	?	?	0	0	1	?	1	0	0	2	2	1	1
Amia calva	1	0	1	3	1	0	0	0	0	0	0	2	0	0	2
Amphicentrum granulosum	1	0	1	3	0	0	0	0	1	1	0	2	2	1	3
Amphicentrum jurgenai	1	0	0	1	0	0	0	3	1	1	0	2	2	?	?
Beagiascus	1	0	1	3	0	0	0	1	0	1	0	2	2	1	0
Beishanichthys	1	0	0	0	0	0	1	3	1	0	0	2	2	0	1
Boreosomus	1	0	0	1	0	?	1	3	1	?	0	2	1	1	0
Bourbonnella guilloti	1	?	?	?	?	?	?	?	?	?	0	2	2	1	3
Bourbonnella jocelynae	1	?	?	?	?	?	?	?	?	?	0	?	2	0	?
Canobius elegantulus	1	0	0	1	0	0	1	3	1	0	0	2	1	1	1
Cheirodopsis	1	0	?	?	0	0	0	?	1	?	0	2	2	0	?
Cheirolepis canadensis	1	0	0	0	0	0	0	3	0	0	0	2	2	1	0
Cheirolepis trailli	1	0	0	0	0	0	0	3	0	0	0	2	2	1	0
Cheirolepis schultzei	1	0	?	?	0	0	0	?	0	0	0	2	2	1	0
Coccocephalus	1	?	?	?	?	?	?	?	?	?	0	2	0	1	0
Cuneognathus	1	0	?	?	?	?	?	?	?	?	0	2	1	1	?
Cycloptychius	1	0	0	0	0	0	1	3	1	?	0	1	2	1	0
Cyranhoris	1	1	2	4	0	2	2	4	2	2	0	1	1	1	0
Dialipina	1	0	1	3	0	0	0	?	?	0	0	2	0	1	0
Dictyopyge	1	?	?	?	?	?	?	?	?	?	0	1	2	1	0
Discoserra	1	0	1	3	0	0	0	0	0	0	0	2	0	0	1
Donnrosenia	1	0	0	1	0	?	1	3	0	?	0	2	1	1	?
Ebenaqua	1	1	2	4	2	2	2	4	2	2	0	2	1	1	3
Elonichthys' palatinus	1	0	A	C	0	0	0	0	0	0	0	2	1	1	0
Gogosardinia	1	0	0	1	0	0	1	3	1	0	0	2	1	1	0
Gonatodus	1	0	0	2	0	0	0	0	0	0	0	2	0	1	0
Guildayichthys	1	0	1	3	0	0	0	0	0	0	0	2	0	0	1
Guntherichthys	1	?	?	?	?	?	?	?	?	?	0	?	1	?	?
Haploepis ovoidea	1	?	?	?	?	?	?	?	?	?	0	2	0	1	?
Howqualepis	1	0	0	1	0	1	1	3	1	1	0	2	1	1	0
Kalops diophrys	1	0	1	3	0	0	0	0	0	0	0	2	1	1	0
Kalops monophrys	1	0	1	3	0	0	0	0	0	0	0	2	1	1	0
Kentuckia deani	1	0	0	0	0	0	1	3	1	0	0	2	1	1	?
Lepisosteus	1	0	1	3	1	0	0	2	1	0	0	2	0	0	0
Limnomis	1	0	0	1	?	1	0	3	1	0	0	2	1	0	0
Lineagruan judithi	1	0	1	3	0	0	0	0	0	1	0	2	1	1	0
Lineagruan snowyi	1	0	1	3	0	0	0	0	0	?	0	2	1	0	0
Mansfieldiscus	1	0	1	3	0	0	0	1	0	0	0	2	1	0	0

	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**
Melanecta anneae	1	0	0	1	?	1	1	3	1	1	0	2	1	1	0
Mesopoma carricki	1	0	?	?	0	0	1	?	1	0	0	2	1	1	0
Mesopoma planti	1	0	0	1	0	?	1	3	1	?	0	2	1	1	0
Microhaplolepis	1	?	?	?	?	?	?	?	?	?	0	2	2	0	?
Mimia	1	0	0	1	0	0	1	3	1	0	0	2	1	1	0
Moythomasia	1	0	0	A	0	0	0	3	1	0	0	2	2	1	0
New Brunswick Fish	1	0	0	2	0	0	0	0	1	1	0	2	2	1	?
Novogonatodus	1	?	?	?	?	?	?	?	?	?	0	1	2	1	0
Osorioichthys	1	0	0	1	0	0	1	3	1	0	0	2	1	1	1
Palaeoniscum	1	0	0	0	0	0	1	3	1	?	0	1	1	1	0
Parahaplolepis	1	0	?	?	?	?	?	?	1	0	0	2	2	0	?
Paramblypterus	1	0	?	?	0	0	1	?	1	?	0	2	2	0	?
Paramesolepis	1	0	0	0	0	0	0	0	1	?	0	2	2	1	1
Paratarrasius	1	0	1	3	0	0	0	0	0	0	0	2	1	0	0
Platysomus gibbosus	1	?	?	?	?	?	?	?	?	?	0	2	2	1	3
Platysomus parvulus	1	?	?	?	?	?	?	?	?	?	0	2	2	1	1
Platysomus schultzei	1	0	1	3	0	0	0	?	0	1	0	2	1	1	3
Platysomus striatus	1	0	0	1	0	0	0	3	1	?	0	2	2	0	1
Platysomus superbus	1	?	?	?	?	?	?	?	?	?	0	2	2	0	3
Platysomus swaffordae	1	0	1	3	0	0	0	0	0	1	0	2	2	1	3
Polypterus bichir	1	0	0	1	1	0	1	3	1	0	0	2	0	0	1
Proceramala	1	0	?	?	?	?	?	?	?	?	0	2	2	1	0
Pteronisculus	1	0	1	3	0	0	0	0	0	0	0	?	1	1	0
Redfieldius	1	?	?	?	?	?	?	?	?	?	0	1	2	1	0
Rhadinichthys	1	0	0	0	0	0	1	3	1	0	0	1	1	1	0
Spinofacia	1	?	?	?	?	?	?	?	?	?	0	?	1	0	?
Stegotrachelus	1	0	?	?	0	0	?	?	?	0	0	2	1	0	0
Tarrasius	1	0	?	?	0	0	0	?	0	0	0	2	2	1	0
Tegeolepis	1	0	A	C	0	0	0	1	0	0	0	1	0	1	0
Wendyichthys dicksoni	1	1	2	4	2	2	2	4	2	2	0	2	1	1	0
Wendyichthys lautreci	1	1	2	4	2	2	2	4	2	2	0	2	1	1	0
Woodichthys	1	0	0	1	0	?	1	3	1	0	0	2	1	1	0
Polydon spathula	1	1	2	4	2	2	2	4	2	2	1	4	3	2	4
Solnhofenamia	1	0	1	3	?	0	0	0	1	0	0	2	1	0	0
Obaichthys	1	0	?	?	1	?	0	?	?	?	0	2	0	0	1
Chondrosteus	?	1	2	4	2	2	2	4	2	2	1	4	3	2	4

	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Onychodus	2	5	0	0	0	1	1	0	0	0	0	1	1	1	1
Diabolepis	?	?	?	?	?	?	?	?	?	?	0	1	1	0	?
Miguashaia	0	5	2	4	3	3	5	?	0	0	0	?	1	1	0
Psarolepis	0	5	0	?	0	1	?	0	0	?	0	?	1	1	1
Acipenser	3	?	2	4	3	3	5	2	0	?	1	0	0	0	?
Aeduella blainvillei	0	?	0	2	0	0	4	0	0	?	1	?	?	?	?
Aesopichthys	0	3	0	2	0	2	0	0	0	?	1	0	?	?	?
Amblypterus latus	0	?	0	1	0	1	?	0	0	?	1	?	?	?	?
Amia calva	0	5	1	0	0	0	0	0	1	0	1	1	0	0	0
Amphicentrum granulosum	3	?	0	3	0	1	2	0	0	?	1	0	?	?	2
Amphicentrum jurgenai	?	?	0	3	0	0	?	0	0	?	1	?	?	?	?
Beagiascus	2	0	0	1	0	2	0	0	0	?	1	?	?	?	?
Beishanichthys	0	?	0	1	0	0	0	0	0	?	1	?	?	?	?
Boreosomus	0	?	0	1	0	1	0	0	0	?	1	1	?	?	?
Bourbonnella guilloti	0	?	0	2	0	0	4	0	0	?	1	?	?	?	?
Bourbonnella jocelynae	?	3	0	2	0	0	?	0	0	?	1	?	?	?	?
Canobius elegantulus	0	?	0	2	0	2	0	0	0	0	1	?	?	?	?
Cheirodopsis	?	?	0	3	0	0	?	0	0	?	1	?	?	?	?
Cheirolepis canadensis	0	3	0	1	0	2	0	0	0	0	1	1	0	0	0
Cheirolepis trailli	?	3	0	1	0	2	0	0	0	0	1	1	0	0	0
Cheirolepis schultzei	?	1	0	1	0	1	0	0	0	?	1	?	?	?	?
Coccocephalus	2	?	0	1	0	2	0	0	0	?	1	1	?	?	?
Cuneognathus	?	1	0	1	0	1	0	0	0	?	1	?	?	?	?
Cycloptychius	0	?	0	1	0	2	0	0	0	?	1	?	?	?	?
Cyranhoris	1	2	0	1	0	2	0	0	0	0	1	0	?	?	?
Dialipina	0	1	0	0	0	0	0	?	0	?	?	?	?	?	0
Dictyopyge	0	?	0	3	0	1	0	0	0	?	1	?	?	?	?
Discoserra	0	1	0	0	2	0	0	0	0	1	1	0	?	?	?
Donnrosenia	?	?	0	1	0	2	0	0	0	?	1	1	?	?	?
Ebenaqua	3	1	0	0	2	0	3	0	0	?	1	0	?	?	?
Elonichthys' palatinus	0	?	0	1	0	2	0	0	0	?	1	?	?	?	?
Gogosardinia	0	1	0	1	0	2	0	0	0	?	1	0	?	?	?
Gonatodus	0	0	0	1	0	2	0	0	0	?	1	?	?	?	?
Guildayichthys	0	1	0	0	1	0	0	0	0	1	1	?	?	?	?
Guntherichthys	0	0	0	1	0	2	0	0	0	?	1	?	?	?	?
Haploepis ovoidea	?	0	0	0	0	0	?	0	0	?	1	?	?	?	?
Howqualepis	2	2	0	1	0	1	0	0	0	0	1	1	0	0	2
Kalops diophrys	0	0	0	1	0	2	0	0	0	?	1	0	?	?	?
Kalops monophrys	0	0	0	1	0	2	0	0	0	?	1	0	?	?	?
Kentuckia deani	?	?	0	1	0	2	?	0	0	?	1	?	?	?	?
Lepisosteus	0	5	?	0	2	0	0	0	1	0	1	1	0	0	1
Limnomis	2	?	0	1	0	2	0	0	0	?	1	?	?	?	?
Lineagruan judithi	0	1	0	2	0	2	0	0	0	?	1	?	?	?	?
Lineagruan snowyi	1	1	0	1	0	2	0	0	0	?	1	?	?	?	?
Mansfieldiscus	1	0	0	1	0	1	0	0	0	?	1	0	0	0	?

	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Melanecta anneae	1	0	0	1	0	1	?	0	0	?	1	?	?	?	?
Mesopoma carricki	0	?	0	1	0	2	0	0	0	?	1	1	?	?	?
Mesopoma planti	0	?	0	1	0	1	0	0	0	?	1	?	?	?	?
Microhaplolepis	0	?	0	3	0	0	?	0	0	?	1	?	?	?	?
Mimia	0	3	0	1	0	2	0	0	0	0	1	0	0	0	0
Moythomasia	0	?	0	1	0	2	0	0	0	?	1	?	?	?	?
New Brunswick Fish	0	3	0	1	0	2	0	0	0	?	1	?	?	?	?
Novogonatodus	?	1	0	2	0	2	0	0	0	?	1	0	?	?	?
Osorioichthys	0	3	0	2	0	1	0	0	0	?	1	1	?	?	?
Palaeoniscum	?	?	0	1	0	2	0	0	0	?	1	?	?	?	?
Parahaplolepis	0	?	0	2	0	0	?	0	0	?	1	?	?	?	?
Paramblypterus	0	?	0	1	0	1	?	0	0	?	1	?	?	?	?
Paramesolepis	0	0	0	3	0	0	?	0	0	?	1	?	?	?	?
Paratarrasius	0	0	0	1	0	0	0	0	0	0	1	1	?	?	?
Platysomus gibbosus	3	0	0	2	1	0	3	0	0	?	1	?	?	?	?
Platysomus parvulus	0	?	0	3	1	0	0	0	0	?	1	?	?	?	?
Platysomus schultzei	3	1	0	2	1	0	3	0	0	?	1	?	?	?	?
Platysomus striatus	0	?	0	2	0	0	0	0	0	?	1	?	?	?	?
Platysomus superbus	3	?	0	3	0	0	3	0	0	?	1	?	?	?	?
Platysomus swaffordae	3	0	0	2	2	0	3	0	0	?	1	?	?	?	?
Polypterus bichir	0	4	0	0	0	0	?	1	0	0	1	0	0	0	0
Proceramala	1	0	0	2	0	2	0	0	0	?	1	?	?	?	?
Pteronisculus	0	3	0	1	0	2	0	0	0	?	1	?	?	?	2
Redfieldius	0	2	0	1	0	1	0	0	0	?	1	?	?	?	?
Rhadinichthys	0	3	0	1	0	2	0	0	0	?	1	?	?	?	?
Spinofacia	1	?	0	1	0	2	0	0	0	?	1	?	?	?	?
Stegotrachelus	0	?	0	1	0	2	0	0	0	?	1	?	?	?	?
Tarrasius	0	?	0	2	0	2	0	0	0	?	1	?	?	?	?
Tegeolepis	2	?	0	1	0	1	0	0	0	?	1	1	?	?	?
Wendyichthys dicksoni	1	3	0	1	0	2	0	0	0	0	1	?	?	?	?
Wendyichthys lautreci	0	1	0	1	0	1	0	0	0	?	1	?	?	?	?
Woodichthys	0	1	0	1	0	2	0	0	0	?	1	1	?	?	?
Polydon spathula	?	?	2	4	3	3	?	2	0	?	1	0	1	0	?
Solnhofenamia	0	5	0	3	0	0	1	0	1	?	1	0	?	?	0
Obaichthys	0	?	1	0	2	0	?	0	?	?	1	0	?	?	1
Chondrosteus	3	?	2	4	3	3	5	2	0	?	1	0	?	?	?

	31	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**
Onychodus	0	1	0	0	0	3	0	0	0	5	4	0	?	0	0
Diabolepis	0	0	0	0	0	3	1	0	?	?	?	?	?	?	0
Miguashaia	0	0	0	0	0	3	0	0	?	?	?	?	?	?	0
Psarolepis	0	1	0	0	0	3	0	0	0	0	0	1	1	1	0
Acipenser	0	0	?	2	0	?	1	2	?	?	?	?	?	0	0
Aeduella blainvillei	0	0	?	?	0	?	0	0	0	0	0	0	?	0	0
Aesopichthys	1	0	?	1	0	0	1	0	0	0	0	0	2	0	1
Amblypterus latus	?	0	?	1	0	1	0	0	0	0	0	0	2	0	0
Amia calva	1	0	1	1	0	3	0	0	0	0	0	0	0	0	0
Amphicentrum granulosum	0	0	?	2	0	?	1	5	0	0	0	0	?	0	0
Amphicentrum jurgenai	?	0	?	?	?	?	1	5	0	0	0	0	?	0	0
Beagiascus	?	0	?	0	0	0	1	0	0	0	0	0	0	0	0
Beishanichthys	0	0	1	1	0	?	1	0	0	2	1	0	?	0	0
Boreosomus	0	0	1	0	0	?	0	1	0	2	1	0	0	0	0
Bourbonnella guilloti	0	0	?	?	0	?	0	0	?	?	?	?	?	?	?
Bourbonnella jocelynae	?	0	?	?	0	1	?	?	0	?	?	?	?	?	?
Canobius elegantulus	?	0	?	?	0	?	1	0	0	0	0	0	1	0	0
Cheirodopsis	?	0	?	?	0	?	1	5	0	0	0	0	1	0	0
Cheirolepis canadensis	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0
Cheirolepis trailli	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0
Cheirolepis schultzei	0	0	0	0	0	0	0	0	0	?	?	0	?	?	?
Coccocephalus	1	0	1	0	0	1	?	0	0	?	?	?	?	?	?
Cuneognathus	?	0	?	0	0	0	0	1	0	0	0	?	0	?	0
Cycloptychius	?	0	?	0	0	?	1	1	0	2	1	0	?	0	0
Cyranhoris	?	0	?	1	0	0	1	3	0	0	0	0	2	0	1
Dialipina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dictyopyge	?	0	?	?	0	?	?	1	?	?	?	?	?	?	?
Discoserra	0	0	?	1	0	0	1	4	0	5	4	0	2	0	0
Donnrosenia	?	0	?	0	0	0	1	1	0	0	0	0	?	0	0
Ebenaqua	0	0	?	2	?	0	1	4	0	0	0	0	2	0	0
Elonichthys' palatinus	?	0	?	0	0	?	1	0	0	B	A	0	2	0	0
Gogosardinia	?	0	1	0	0	0	?	1	0	0	0	0	2	0	0
Gonatodus	?	0	1	1	0	?	0	0	0	2	1	0	0	0	0
Guildayichthys	0	0	?	1	0	0	1	4	0	5	4	0	0	0	0
Guntherichthys	0	0	?	?	0	1	?	0	?	?	?	?	?	?	?
Haploepis ovoidea	?	0	?	?	0	1	0	0	0	?	?	?	?	?	0
Howqualepis	0	1	1	0	0	0	1	1	0	0	0	1	2	1	0
Kalops diophrys	?	0	?	0	0	0	1	0	0	3	2	0	0	0	0
Kalops monophrys	?	0	?	0	0	0	1	0	0	3	2	0	0	0	0
Kentuckia deani	0	?	?	0	0	?	1	0	0	2	1	0	0	0	0
Lepisosteus	1	0	1	1	0	3	1	2	0	0	0	0	?	0	0
Limnomis	0	0	?	0	0	0	1	1	0	0	0	1	0	1	0
Lineagruan judithi	?	0	?	?	0	0	1	0	0	0	0	0	0	0	0
Lineagruan snowyi	?	0	?	?	0	?	1	0	0	0	0	0	0	0	0
Mansfieldiscus	?	0	?	0	0	0	1	1	0	2	1	0	?	0	0

	31	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**
Melanecta anneae	?	0	?	0	0	?	0	1	0	0	0	1	2	1	0
Mesopoma carricki	?	0	?	1	0	?	?	1	0	0	0	0	?	0	0
Mesopoma planti	?	0	?	?	0	?	1	1	0	0	0	0	0	0	0
Microhaplolepis	?	0	?	?	0	1	0	0	0	?	?	?	?	?	0
Mimia	0	0	1	0	0	0	0	1	0	0	0	0	2	0	0
Moythomasia	?	0	?	0	0	?	0	0	0	A	A	0	1	0	0
New Brunswick Fish	?	0	?	0	0	0	1	0	0	2	1	0	0	0	0
Novogonatodus	0	0	?	?	0	0	?	?	?	?	?	?	?	?	?
Osorioichthys	?	0	?	1	0	?	0	0	0	0	0	0	2	0	0
Palaeoniscum	?	0	?	?	0	?	1	0	0	2	1	0	0	0	0
Parahaplolepis	?	0	?	?	0	1	0	1	0	?	?	0	?	0	0
Paramblypterus	?	0	?	?	0	0	0	0	0	0	0	0	2	0	0
Paramesolepis	?	0	?	1	0	?	0	0	0	2	1	0	?	0	0
Paratarrasius	?	0	?	?	0	0	1	0	0	3	2	0	?	0	0
Platysomus gibbosus	?	0	?	2	?	?	1	4	0	0	0	0	2	0	0
Platysomus parvulus	?	0	?	1	0	?	1	4	?	?	?	?	?	?	?
Platysomus schultzei	?	0	?	2	1	0	1	4	0	0	0	0	?	0	0
Platysomus striatus	?	0	?	1	0	?	1	4	0	0	0	0	2	0	0
Platysomus superbus	?	0	?	2	?	?	?	4	0	0	0	0	2	0	0
Platysomus swaffordae	?	0	?	2	?	0	1	4	0	0	0	0	?	0	0
Polypterus bichir	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0
Proceramala	?	0	?	?	0	0	1	0	0	?	?	?	?	?	0
Pteronisculus	0	0	1	1	0	0	1	1	0	0	0	0	1	0	0
Redfieldius	?	0	?	?	0	0	1	1	0	?	?	0	2	0	0
Rhadinichthys	?	0	?	0	0	?	1	1	0	2	1	0	0	0	0
Spinofacia	?	0	?	0	0	1	?	0	0	0	0	?	0	0	0
Stegotrachelus	?	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Tarrasius	0	0	?	?	0	0	1	0	0	3	2	0	?	0	0
Tegeolepis	0	0	1	0	0	?	1	2	0	B	A	0	0	0	0
Wendyichthys dicksoni	?	0	?	1	0	0	1	3	0	0	0	0	1	0	1
Wendyichthys lautreci	?	0	?	0	0	0	1	3	0	0	0	0	?	0	1
Woodichthys	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0
Polydon spathula	0	0	?	?	0	?	1	2	?	?	?	?	?	?	0
Solnhofenamia	0	0	1	1	0	3	0	0	0	0	0	0	1	0	0
Obaichthys	0	0	?	1	0	?	?	2	?	?	?	?	?	?	?
Chondrosteus	0	0	?	2	0	?	?	?	?	?	?	?	?	?	?

	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Onychodus	0	0	0	0	2	0	0	0	2	2	1	0	0	0	0
Diabolepis	0	0	?	?	?	0	?	?	?	2	1	3	?	0	1
Miguashaia	0	0	0	0	2	0	0	0	2	2	1	0	0	0	0
Psarolepis	0	?	?	?	?	?	?	?	?	1	?	0	?	0	0
Acipenser	0	0	3	0	2	1	?	?	?	2	1	0	0	0	0
Aeduella blainvillei	0	0	2	0	2	0	1	5	3	2	1	0	2	0	0
Aesopichthys	0	0	2	1	0	1	1	5	3	2	1	0	1	0	2
Amblypterus latus	0	0	2	?	?	1	1	5	3	2	1	0	2	0	1
Amia calva	0	0	2	0	2	0	1	5	3	2	1	0	2	0	1
Amphicentrum granulosum	0	0	2	1	0	1	1	5	3	2	1	0	2	0	?
Amphicentrum jurgenai	0	0	2	?	0	0	1	5	3	2	1	0	2	?	2
Beagiascus	0	0	2	0	0	1	1	5	3	2	1	0	2	0	2
Beishanichthys	0	0	2	1	0	0	1	5	3	2	1	0	0	0	2
Boreosomus	0	0	2	1	0	0	1	5	3	2	1	0	2	0	0
Bourbonnella guilloti	0	0	2	?	?	0	1	5	3	2	1	0	2	0	0
Bourbonnella jocelynae	?	?	?	?	?	?	1	5	3	2	1	0	?	0	2
Canobius elegantulus	0	0	2	1	0	1	1	5	3	2	1	0	1	0	1
Cheirodopsis	0	0	2	1	0	1	1	5	3	2	1	0	2	0	1
Cheirolepis canadensis	0	0	2	0	?	0	0	0	2	2	1	0	1	0	0
Cheirolepis trailli	0	0	2	1	0	1	0	2	0	0	1	0	1	1	0
Cheirolepis schultzei	0	0	2	0	?	0	?	?	?	2	1	0	1	0	0
Coccocephalus	0	0	2	1	0	1	1	5	3	2	1	0	?	1	2
Cuneognathus	0	0	2	1	0	1	1	5	3	1	1	0	2	0	1
Cycloptychius	0	0	2	1	0	1	1	5	3	2	1	0	2	0	1
Cyranhoris	0	0	2	1	0	1	1	5	3	2	1	0	2	0	2
Dialipina	0	0	2	0	2	?	0	2	0	2	1	0	?	1	1
Dictyopyge	1	?	?	?	?	?	?	?	?	2	1	0	2	0	1
Discoserra	0	0	1	1	0	1	0	2	0	2	1	0	0	0	2
Donnrosenia	0	0	2	1	0	1	1	5	3	1	1	0	2	0	0
Ebenaqua	0	0	2	?	?	0	1	5	3	2	1	0	2	0	2
Elonichthys' palatinus	0	0	2	1	0	0	1	5	3	2	1	0	2	0	0
Gogosardinia	0	0	2	1	0	1	0	4	2	1	1	0	?	1	0
Gonatodus	0	0	2	1	0	1	1	5	3	2	1	0	0	0	2
Guildayichthys	0	0	0	1	0	1	0	2	0	2	1	1	1	0	1
Guntherichthys	0	0	2	1	0	1	?	?	?	2	1	0	?	0	1
Haploepis ovoidea	0	0	2	1	1	0	1	5	3	1	1	0	2	0	2
Howqualepis	0	0	2	1	0	1	1	5	3	1	1	0	2	0	0
Kalops diophrys	0	0	2	1	0	0	1	5	3	2	1	0	0	0	2
Kalops monophrys	0	0	2	1	0	0	1	5	3	2	1	0	0	0	2
Kentuckia deani	0	0	2	1	0	1	1	5	3	1	1	0	2	1	0
Lepisosteus	0	0	2	0	2	0	1	5	3	2	1	0	0	0	0
Limnomis	0	0	2	1	0	1	1	5	3	1	1	0	2	0	1
Lineagruan judithi	0	0	2	1	0	1	1	5	3	2	1	0	2	0	2
Lineagruan snowyi	0	0	2	1	0	1	1	5	3	2	1	0	2	0	2
Mansfieldiscus	0	0	2	1	0	1	1	5	3	2	1	0	2	0	2

	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Melanecta anneae	0	0	2	1	0	0	1	5	3	?	?	0	2	0	1
Mesopoma carricki	0	0	2	1	0	1	1	5	3	2	1	0	2	0	?
Mesopoma planti	0	0	2	1	0	1	1	5	3	2	1	0	2	0	?
Microhaplolepis	0	0	2	1	1	0	1	5	3	1	1	0	2	0	2
Mimia	0	0	2	1	0	1	1	5	3	1	1	0	2	1	0
Moythomasia	0	0	2	1	0	1	1	5	3	1	1	0	2	1	0
New Brunswick Fish	0	0	2	1	0	1	1	5	3	2	1	0	0	0	1
Novogonatodus	0	0	2	?	?	1	?	?	?	?	?	?	?	?	?
Osorioichthys	0	0	2	1	0	1	1	5	3	2	1	0	2	0	0
Palaeoniscum	0	0	2	1	0	0	1	5	3	2	1	0	0	0	1
Parahaplolepis	0	0	2	1	1	0	1	5	3	?	?	0	2	0	2
Paramblypterus	0	0	1	1	0	1	1	5	3	2	1	0	2	0	1
Paramesolepis	0	0	2	1	0	1	1	5	3	2	1	0	2	0	1
Paratarrasius	0	0	A	1	0	A	1	5	3	2	1	A	0	0	2
Platysomus gibbosus	0	0	2	1	0	0	1	5	3	2	1	0	2	0	2
Platysomus parvulus	0	0	?	1	0	0	?	?	?	?	?	0	2	?	2
Platysomus schultzei	0	0	2	1	0	1	1	5	3	2	1	0	2	0	0
Platysomus striatus	0	0	2	1	0	0	1	5	3	2	1	0	2	0	2
Platysomus superbus	0	0	2	1	0	1	1	5	3	2	1	0	2	0	2
Platysomus swaffordae	0	0	2	1	0	0	1	5	3	2	1	0	2	0	0
Polypterus bichir	0	0	0	0	2	0	1	5	3	2	1	0	2	0	0
Proceramala	0	0	2	1	?	1	1	5	3	2	1	0	2	0	2
Pteronisculus	0	0	2	1	0	1	1	5	3	2	1	0	2	0	1
Redfieldius	1	0	2	1	0	0	1	5	3	2	1	0	?	0	3
Rhadinichthys	0	0	2	1	0	1	1	5	3	2	1	0	2	1	1
Spinofacia	0	0	2	1	0	1	1	5	3	2	1	0	2	?	2
Stegotrachelus	0	0	2	1	0	1	1	5	3	1	1	0	2	0	1
Tarrasius	0	0	A	0	2	A	1	5	3	2	1	A	0	0	1
Tegeolepis	0	0	2	0	2	1	1	5	3	2	1	0	2	0	0
Wendyichthys dicksoni	0	0	2	1	0	1	1	5	3	2	1	0	2	0	2
Wendyichthys lautreci	0	0	2	1	0	1	1	5	3	2	1	0	2	?	?
Woodichthys	0	0	2	1	0	1	1	5	3	2	1	0	2	0	2
Polydon spathula	0	1	4	2	3	2	?	?	?	1	1	0	?	0	0
Solnhofenamia	0	0	2	0	3	0	1	5	3	2	1	0	0	0	1
Obaichthys	0	?	?	?	?	?	?	?	?	2	1	0	0	0	0
Chondrosteus	0	?	?	?	?	?	?	?	?	2	1	0	?	?	2

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Onychodus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Diabolepis	?	?	0	0	?	?	0	?	?	1	2	?	?	3	?
Miguashaia	0	0	0	1	0	0	0	0	0	1	2	2	?	3	1
Psarolepis	?	0	3	1	?	?	0	?	?	?	?	?	?	?	?
Acipenser	1	0	0	1	0	4	0	1	2	1	?	2	1	3	1
Aeduella blainvillei	2	0	0	1	0	1	0	2	3	1	3	1	4	3	1
Aesopichthys	2	0	0	1	0	0	0	2	3	1	1	1	2	2	2
Amblypterus latus	2	0	0	1	0	0	0	2	3	1	2	1	2	2	2
Amia calva	2	0	0	1	0	1	0	2	3	1	2	2	2	3	1
Amphicentrum granulosum	2	2	0	1	3	5	0	2	3	1	3	1	1	3	1
Amphicentrum jurgenai	2	0	0	1	0	?	0	2	3	1	?	1	2	3	1
Beagiascus	2	0	0	1	1	3	0	2	3	1	1	1	1	2	2
Beishanichthys	2	0	0	1	0	2	0	1	0	1	?	2	3	2	1
Boreosomus	2	0	0	1	0	2	0	2	3	1	3	2	4	2	2
Bourbonnella guilloti	2	0	0	1	0	1	0	2	3	1	3	1	4	3	1
Bourbonnella jocelynae	2	0	0	1	0	1	0	?	?	1	1	?	1	?	1
Canobius elegantulus	2	0	0	1	0	1	0	2	3	1	2	1	2	3	1
Cheirodopsis	2	0	0	1	0	1	0	2	3	1	3	1	1	2	1
Cheirolepis canadensis	1	0	0	1	0	1	0	1	2	1	3	2	4	1	1
Cheirolepis trailli	0	0	0	1	0	1	0	1	0	1	3	2	4	1	1
Cheirolepis schultzei	1	0	0	1	0	1	0	1	2	1	3	2	4	1	1
Coccocephalus	2	0	0	1	0	3	0	?	?	1	3	1	2	?	1
Cuneognathus	2	0	0	1	0	1	0	2	3	1	?	1	?	?	2
Cycloptychius	2	0	0	1	0	1	0	2	3	1	1	1	1	2	1
Cyranhoris	2	0	0	1	0	2	0	2	3	1	1	1	2	2	2
Dialipina	2	0	0	1	?	?	0	?	?	1	1	?	1	3	1
Dictyopyge	2	0	0	1	0	2	0	2	3	1	2	?	2	3	1
Discoserra	1	0	0	1	0	3	1	1	2	1	?	2	?	3	2
Donnrosenia	1	0	0	1	0	1	0	2	3	1	1	0	4	1	2
Ebenaqua	2	0	0	1	0	2	0	2	3	1	2	2	1	2	1
Elonichthys' palatinus	2	0	0	1	0	2	0	2	3	1	1	2	1	3	1
Gogosardinia	1	?	0	1	?	?	0	?	?	1	?	?	?	?	2
Gonatodus	2	0	0	1	0	1	0	1	0	1	2	2	2	2	1
Guildayichthys	2	0	0	1	0	1	1	1	0	1	2	1	?	3	2
Guntherichthys	2	?	0	1	?	?	0	?	?	?	?	?	?	?	?
Haploepis ovoidea	1	0	0	1	0	1	0	2	3	1	3	1	4	2	1
Howqualepis	2	0	0	1	0	0	0	2	3	1	1	1	4	1	2
Kalops diophrys	2	0	0	1	2	3	0	1	1	1	2	2	1	2	1
Kalops monophrys	2	0	0	1	0	0	0	1	0	1	2	2	2	2	1
Kentuckia deani	2	0	0	1	0	?	0	2	3	1	?	?	?	2	2
Lepisosteus	2	0	0	1	0	2	0	1	0	1	2	1	2	2	1
Limnomis	2	0	0	1	0	1	0	2	3	1	1	1	4	1	2
Lineagruan judithi	2	0	0	1	1	3	0	2	3	1	1	2	1	2	2
Lineagruan snowyi	2	0	0	1	1	3	0	2	3	1	1	?	1	2	2
Mansfieldiscus	2	0	0	1	0	1	0	2	3	1	1	1	1	2	1

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Melanecta anneae	2	?	0	1	?	?	0	2	3	1	?	?	1	?	1
Mesopoma carricki	2	0	0	1	0	2	0	2	3	1	1	1	4	?	1
Mesopoma planti	2	0	0	1	0	?	0	2	3	1	1	1	1	2	1
Microhaplolepis	2	0	2	1	0	1	0	2	3	1	3	1	4	2	1
Mimia	1	0	0	1	0	1	0	2	3	1	1	1	1	2	2
Moythomasia	2	0	0	1	0	2	0	2	3	1	1	1	1	1	2
New Brunswick Fish	2	0	0	1	0	?	0	1	2	1	2	2	2	2	1
Novogonatodus	?	?	?	1	?	?	?	2	3	1	1	1	?	2	1
Osorioichthys	1	0	0	1	0	2	0	2	3	1	1	1	2	2	2
Palaeoniscum	2	0	0	1	0	2	0	1	0	1	2	2	3	3	2
Parahaplolepis	1	0	2	1	0	1	0	2	3	1	3	1	4	2	1
Paramblypterus	2	0	0	1	1	3	0	2	2	1	2	1	1	2	2
Paramesolepis	2	0	0	1	0	1	0	2	3	1	3	?	4	2	2
Paratarrasius	2	0	0	1	1	3	0	1	1	1	1	2	1	2	2
Platysomus gibbosus	2	0	0	1	0	2	0	2	3	1	2	2	?	2	1
Platysomus parvulus	2	?	0	1	?	?	0	2	3	1	2	2	1	3	1
Platysomus schultzei	2	1	0	1	3	5	0	2	3	1	3	1	4	?	1
Platysomus striatus	2	0	0	1	0	2	0	2	3	1	2	2	2	3	1
Platysomus superbus	2	0	0	1	0	2	0	2	3	1	2	?	1	2	1
Platysomus swaffordae	2	0	0	1	0	1	0	2	3	?	?	?	?	?	?
Polypterus bichir	2	0	0	1	0	3	0	2	3	1	2	2	?	3	?
Proceramala	2	0	0	1	1	3	0	2	3	1	1	1	1	2	2
Pteronisculus	2	0	0	1	0	2	0	2	3	1	2	1	2	2	2
Redfieldius	2	0	1	1	0	1	0	?	?	1	2	2	2	2	1
Rhadinichthys	2	0	0	1	0	2	0	2	3	1	1	1	2	2	1
Spinofacia	2	0	0	1	0	1	0	2	3	1	1	1	2	2	1
Stegotrachelus	2	0	0	1	0	1	0	3	3	1	1	1	1	1	2
Tarrasius	2	0	0	1	0	1	0	1	0	1	1	2	1	2	2
Tegeolepis	2	?	0	1	?	?	0	2	3	1	1	1	2	3	2
Wendyichthys dicksoni	2	0	0	1	0	2	0	2	3	1	1	1	2	2	2
Wendyichthys lautreci	?	?	0	1	?	?	0	2	3	1	?	1	?	?	1
Woodichthys	2	0	0	1	0	2	0	2	3	1	?	?	2	2	2
Polydon spathula	0	0	0	1	0	?	0	1	0	1	1	2	?	3	1
Solnhofenamia	2	0	0	1	0	1	0	1	0	1	2	2	3	3	1
Obaichthys	2	0	0	1	0	?	0	?	0	1	2	?	3	3	1
Chondrosteus	2	0	0	1	0	3	0	2	3	1	?	?	2	3	1

	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Onychodus	1	3	4	2	2	0	0	0	1	?	?	0	0	3	?
Diabolepis	1	?	?	?	?	0	2	?	?	?	?	?	?	?	?
Miguashaia	1	3	4	2	2	0	2	0	1	0	1	0	0	3	?
Psarolepis	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?
Acipenser	0	1	3	1	0	1	1	?	?	?	?	1	0	3	?
Aeduella blainvillei	0	0	?	?	0	1	2	0	?	?	?	1	?	1	?
Aesopichthys	0	2	1	?	0	1	2	2	1	1	3	1	0	2	2
Amblypterus latus	0	2	1	0	0	1	2	0	?	?	?	1	0	0	?
Amia calva	0	2	0	0	0	1	2	2	1	1	1	1	?	?	2
Amphicentrum granulosum	0	1	1	1	0	1	2	0	1	1	4	1	0	3	2
Amphicentrum jurgenai	0	0	1	?	0	1	2	0	1	0	3	1	0	3	2
Beagiascus	0	2	2	0	0	1	2	0	1	1	2	1	0	0	2
Beishanichthys	0	1	1	0	0	1	2	0	1	0	5	1	0	0	2
Boreosomus	0	1	1	1	0	1	2	0	1	0	5	1	0	4	2
Bourbonnella guilloti	0	0	1	0	0	1	2	?	?	?	?	1	0	?	?
Bourbonnella jocelynae	0	1	1	0	0	1	2	?	?	?	?	1	?	?	?
Canobius elegantulus	0	2	1	0	0	1	?	0	1	0	1	1	0	0	2
Cheirodopsis	0	2	1	0	0	1	2	0	?	?	?	1	0	3	2
Cheirolepis canadensis	0	0	0	0	0	1	?	0	1	0	1	1	0	3	2
Cheirolepis trailli	0	0	0	0	0	1	1	0	1	0	1	1	1	3	2
Cheirolepis schultzei	0	1	1	0	0	1	?	0	1	?	?	1	1	3	2
Coccocephalus	0	1	1	?	0	1	?	0	1	1	2	1	?	?	?
Cuneognathus	0	1	1	1	0	1	?	0	?	?	?	1	0	3	?
Cycloptychius	0	2	1	0	0	1	2	0	1	0	3	1	0	0	4
Cyranhoris	0	2	1	1	0	1	2	0	1	1	1	1	0	0	2
Dialipina	0	2	?	1	0	1	1	0	?	?	?	?	?	?	?
Dictyopyge	0	2	1	1	0	1	2	0	?	?	?	1	0	1	?
Discoserra	0	?	0	?	0	1	?	0	1	1	5	1	0	0	2
Donnrosenia	0	1	0	0	0	1	0	0	1	0	1	1	0	3	?
Ebenaqua	0	1	0	0	0	1	2	0	1	1	5	1	0	3	2
Elonichthys' palatinus	0	0	1	1	0	1	2	0	1	1	2	1	0	0	2
Gogosardinia	0	0	?	?	0	1	0	0	1	0	3	1	0	3	?
Gonatodus	0	2	0	0	0	1	?	0	1	0	1	1	0	0	2
Guildayichthys	0	0	0	?	0	1	2	0	1	1	5	1	0	0	2
Guntherichthys	0	2	1	0	0	1	?	?	1	?	2	1	?	?	?
Haploepis ovoidea	0	0	0	1	0	1	2	0	?	?	?	1	0	1	?
Howqualepis	0	1	1	1	0	1	0	0	1	0	1	1	0	3	2
Kalops diophrys	0	2	1	1	0	1	2	0	1	1	1	1	0	0	2
Kalops monophrys	0	2	1	1	0	1	2	0	1	1	1	1	0	0	2
Kentuckia deani	0	0	1	0	0	1	0	?	1	0	5	1	?	?	?
Lepisosteus	0	0	0	0	0	1	2	0	1	1	1	1	?	?	2
Limnomis	0	0	1	1	0	1	2	0	1	0	?	1	0	3	1
Lineagruan judithi	0	2	0	0	0	1	2	0	1	1	2	1	0	0	2
Lineagruan snowyi	0	2	0	0	0	1	?	0	1	1	2	1	0	0	2
Mansfieldiscus	0	1	2	0	0	1	2	0	1	0	5	1	0	1	2

	76	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**
Melanecta anneae	0	0	?	0	0	1	?	0	1	0	5	1	0	?	?
Mesopoma carricki	0	1	1	1	0	1	2	0	?	?	?	1	0	1	2
Mesopoma planti	0	2	?	1	0	1	2	0	1	0	3	1	0	1	2
Microhaplolepis	2	0	0	1	1	1	2	0	?	?	?	1	0	1	?
Mimia	0	0	1	0	0	1	?	0	1	0	3	1	0	3	2
Moythomasia	0	0	1	0	0	1	?	0	1	0	5	1	0	0	2
New Brunswick Fish	0	2	?	0	0	1	2	0	1	1	4	1	0	0	2
Novogonatodus	?	?	?	?	?	?	?	0	?	?	?	?	0	0	?
Osorioichthys	0	0	1	0	0	1	?	0	1	0	1	1	0	0	2
Palaeoniscum	0	2	1	?	0	1	2	0	1	0	5	1	0	0	2
Parahaplolepis	2	0	1	1	1	1	2	0	?	?	?	1	0	1	?
Paramblypterus	0	1	1	?	0	1	?	0	?	?	?	1	0	0	?
Paramesolepis	0	0	1	0	0	1	2	0	1	0	3	1	0	3	2
Paratarrasius	0	1	0	1	0	1	?	1	1	1	5	1	0	0	2
Platysomus gibbosus	0	0	0	1	0	1	?	0	1	1	4	1	0	0	2
Platysomus parvulus	0	?	1	?	0	1	2	0	?	?	?	1	0	3	?
Platysomus schultzei	0	0	1	1	0	1	2	0	1	1	5	1	0	3	2
Platysomus striatus	0	1	1	1	0	1	2	0	1	0	3	1	0	3	2
Platysomus superbus	0	2	0	0	0	1	2	0	1	1	3	1	0	3	2
Platysomus swaffordae	?	?	?	?	?	?	?	0	1	1	5	1	0	3	?
Polypterus bichir	?	?	?	?	?	?	2	0	1	0	?	1	?	?	?
Proceramala	0	2	1	0	0	1	2	0	?	?	?	1	0	0	2
Pteronisculus	0	2	1	1	0	1	2	0	1	1	5	1	0	0	2
Redfieldius	0	1	1	1	0	1	2	0	1	1	2	1	0	2	2
Rhadinichthys	0	2	1	0	0	1	2	0	1	0	3	1	0	0	2
Spinofacia	0	1	?	0	0	1	2	0	1	1	2	1	0	0	2
Stegotrachelus	0	0	1	1	0	1	2	0	?	?	?	1	0	3	2
Tarrasius	0	0	1	1	0	1	2	0	?	?	?	1	0	3	?
Tegeolepis	0	0	1	0	0	1	2	0	1	1	4	1	0	2	2
Wendyichthys dicksoni	0	2	1	1	0	1	2	0	1	1	2	1	0	0	2
Wendyichthys lautreci	0	?	1	?	0	1	2	0	1	1	2	1	?	0	?
Woodichthys	0	2	1	0	0	1	2	0	1	0	5	1	0	3	2
Polydon spathula	?	?	?	?	?	1	?	2	?	?	?	1	0	3	2
Solnhofenamia	0	2	0	0	0	1	2	2	1	1	5	1	?	?	2
Obaichthys	0	0	0	0	0	1	2	2	?	?	?	1	0	?	2
Chondrosteus	0	?	?	?	0	1	?	?	?	?	?	1	1	4	?

	91	92	93	94	95	96	97	098	099	100	101	102	103	104	105
Onychodus	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0
Diabolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Miguashaia	?	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Psarolepis	?	0	0	0	0	0	?	?	?	?	?	?	?	0	?
Acipenser	?	0	0	0	0	0	?	?	1	0	0	0	1	0	0
Aeduella blainvillei	?	1	3	2	2	2	1	4	1	1	2	0	1	0	0
Aesopichthys	3	1	1	1	2	?	0	1	1	1	2	0	1	1	0
Amblypterus latus	0	1	1	1	0	2	0	?	1	0	0	0	1	1	0
Amia calva	2	0	0	0	0	0	1	4	1	1	2	0	1	0	0
Amphicentrum granulosum	0	0	0	0	0	0	?	?	1	1	2	0	1	0	0
Amphicentrum jurgenai	0	0	0	0	0	0	0	1	1	?	?	0	1	0	0
Beagiascus	0	1	3	2	1	2	0	1	1	?	?	0	1	1	1
Beishanichthys	?	1	1	1	1	2	?	?	1	0	1	0	1	1	0
Boreosomus	0	1	2	1	1	1	0	?	1	1	2	0	1	1	0
Bourbonnella guilloti	?	?	?	?	?	?	1	4	1	1	2	0	1	0	0
Bourbonnella jocelynae	?	?	?	?	?	?	?	?	1	1	2	0	1	1	0
Canobius elegantulus	0	1	1	1	2	2	?	?	1	1	2	0	1	0	0
Cheirodopsis	0	0	0	0	0	0	?	?	1	1	2	0	1	1	0
Cheirolepis canadensis	0	0	0	0	0	0	0	1	1	1	2	0	1	1	0
Cheirolepis trailli	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0
Cheirolepis schultzei	0	0	0	0	0	0	0	?	1	1	2	0	0	1	0
Coccocephalus	?	?	?	?	?	?	0	?	1	?	?	0	?	?	0
Cuneognathus	?	0	0	0	0	0	?	?	1	0	0	0	1	1	0
Cycloptychius	0	1	1	1	1	2	?	?	1	1	2	0	1	1	0
Cyranhoris	0	1	1	1	1	2	0	1	1	?	?	0	1	1	0
Dialipina	?	?	?	?	?	?	?	?	1	?	?	0	?	0	?
Dictyopyge	1	1	1	1	1	1	?	?	1	1	2	0	1	0	0
Discoserra	3	1	3	2	2	2	0	0	1	1	2	0	0	0	0
Donnrosenia	?	0	0	0	0	0	?	?	1	0	0	0	?	?	0
Ebenaqua	0	0	0	0	0	0	?	?	1	?	?	2	0	0	0
Elonichthys' palatinus	1	1	1	1	1	2	0	1	1	1	2	0	1	0	0
Gogosardinia	?	0	0	0	0	0	?	?	1	0	0	0	1	1	0
Gonatodus	0	1	1	1	1	2	0	1	1	1	2	0	1	2	0
Guildayichthys	0	1	3	3	1	2	0	0	1	1	2	0	0	0	0
Guntherichthys	?	?	?	?	?	?	0	?	1	?	?	?	1	1	0
Haploepis ovoidea	0	1	1	1	1	1	1	4	1	1	2	0	1	1	0
Howqualepis	0	0	0	0	0	0	0	?	1	0	0	0	1	1	0
Kalops diophrys	1	1	3	2	1	2	0	3	1	1	2	0	0	1	0
Kalops monophrys	?	1	2	2	0	2	0	3	1	?	?	0	1	1	0
Kentuckia deani	?	0	0	0	0	0	?	?	1	1	2	0	1	1	0
Lepisosteus	2	1	3	3	1	0	1	4	1	0	0	0	1	0	0
Limnomis	0	0	0	0	0	0	?	?	1	?	?	0	1	1	0
Lineagruan judithi	0	1	1	1	1	2	0	3	1	?	?	0	1	1	1
Lineagruan snowyi	0	1	2	2	1	2	?	?	1	?	?	0	1	1	1
Mansfieldiscus	0	1	1	1	1	2	?	?	1	?	?	0	1	1	0

	91	92	93	94	95	96	97	098	099	100	101	102	103	104	105
Melanecta anneae	?	?	?	?	?	?	0	?	1	?	?	0	1	?	0
Mesopoma carricki	0	1	1	1	1	1	?	?	1	?	?	0	1	1	0
Mesopoma planti	0	1	1	1	?	1	?	?	1	0	0	0	1	1	0
Microhaplolepis	0	1	1	1	1	1	1	4	1	1	2	0	1	0	0
Mimia	0	0	0	0	0	0	0	1	1	0	0	0	?	1	0
Moythomasia	0	1	1	1	1	2	0	1	1	?	?	0	1	1	0
New Brunswick Fish	0	1	3	3	1	2	0	?	1	1	2	0	1	1	0
Novogonatodus	?	1	1	1	1	2	?	?	1	1	2	0	1	1	?
Osorioichthys	0	1	1	1	1	2	0	1	1	0	0	0	1	1	0
Palaeoniscum	0	1	2	1	1	2	?	?	1	?	?	0	1	0	0
Parahaplolepis	0	1	1	1	1	1	1	4	1	0	1	0	1	0	0
Paramblypterus	0	1	3	3	2	2	0	?	1	0	0	0	?	2	0
Paramesolepis	0	0	0	0	0	0	?	?	1	?	?	0	1	1	0
Paratarrasius	0	1	3	3	1	2	?	?	1	1	2	0	1	2	0
Platysomus gibbosus	0	1	1	1	1	1	?	?	1	?	?	2	0	0	0
Platysomus parvulus	?	0	0	0	0	0	?	?	1	1	2	0	1	0	0
Platysomus schultzei	0	0	0	0	0	0	0	1	1	?	?	1	1	0	0
Platysomus striatus	0	0	0	0	0	0	?	?	1	1	2	0	1	0	0
Platysomus superbus	0	0	0	0	0	0	?	?	1	?	?	0	1	0	0
Platysomus swaffordae	0	0	0	0	0	0	?	?	1	?	?	1	1	?	?
Polypterus bichir	?	0	0	0	0	0	1	4	1	0	0	0	?	0	?
Proceramala	0	1	3	2	1	2	0	1	1	1	2	0	1	1	0
Pteronisculus	0	1	1	1	1	2	0	1	1	0	0	0	0	1	0
Redfieldius	0	1	1	1	1	1	?	?	1	?	?	0	1	1	0
Rhadinichthys	0	1	1	1	1	2	?	?	1	1	2	0	1	1	0
Spinofacia	0	1	1	1	1	1	0	?	1	?	?	0	1	1	0
Stegotrachelus	0	0	0	0	0	0	0	?	1	?	?	0	1	1	0
Tarrasius	?	0	0	0	0	0	0	?	1	1	2	0	1	1	0
Tegeolepis	1	0	0	0	0	0	?	?	1	1	2	0	1	0	0
Wendyichthys dicksoni	0	1	1	1	1	2	0	1	1	0	0	0	1	1	0
Wendyichthys lautreci	?	1	?	?	?	2	0	1	1	?	?	?	1	1	0
Woodichthys	0	0	0	0	0	0	0	1	1	?	?	0	1	1	0
Polydon spathula	?	0	0	0	0	0	1	4	1	1	2	0	1	0	0
Solnhofenamia	1	1	1	1	?	1	0	2	1	1	2	0	1	0	0
Obaichthys	2	1	1	1	2	1	1	4	1	0	1	0	1	0	0
Chondrosteus	0	0	0	0	0	0	0	?	1	0	?	0	1	0	0

	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Onychodus	0	2	2	0	3	0	2	1	0	0	0	0	0	0	0
Diabolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Miguashaia	0	2	2	0	4	0	4	?	0	0	0	0	0	1	0
Psarolepis	0	2	2	0	0	?	0	?	?	?	?	?	?	?	?
Acipenser	2	3	3	2	5	4	5	2	0	0	0	0	1	2	2
Aeduella blainvillei	?	?	?	0	?	1	1	1	0	0	0	0	0	0	1
Aesopichthys	1	1	0	0	1	1	0	1	0	0	0	0	0	1	1
Amblypterus latus	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1
Amia calva	0	2	2	0	2	3	4	0	0	0	0	1	0	1	1
Amphicentrum granulosum	0	1	2	0	1	2	1	1	0	0	0	0	0	0	1
Amphicentrum jurgenai	0	1	2	0	1	2	0	1	0	0	0	0	0	0	1
Beagiascus	1	0	0	0	0	1	0	1	2	2	1	0	0	0	1
Beishanichthys	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1
Boreosomus	1	1	0	0	0	1	0	0	0	0	0	0	0	1	1
Bourbonnella guilloti	1	1	1	0	0	?	0	1	0	0	0	0	0	0	1
Bourbonnella jocelynae	1	1	1	0	0	?	0	1	0	0	0	0	0	0	1
Canobius elegantulus	1	1	1	0	1	1	0	1	0	0	0	0	0	1	1
Cheirodopsis	1	1	1	0	1	2	0	1	0	0	0	0	0	0	1
Cheirolepis canadensis	1	0	0	0	3	2	0	0	5	2	1	0	0	0	1
Cheirolepis trailli	1	0	0	0	3	2	0	0	2	2	1	0	0	0	1
Cheirolepis schultzei	0	0	0	0	3	2	3	0	5	2	1	0	0	0	1
Coccocephalus	1	0	0	0	0	?	0	?	?	?	?	?	0	0	1
Cuneognathus	1	0	0	0	0	?	0	1	0	0	0	0	0	0	1
Cycloptychius	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Cyranhoris	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Dialipina	?	?	?	?	?	?	2	?	?	?	?	0	1	3	2
Dictyopyge	1	1	1	0	0	2	0	1	0	0	0	0	0	2	1
Discoserra	0	2	2	1	2	1	2	1	0	0	0	1	0	0	1
Donnrosenia	?	?	?	?	?	?	?	0	5	3	1	0	0	0	1
Ebenaqua	0	2	2	A	2	2	1	0	0	0	0	0	0	0	1
Elonichthys' palatinus	1	0	0	0	0	1	0	0	5	2	1	0	0	0	1
Gogosardinia	1	0	0	0	0	2	0	0	0	0	0	0	0	1	1
Gonatodus	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1
Guildayichthys	0	2	2	1	2	1	2	1	0	0	0	1	0	0	1
Guntherichthys	?	?	?	?	?	?	?	?	0	0	0	0	0	0	?
Haploepis ovoidea	0	1	2	0	1	2	1	1	0	0	0	0	0	0	1
Howqualepis	1	0	0	0	0	2	0	0	0	0	0	0	0	0	1
Kalops diophrys	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Kalops monophrys	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Kentuckia deani	1	0	0	0	0	?	0	1	5	2	1	0	0	0	1
Lepisosteus	0	2	2	0	2	?	2	1	0	0	0	0	0	1	1
Limnomis	1	0	0	0	0	2	0	0	0	0	0	0	0	0	1
Lineagruan judithi	1	1	1	0	0	1	0	1	2	3	2	0	0	0	1
Lineagruan snowyi	1	0	0	0	0	1	0	1	3	3	2	0	0	0	1
Mansfieldiscus	1	0	0	0	0	1	0	1	5	2	1	0	0	0	1

	106	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**	**119**	**120**
Melanecta anneae	1	0	0	0	0	?	0	1	0	0	0	0	0	0	1
Mesopoma carricki	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1
Mesopoma planti	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1
Microhaplolepis	0	1	2	0	1	1	1	0	0	0	0	0	0	0	1
Mimia	1	0	0	0	0	2	0	0	0	0	0	0	0	1	1
Moythomasia	1	0	0	0	0	1	0	1	?	?	?	0	0	0	1
New Brunswick Fish	1	0	0	0	0	1	0	?	2	2	1	0	0	0	1
Novogonatodus	1	1	0	0	0	1	0	?	0	0	0	0	0	0	1
Osorioichthys	1	0	0	0	0	1	0	1	0	0	0	0	0	2	1
Palaeoniscum	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Parahaplolepis	0	1	2	0	0	1	1	1	0	0	0	0	0	1	1
Paramblypterus	1	?	?	0	0	1	0	0	0	0	0	0	0	0	1
Paramesolepis	0	1	2	0	1	2	2	1	0	0	0	0	0	1	1
Paratarrasius	1	0	0	0	0	1	0	1	1	3	1	0	0	1	1
Platysomus gibbosus	0	2	2	1	2	1	4	0	0	0	0	0	0	0	1
Platysomus parvulus	1	1	?	0	1	2	0	1	0	0	0	0	0	0	1
Platysomus schultzei	0	2	2	0	2	5	4	0	0	0	0	0	0	0	1
Platysomus striatus	1	1	1	0	1	2	3	1	0	0	0	0	0	0	1
Platysomus superbus	1	1	1	0	1	2	0	1	0	0	0	0	0	0	1
Platysomus swaffordae	0	2	2	1	2	5	0	?	0	0	0	0	0	0	1
Polypterus bichir	1	1	2	0	1	?	?	1	0	0	0	0	0	1	1
Proceramala	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1
Pteronisculus	1	0	0	0	0	1	0	0	1	3	1	0	0	0	1
Redfieldius	1	0	0	0	0	2	2	1	0	0	0	0	0	1	1
Rhadinichthys	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Spinofacia	1	0	0	0	0	1	0	?	0	0	0	0	0	0	1
Stegotrachelus	1	0	0	0	0	2	0	1	5	2	1	0	0	0	1
Tarrasius	0	1	0	0	1	2	0	0	0	0	0	0	0	0	1
Tegeolepis	1	0	0	0	0	2	0	0	0	0	0	0	0	?	1
Wendyichthys dicksoni	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Wendyichthys lautreci	1	0	0	0	0	1	0	?	0	0	0	0	0	0	1
Woodichthys	1	0	0	0	0	2	0	0	0	0	0	0	0	0	1
Polydon spathula	2	3	3	2	5	4	5	2	0	0	0	0	1	3	2
Solnhofenamia	0	2	2	0	2	3	4	1	0	0	0	1	0	1	1
Obaichthys	0	2	2	0	2	3	1	0	0	0	0	0	0	0	1
Chondrosteus	?	?	?	?	?	?	?	?	0	0	0	0	0	1	?

	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
Onychodus	1	1	1	1	1	2	2	2	0	1	?	0	0	3	0
Diabolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Miguashaia	1	?	1	1	1	2	2	2	1	0	0	0	0	3	0
Psarolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Acipenser	4	2	?	?	0	1	1	1	1	0	0	1	2	2	1
Aeduella blainvillei	2	0	3	1	0	1	3	1	0	0	0	0	?	0	?
Aesopichthys	1	1	1	2	0	0	1	1	0	0	0	0	?	?	?
Amblypterus latus	1	0	2	1	0	0	0	1	?	0	0	?	?	?	1
Amia calva	1	0	2	?	0	0	0	1	0	0	0	1	2	2	1
Amphicentrum granulosum	3	3	2	1	0	0	0	?	?	?	?	?	?	?	1
Amphicentrum jurgenai	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?
Beagiascus	1	0	0	0	0	0	1	0	0	1	?	0	?	1	?
Beishanichthys	1	1	1	1	0	0	0	1	?	?	?	0	?	1	?
Boreosomus	1	0	1	1	0	0	1	1	0	0	0	1	2	2	1
Bourbonnella guilloti	2	1	1	0	0	1	3	1	0	0	0	0	?	?	?
Bourbonnella jocelynae	3	1	1	1	0	?	?	?	?	?	?	?	?	?	?
Canobius elegantulus	2	1	1	1	0	0	0	1	?	?	?	?	?	?	?
Cheirodopsis	3	1	2	1	0	0	0	1	?	?	?	?	?	?	?
Cheirolepis canadensis	1	0	0	0	0	0	0	?	0	0	0	0	0	1	0
Cheirolepis trailli	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Cheirolepis schultzei	1	0	4	2	0	0	0	0	?	?	?	?	?	?	?
Coccocephalus	?	?	3	?	?	?	?	?	?	?	?	?	?	?	?
Cuneognathus	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?
Cycloptychius	2	1	2	4	0	0	0	1	?	0	0	?	?	?	?
Cyranhoris	1	1	1	0	0	0	0	0	0	1	1	0	1	0	1
Dialipina	4	2	?	?	?	?	?	?	1	0	0	0	0	?	0
Dictyopyge	3	1	1	2	2	1	3	1	0	?	?	?	?	?	?
Discoserra	5	0	5	5	0	0	?	?	?	0	0	0	?	?	1
Donnrosenia	1	1	2	1	0	0	0	?	0	0	0	0	?	1	?
Ebenaqua	1	0	2	4	2	2	2	1	0	0	0	1	2	2	1
Elonichthys' palatinus	1	0	2	1	0	0	1	0	0	0	0	0	?	1	?
Gogosardinia	1	?	3	4	0	0	0	?	?	0	0	0	1	0	?
Gonatodus	1	1	0	0	0	0	1	0	0	0	0	?	?	?	0
Guildayichthys	5	0	5	5	0	1	0	1	1	0	0	0	0	1	1
Guntherichthys	1	?	2	4	0	0	0	?	0	?	?	?	?	?	1
Haploepis ovoidea	1	1	1	1	0	1	3	1	0	0	0	0	0	1	?
Howqualepis	1	1	2	1	0	0	1	0	0	0	0	0	1	1	1
Kalops diophrys	0	1	?	1	0	0	1	0	0	0	0	0	1	0	?
Kalops monophrys	0	1	1	2	0	0	1	0	0	0	0	0	1	1	?
Kentuckia deani	1	?	1	1	0	0	0	?	0	0	0	0	?	?	?
Lepisosteus	0	0	2	4	0	1	1	1	1	0	0	1	2	2	1
Limnomis	0	0	2	1	0	0	?	?	0	0	0	0	1	1	?
Lineagruan judithi	1	0	3	4	0	0	1	1	0	1	2	0	0	1	?
Lineagruan snowyi	1	0	3	4	0	0	1	0	0	1	2	0	0	1	?
Mansfieldiscus	1	1	1	?	0	0	?	?	0	0	0	0	1	1	?

	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135
Melanecta anneae	1	?	1	1	0	?	?	?	?	?	?	?	?	?	?
Mesopoma carricki	2	0	1	0	0	0	0	1	?	?	?	?	?	?	?
Mesopoma planti	2	?	1	0	0	0	0	1	?	?	?	?	?	?	?
Microhaplolepis	?	1	?	?	?	1	?	?	0	0	0	0	0	1	?
Mimia	2	0	2	0	0	0	1	0	0	0	0	0	0	1	0
Moythomasia	1	0	2	3	0	0	0	0	0	0	0	0	1	1	?
New Brunswick Fish	1	?	1	0	0	0	0	?	0	0	0	0	1	1	?
Novogonatodus	1	?	2	0	?	?	?	?	?	?	?	?	?	?	?
Osorioichthys	2	0	1	1	0	0	1	0	0	0	0	0	1	1	?
Palaeoniscum	2	0	3	1	0	0	?	1	?	?	?	?	?	?	?
Parahaplolepis	3	0	1	1	0	1	0	1	0	0	0	0	0	1	?
Paramblypterus	1	1	1	1	0	0	?	1	0	0	0	0	?	?	?
Paramesolepis	3	1	2	1	0	0	0	1	?	?	?	?	?	?	?
Paratarrasius	1	1	1	1	0	0	1	0	0	0	0	0	2	2	0
Platysomus gibbosus	0	0	2	4	0	?	?	?	?	?	?	?	?	?	?
Platysomus parvulus	1	?	2	1	0	?	0	?	?	?	?	?	?	?	?
Platysomus schultzei	0	0	2	4	1	2	2	2	1	0	0	1	2	2	1
Platysomus striatus	2	1	0	0	0	0	0	?	?	?	?	?	?	?	?
Platysomus superbus	3	1	2	1	0	0	0	1	0	?	?	0	?	?	1
Platysomus swaffordae	0	0	2	4	0	?	?	?	?	?	?	?	?	?	?
Polypterus bichir	1	0	1	4	1	2	2	2	1	0	0	0	0	3	1
Proceramala	1	1	2	1	0	1	0	0	?	?	?	?	?	?	?
Pteronisculus	1	0	1	1	0	0	0	0	0	0	0	?	?	?	1
Redfieldius	3	0	?	2	2	1	3	1	?	?	?	?	?	?	?
Rhadinichthys	1	1	2	1	0	0	0	1	?	?	?	?	?	?	?
Spinofacia	1	?	3	4	0	0	?	?	0	1	1	0	0	1	?
Stegotrachelus	0	0	?	0	0	0	0	0	?	0	0	0	?	1	?
Tarrasius	1	1	1	0	0	0	0	1	?	?	?	?	?	?	?
Tegeolepis	?	0	?	?	0	0	0	0	0	0	0	1	2	2	1
Wendyichthys dicksoni	1	1	3	4	0	0	1	0	0	1	1	0	0	1	0
Wendyichthys lautreci	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Woodichthys	1	1	2	2	0	0	0	?	?	0	0	0	1	1	0
Polydon spathula	4	2	?	?	0	1	3	1	1	0	0	1	2	2	1
Solnhofenamia	1	1	2	?	0	0	0	0	0	0	0	1	2	2	1
Obaichthys	1	1	2	4	0	1	0	1	1	0	0	1	2	2	1
Chondrosteus	3	?	2	4	0	?	0	1	?	?	?	?	?	?	1

	136	**137**	**138**	**139**	**140**	**141**	**142**	**143**	**144**	**145**	**146**	**147**	**148**	**149**	**150**
Onychodus	0	0	?	?	?	?	0	2	1	0	0	?	?	?	0
Diabolepis	0	0	?	0	3	?	0	1	0	1	?	?	?	?	?
Miguashaia	0	1	?	?	?	?	?	2	1	?	?	?	0	0	0
Psarolepis	0	1	?	0	0	?	?	?	0	?	?	?	?	?	0
Acipenser	?	0	0	?	?	?	?	3	1	1	1	?	0	0	1
Aeduella blainvillei	?	?	?	?	?	?	?	3	0	?	1	?	0	0	1
Aesopichthys	?	?	?	0	0	0	1	1	0	0	1	?	0	0	1
Amblypterus latus	?	0	?	?	?	?	?	?	?	?	?	?	?	?	1
Amia calva	0	0	1	0	0	0	0	0	1	0	2	?	0	0	1
Amphicentrum granulosum	0	0	?	?	?	?	1	0	0	?	1	?	0	2	1
Amphicentrum jurgenai	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Beagiascus	?	?	?	0	0	0	1	1	0	0	0	?	?	0	1
Beishanichthys	?	?	?	0	4	0	1	1	0	?	1	?	0	0	1
Boreosomus	1	0	?	0	?	?	1	0	0	0	1	?	0	0	1
Bourbonnella guilloti	?	?	?	?	?	?	?	1	0	?	1	?	0	0	1
Bourbonnella jocelynae	?	?	?	?	?	?	?	?	?	?	1	?	?	?	1
Canobius elegantulus	?	?	?	0	0	?	1	0	0	?	1	?	0	0	1
Cheirodopsis	?	?	?	?	?	?	1	0	0	?	1	?	0	0	1
Cheirolepis canadensis	0	0	1	0	5	0	?	0	0	0	1	0	0	0	1
Cheirolepis trailli	0	0	1	0	5	0	0	0	0	1	0	0	0	0	1
Cheirolepis schultzei	?	?	?	?	?	?	0	0	?	?	1	?	?	?	1
Coccocephalus	?	?	?	0	?	?	1	0	0	0	1	?	1	0	1
Cuneognathus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Cycloptychius	?	?	?	0	4	0	1	0	0	0	1	?	0	0	1
Cyranhoris	?	?	?	0	0	0	1	1	0	0	0	0	1	0	1
Dialipina	?	?	?	?	?	?	?	1	0	?	1	0	?	?	?
Dictyopyge	?	?	?	?	?	?	?	1	0	?	1	?	0	0	1
Discoserra	?	?	?	?	?	?	?	0	0	?	?	?	1	?	1
Donnrosenia	?	?	?	?	?	?	?	0	?	0	?	?	?	?	1
Ebenaqua	?	0	?	?	?	?	?	0	0	0	1	?	?	0	1
Elonichthys' palatinus	?	0	?	?	?	?	1	0	0	0	1	?	0	0	1
Gogosardinia	?	1	?	0	0	0	1	1	?	0	?	?	?	?	1
Gonatodus	?	?	?	0	4	0	1	0	0	0	1	?	0	0	1
Guildayichthys	?	?	?	?	?	?	?	0	0	?	0	1	0	1	1
Guntherichthys	?	0	?	?	?	?	?	?	?	0	?	?	?	?	?
Haploepis ovoidea	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Howqualepis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Kalops diophrys	?	?	?	0	1	0	1	1	0	0	1	?	1	0	1
Kalops monophrys	?	0	?	0	1	0	1	1	0	0	1	?	1	0	1
Kentuckia deani	?	?	?	0	4	0	0	0	0	0	0	?	0	0	1
Lepisosteus	0	1	1	0	?	0	0	1	1	0	1	0	0	0	1
Limnomis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Lineagruan judithi	?	?	?	0	0	0	1	1	?	0	?	?	?	?	1
Lineagruan snowyi	?	?	?	0	0	0	1	1	0	0	0	?	?	?	1
Mansfieldiscus	?	?	?	?	?	?	1	0	0	0	1	?	0	0	1

	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
Melanecta anneae	?	?	?	0	0	0	1	1	0	?	1	?	?	?	1
Mesopoma carricki	?	?	?	0	0	?	?	?	?	?	1	?	?	0	1
Mesopoma planti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Microhaplolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Mimia	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1
Moythomasia	?	?	?	?	?	?	1	0	0	?	0	?	?	?	1
New Brunswick Fish	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?
Novogonatodus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Osorioichthys	?	?	?	0	0	0	1	0	0	0	0	?	?	?	1
Palaeoniscum	?	0	?	0	4	0	1	0	0	0	0	?	0	0	1
Parahaplolepis	?	?	?	?	?	?	?	1	?	?	?	?	?	?	1
Paramblypterus	?	?	?	?	?	?	?	0	0	?	1	0	0	0	1
Paramesolepis	?	?	?	0	4	0	1	0	0	0	0	?	0	0	1
Paratarrasius	?	?	?	0	0	0	1	3	1	0	0	?	0	0	1
Platysomus gibbosus	?	?	?	?	?	?	1	0	0	0	1	?	?	0	1
Platysomus parvulus	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?
Platysomus schultzei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Platysomus striatus	?	?	?	?	?	?	1	0	0	0	1	?	?	0	1
Platysomus superbus	0	0	?	?	?	?	1	0	0	0	1	?	?	0	1
Platysomus swaffordae	?	?	?	?	?	?	1	1	?	?	?	?	?	?	1
Polypterus bichir	0	0	1	0	0	0	0	0	0	0	?	?	0	0	?
Proceramala	?	?	?	?	?	?	1	?	?	?	?	0	?	?	1
Pteronisculus	?	0	0	0	0	0	1	0	0	0	0	?	1	0	1
Redfieldius	?	0	?	?	?	?	?	1	0	?	1	?	0	0	1
Rhadinichthys	?	?	?	0	4	0	1	0	0	0	1	?	0	0	1
Spinofacia	?	?	?	0	0	0	1	1	?	0	?	?	?	?	1
Stegotrachelus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Tarrasius	?	?	?	0	1	0	?	0	0	?	1	0	0	0	1
Tegeolepis	?	0	?	?	?	?	?	0	0	0	0	?	?	?	1
Wendyichthys dicksoni	?	0	?	0	0	0	1	0	0	0	0	?	1	0	1
Wendyichthys lautreci	?	?	?	?	?	?	1	1	0	0	1	0	?	?	1
Woodichthys	0	0	1	0	0	0	1	1	0	0	?	0	0	0	1
Polydon spathula	1	1	1	?	?	?	?	?	1	1	?	?	1	0	1
Solnhofenamia	1	0	1	0	0	0	?	0	1	0	1	?	0	0	1
Obaichthys	1	1	1	?	?	?	?	?	?	?	?	?	?	?	1
Chondrosteus	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165
Onychodus	?	?	?	0	1	0	0	0	0	1	0	0	1	0	0
Diabolepis	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?
Miguashaia	?	?	?	0	1	1	0	0	0	0	1	0	1	0	0
Psarolepis	?	?	?	1	1	0	?	?	?	0	0	0	0	0	?
Acipenser	0	?	?	?	?	?	1	?	0	0	0	0	1	0	0
Aeduella blainvillei	1	0	0	1	0	?	0	?	0	1	0	0	?	0	?
Aesopichthys	0	0	0	1	0	?	0	?	1	1	0	0	0	0	0
Amblypterus latus	0	?	?	1	0	?	1	?	0	1	0	1	?	0	?
Amia calva	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0
Amphicentrum granulosum	0	1	0	1	0	?	1	?	?	1	0	0	0	0	0
Amphicentrum jurgenai	?	?	?	?	?	?	1	?	0	?	0	0	0	0	?
Beagiascus	0	?	0	1	?	?	1	?	1	1	0	0	0	0	0
Beishanichthys	1	?	0	1	0	?	1	?	0	0	0	0	?	0	?
Boreosomus	1	0	0	1	0	?	0	?	0	1	0	0	0	0	0
Bourbonnella guilloti	0	0	0	1	0	?	0	?	0	1	0	0	0	0	?
Bourbonnella jocelynae	?	?	?	1	?	?	0	?	0	1	0	0	0	0	0
Canobius elegantulus	0	?	0	1	0	?	?	?	0	0	0	0	?	0	?
Cheirodopsis	?	0	0	1	0	?	1	?	0	0	0	?	0	0	0
Cheirolepis canadensis	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Cheirolepis trailli	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0
Cheirolepis schultzei	?	?	0	1	0	?	0	0	1	?	0	?	0	0	0
Coccocephalus	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?
Cuneognathus	?	?	?	?	?	?	?	?	1	?	0	0	0	0	0
Cycloptychius	0	?	0	1	0	?	1	?	0	0	0	0	?	0	?
Cyranhoris	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0
Dialipina	?	?	?	?	?	?	0	0	0	0	?	1	1	?	0
Dictyopyge	1	?	0	1	0	1	1	?	0	1	0	0	?	0	0
Discoserra	0	1	2	?	0	1	0	0	1	0	0	1	0	0	1
Donnrosenia	?	?	?	?	0	?	1	?	?	0	0	0	0	0	0
Ebenaqua	0	0	?	?	0	?	0	?	0	1	0	?	0	0	1
Elonichthys' palatinus	0	1	0	1	0	?	1	?	1	1	0	?	?	0	0
Gogosardinia	1	0	?	?	0	?	1	1	?	0	0	0	0	0	0
Gonatodus	1	0	0	1	0	?	0	?	0	1	0	1	0	0	0
Guildayichthys	0	1	2	1	0	1	0	0	1	0	0	1	0	0	1
Guntherichthys	?	?	?	?	?	?	?	?	1	1	0	0	0	0	?
Haploepis ovoidea	1	0	?	?	0	?	1	?	0	0	0	1	0	1	0
Howqualepis	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0
Kalops diophrys	1	0	0	1	0	?	0	?	1	0	0	1	0	0	0
Kalops monophrys	1	0	0	1	0	?	0	?	1	0	0	1	0	0	0
Kentuckia deani	?	?	1	1	0	?	?	?	0	0	0	?	?	?	0
Lepisosteus	0	1	0	1	0	1	1	1	0	1	0	0	0	0	1
Limnomis	?	?	?	?	?	?	1	?	1	1	0	0	0	0	0
Lineagruan judithi	0	?	0	1	?	?	1	?	1	1	0	0	0	0	0
Lineagruan snowyi	?	?	0	1	?	?	1	?	1	1	0	0	0	0	0
Mansfieldiscus	?	?	0	1	0	?	1	?	1	0	0	0	0	0	0

	151	**152**	**153**	**154**	**155**	**156**	**157**	**158**	**159**	**160**	**161**	**162**	**163**	**164**	**165**
Melanecta anneae	?	?	0	1	0	?	1	1	0	1	0	0	0	0	0
Mesopoma carricki	?	?	?	?	?	?	1	?	?	0	0	?	0	0	0
Mesopoma planti	?	?	?	?	?	?	1	?	?	0	0	?	0	0	?
Microhaplolepis	1	0	?	?	0	?	1	?	0	0	0	0	0	1	0
Mimia	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0
Moythomasia	1	0	0	1	0	1	1	1	1	0	0	1	0	0	0
New Brunswick Fish	?	?	?	?	?	?	1	?	1	0	0	?	0	0	?
Novogonatodus	?	?	?	?	?	?	1	?	0	1	0	1	?	0	0
Osorioichthys	0	1	1	1	0	?	0	?	1	0	0	1	0	0	0
Palaeoniscum	0	?	0	1	0	?	1	?	0	0	0	?	0	0	?
Parahaplolepis	0	0	?	?	0	?	1	?	0	0	0	0	0	1	0
Paramblypterus	?	0	?	1	0	?	1	?	0	0	0	?	?	?	0
Paramesolepis	?	?	0	1	0	?	?	?	0	0	0	?	0	0	?
Paratarrasius	?	?	0	1	0	?	0	?	1	0	0	?	?	0	0
Platysomus gibbosus	?	?	?	?	0	?	1	?	?	?	0	?	0	?	?
Platysomus parvulus	?	?	?	?	?	?	1	?	0	1	0	0	0	0	0
Platysomus schultzei	?	?	?	?	?	?	1	?	0	1	0	0	0	0	0
Platysomus striatus	?	?	0	1	0	?	1	?	0	0	0	0	0	0	?
Platysomus superbus	?	?	0	1	0	?	1	?	0	0	0	0	0	0	0
Platysomus swaffordae	?	?	?	0	0	?	1	?	?	0	0	0	0	0	0
Polypterus bichir	1	0	2	1	0	1	0	0	0	0	0	0	1	0	0
Proceramala	0	0	1	1	?	?	0	?	1	1	0	0	0	0	0
Pteronisculus	1	1	1	1	0	1	0	?	1	0	0	0	0	0	0
Redfieldius	?	?	2	1	0	?	1	?	0	0	0	?	0	0	0
Rhadinichthys	0	?	0	1	0	?	1	?	0	0	0	?	0	0	0
Spinofacia	?	?	?	?	?	?	1	?	1	?	?	?	?	?	?
Stegotrachelus	?	?	?	?	?	?	1	?	1	1	0	0	0	0	0
Tarrasius	?	1	0	1	0	?	0	0	0	1	0	1	1	0	0
Tegeolepis	0	?	0	1	0	?	1	?	?	?	0	?	?	?	?
Wendyichthys dicksoni	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
Wendyichthys lautreci	?	?	?	?	0	1	1	?	0	0	0	0	?	0	0
Woodichthys	0	?	1	1	0	1	1	1	0	0	0	0	0	0	0
Polydon spathula	0	1	?	?	1	1	1	?	0	0	0	0	1	0	0
Solnhofenamia	0	1	0	1	0	1	1	?	0	0	0	1	1	0	0
Obaichthys	?	?	?	?	?	?	1	?	0	0	0	1	0	0	0
Chondrosteus	?	?	?	?	0	?	1	?	0	0	0	?	1	0	0

	166	**167**	**168**	**169**	**170**	**171**	**172**	**173**	**174**	**175**	**176**	**177**	**178**	**179**	**180**
Onychodus	?	?	1	0	0	0	0	0	3	0	3	0	0	0	5
Diabolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Miguashaia	1	0	1	0	0	0	0	0	3	0	3	0	0	?	5
Psarolepis	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
Acipenser	1	2	0	0	1	1	?	0	2	0	0	0	0	2	0
Aeduella blainvillei	?	?	?	0	1	1	?	1	0	2	0	0	3	2	0
Aesopichthys	0	?	1	1	1	1	?	1	1	2	0	1	1	1	1
Amblypterus latus	?	?	?	0	?	1	?	?	?	?	?	?	?	2	0
Amia calva	0	?	0	0	0	0	1	0	3	0	3	0	1	2	4
Amphicentrum granulosum	?	?	1	3	?	1	?	?	3	0	3	0	1	1	2
Amphicentrum jurgenai	?	?	?	3	?	?	?	?	?	?	2	?	1	1	2
Beagiascus	1	?	1	0	1	1	?	1	0	1	0	0	0	2	0
Beishanichthys	?	?	?	0	0	0	0	0	1	?	?	0	1	2	4
Boreosomus	0	?	1	0	1	1	?	0	3	0	3	0	0	2	0
Bourbonnella guilloti	?	?	?	0	1	1	?	1	0	2	0	0	3	2	0
Bourbonnella jocelynae	?	?	1	0	?	0	0	1	0	2	0	0	?	2	0
Canobius elegantulus	?	?	?	0	1	1	?	?	2	2	0	0	0	1	0
Cheirodopsis	?	?	1	1	1	1	?	1	3	0	3	0	1	2	0
Cheirolepis canadensis	0	1	1	0	1	1	1	0	0	2	0	0	1	0	0
Cheirolepis trailli	0	1	1	0	0	1	1	0	0	2	0	0	1	0	0
Cheirolepis schultzei	0	1	1	?	?	1	1	?	?	?	?	?	?	?	?
Coccocephalus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cuneognathus	?	?	?	0	?	1	?	?	?	?	?	?	0	2	?
Cycloptychius	?	?	?	0	1	1	?	?	0	?	0	0	0	0	1
Cyranhoris	1	2	1	0	1	1	?	1	0	1	0	2	0	2	0
Dialipina	?	?	?	0	1	1	?	1	0	?	?	0	0	1	0
Dictyopyge	?	?	?	0	1	1	?	1	3	0	3	0	0	2	0
Discoserra	2	3	1	2	1	0	0	?	2	?	1	1	1	2	4
Donnrosenia	1	?	1	0	1	1	?	?	0	?	0	0	?	2	?
Ebenaqua	2	3	1	3	1	0	0	?	2	2	1	0	1	1	2
Elonichthys' palatinus	?	?	1	0	?	?	?	?	?	?	?	0	0	2	0
Gogosardinia	1	?	1	0	1	1	?	?	?	2	0	?	0	?	?
Gonatodus	?	?	1	0	1	1	?	?	0	?	0	0	0	2	0
Guildayichthys	2	3	1	2	1	?	?	1	2	?	1	1	1	2	4
Guntherichthys	?	?	?	0	1	0	0	1	0	2	0	0	0	2	0
Haploepis ovoidea	0	1	1	0	1	1	?	1	0	1	0	0	0	2	0
Howqualepis	1	1	1	0	1	1	1	1	0	?	0	0	0	1	0
Kalops diophrys	1	2	1	0	1	1	?	1	0	2	0	0	0	2	0
Kalops monophrys	1	2	1	0	1	1	?	1	2	2	0	0	0	2	0
Kentuckia deani	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
Lepisosteus	2	3	?	0	0	0	1	0	?	?	?	0	1	0	5
Limnomis	1	0	1	0	1	0	0	0	2	2	0	0	0	2	0
Lineagruan judithi	0	?	1	0	1	1	?	1	0	1	0	2	0	2	0
Lineagruan snowyi	1	?	1	0	1	1	?	0	3	0	3	2	0	2	0
Mansfieldiscus	1	?	1	0	1	1	?	?	0	?	?	?	0	2	0

	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
Melanecta anneae	1	?	?	0	1	1	?	1	1	2	0	0	0	2	0
Mesopoma carricki	?	?	?	0	1	1	?	1	3	0	3	0	0	1	0
Mesopoma planti	?	?	?	0	1	1	?	1	?	?	?	?	?	?	?
Microhaplolepis	?	?	1	0	1	1	?	1	0	1	0	0	?	1	?
Mimia	1	2	1	0	1	1	1	0	2	2	0	0	0	1	0
Moythomasia	?	?	1	0	1	1	?	1	2	2	0	3	0	1	0
New Brunswick Fish	?	?	?	0	?	1	?	?	1	2	0	0	?	2	?
Novogonatodus	1	?	?	2	1	1	?	1	?	?	?	0	?	2	?
Osorioichthys	1	2	1	0	?	1	?	?	?	?	?	?	?	?	?
Palaeoniscum	?	?	?	0	1	1	?	?	0	2	0	0	0	2	0
Parahaplolepis	0	1	1	0	1	1	?	1	0	2	0	0	0	1	0
Paramblypterus	?	?	?	0	1	1	?	1	0	?	0	0	0	2	0
Paramesolepis	?	?	1	1	1	1	?	1	2	2	0	0	1	2	0
Paratarrasius	0	1	1	4	0	0	0	0	3	0	3	0	2	2	4
Platysomus gibbosus	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?
Platysomus parvulus	?	?	?	3	1	?	?	?	1	?	2	0	0	2	1
Platysomus schultzei	1	?	1	2	1	0	0	?	2	2	2	0	1	1	2
Platysomus striatus	?	?	?	1	1	?	?	?	3	0	3	0	1	2	1
Platysomus superbus	1	?	1	1	?	1	?	?	3	0	3	0	0	2	2
Platysomus swaffordae	1	?	1	2	?	?	?	?	1	2	2	?	?	?	?
Polypterus bichir	1	2	1	4	0	0	0	0	0	1	0	2	2	2	4
Proceramala	?	?	1	1	1	1	?	1	2	2	0	0	1	2	1
Pteronisculus	2	2	1	0	1	1	?	0	0	?	0	0	0	2	0
Redfieldius	?	?	1	0	1	1	?	1	2	1	0	0	0	1	0
Rhadinichthys	?	?	1	0	1	1	?	?	0	2	0	0	0	1	0
Spinofacia	?	?	1	0	1	1	?	1	3	0	3	0	0	?	0
Stegotrachelus	1	?	1	0	1	1	?	1	2	2	0	0	0	2	0
Tarrasius	?	?	1	4	0	0	0	0	3	0	3	0	2	2	4
Tegeolepis	?	?	?	0	?	?	?	?	?	?	?	?	?	1	0
Wendyichthys dicksoni	1	1	1	0	1	1	?	1	0	1	0	2	0	2	0
Wendyichthys lautreci	1	?	1	0	1	1	?	1	1	1	0	0	0	2	0
Woodichthys	1	?	?	0	1	1	1	1	0	0	3	0	0	2	0
Polydon spathula	1	1	1	0	1	0	0	0	3	0	3	0	0	2	0
Solnhofenamia	?	?	?	0	?	0	0	?	?	?	?	0	0	2	4
Obaichthys	1	1	1	0	?	1	?	?	?	?	?	0	0	1	0
Chondrosteus	0	?	?	0	?	?	?	0	3	0	3	0	0	2	0

	181	**182**	**183**	**184**	**185**	**186**	**187**	**188**	**189**	**190**	**191**	**192**	**193**	**194**	**195**
Onychodus	0	0	0	1	0	0	0	?	0	2	0	2	0	0	0
Diabolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Miguashaia	0	0	0	1	0	0	0	?	0	0	0	2	0	0	0
Psarolepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Acipenser	1	0	0	1	1	0	?	?	0	0	0	1	1	2	?
Aeduella blainvillei	1	0	0	1	1	0	1	?	1	0	0	1	1	2	0
Aesopichthys	1	0	1	1	0	1	1	?	1	0	0	1	1	2	0
Amblypterus latus	1	?	0	1	?	0	?	?	?	0	0	?	1	2	0
Amia calva	1	0	0	2	0	0	0	1	0	4	0	2	0	0	0
Amphicentrum granulosum	1	0	1	3	?	1	?	?	0	0	0	0	1	2	0
Amphicentrum jurgenai	1	0	1	3	?	1	?	?	?	0	?	0	1	2	0
Beagiascus	1	0	0	2	1	0	1	?	1	0	0	1	1	2	0
Beishanichthys	1	0	0	1	0	1	0	?	1	4	0	4	1	2	0
Boreosomus	1	0	0	1	0	1	1	?	1	0	0	0	1	2	0
Bourbonnella guilloti	1	0	0	1	1	0	1	?	1	0	0	1	1	2	0
Bourbonnella jocelynae	1	0	0	1	1	?	?	?	?	?	?	?	?	?	0
Canobius elegantulus	1	0	?	?	1	0	1	?	1	0	0	1	1	2	0
Cheirodopsis	1	0	0	1	?	1	1	?	1	0	0	1	1	2	0
Cheirolepis canadensis	1	0	0	0	?	0	?	?	1	0	0	4	1	2	1
Cheirolepis trailli	1	0	0	0	1	0	1	?	1	0	0	0	1	2	1
Cheirolepis schultzei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Coccocephalus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cuneognathus	1	?	1	1	?	1	1	?	?	0	0	1	1	2	0
Cycloptychius	1	0	0	0	1	0	1	?	1	0	0	1	1	2	0
Cyranhoris	1	0	0	1	1	0	0	?	1	0	0	1	1	2	0
Dialipina	0	?	0	0	1	0	1	?	0	1	0	?	0	1	0
Dictyopyge	1	0	0	1	1	0	1	?	0	0	0	0	1	2	0
Discoserra	1	0	0	2	1	1	?	1	0	4	1	4	1	0	0
Donnrosenia	1	?	0	0	?	0	?	?	?	0	0	?	1	0	0
Ebenaqua	1	0	0	2	1	1	1	?	1	0	0	0	1	2	0
Elonichthys' palatinus	1	0	0	?	?	0	?	?	?	0	0	1	1	2	0
Gogosardinia	1	?	0	1	?	0	1	?	1	0	0	?	?	?	0
Gonatodus	1	0	0	0	?	1	?	?	1	0	0	0	1	2	0
Guildayichthys	1	0	0	2	?	1	?	?	1	4	1	4	1	2	0
Guntherichthys	1	0	0	?	1	0	1	?	1	0	0	4	?	?	0
Haploepis ovoidea	1	1	0	1	1	0	1	?	1	0	0	1	1	2	0
Howqualepis	1	0	0	0	?	0	1	?	1	0	0	0	1	2	0
Kalops diophrys	1	0	0	1	1	0	0	?	1	0	0	1	1	2	0
Kalops monophrys	1	0	0	1	1	0	1	?	1	0	0	1	1	2	0
Kentuckia deani	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lepisosteus	1	1	0	2	0	0	0	0	0	4	0	2	1	2	0
Limnomis	1	0	1	2	1	0	1	?	0	0	0	1	1	2	0
Lineagruan judithi	1	0	0	?	1	0	1	?	1	0	0	1	1	2	0
Lineagruan snowyi	1	0	0	?	1	0	1	?	1	0	0	1	1	2	0
Mansfieldiscus	1	0	0	1	1	0	1	?	1	0	0	0	1	2	0

	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195
Melanecta anneae	1	0	0	1	?	0	1	?	1	0	0	1	1	2	0
Mesopoma carricki	1	0	0	1	1	0	1	?	1	0	0	1	1	2	0
Mesopoma planti	?	0	?	?	1	?	1	?	1	0	0	?	?	?	0
Microhaplolepis	1	?	0	1	?	1	1	?	1	0	0	4	?	?	0
Mimia	1	0	0	1	1	0	1	0	1	0	0	1	1	2	0
Moythomasia	1	0	0	1	1	0	1	?	1	0	0	1	1	2	0
New Brunswick Fish	1	?	0	0	?	?	?	?	?	?	?	?	?	?	0
Novogonatodus	?	?	0	0	1	?	?	?	?	?	?	?	?	?	0
Osorioichthys	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Palaeoniscum	1	0	0	0	?	0	?	?	1	0	0	1	1	2	0
Parahaplolepis	1	1	0	1	1	1	1	?	1	0	0	4	1	2	0
Paramblypterus	1	0	0	0	?	?	?	?	?	0	0	?	1	2	0
Paramesolepis	1	0	?	?	?	1	1	?	1	0	0	1	1	2	0
Paratarrasius	1	0	1	3	0	2	0	?	0	3	0	3	0	1	1
Platysomus gibbosus	1	?	0	1	?	1	?	?	?	0	?	?	?	?	0
Platysomus parvulus	1	0	0	1	?	0	?	?	?	0	0	0	1	2	?
Platysomus schultzei	1	0	1	3	?	1	?	?	?	0	0	0	1	2	0
Platysomus striatus	1	0	0	1	?	1	?	?	1	0	0	0	1	2	0
Platysomus superbus	1	0	0	1	?	0	?	?	1	0	0	1	1	2	0
Platysomus swaffordae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Polypterus bichir	1	2	0	1	0	1	1	1	0	2	0	2	1	2	0
Proceramala	1	0	0	1	0	1	?	?	1	0	0	1	1	2	0
Pteronisculus	1	0	0	1	1	0	1	?	1	0	0	0	1	2	0
Redfieldius	1	0	0	1	1	1	1	?	1	0	0	0	1	2	0
Rhadinichthys	1	0	0	0	1	0	1	?	1	0	0	1	1	2	0
Spinofacia	1	0	0	1	?	?	0	?	1	0	0	?	1	2	0
Stegotrachelus	1	0	0	1	1	0	1	?	1	0	0	1	1	2	0
Tarrasius	1	0	1	3	0	2	0	?	0	3	0	3	0	1	1
Tegeolepis	1	0	0	?	?	?	?	?	?	?	?	?	?	?	0
Wendyichthys dicksoni	1	0	0	1	1	0	0	?	1	0	0	1	1	2	0
Wendyichthys lautreci	1	0	0	1	1	1	1	?	1	0	0	1	1	2	0
Woodichthys	1	0	0	1	1	0	1	?	1	0	0	1	1	2	0
Polydon spathula	1	0	0	1	0	0	0	?	0	0	0	0	1	2	0
Solnhofenamia	1	0	0	2	?	0	?	1	?	4	0	2	1	2	0
Obaichthys	1	1	0	?	?	0	?	?	?	4	0	2	1	2	0
Chondrosteus	1	0	0	?	0	0	?	?	?	0	0	0	1	2	0

	196	197	198	199	200	201	202	203	204	205	206	207	208	209
Onychodus	2	0	2	0	2	2	0	1	0	0	0	0	0	2
Diabolepis	?	?	?	?	?	?	0	1	?	?	?	?	0	?
Miguashaia	2	0	2	0	2	2	0	?	0	0	0	0	0	2
Psarolepis	1	?	?	?	1	0	0	0	?	?	?	?	0	?
Acipenser	4	1	?	?	0	0	1	1	0	0	?	?	0	1
Aeduella blainvillei	1	1	?	?	1	0	1	1	0	0	0	0	0	0
Aesopichthys	1	1	0	1	0	0	1	1	0	0	0	1	0	0
Amblypterus latus	1	1	?	?	1	?	1	1	0	0	0	0	0	0
Amia calva	2	0	2	0	2	2	0	1	0	0	0	0	0	2
Amphicentrum granulosum	1	1	?	?	?	?	1	1	0	0	0	0	0	0
Amphicentrum jurgenai	1	1	?	?	?	?	1	1	0	?	?	?	0	0
Beagiascus	1	1	?	1	0	0	1	1	0	1	0	1	0	0
Beishanichthys	1	1	1	?	1	0	1	1	0	0	0	0	0	0
Boreosomus	1	1	?	?	1	0	1	1	0	0	0	1	0	0
Bourbonnella guilloti	1	1	?	?	1	0	1	1	0	0	0	0	0	0
Bourbonnella jocelynae	1	?	?	?	1	0	1	1	0	0	0	1	0	0
Canobius elegantulus	1	1	?	?	0	0	1	1	0	0	0	0	0	0
Cheirodopsis	1	1	?	?	?	?	1	1	0	0	1	0	0	0
Cheirolepis canadensis	0	0	2	0	2	2	1	1	0	0	0	0	0	0
Cheirolepis trailli	0	0	2	0	2	2	1	1	0	0	0	0	0	0
Cheirolepis schultzei	0	0	?	0	2	2	1	1	0	0	0	0	0	0
Coccocephalus	?	?	?	?	?	?	1	1	?	?	?	?	0	0
Cuneognathus	1	?	?	?	?	0	1	1	0	?	0	1	0	0
Cycloptychius	1	1	?	?	?	?	1	1	0	0	0	0	0	0
Cyranhoris	1	1	?	?	0	0	1	1	0	0	0	1	0	0
Dialipina	1	1	1	1	0	?	1	1	0	0	0	0	0	0
Dictyopyge	1	1	?	?	0	0	1	1	0	0	0	0	0	0
Discoserra	1	1	0	?	0	0	1	1	0	0	1	0	0	0
Donnrosenia	1	1	0	1	0	0	1	1	0	0	0	1	0	0
Ebenaqua	1	1	?	?	1	0	1	1	0	0	1	0	0	0
Elonichthys' palatinus	1	1	?	?	0	0	1	1	0	?	?	?	0	0
Gogosardinia	1	1	?	1	0	0	1	1	0	0	0	1	0	0
Gonatodus	1	1	?	1	0	0	1	1	0	0	0	0	0	0
Guildayichthys	1	1	1	?	0	0	1	1	0	0	1	0	0	0
Guntherichthys	3	1	?	?	1	0	1	1	0	0	0	0	0	0
Haploepis ovoidea	1	1	?	?	0	0	1	1	0	0	1	0	0	0
Howqualepis	1	1	1	1	0	0	1	1	0	0	0	0	0	0
Kalops diophrys	1	1	1	?	0	0	1	1	0	1	0	0	0	0
Kalops monophrys	1	1	1	?	0	0	1	1	0	0	0	0	0	0
Kentuckia deani	?	?	?	?	?	?	?	1	?	?	?	?	0	0
Lepisosteus	1	1	1	0	1	0	1	1	0	1	0	0	0	0
Limnomis	1	1	1	1	0	0	1	1	0	0	0	0	0	0
Lineagruan judithi	1	1	?	1	0	0	1	1	0	1	0	1	0	0
Lineagruan snowyi	1	1	?	1	0	0	1	1	0	1	0	1	0	0
Mansfieldiscus	1	1	1	1	0	0	1	1	0	0	0	0	0	0

	196	**197**	**198**	**199**	**200**	**201**	**202**	**203**	**204**	**205**	**206**	**207**	**208**	**209**
Melanecta anneae	1	?	?	?	?	?	1	1	0	0	0	0	0	0
Mesopoma carricki	1	1	?	1	0	0	1	1	0	?	0	0	0	0
Mesopoma planti	1	1	?	1	1	0	1	1	0	?	?	?	0	0
Microhaplolepis	1	1	?	?	0	0	1	1	0	0	1	1	0	0
Mimia	1	1	1	1	0	0	1	1	0	0	0	0	0	0
Moythomasia	1	1	?	1	0	0	1	1	0	0	0	0	0	0
New Brunswick Fish	1	1	?	?	0	1	1	1	0	0	0	0	0	0
Novogonatodus	1	1	1	1	0	0	1	1	?	?	0	0	0	0
Osorioichthys	1	1	?	?	0	0	1	1	0	?	?	?	0	0
Palaeoniscum	1	1	?	1	0	?	1	1	0	?	0	0	0	0
Parahaplolepis	1	1	?	?	1	0	1	1	0	0	1	1	0	0
Paramblypterus	1	1	1	1	0	0	1	1	0	1	0	0	0	0
Paramesolepis	1	?	?	?	?	?	1	1	0	0	0	0	0	0
Paratarrasius	1	?	?	?	?	0	1	1	0	1	0	0	0	0
Platysomus gibbosus	1	1	?	?	?	?	1	1	0	?	?	?	0	0
Platysomus parvulus	?	?	?	?	?	?	1	1	0	?	?	?	0	0
Platysomus schultzei	1	1	?	1	0	0	1	1	0	0	0	0	0	0
Platysomus striatus	1	1	0	1	1	0	1	1	0	0	0	0	0	0
Platysomus superbus	1	1	?	?	?	?	1	1	0	1	0	0	0	0
Platysomus swaffordae	1	1	?	1	1	0	1	1	0	?	0	3	0	0
Polypterus bichir	1	1	1	1	1	0	1	1	0	0	0	0	0	0
Proceramala	1	1	1	1	0	0	1	1	0	1	1	0	0	0
Pteronisculus	1	1	?	?	0	0	1	1	0	0	0	0	0	0
Redfieldius	1	1	?	?	0	0	1	1	0	0	0	1	0	0
Rhadinichthys	1	1	?	?	?	?	1	1	0	0	0	0	0	0
Spinofacia	1	1	?	1	0	0	1	1	0	0	0	1	0	0
Stegotrachelus	1	1	?	1	0	0	1	1	0	0	0	0	0	0
Tarrasius	1	?	?	?	?	0	?	1	0	0	0	0	0	0
Tegeolepis	1	1	?	1	?	?	?	1	?	?	?	?	0	0
Wendyichthys dicksoni	1	1	?	?	0	0	1	1	0	1	0	1	0	0
Wendyichthys lautreci	1	1	?	?	0	0	1	1	0	0	1	1	0	0
Woodichthys	1	1	?	1	0	0	1	1	0	?	0	0	0	0
Polydon spathula	4	?	?	?	2	2	1	1	0	0	2	4	1	1
Solnhofenamia	2	?	?	?	2	2	0	1	0	?	?	?	0	2
Obaichthys	1	1	0	1	1	0	1	1	0	1	0	0	0	0
Chondrosteus	1	?	?	?	1	0	1	1	0	0	2	4	0	1

Appendix 2—Characters and character states that define the clades for the tree presented in Figure 9. Bootstrap values (B) above zero are given.

Node 1 Actinopterygii
B=52

26(1) splenial absent
28(0) prearticular anterior end far from symphysis
76(0) dermopterotic/supratemporotabular present
81(1) tabular absent
155(0) mandibular canal through dentary
156(1) mandibular canal not through posterior infradentary
202(1) ganoine present

Node 2 "Recent" fish
5(1) premaxilla nasal process present
27(0) surangular absent
33(1) acrodin caps on teeth present
97(1) sclerotic ring absent
98(4) sclerotic plates absent
124(4) convex subopercular lower suture
135(1) long parasphenoid

Polypterus bichir
3(0) premaxilla is part of complex bone
4(1) complex premaxilla is a premaxillo-lachrymal
7(1) premaxilla is part of orbit
8(3) premaxilla is part of complex bone with lachrymal
15(1) teeth only on anterior part of maxilla
17(4) absence of ornamentation maxilla and preoperculum
23(1) maxilla with canal, is complex bone with infraorbitals
36(2) little or no ganoine ornamentation on skull roof
37(0) short preparietal relative length
58(2), 68(2) dealing with absence of supraorbital bones
69(3) supraorbital series absent
106(1) preoperculum with distinct anterodorsal and ventral regions
107(1) preoperculum anterodorsal region subvertical or vertical
151(1) horizontal pit line present
152(0) vertical preopercular pit line present
153(2) preopercular canal to postotic region
167(2) clavicle contact elongate
169 (4) body form blade-like
174(0) few predorsal scutes/ridge scales
175(1) body scales to dorsal ridge scales are one to one
176(0) dorsal ridge scales without a spine/spike
177(2) dorsal fin base with guard scales
178(2) dorsal fin merged with caudal
182(2) number of dorsal fin rays dorsal finlets
186(1) anal fin base of anal fin ends close to caudal fin
187(1) scutes and basal fulcra between anal and caudal fins present
190(2) diphycercal caudal fin

Node 3 Chondrostei + Holostei
B=8
83(2) cheek fit with thick-peripheral gaps
123(2) concave subopercular upper suture
126(1) branchiostegals rays not below mandible
132(1) lateral gular absent
133(2) lateral gular shape, none lateral gular absent
144(1) supraorbital canal in contact with otic

157(1) pectoral fin not lobed

Node 4 Chondrostei

B=99

2(1), 3(2), 4(4), 5(2), 6(2), 7(2), 8(4), 9(2), 10(2) dealing with absence of premaxilla
11(1), 12(4), 13(3), 14(2), 15(4), 16(3), 19(4), 20(3), 21(3), 23(2), dealing with absence of maxilla
34(2) dentary and maxillary teeth absent on oral rim
192(0) cleft equilobate caudal outline
206(2) flank scales absent
207(4) ventrolateral flank scales absent
209(1) rhombic scale limited to caudal region

†*Chondrosteus acipenseroides*

60(2) postparietal short and rectangular
68(2) supraorbital bones absent
69(3) supraorbital series absent
88(1) postorbital notch in jugal/IO3 present
89(4) Jugal/IO3 contacts suborbital ventrally
97(0) sclerotic ring present
166(0) clavicle length short

Node 5 Acipenseriformes

B=55

118(1) operculum absent
196(4) round based and rhombic scales

Acipenser brevirostrum

69(2) supraorbital series is a single bone
138(0) parasphenoid not sutured to vomer
167(2) clavicle contact elongate
168(0) interclavicle present
171(1) fringing fulcra present
174(2) predorsal scutes/dorsal ridge scales complete to occiput
176(0) dorsal ridge scales without a spine/spike
185(1) scutes and/or basal fulcra between pelvic and anal fins present
192(1) caudal outline strongly inequilobate

Polydon spathula

28(1) prearticular anterior end near symphysis
47(1), 49(2), 50(3) dealing with the absence of nasal bones
55(1) pineal opening in parietal area
100(1) quadratojugal absent
137(1) posterior ascending process absent
148(1) supratemporal commissure not across midline
201(2) ventral edges of scales not applicable because rhombic ganoid scales missing
208(1) stellate bones in snout present

Node 6 Holostei

B=26

24(1) supramaxillae present
79(0) ventral protuberance of dermopterotic/supratemporotabular present
91(2) more than two infraorbital bones ventral to orbit
184(2) Pelvic fin with reduced base
190(4) abbreviated heterocercal caudal fin shape

Node 7 Amiiformes

B=41

37(0) preparietal relative length short
60(1) postparietal square shaped
77(2) more than 1/3 of dermopterotic/supratemporotabular contacts parietal
100(1) quadratojugal absent
112(4) preoperculum widest anteroventrally
117(1) interoperculum present

126(0) branchiostegal rays between mandible
129(0) median gular present
196(2) scale shape rounded
200(2) posterior edges of rhombic scales, not applicable, not ganoid
201(2) ventral edges of scales-not applicable, not ganoid
202(0) ganoine-absent
209(2) rhombic scale limits-rhombic scales absent

Amia calva

9(0) premaxilla not in contact with nasals
15(2) maxillary teeth only on maxillary body, not anterior articulary region
27(1) surangular present
31(1) coronoid process present
58(2), 68(2), 69(3) dealing with absence of supraorbital bones
113(0) gap between operculum and skull roof bones present
146(2) otic canal trajectory in one bone
178(1) rear of dorsal fin close to caudal fin
193(0) epichordal fin rays of caudal fin present
194(0) epichordal fin rays of caudal fin short

†Solnhofenamia elongata

13(1) height of posterior part of maxilla is medium
19(3) high triangular posterior plate of the maxilla
22(1) pleurodont maxillary teeth
43(1) median rostral with anterior and posterior margins of equal width
50(3) notched nasals absent
86(5) rectangular lachrymal
91(1) two infraorbital bones ventral to orbit
96(1) maxilla not in contact with suborbitals
97(0) sclerotic ring present
98(2) two sclerotic plates
128(0) 12 or more branchiostegal rays per side
162(1) dorsal end of cleithrum broad and round

Node 8 Lepisosteiformes
B=48

20(2) maxilla posterior end is preorbital
30(1) dentition on coronoids arranged in narrow marginal tooth rows
137(1) posterior ascending process absent
182(1) number of dorsal fin rays is 10 or less
205(1) enlarged postcleithral scales present

Lepisosteus osseus

27(1) surangular present
31(1) coronoid process present
74(2) dermosphenotic not in contact with dermohyal
83(0) cheek fit is tight abutting
121(0) operculum three times deeper than suboperculum or more
127(1) first branchiostegal ray deeper than second
160(1) postcleithrum absent
165(1), 166(2), 167(3) dealing with the absence of a clavicle
178(1) rear of dorsal fin close to caudal

†Obaichthys decoratus

15(1) teeth only on anterior part of maxilla
96(1) maxilla not in contact with suborbitals
112(1) preoperculum widest midbone
113(0) gap between operculum and skull roof bones present
119(0) first axis of operculum longer than second

162(1) dorsal end of cleithrum broad and round
171(1) fringing fulcra present
198(0) peg and socket articulation-broad

Node 9 Palaeonisci

B=2

36(0) dense ganoine ornamentation on skull roof
86(5) rectangular lachrymal
126(0) Branchiostegal rays between mandible
162(1) dorsal end of cleithrum broad and round

Node 10 Tarrasiiformes

B=48

40(3) median rostral bones
41(2) 2 rostral bones, dorsal and ventral, both separate and distinct
74(2) dermosphenotic not in contact with dermohyal
112(0) preoperculum widest anterodorsally
169(4) blade like body form
178(2) dorsal fin merged with caudal
183(1) Pelvic fin absent
186(2) anal fin base merged with caudal fin
190(3) hypocercal caudal fin shape
194(1) epichordal fin rays of caudal fin elongated
195(1) micromeric scales

Paratarrasius hibbardi

49(1) nasal bones with notches
60(2) postparietal short and rectangular
65(1) two separate extrascapular rows
69(1) double series of supraorbital bones
77(1) anterior 1/3 of dermopterotic/supratemporotabular in contact with parietal
83(1) thin overlapping cheek fit
89(0) jugal/infraorbital three contacts suborbital bones posteriorly
92(1) suborbital bones present
93(3) more than 6 suborbital bones
94(3) suborbitals arranged in many rows
95(1) suborbital fit is sutured
96(2) maxilla contacts suborbital bones
106 (1) preoperculum with distinct anterodorsal and ventral regions
114(1) antopercular bones do not extend to bottom of operculum
115(3) antopercular width tapers ventrally
116(1) antopercular as thick as adjacent bones
127(1) first branchiostegal ray deeper than second
143(3) supraorbital canal into dermopterotic/supratemporotabular
144(1) supraorbital canal in contact with otic
159(1) presupracleithrum present
205(1) enlarged postcleithral scales present

Tarrasius problematicus

14(1) maxilla ventral margin curved
21(2) maxilla with strong posteroventral process
78(1) dermopterotic/supratemporotabular ventrally in contact with operculum
110(1) preoperculum contacts posterior margin of maxilla
113(0) gap between operculum and skull roof bones present
124(0) horizontal subopercular lower suture
140(1) ethmoid commissure through median ventral rostral
146(1) otic canal trajectory in two bones
160(1) postcleithrum absent

Node 11 Palaeonisci minus Tarrasiiformes

53(2) postrostral number is one
54(0) median postrostral
170(1) basal fulcra between dorsal and caudal fins present

173(1) basal fulcra or scutes anterior to dorsal fin present
185(1) scutes or basal fulcra between pelvic and anal fins present

Node 12 Guildayichthyiformes
B=99

15(1) maxillary teeth only on anterior part of bone
25(1) adductor mandibulae fossa on most of mandible
38(4) sharp snout shape
40(5) paired and median rostral bones
41(4) paired and median rostral bones
49(1) nasal bones with notches
67(1) dermal supraoccipital present
89(0) jugal/infraorbital three contact contacts suborbital posteriorly
92(1) suborbital bones present
93(3) more than 6 suborbital bones present
96(2) maxilla contacts suborbitals
109(1) two preopercular bones
110(2) preoperculum not in contact with maxilla
117(1) interoperculum present
121(5), 123(5), 124(5) dealing with absence of a suboperculum
135(1) long parasphenoid
153(2) preopercular canal to postotic region
159(1) presupracleithrum present
165(1), 166(2), 167(3) dealing with absence of a clavicle
169(2) round body form
177(1) dorsal fin with a scaled lobe
178(1) rear of dorsal fin close to caudal
186(1) anal fin base ends close to caudal
190(4) abbreviated heterocercal caudal fin
191(1) caudal fin rays webbed
211(1) flank scales deep

Discoserra pectinodon

43(2) median rostral bone narrowing anteriorly
48(1) nasal bone number is two on each side
60(2) postparietal bones short and rectangular
61(1) postparietal bone almost equal in size to parietal
69(2) supraorbitals present as single bone
91(3) only infraorbital 3/posteroventral infraorbital ventral to the orbit
148(1) supratemporal commissure not across midline
194(0) epichordal fin rays of caudal fin short
198(0) peg and socket articulation broad

Guildayichthys carnegiei

57(1) two pairs of parietals
72(1) dermosphenotic contacts nasal
126(1) branchiostegal rays not below mandible
189(1) caudal fin with hinge line

Node 13 Palaeoniscomorpha

14(1) ventral margin of maxilla is curved
48(2) single nasal bone on each side
171(1) fringing fulcra present
180(0) triangular dorsal fin shape

Dialipina salgueiroensis

59(1) postparietal with pointed anterolateral process
77(2) more than 1/3 of dermopterotic/supratemporotabular bone contacts parietal
118(1), 119(3), 120(2), 121(4), 122(2) dealing with the absence of an operculum
143(1) supraorbital canal into parietal
146(1) otic canal trajectory into two bones
181(0) two dorsal fins
190(1) triphycercal caudal fin
194(1) epichordal fin rays of caudal fin elongated

Node 14 Palaeonisciformes

3(0) premaxilla part of complex bone
19(1) maxilla posterior plate is a moderate rectangular plate
21(2) strong posteroventral process of the maxilla
60(0) Postparietal long and rectangular
79(0) ventral protuberance of dermopterotic/supratemporotabular present
112(0) preoperculum widest anterodorsally
129(0) median gular present
162(0) cleithrum dorsal end is pointed
189(1) caudal fin with hinge line

Node 15 Cheirolepididae
B=96

13(2) height of posterior part of maxilla is high
71(3) shape of dermosphenotic elongate
74(1) dermosphenotic in contact with dermohyal
86(1) rhombic lachrymal
110(3) preoperculum contacts dorsal margin of maxilla
115(2) antopercular bone widens ventrally
116(1) antopercular bone as thick as adjacent bones
140(5) ethmoid commissure absent
151(1) horizontal pit line present
173(0) basal fulcra anterior to dorsal fin absent
178(1) rear of dorsal fin close to caudal fin
179(0) dorsal fin originates behind anal fin
195(1) micromeric scales
196(0) 'acanthodian shaped' scales
197(0) peg and socket articulation absent
198(2) peg and socket articulation absent
200(2) posterior edges of rhombic scales not applicable, not rhombic ganoid scales
201(2) ventral edges of scales not applicable, not rhombic ganoid scales

Cheirolepis trailli

49(1) nasal with notches
56(0) pineal opening in postrostral area
59(1) postparietal with pointed anterolateral process
100(0) quadratojugal present
101(0) quadratojugal small
134(0) lateral gular similar in size to branchiostegal rays
145(1) supraorbital and infraorbital canals not in contact rostrally
170(0) basal fulcra between dorsal and caudal fins absent
192(0) cleft equilobate caudal outline

Node 16 *Cheirolepis canadensis + C schultzei*
B=16

51(0) rear of nasal bones preorbital
69(2) supraorbitals present as a single bone
146(1) otic canal trajectory in 2 bones

Cheirolepis schultzei

21(1) slightly developed posteroventral process of the maxilla
77(1) anterior 1/3 of dermopterotic/supratemporotabular bone in contact with parietal bone
78(1) dermopterotic/supratemporotabular ventrally in contact with operculum
106(0) preoperculum without distinct regions
112(3) preoperculum cinched in middle
159(1) presupracleithrum present

Node 17 *Tegeolepis* through rest (minus *Cheirolepis*)

33(1) acrodin caps on teeth present
52(1), 53(5), 54(3) dealing with the absence of postrostral bones

68(2), 69(3) dealing with the absence of supraorbital bones
72(1) dermosphenotic contacts nasal
78(1) dermopterotic/supratemporotabular ventrally in contact with operculum
157(1) pectoral fin not lobed

Tegeolepis clarki

8(1) premaxilla contacts ventral margin lachrymal bone
12(1) maxilla anterior end is orbital
16(2) marginal teeth orientation is posteriad
21(1) slightly developed posteroventral process of maxilla
38(2) elongated snout
86(4) triangular shaped lachrymal
89(2) jugal/infraorbital three not in contact with suborbitals
91(1) two infraorbital bones ventral to orbit
132(1), 134(2) dealing with absence of lateral gular
135(1) long parasphenoid

Node 18 *Kentuckia* through rest (minus *Tegeolepis*, Cheirolepids)

7(1) premaxilla part of orbit
9(1) premaxilla in contact with nasal
13(1) medium height of posterior part of maxilla
49(1) nasal bone with notches
74(2) dermosphenotic not in contact with dermohyal

Kentuckia deani

59(1) postparietal with pointed anterolateral process
113(1) gap between operculum and skull roof bones absent
114(5) antopercular bone(s) extend(s) to ventral half of operculum
115(2) antopercular bone widens ventrally
116(1) antopercular bones as thick as adjacent bones
140(4) ethmoid commissure through paired complex bone
168(0) interclavicle present

Node 19 *Woodichthys* through rest

38(1) snout shape sharp bump
123(2) subopercular upper suture concave
142(1) supraorbital canal trajectory between medial and lateral nasal openings

Woodichthys bearsdeni

36(1) ganoine ornamentation on skull roof bones moderate
60(2) postparietal short and rectangular
66(2) extrascapular number is four
77(2) more than 1/3 of the dermopterotic/supratemporotabular bone contacts parietal
122(1) operculum in contact with lateral extrascapular
124(2) concave subopercular lower suture
143(1) supraorbital canal into parietal

Node 20 (*Gogosardina* + *Mimia*) through rest

43(2) median rostral shape narrowing anteriorly
159(1) presupracleithrum present

Node 21 *Gogosardinia* + *Mimia*

B=66

27(0) surangular absent
59(1) postparietal with pointed anterolateral process
61(1) Postparietal relative size almost equal to f/p
86(3) lachrymal shape vertical pillar
1191) opercular shape both axes approximately equal

137(1) posterior ascending process absent

Gogosardinia coatesi

52(0) postrostral bones present
53(4) postrostral number four
54(2) postrostral number more than 2 bones
123(3) sigmoidal subopercular upper suture
134(0) lateral gular similar in size to branchiostegal ray
143(1) supraorbital canal into parietal
151(1) horizontal pit line present
207(1) ventrolateral flank scales narrow

Mimipiscis toombsi

17(3) maxilla-preoperculum ornamentation of ridges and tubercles of ganoine
121(2) operculum about same height as suboperculum
127(1) first branchiostegal ray deeper than second
133(0) lateral gular similar in size to branchiostegal ray

Node 22 (*Donrosennia* + *Howqualepis*) through rest

30(2) dentition on coronoids arranged in single tooth row
74(1) dermosphenotic in contact with dermohyal
135(1) long parasphenoid
138(0) parasphenoid not sutured to vomer

Node 23 *Donnrosenia* + *Howqualepis* B=13

73(4) dermosphenotic longer than dermopterotic/supratemporotabular
77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal
86(1) rhombic lachrymal
122(1) operculum in contact with lateral extrascapular
184(0) pelvic fin with long base

Donnrosenia schaefferi

9(0) premaxilla not in contact with nasal
61(1) postparietal almost equal in size to parietal
72(0) dermosphenotic contact absent
78(0)dermopterotic/supratemporotabular not in contact with the operculum
114(5) antopercular bone(s) extend(s) to ventral half of operculum
115(3) antopercular bone(s) taper(s) ventrally
116(1) antopercular bone(s) as thick as adjacent bones
194(0) epichordal fin rays of caudal fin short
198(0) peg and socket articulation broad
207(1) ventrolateral flank scales narrow

Howqualepis rostridens

21(1) slightly developed posteroventral process of maxilla
32(1) parasymphysial teeth on dentary present
42(1) median rostral contributes to jaw margin
44(1) teeth present on rostral
66(0) extrascapular number three
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
127(1) first branchiostegal ray deeper than second ray

Node 24 [*Cuneognathus* + (*Limnomis* + *Stegotrachelus*)] + rest

113(1) gap between operculum and skull roof bones absent
172(0) fringing fulcra absent

Node 25 Stegotrachelus + (*Limnomis* + (*Cuneognathus* + *Melanecta*))

43(0) median rostral bone widens anteriorly
60(1) Postparietal squared
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
160(1) postcleitrum absent

Stegotrachelus finlayi

68(3) supraorbital bones absent
114(5) antopercular bone(s) extend(s) to ventral half of operculum
115(2) antopercular bone(s) widen(s) ventrally
116(1) antopercular bones as thick as adjacent bones

Node 26 *Limnomis delaneyi* + (*Cuneognathus* + *Melanecta*)

6(1) premaxillae separated medially
42(1) median rostral contributes to jaw margin
44(1) teeth present on rostral bone

Limnomis delaneyi

7(0) premaxilla not part of orbit
73(4) dermosphenotic larger than dermopterotic/supratemporotabular
113(0) gap between operculum and skull roof bones present
171(0) fringing fulcra absent
173(0) basal fulcra anterior to dorsal fin absent
184(2) pelvic fin with reduced base
189(0) caudal fin without hinge line

Node 27 *Cuneognathus gardineri* + *Melanecta*

21(1) slightly developed posteroventral process of maxilla
37(0) preparietal relative length short

Cuneognathus gardineri

77(1) anterior 1/3 of dermopterotic/supratemporotabular bone contacts parietal
124(0) horizontal subopercular lower suture
186(1) anal fin l ends close to caudal fin
207(1) ventrolateral flank scales narrow

Melanecta

17(0) maxilla preopercular ornamentation of circumferential ridges of ganoine
43(2) median rostral bone narrows anteriorly
51(0) rear of nasal bone preorbital
75(1) dermosphenotoic present as one bone
79(0) ventral protuberance of dermopterotic/supratemporotabular present
159(0) presupracleithrum absent

Node 28 *Moythomasia* through rest

66(2) extrascapular number is four
89(0) jugal/infraorbital three contacts suborbital posteriorly
92(1) suborbital bones present
93(1) suborbitals present as 1 to 3 bones
94(1) suborbitals arranged in one row
95(1) suborbital fit is sutured
96(2) maxilla contacts suborbitals
111(1) preoperculum anteriorly in contact with suborbital
162(1) dorsal end of cleithrum broad and round

Moythomasia nitida

7(0) premaxilla not part of orbit
13(2) height of posterior part of maxilla is high
43(1) median rostral bone with anterior and posterior margins of equal width
59(1) postparietal with pointed anterolateral process

124(3) sigmoidal subobpercular lower suture
151(1) horizontal pit line present
177(3) dorsal fin base with smaller scales

Node 29 *Osorioichthys* through rest

34(1) dentary and maxillary teeth not organized in two series
55(2) pineal opening position absent
73(2) dermopterotic/supratemporotabular longer than dermosphenotic
74(2) dermosphenotic not in contact with dermohyal
123(1) diagonal subopercular upper suture

Osorioichthys marginis

15(1) maxillary teeth present only on anterior part of maxilla
19(2) posterior plate of maxilla is high and rounded
21(1) slightly developed posteroventral process of maxilla
61(1) postparietal almost equal in size to parietal
86(1) lachrymal is rhombic
119(2) second axis of operculum is longer than first
121(2) operculum about the same height as suboperculum
127(1) first branchiostegal ray deeper than second
152(1) vertical preopercular pit line absent
153(1) preopercular canal to postorbital corner
157(0) pectoral fin is lobe based

Node 30 Minus *Osorioichthys* (*Pteroniscul us* through the rest) Carbopermoichtyidae

27(0) surangular absent
60(1) Postparietal squared
77(2) more than 1/3 of dermopterotic/supratemporotabular contacts parietal bone

Node 31 *Pteronisculus* + *Guntherichthys* + (Aesopichthyidae + (*Elonichthys* + *Mansfieldiscus sweeti*)) + *Cyranorhis* + (*Wendyichthys dicksoni* + *Wendyichthys lautreci*)) + (*Coccocephalus* + *Spinofacia*) + (*Beagiascus Lineagruan*)

3(1) premaxilla is a separate and distinct bone
4(3) premaxilla not part of complex bone
7(0) premaxilla not part of orbit
8(0) posterior margin of premaxilla contacts lachrymal bone
9(0) premaxilla not in contact with nasal bone
85(1) lachrymal is a separate and distinct bone
162(0) dorsal end of cleithrum is pointed

Pteronisculus stensioei

38(1) snout shape is a sharp bump
43(1) median rostral bone with anterior and posterior margins of equal lengths
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
103(0) postspiracular present
113(0) gap between operculum and skull roof bones present
114(1) antopercular bone(s) do not extend down to bottom of operculum
115(3) antopercular bone width-anteoperculuar bone(s) taper(s) ventrally
116(1) antopercular bones as thick as as adjacent bones
151(1) horizontal pit line present
152(1) vertical preopercular pit line absent
153(1) preopercular canal postorbital corner
157(0) pectoral fin is lobe based

166(2) clavicle length, not applicable, clavicles absent
173(0) basal fulcra anterior to dorsal fin absent
192(0) caudal outline is cleft equilobate

Node 32 *Guntherichthys* + (Aesopichthyidae + (*Elonichthys* + *Mansfieldiscus sweeti*)) + *Cyranorhis* + (*Wendyichthys dicksoni* + *Wendyichthys lautreci*)) + ((*Coccocephalus* + *Spinofacia*) + (*Beagiascus Lineagruan*))

17(0) maxilla preoperculum ornamentation is circumferential ridges of ganoine
86(2) lachrymal is inverted L shaped
160(1) postcleithrum absent

Guntherichthys lehiensis

36(1) moderate ganoine ornamentation on skull roof bones
171(0) fringing fulcra absent
192(4) caudal outline not cleft
196 (3) scale shape round and rhombic
200(1) posterior edges of rhombic scales are straight

Node 33 (Aesopichthyidae + (*Elonichthys* + *Mansfieldiscus sweeti*)) + *Cyranorhis* + (*Wendyichthys dicksoni* + *Wendyichthys lautreci*)) + (*Coccocephalus* + *Spinofacia*) + (*Beagiascus Lineagruan*)

31(1) coronoid process present
60(2) postparietal short and rectangular
127(1) first branchiostegal deeper than second branchiostegal ray

Node 34 Aesopichthyidae + (*Elonichthys* + *Mansfieldiscus sweeti*)

100(1), 101(2) dealing with absence of quadratojugal
146(1) otic canal in two bones

Node 35 Aesopichthyidae
B=29

13(2) height of posterior part of maxilla is high
19(2) posterior plate of maxilla is high and rounded
107(1) preoperculum anterodorsal region-subvertical or vertical
157(0) pectoral fin is lobe based
169(1) deep body form
178(1) rear of dorsal fin close to caudal
180(1) dorsal fin shape is sigmoidal
185(0) scutes or basal fulcra between P2 and anal absent
186(1) anal fin ends close to caudal fin

Aesopichthys erinaceus

17(3) maxilla preoperculum ornamentation is ridges and tubercles of ganoine
45(1) rostral notch present
58(1) parietal not in contact with supraorbital
83(2) cheek fit is thick peripheral gaps
89(2) jugal/infraorbital 3 not in contact with suborbital
91(3) infraorbital bones ventral to orbit is only infraorbital 3/posteroventral infraorbital
95(2) suborbital fit is loose with gaps
110(1) preoperculum contacts posterior margin of maxilla
119(1) both axes of operculum approximately equal
124(2) concave subopercular lower suture
128(1) fewer than 12 branchiostegal rays per side
177(1) dorsal fin base is a scaled lobe
179(1) dorsal fin originates at same level as anal
183(1) pelvic fin absent
198(0) peg and socket articulation broad
207(1) ventrolateral flank scales narrow

Proceramala montanensis

65(1) two separate extrascapular rows
93(3) suborbital number is more than six
94(2) suborbital bones arranged in two rows
126(1) branchiostegal rays not below mandible
127(0) first branchiostegal ray as deep as second
153(1) preopercular canal to postorbital corner
205(1) enlarged postcleithral scales present
206(1) flank scales deep

Node 36 *Elonichthys* + *Mansfieldiscus sweeti*

34(0) dentary and maxillary teeth-in two series
75(1) dermosphenotic number-one bone
114(5) antopercular extent-located on the ventral half of the operculum
115(2) antopercular width-antopercular bones widens ventrally
116(1) antopercular bones as thick as adjacent bones

'Elonichthys' palatinus

51(0) rear of nasal bones preorbital
60(0) postparietal long and rectangular
72(2) dermosphenotic not in contact with nasal bone
74(3) dermosphenotic not in contact with dermohyal because dermohyal absent
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
91(1) number of infraorbital bones ventral to orbit is two
104(0) dermohyal absent
113(0) gap between operculum and skull roof bones present

Mansfieldiscus sweeti

8(1) premaxilla contacts ventrally lachrymal bone
14(0) ventral margin of maxilla is straight
21(1) slightly developed posteroventral process of maxilla
38(1) snout shape is a sharp bump
66(1) extrascapular number is two
78(2)dermopterotic/supratemporotabular ventroposteriorly in contact with operculum
85(0) lachrymal is part of complex bone
86(5) lachrymal is rectangular
89(1) jugal/infraorbital 3 contacts suborbital posterodorsally
160(0) postcleithrum present
192(0) caudal outline is cleft equilobate

Node 37 *(Cyranorhis + (Wendyichthys dicksoni + Wendyichthys lautreci)) + ((Coccocephalus + Spinofacia) + (Beagiascus Lineagruan))*

B=3

17(1) maxilla preoperculum ornamentation is mainly vertical ridges of ganoine
130(1) extralateral gular present
131(1) extralateral gular begins at anterior most tip of median gular
175(1) body scales to dorsal ridge scales is one to one
207(1) ventrolateral flank scales narrow

Node 38 (*Coccocephalus* + *Spinofacia*) + *Beagiascus Lineagruan*

34(0) dentary and maxillary teeth are in two series
43(0) median rostral widens anteriorly
66(3) extrascapular number is more than 4

Node 39 *Beagiascus Lineagruan judithi Lineagruan snowyi*

B=63

65(1) extrascapular rows two separate rows
73(1) almost equal length of dermopterotic/supratemporotabular and dermosphenotic
78(0) dermopterotic/supratemporotabular not in contact with operculum
105(1) supraopercular bone present
114(2) antopercular bones extend to bottom of operculum
115(3) antopercular bones taper in width ventrally
116(2) antopercular bone thickness is extremely thin
131(2) extralateral gular begins at midpoint of median gular
205(1) enlarged postcleithral scales present

Beagiascus pulcherrimus

8(1) premaxilla contacts ventrally lachrymal bones
13(2) height of posterior part of maxilla is high
16(2) marginal teeth orientation is posteriad
17(0) maxilla pop ornamentation is circumferential ridges
49(0) nasal bones without notches
78(2)dermopterotic/supratemporotabular ventroposteriorly in contact with operculum
93(3) suborbital number is more than six
115(2) antopercular bone(s) widen(s) ventrally
116(1) antopercular bone(s) as thick as adjacent bones
123(0) horizontal subopercular upper suture
124(0) horizontal subopercular lower suture

Lineagruan judithi

16(0) marginal teeth orientation is vertical
19(2) high rounded posterior plate of maxilla
72(2) dermosphenotic not in contact with nasal
98(3) sclerotic plate number is three
107(1) preoperculum anterodorsal region is subvertical or vertical
108(1) preopercular angle is narrower than 90°
128(1) fewer than 12 branchiostegal rays per side
166(0) clavicle length is short

Lineagruan snowyi

14(0) ventral margin of maxilla is straight
93(2) suborbital number is four to six
114(3) antopercular bones extend to bottom of suboperculum
173(0) basal fulcra anterior to dorsal fin absent
174(3) predorsal scutes/dorsal ridge scales absent
175(0) number of body scales to dorsal ridge scales not applicable because dorsal ridge scales absent
176(3) dorsal ridge scales absent

Node 40 *Coccocephalus* + *Spinofacia*

B=16

36(1) ganoine ornamentation on skull roof bones-moderate
75(1) dermosphenotic one bone
77(1)dermopterotic/supratemporotabular not in contact with parietal

Node 41 *Cyranorhis* + *(Wendyichthys dicksoni* + *Wendyichthys lautreci)*

B=26

2(1), 3(2), 4(4), 6(2), 7(2), 8(4), 9(2) dealing with the absence of premaxillary bones
38(3) snout shape is notched

45(1) rostral notch present
79(1) ventral protuberance of dermopterotic/supratemporotabular absent

Cyranorhis bergeraci

12(1) anterior end of maxilla is orbital
17(2) maxilla preopercular ornamentation is mainly tuberculations
86(1) lachrymal is rhombic
124(0) horizontal subopercular lower suture
127(0) first branchiostegal ray is as deep as second
134(0) lateral gular is similar in size to branchiostegal rays
162(1) dorsal end of cleithrum is broad and round

Node 42 *Wendyichthys dicksoni + W. lautreci*

B=5

5(2) premaxilla nasal process absent because premaxilla absent
159(0) presupracleithrum absent
160(0) postcleithrum present

Wendyichthys dicksoni

17(3) max pop ornamentation is ridges and tubercles of ganoine
143(0) supraorbital canal into postparietal
205(1) enlarged postcleithral scales present

Wendyichthys lautreci

16(0) marginal teeth orientation is vertical
21(1) slightly developed posteroventral process of maxilla
34(0) dentary and maxillary teeth in two series
75(1) one dermosphenotic bone
146(1) otic canal in two bones
174(1) many predorsal scutes/dorsal ridge scales
186(1) anal fin ends close to caudal fin
206(1) flank scales are deep

Node 43 Ambylpteridae through deep bodied

128(1) less than 12 branchiostegal rays per side
146(1) otic canal trajectory in two bones
159(0) presupracleithrum absent

Node 44 Ambylpteridae

B=11

13(2) height of posterior part of maxilla is high
21(1) slightly developed posteroventral process of maxilla
113(0) gap between operculum and skull roof bones present

Amblypterus latus

36(1) moderate ganoine ornamentation on skull roof bones
123(2) concave subopercular upper suture
160(1) postcleithrum absent
200(1) posterior edges of rhombic scales are straight

Paramblypterus decorus

14(0) ventral margin of maxilla is straight
48(1) nasal number is two bones on each side
65(1) two separate extrascapular rows
69(2) supraorbital present as single bone
73(1) length of dermosphenotic almost equal to dermopterotic/supratemporotabular
77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal bone
93(3) suborbital number is more than six
94(3) suborbital bones arranged in many rows
104(2) dermohyal in a series
184(0) pelvic fin with long base

205(1) enlarged postcleithral scales present

Node 45 *Rhadinichthys* through deep bodied

43(0) median rostral bone widens anteriorly
75(1) one dermosphenotic bone
100(1), 101(2) dealing with the absence of a quadratojugal

Node 46 (*Rhadinichthys* + (*Cycloptychius* + *Novogonatodus*)) + (*Palaeoniscum* + (New Brunswick + (*Gonatodus* + *Kalops*)))

4(0) a complex premaxilla present as a ventral-rostro-premaxillo-lachrymal
34(0) dentary and maxillary teeth in two series
40(2) median and complex rostral bones present
41(1) 2 rostral bones, a dorsal and ventral bone, ventral part of complex bone
140(4) ethmoid commissure through paired complex bone
184(0) pelvic fin with long base

Node 47 *Rhadinichthys* + (*Cycloptychius* + *Novogonatodus*)

B=4

38(1) snout shape is a sharp bump
86(3) lachrymal shape is a vertical pillar
127(2) concave subopercular upper suture

Rhadinichthys canobiensis

59(1) postparietal with pointed anterolateral process
179(1) dorsal fin originates at same level as anal

Node 48 *Cycloptychius* + *Novogonatodus*

B=2

13(2) height of posterior margin of maxilla is high

Cycloptychius concentricus

121(2) operculum is about the same height as suboperculum
162(0) dorsal end of cleithrum ispointed
179(0) dorsal fin originates behind anal

Novogonatodus kasantsevae

19(2) posterior plate of maxilla is high and rounded
107(1) preoperculum anterodorsal region is subvertical or vertical
160(1) postcleithrum absent
169(2) round body form

Node 49 *Palaeoniscum* through rest

58(0) parietal contacts supraorbital
68(1) supraorbital bones present without canal
69(0) supraorbitals single series
72(2) dermosphenotic contact not in contact with nasal

Palaeoniscum freieslebeni

51(0) rear of nasal bones-preorbital
73(3) dermosphenotic relative size-dermopterotic/supratemporotabular more than two times longer than dermosphenotic
74(3) dermosphenotic not in contact with dermoyhal because no dermohyal present
75(1) dermosphenotic one bone
104(0) dermohyal absent
121(2) operculum about same height as suboperculum
123(3) sigmoidal subopercular upper suture
146(0) otic canal in three bones

Node 50 (New Brunswick + (*Gonatodus* + *Kalops*)

4(2) complex premaxilla present as of a ventral rostro-premaxilla
8(0) posterior margin of premaxilla contacts lachrymal bone

New Brunswick fish

10(1) premaxillary teeth absent in midline
13(0) height of posterior part of maxilla is low
69(2) supraorbital present as single bone
94(3) suborbital bones arranged in many rows
114(2) antopercular bones extend to bottom of operculum
115(2) antopercular bone widen ventrally
116(1) antopercular bones as thick as as adjacent bones
174(1) many predorsal scutes/dorsal ridge scales
201(1) ventral edges of scales are serrated

Node 51 *Gonatodus +Kalops*

B=1

9(0) premaxillae, relation of-premaxilla not in contact with nasal bone
17(0) maxilla preoperculum ornamentation-circumferential ridges of ganoine
60(2) postparietal is short and rectangular
127(1) first branchiostegal ray is deeper than second branchiostegal ray
157(0) pectoral fin is lobe based

Gonatodus punctatus

13(0) height of posterior part of maxilla is low
34(1) dentary and maxillary teeth not in two series
37(0) preparietal relative length is short
78(0) dermopterotic/supratemporotabular not in contact with operculum
104(2) dermohyal in a series
107(1) preoperculum anterodorsal region is subvertical or vertical
123(0) horizontal subopercular upper suture
160(1) postcleithrum absent
186(1) anal fin ends close to caudal fin
192(0) caudal outline is cleft equilobate

Node 52 *Kalops monophrys + Kalops diophrys*

B=85

3(1) premaxilla is separate and distinct
4(3) premaxilla not part of complex bone
40(3) 2 median rostral bones
41(2) 2 rostral bones, dorsal and ventral, both separate, distinct
51(0) rear of nasal bones is preorbital
79(1) ventral protuberance off of dermopterotic/supratemporotabular absent
94(2) suborbital bones arranged in two rows
98(3) sclerotic plate number is three
113(0) gap between operculum and skull roof bones present
121(0) operculum three times deeper than suboperculum or more
140(1) ethmoid commissure through median ventral rostral
143(1) supraorbital canal into parietal bone
148(1) supratemporal commissure not across midline
184(1) pelvic fin with short base

Kalops diophrys

65(2) extrascapular rows-two rows share median bone
69(1) supraorbital bones present as double series

73(1) dermosphenotic almost equal in size to dermopterotic/supratemporotabular
103(0) postspiracular present
134(0) lateral gular similar in size to branchiostegal ray
187(0) scutes and basal fulcra between anal and caudal fins absent
205(1) enlarged postcleithral scales present

Kalops monophrys

95(0) suborbital fit is absent
174(2) predorsal scutes/dorsal ridge scales are complete to occiput

Node 53 *Mesopoma* through deep bodied

107(1) preoperculum anterodorsal region is subvertical or vertical
121(2) operculum approximately same height as suboperculum
133(2) lateral gular shape is none, lateral gulars absent
162(0) dorsal end of cleithrum is pointed

Node 54 *Mesopoma Boreosomus* Redfieldiids

B=1

27(1) surangular present
38(1) snout shape is a sharp bump
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
89(1) jugal/infraorbital 3 contacts suborbital posterodorsally
96(1) maxilla not in contact with suborbital
113(0) gap between operculum and skull roof bones present
175(0) number of body scales to dorsal ridge scales is not applicable, dorsal ridge scales absent

Mesopoma carricki

179(1) dorsal fin originates at same level as anal fin

Mesopoma planti

73(1) dermosphenotic almost equal in size to dermopterotic/supratemporotabular
86(3) lachrymal shape is a vertical pillar
100(0) quadratojugal present
101(0) small quadratojugal
107(0) preoperculum anterodorsal region is subhorizontal
200(1) posterior edges of rhombic scales-straight

Node 55 *Boreosomus* + Redfieldiids

B=2

51(0) rear of nasal bones preorbital
72(2) dermosphenotic not in contact with nasal
192(0) caudal outline is cleft equilobate

Boreosomus piveteaau

37(0) preparietal relative length is short
60(0) postparietal long and rectangular
75(1) one dermosphenotic bone
89(4) Jugal/infraorbital 3 contacts suborbital ventrally
93(2) suborbital number is four to six
157(0) pectoral fin is lobe based
173(0) basal fulcra anterior to dorsal fin absent
185(0) scutes or basal fulcra between pelvic and anal fin absent
200(1) posterior edges of rhombic scales are straight

Node 56 Redfieldiids

B=53

12(1) maxilla anterior end is orbital
13(2) height of posterior part of maxilla is high
46(1) tuberculated snout present
111(2) preoperculum anteriorly in contact with infraorbitals, extensively

113(1) gap between operculum and skull roof bones absent
125(2) branchiostegal rays present as 1/branchiostegal plate
126(1) branchiostegal rays not below mandible
143(1) supraorbital canal into parietal

Dictyopyge sp.

19(3) high triangular posterior plate of maxilla
74(3) dermosphenotic not in contact with dermohyal because dermohyal absent
91(1) number of infraorbital bones ventral to orbit is two
104(0) dermohyal absent
108(1) preopercular angle is narrower than 90°
119(2) second axis of operculum longer than first
122(1) operculum in contact with lateral extrascapular
189(0) caudal fin without hinge line

Redfieldius gracilis

60(3) postparietal rounded
63(1) three postparietals bones, one per side and a median bone
66(1) extrascapular number is two
89(2) jugal/infraorbital 3 not in contact with suborbital
107(0) preoperculum anterodorsal region is subhorizontal
112(2) preoperculuar width is even
153(2) preopercular canal to postotic region
174(2) predorsal scutes/dorsal ridge scales are complete to occiput
175(1) body scales to dorsal ridge scales are one to one
176(0) dorsal ridge scales without a spine or spike
179(1) dorsal fin originates at same level as anal

Node 57 *Canobius* through rest

15(1) maxillary teeth only on anterior part of bone
19(2) posterior plate of maxilla is high and rounded
43(1) median rostral with anterior and posterior margins of equal width 66(1) extrascapular number is two
108(1) preopercular angle is narrower than 90

Canobius elegantulus

58(1) parietal not in contact with supraorbital
74(3) dermosphenotic not in contact with dermohyal because dermohyal is absent
86(1) lachrymal is rhombic
95(2) suborbital fit is loose with gaps
104(0) dermohyal absent
179(1) dorsal fin originates at same level as anal fin

Node 58 Aeduellids through rest

13(2) height of posterior part of maxilla is high
21(0) maxilla posteroventral process absent
121(3) suboperculum deeper than operculum
140(4) ethmoid commissure through paired complex bone
200(1) posterior edges of rhombic scales are straight

Node 59 (*Bourbonnella jocelynae + Beishanichthys) + (Aeduella blainvilli + Bourbonnella guilloti) + Haplolepidae*

36(1) moderate ganoine ornamentation on skull roof bones
51(0) rear of nasal bones preorbital
60(2) Postparietal short and rectangular
143(1) supraorbital canal into parietal
151(1) horizontal pit line present

Node 60 *(Aeduella blainvilli + Bourbonnella guilloti)* + Haplolepidae

B=6

37(0) preparietal relative length is short
89(1) jugal/infraorbital 3 contacts suborbital bone(s) posterodorsally
126(1) branchiostegal rays not between the mandibles

Node 61
Aeduellidae
Aeduella blainvilli + Bourbonnella guilloti

B=63

60(0) Postparietal long and rectangular
74(3) dermosphenotic not in contact with dermohyal because dermohyal is absent
121(2) operculum about same height as suboperculum
157(0) pectoral fin is lobe based
160(1) postcleithrum absent

Aeduella blainvillei

122(0) operculum not in contact with lateral extrascapulars
123(3) sigmoidal subopercular upper suture
143(3) supraorbital canal into dermopterotic/supratemporotabular

Bourbonnella guilloti

124(0) horizontal subopercular lower suture
151(0) horizontal pit line absent

Node 62 Haplolepidae

B=85

55(1) pineal opening in parietal area
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
96(1) maxilla not in contact with suborbital bone(s)
106(0) preoperculum without distinct regions
108(2) preopercular angle-n/a, no distinct regions
164(1) cleithrum dorsal arm stout and wide
182(1) number of dorsal fin rays 10 or less
206(1) flank scales deep

Haplolepis corrugata

13(0) height of posterior part of maxilla is low
19(0) posterior plate of maxilla not differentiated
111(2) preoperculum anteriorly in contact with infraorbitals, extensively
121(1) operculum two times deeper than suboperculum
162(1) dorsal end of cleithrum broad and round

Node 63 *Microhaplolepis + Parahaplolepis*

B=69

14(0) ventral margin of maxilla is straight
63(2), 76(2), 80(1) dealing with fusion of postparietal to dermopterotic/supratemporotabular
179(1) dorsal fin originates at same level as anal
192(4) caudal fin is not cleft
207(1) ventrolateral flank scales narrow

Microhaplolepis ovoidea

19(3) high triangular posterior plateof maxilla
113(0) gap between operculum and skull roof bones present

Parahaplolepis tuberculata

38(1) snout shape is sharp bump
100(0) quadratojugal present
101(1) large quadratojugal
119(1) both axes of operculum approximately equal in size

122(0) operculum not in contact with lateral extrascapulars
151(0) horizontal pit line absent

Node 64 *Beishanichthys + Bourbonnella joceylnae*
B=2

14(0) maxilla ventral margin is straight
171(0) fringing fulcra absent

Beishanichthys brevicaudalis

19(1) moderate rectangular posterior plate of maxilla
66(2) extrascapular number is four
100(0) quadratojugal present
101(1) large quadratojugal
121(1) operculum is two times deeper than suboperculum
173(0) basal fulcra anterior to dorsal fin absent
174(1) many predorsal scutes/dorsal ridge scales
180(4) dorsal fin long and low
185(0) scutes or basal fulcra between pelvic and anal fins absent

Bourbonnella jocelynae

157(0) pectoral fin lobe based
160(1) postcleithrum absent
207(1) ventrolateral flanks scales narrow

Node 65 "Deep Bodied" *Paramesolepis Cheirodopsis* + Platysomids + Amphicentrids *Ebenaqua*
B=3

7(0) premaxilla not part of orbit
19(3) high triangular shaped posterior plate of maxilla
86(3) lachrymal shape is a vertical pillar
89(3), 92(0), 93(0), 94(0), 95(0), 96(0) dealing with absence of suborbital bones
111(2) preoperculum anteriorly in contact with infraorbitals; extensive
123(2) concave subopercular upper suture
169(1) deep body form

Paramesolepis tuberculata

8(0) premaxilla contacts posteriorly lachrymal bone
40(2) rostral bones present as median and complex bone
41(1) 2 rostral bones-dorsal and ventral, ventral part of complex bone
75(1) dermosphenotic present as one bones
106(0) preoperculum without distinct regions
108(2) preopercular angle-n/a no distinct regions
112(2) preoperculum width is even
146(0) otic canal in 3 bones

Node 66 *Cheirodopsis* + Platysomids + Amphicentrids *Ebenaqua*
B=1

14(0) maxilla ventral margin-straight
175(0), 176(3) dealing with absence of dorsal ridge scales

Cheirodopsis geikiei

206(1) flank scales are deep

Node 67 Platysomids + Amphicentrids *Ebenaqua*
B=1

43(2) median rostral bone narrows anteriorly
60(2) Postparietal shape-short and rectangular
66(2) extrascapular number-four
71(2) dermosphenotic shape-rectangular
104(0) dermohyal-absent

Platysomus superbus

15(3) maxillary teeth not on oral rim of maxilla
16(3) marginal teeth absent
22(3) maxillary teeth absent
34(2) dentary and maxillary teeth absent from oral rim

78(0)
dermopterotic/supratemporotabular not in contact with operculum
85(1) lachrymal is a separate and distinct bone
178(0) rear of dorsal fin far from caudal fin
186(0) anal fin ends far from caudal fin
205(1) enlarged postcleithral scales present

Node 68 *Platysomus striatus* to *Platysomus swaffordae*

B=1

51(0) rear of nasal bones preorbital
74(3) dermosphenotic does not contact dermohyal because dermohyal absent
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
192(0) cleft equilobate caudal outline

Platysomus striatus

19(2) maxilla posterior plate is high and rounded
73(2)
dermopterotic/supratemporotabular longer than dermosphenotic
112(3) preoperculum cinched in middle
123(0) horizontal subopercular upper suture
124(0) horizontal subopercular lower suture

Node 69 *Platysomus parvulus* to *swaffordae*

B=2

14(1) curved ventral margin of maxilla
160(1) postcleithrum absent
169(3) angulate body form
176(2) dorsal ridge scales are peg like

Platysomus parvulus

20(1) maxilla posterior end is orbital
174(1) many predorsal scutes/dorsal ridge scales
178(0) rear of dorsal fin far from caudal fin
186(0) anal fin base ends far from caudal fin

Node 70 *Amphicentrum jurgeni* to *Platysomus swaffordae*

B=9

106(0) preoperculum without distinct regions
179(1) dorsal fin originates at same level as anal fin
183(1), 184(3), dealing with absence of pelvic fin absent

Amphicentrum jurgenai

73(2)dermopterotic/supratemporotabular longer than dermosphenotic

Node 71 *Amphicentrum granulosum* to *Platysomus swaffordae*

B=3

3(1) premaxilla separate and distinct
4(3) premaxilla not part of complex bone
8(0) premaxilla contacts posteriorly lachrymal bone
85(1) lachrymal separate and distinct bone

Amphicentrum granulosum

21(1) slightly developed posteroventral process of maxilla
51(1) rear of nasal bones-midorbital
62(2), 65(3), **149(2) dealing with absenc of extrascapular bones**
152(1) vertical preopercular pit line absent
176(3) dorsal ridge scales absent
189(0) caudal fin without hinge line

Node 72 *Ebenaqua Platysomus gibbosus Platysomus schultzei Platysomus swaffordae*

B=30

19(2) high rounded maxilla posterior plate

20(1/2) maxilla posterior process is slightly developed or strong 107(2) preoperculum anterodorsal region not differentiatied, not applicable
110(2) preoperculum not in contact with maxilla
113(0) gap between operculum and skull roof-bones present
124(4) subopercular lower suture convex
126(2), 127(2) dealing with absence of branchiostegal rays
171(0) fringing fulcra absent
174(2) predorsal scutes/dorsal ridge scales complete to occiput
175(2) body scales to dorsal ridge scales arranged with more than 1 body scale row to dorsal ridge scale

Node 73 *Ebenaqua* + *Platysomus gibbosus*

B=16

72(2) dermosphenotic not in contact with nasals
78(0) dermopterotic/supratemporotabular not in contact with operculum
103(0) postspiracular present
183(0) pelvic fin present

Ebenaqua ritchiei

13(1) medium height of posterior part of maxilla
17(1) maxilla pop ornamentation is mainly vertical ridges
19(0) maxilla posterior plate not differentiated
79(0) ventral protuberance of dermopterotic/supratemporotabular present
125(2) branchiostegal plate present
157(0) pectoral fin is lobe based

Platysomus gibbosus

89(0) jugal/infraorbital 3 contacts suborbital posteriorly
92(1) suborbital bones present
93(1) suborbital number present as 1 to 3 bones
94(1) suborbitals arranged in one row
95(1) suborbital fit is sutured
96(1) maxilla not in contact with suborbitals
111(1) preoperculum anteriorly contacts suborbitals
169(1) deep body form

Node 74 *Platysomus schultzei* + *Platysomus swaffordae*

B=27

60(0) Postparietal long rectangular
111(5) preoperculum anteriorly in contact with platysomid qj/so
169(2) round body form

Platysomus schultzei

13(1) medium height of posterior part of maxilla
17(1) maxilla pop ornamentation of mainly vertical ridges
51(1) rear of nasal bones midorbital
62(1) postparietal not in contact with lateral extrascapulars
65(3) extrascapular rows absent
125(1) branchiostegal rays absent
200(0) posterior edges of rhombic scales are serrated

Platysomus swaffordae

160(0) postcleithrum present
174(1) many predorsal scutes/dorsal ridges scales
207(3) ventrolateral flank scales shorter

Appendix 3—Characters and character states that define the clades for the tree presented in Figure 10. Bootstrap values (B) above zero are given.

Node 1 Palaeonisci

B=65

26(1) splenial absent
36(0) dense ganoine ornamentation on skull roof bones
51(1) rear of nasal bones preorbital
71(1) dermosphenotic is T-shaped
76(0) dermopterotic/supratemporotabular present
81(1) tabular absent
155(0) mandibular canal trajectory through dentary
156(1) mandibular canal trajectory not through posterior infradentary
202(1) ganoine present

Node 2 *Tarrasius* + (*Paratarrasius* + Guildayichthyidae)

B=1

40(3) median rostral bones
41(2) 2 rostral bones, dorsal and ventral, both separate and distinct
75(2) 2 dermosphenotic bones, a dorsal and ventral dermosphenotic
169(4) blade like body form
178(2) dorsal fin merged with caudal
186(2) anal fin merged with caudal fin
190(3) hypocercal caudal fin

Tarrasius problematicus

13(2) height of posterior part of maxilla is high
19(2) maxilla posterior plate is high and rounded
104(1) dermohyal present as single bone
107(1) POP anterodorsal regionis subvertical or vertical
110(1) Preoperculum contacts posterior margin of maxilla
124(0) horizontal subopercular lower suture
140(1) ethmoid commissure through median ventral rostral
146(1) otic canal in two bones
160(1) postcleithrum absent

Node 3 *Paratarrasius hibbardi* + [*Discoserra pectinodon* + *Guildayichthys carnegiei*]

B=1

14(0) maxilla ventral margin is straight
49(1) nasal bones with notches
50(0) nasals notched on medial and/or lateral borders
89(0) jugal/infraorbital 3 contacts suborbital bones posteriorly
92(1) suborbital bones are present
93(3) more than 6 suborbital bones present
94(3) suborbital bones arranged in many rows
95(1) suborbital fit is sutured
96(2) maxilla contacts suborbital
111(1) Preoperculum anteriorly in contact with suborbitals
159(1) presupracleithrum present

Paratarrasius hibbardi

13(1) height of posterior part of maxilla is medium
17(0) maxilla preoperculum ornamentation is circumferential ridges
19(1) maxilla posterior plate is a moderate rectangular plate
65(1) two separate extrascapular rows
69(1) supraorbital bones present in a double series
77(1) anterior 1/3 of dermopterotic/supratemporotabular bone is in contact with parietal

83(1) cheek fit is thin overlapping
104(2) dermohyal present in a series
106(1) preoperculum with distinct anterodorsal and ventral regions
114(1) antopercular bone(s) do not extend to bottom of operculum
115(3) antopercular bone(s) taper(s) ventrally
116(1) antopercular bones as thick as adjacent bones
119(1) both axes of operculum approximately equal
127(1) first branchiostegal ray deeper than second branchiostegal
133(2), 134(2) dealing with absence of lateral gular
143(3) supraorbital canal into dermopterotic/supratemporotabular
144(1) supraorbital canal in contact with otic
205(1) enlarged postcleithral scales present

Node 4 Guildayichthyiformes

B=99

15(1) maxillary teeth only on anterior part of bone
25(1) adductor mandibulae fossa on most of mandible
38(4) snout shape is sharp
40(5) rostral bones present as paired and median bones
41(4) rostral condition is paired and median bones
67(1) dermal supraoccipital present
103(0) postspiracular present
108(2) preopercular angle n/a, no distinct regions
109(1) preoperculum number is two
110(2) preoperculum not in contact with maxilla
112(2) preoperculum even in width
117(1) interoperculum present
121(5) opercular size compared to suboperculum n/a because suboperculum absent
122(0) operculum not in contact with lateral extrascapulars
123(5), 124(5) dealing with absence of suboperculum
135(1) long parasphenoid
153(2) preopercular canal to postotic region
165(1), 167(3) dealing with absence of clavicle
169(2) round body form
170(1) basal fulcra between dorsal and caudal fins present
174(2) predorsal scutes/dorsal ridge scales are complete to occiput
176(1) dorsal ridge scales are spine shaped
177(1) dorsal fin base has scaled lobe
178(1) rear of dorsal fin close to caudal
184(2) pelvic fin with a reduced base
186(1) anal fin ends close to caudal
190(4) caudal fin shape is abbreviated heterocercal
191(1) caudal fin rays webbed
192(4) caudal outline not cleft
193(1) epichordal fin rays of caudal fin absent
206(1) flank scales deep

Discoserra pectinodon

43(2) median rostral bone narrows anteriorly
48(1) nasal number is two on each side
62(1) postparietal size almost equal to parietal
69(2) supraorbitals-single bone
91(3) infraorbital bones ventral to orbit-only the infraorbital 3/posteroventral infraorbital
94(2) suborbital bones arranged in two rows
95(2) suborbital fit is loose with gaps
148(1) supratemporal commissure not across midline
198(0) peg and socket articulation broad

Guildayichthys carnegiei

57(1) parietal number-two pairs of parietals

58(1) parietal not in contact with supraorbital

72(1) dermosphenotic contacts nasal

126(1) branchiostegal rays not below mandible

189(1) caudal fin with hinge line

Node 5 Palaeoniscomorpha

48(2) nasal number is single bone on each side

170(1) basal fulcra between dorsal and caudal fins present

171(1) fringing fulcra present

174(0) few predorsal scutes/dorsal ridge scales

185(1) scutes or basal fulcra between pelvic and anal fins present

187(1) scutes and basal fulcra between anal and caudal fins present

Dialipina salgueiroensis

59(1) postparietal with pointed anterolateral process

77(2) more than 1/3 of dermopterotic/supratemporotabular bone contacts parietal

112(2) preoperculum width even

118(1), 119(3), 120(2), 121(4) dealing with absence of operculum

146(1) otic canal in two bones

190(1) triphycercal caudal fin

Node 6 Palaeonisciformes

B=1

3(0) premaxilla part of complex bone

19(1) maxilla posterior plate of maxilla moderate in size

60(0) Postparietal long and rectangular

79(0) ventral protuberance of dermopterotic/supratemporotabular present

189(1) caudal fin with hinge line

193(1) epichordal fin rays of caudal fin absent

194(2) length of epichordal fin rays of caudal fin absent

Node 7 Cheirolepididae

B=92

13(2) height of posterior part of maxilla is high

71(3) dermosphenotic elongate in shape

74(1) dermosphenotic in contact with dermohyal

110(3) preoperculum contacts dorsal margin of max

115(2) antopercular bone widens ventrally

116(1) antopercular bone as thick as adjacent bone

140(5) ethmoid commissure trajectory absent

151(1) horizontal pit line present

178(1) rear of dorsal fin close to caudal fin

195(1) micromeric scales

196(0) scale shape-acanthodian shape

197(0) peg and socket articulation absent

198(2) peg and socket articulation absent

200(2) posterior edges of rhombic scales not applicable because rhombic ganoid scales absent

201(2) ventral edges of scales-not applicable because rhombic ganoid scales absent

Cheirolepis trailli

49(1) nasal bones with notches

56(0) pineal opening in postrostral area

59(1) postparietal with pointed anterolateral process

100(0) quadratojugal present

101(0) small quadratojugal

134(0) lateral gular similar in size to branchiostegal rays

145(1) supraorbital and infraorbital canals not in contact rostrally

170(0) basal fulcra between dorsal and caudal fins absent

Node 8 *Cheirolepis canadensis + C schultzei*

B=14

51(0) rear of nasal bones preorbital
69(2) supraorbital present as single bone
146(1) otic canal in 2 bones

Cheirolepis schultzei

21(1) posteroventral process of maxilla slightly developed
77(1) anterior 1/3 of dermopterotic/supratemporotabular bone in contact with parietal
106(0) preoperculum without distinct regions
112(3) POP cinched in middle
159(1) presupracleithrum present

Node 9 *Tegeolepis* through rest (minus *Cheirolepis*)

33(1) acrodin caps on teeth present
52(1) postrostral bones absent
68(2), 69(3) dealing with absence of supraorbital bones
72(1) dermosphenotic contacts nasal bone
75(2) dermosphenotic number is two bones, dorsal and ventral dermosphenotic
157(1) pectoral fin not lobed

Tegeolepis clarki

8(1) premaxilla contact ventrally lachrymal bones
12(1) maxilla anterior end is orbital
21(1) posteroventral process of maxilla is a slightly developed process
38(2) snout shape elongated
73(2) dermopterotic/supratemporotabular longer than dermosphenotic
85(1) lachrymal is a separate and distinct bone
89(2) jugal/infraorbital 3 not in contact with suborbitals
91(1) 2 infraorbital bones ventral to orbit
132(1), 134(2), dealing with absence of lateral gular

Node 10 *Kentuckia* through rest (minus *Tegeolepis*, Cheirolepids)

7(1) premaxillary position part of orbit
9(1) premaxilla relation of in contact with nasals
13(1) maxilla height of posterior part medium
49(1) nasal bone with notches
55(1) pineal opening in parietal area
74(2) dermosphenotic not in contact with dermohyal

Kentuckia deani

59(1) postparietal with pointed anterolateral process
113(1) gap between operculum and skull roof bones absent
114(5) antopercular bone extends to ventral half of operculum
115(2) antopercular bone widens ventrally
116(1) antopercular bone as thick as adjacent bones
140(4) ethmoid commissure through paired complex bone
153(1) preopercular canal to postorbital corner
168(0) interclavicle present

Node 11 *Donnrosenia + Howqualepis* through rest

38(1) snout shape sharp bump
100(0) quadratojugal present
101(0) small quadratojugal
123(2) concave subopercular upper suture
142(1) supraorbital canal trajectory between medial and lateral nasal openings
159(1) presupracleithrum present

Node 12 *Donnrosenia + Howqualepis*
B=14

74(1) dermosphenotic in contact with dermohyal
77(1) anterior one third of dermopterotic/supratemporotabular bone contacts the parietal bone
122(1) operculum in contact with lateral extrascapular

Donnrosenia schaefferi

9(0) premaxilla not in contact with nasals
61(1) postparietal almost equal in size to parietal
72(0) dermosphenotic contact absent
78(0)dermopterotic/supratemporotabular not in contact with operculum
114(5) antopercular bone extends to ventral half of operculum
115(3) antopercular bone width tapers ventrally
116(1) antopercular bone as thick as adjacent bones
179(2) dorsal fin originates anterior to anal fin
194(0) epichordal fin rays of caudal fin is short
198(0) peg and socket articulation is broad
207(1) ventrolateral flank scales are narrow

Howqualepis rostridens

21(1) posteroventral process of maxilla is a slightly developed process
32(1) parasymphysial teeth on dentary present
42(1) median rostral contributes to jaw margin
44(1) teeth on rostral present
66(0) extrascapular number is three
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
127(1) first branchiostegal deeper than second branchiostegal

Node 13 (*Gogosardina + Mimia*) through rest

124(0) horizontal subopercular lower suture
158(1) anteriormost pectoral lepidotrichia segmented only distally
167(2) clavicle contact is elongate
184(1) pelvic fin with short base
192(1) caudal outline is strongly inequilobate

Node 14 *Gogosardinia + Mimia*
B=66

27(0) surangular absent
59(1) postparietal with pointed anterolateral process
61(1) postparietal almost equal in size to parietal
119(1) both axes of operculum approximately equal
137(1) posterior ascending process absent

Gogosardinia coatesi

52(0) postrostral bones present
53(4) postrostral number is four
54(2) more than 2 postrostral bones
123(3) sigmoidal subopercular upper suture
124(4) convex supobercular lower suture
134(0) lateral gular similar in size to branchiostegal ray
143(1) supraorbital canal into parietal
151(1) horizontal pit line present
207(1) ventrolateral flank scales narrow

Mimipiscis toombsi

17(3) maxilla-preoperculum ornamentation is ridges and tubercles of ganoine
121(2) operculum about same height as suboperculum

127(1) first branchiostegal ray deeper than second branchiostegal
133(0) lateral gular similar in size to branchiostegal ray

Node 15 [*Cuneognathus* + (*Limnomis* + *Stegotrachelus*)] + rest

60(0) postparietal long and rectangular
82(2) spiracle shape absent
179(2) dorsal fin originates anterior to anal fin

Node 16 *Cuneognathus* + (*Limnomis* + *Stegotrachelus*)

B=4

79(1) ventral protuberance of dermopterotic/supratemporotabular absent

Cuneognathus gardineri

21(1) posteroventral process of maxilla is slightly developed process
37(0) preparietal relative length is short
77(1) anterior 1/3 of dermopterotic/supratemporotabular bone contacts parietal
123(0) horizontal subopercular upper suture-
186(1) anal fin ends close to caudal fin
207(1) ventrolateral flank scales narrow

Node 17 *Limnomis delaneyi* + *Stegotrachelus*

B=16

14(0) ventral margin of maxilla is straight
121(0) operculum three times deeper than suboperculum or more

Limnomis delaneyi

6(1) premaxilla separated medially
16(2) marginal teeth orientation is posteriad
42(1) median rostral contributes to jaw margin
44(1) teeth on rostral present
73(4) dermosphenotic larger than dermopterotic/supratemporotabular
90(1) three infraorbital bones, counting lachrymal
124(1) diagonal subopercular lower suture
171(0) fringing fulcra absent
184(2) pelvic fin with reduced base
189(0) caudal fin without hinge line

Stegotrachelus finlayi

38(0) snout shape is blunt rounded
68(3) supraorbital bones absent
114(5) antopercular extent is ventral half of operculum
115(2) antopercular bones widens ventrally
116(1) antopercular bone as thick as adjacent bones

Node 18 *Woodichthys* through rest

55(2) pineal opening absent
66(2) extrascapular number is four
77(2) more than 1/3 of dermopterotic/supratemporotabular bone contacts parietal
159(0) presupracleithrum absent

Woodichthys bearsdeni

36(1) moderate ganoine ornamentation on skull roof bones
60(2) postparietal is short and rectangular
73(2) dermopterotic/supratemporotabular longer than dermosphenotic
122(1) operculum in contact with lateral extrascapular
124(2) concave subopercular lower suture
143(1) supraorbital canal into parietal
153(1) preopercular canal to postorbital corner

Node 19 *Melanecta* through rest

75(1) dermosphenotoic number is one bone
92(1) suborbital bones present
93(1) suborbital number is 1 to 3
94(1) suborbital bones arranged in one row
95(1) suborbital fit is sutured
111(1) preoperculum anteriorly contacts suborbital
123(1) diagonal subopercular upper suture

Node 20 *Mesopoma planti* + (*Mesopoma carricki*) + *(Boreosomus)*+ Redfieldiidae

B=1

79(1) ventral protuberance of dermopterotic/supratemporotabular absent
128(1) fewer than 12 branchiostegal rays per side

Mesopoma planti

86(3) lachrymal shape is a vertical pillar
200(1) posterior edges of rhombic scales are straight

Node 21 *Mesopoma carricki* + *Boreosomus* + Redfieldiidae

73(4) dermosphenotic relative size dermosphenotic longer than dermopterotic/supratemporotabular
77(1), anterior 1/3 of dermopterotic/supratemporotabular contacts parietal bone
107(1) preoperculum anterodorsal region is subvertical or vertical

Mesopoma carricki

34(1) dentary and maxillary teeth not in two series
179(1) dorsal fin originates at same level as anal fin

Node 22 *Boreosomus* + Redfieldiids

B=3

51(0) rear of nasal bones preorbital
72(2) dermosphenotic not in contact with nasal
192(0) caudal outline is cleft equilobate

Boreosomus piveteaau

37(0) preparietal relative length-short
60(0) postparietal is long and rectangular
75(2) dermosphenotic number is 2, dorsal and ventral dermosphenotic bones
89(4) Jugal/infraorbital 3 contacts suborbital ventrally
93(2) suborbital number is four to six
157(0) pectoral fin is lobe based
173(0) basal fulcra anterior to dorsal fin absent
185(0) scutes or basal fulcra between pelvic and anal fin absent
200(1) posterior edges of rhombic scales are straight

Node 23 Redfieldiids

B=54

12(1) maxilla anterior end is orbital
13(2) height of posterior part of maxilla is high
46(1) tuberculated snout present
73(2) dermopterotic/supratemporotabular longer than dermosphenotic
111(2) preoperculum anteriorly contact infraorbitals, extensively
113(1) gap between operculum and skull roof bones absent
125(2) branchiostegal ray number is 1 ray/branchiostegal plate present
126(1) branchiostegal rays not below mandible
143(1) supraorbital canal into parietal

Dictyopyge sp.

19(3) maxilla posterior plate is high and triangular

74(3) dermosphenotic not in contact with dermohyal because dermohyal absent
77(2) more than 1/3 of dermopterotic/supratemporotabular bone contacts parietal
91(1) 2 infraorbital bones ventral to orbit
104(0) dermohyal absent
108(1) preopercular angle narrower than 90°
119(2) second axis of operculum longer than first
122(1) operculum in contact with lateral extrascapular
189(0) caudal fin without hinge line

Redfieldius gracilis

60(3) postparietal shape is rounded
63(1) postparietals number is three, one bone per side, one median
66(1) extrascapular number is two
89(2) jugal/infraorbital 3 not in contact with suborbital
107(0) preoperculum anterodorsal region is subhorizontal
112(2) preoperculum width is even
153(2) preopercular canal to postotic region
174(2) predorsal scutes/dorsal ridge scales complete to occiput
175(1) number of body scales to dorsal ridge scales is one to one
176(0) dorsal ridge scales with no spine or spike
179(1) dorsal fin originates at same level as anal

Node 24 *Melanecta t*hrough deep bodied

43(2) median rostral bone narrows anteriorly
113(1) gap between operculum and skull roof bones absent
124(1) diagonal subopercular lower suture

Node 25 *Melanecta* + (*Moythomasia* + *Osorioichthys*)

37(0) preparietal relative length is short
77(0) dermopterotic/supratemporotabular not in contact with parietal bone

Melanecta anneae

6(1) premaxillae separated medially
10(1) premaxillary teeth absent in midline
16(1) marginal teeth orientation is forward
42(1) median rostral contributes to jaw margin
44(1) teeth on rostral present
51(0) rear of nasal bones preorbital
143(1) supraorbital canal into parietal
160(1) postcleithrum absent

Node 26 *Moythomasia* + *Osorioichthys*

B=2

60(0) postparietal is long and rectangular
75(2) dermosphenotic number is two, with a dorsal and ventral dermosphenotic
146(0) otic canal into three bones
159(1) presupracleithrum present
162(1) dorsal end of cleithrum broad and round

Moythomasia nitida

7(0) premaxilla not part of orbit
13(2) height of posterior part of maxilla is high
43(1) median rostral with equal widths anteriorly and
55(1) pineal opening in parietal area
59(1) postparietal with pointed anterolateral process
123(2) concave subopercular upper suture
124(3) sigmoidal subobpercular lower suture
151(1) horizontal pit line present

Osorioichthys marginis

15(1) maxillary teeth present only on anterior part of maxilla
19(2) posterior plate of maxilla is high and rounded
34(1) dentary and maxillary teeth not in two series
61(1) size of postparietal almost equal to parietal
73(2) dermopterotic/supratemporotabular longer than dermosphenotic
86(1) lachrymal is rhombic
119(2) operculum second axis longer than first axis
121(2) operculum about same height as suboperculum
127(1) first branchiostegal ray deeper than second branchiostegal ray
152(1) vertical preopercular pit line absent
153(1) preopercular canal to postorbital corner
157(0) pectoral fin is lobe based

Node 27 *Guntherichthys* through deep bodied

27(0) surangular absent
122(1) operculum in contact with lateral extrascapular

Node 28 *Guntherichthys* through *Pteroniscus*

3(1) premaxilla is separate and distinct bone
4(3) complex premaxillae-not part of complex bone
7(0) premaxilla not part of orbit
9(0) premaxilla not in contact with nasal bone
159(1) presupracleithrum present

Node 29 *Guntherichthys* through *Spinofacia*

86(2) lachrymal shape is an inverted L
160(1) postcleithrum absent

Guntherichthys lehiensis

36(1) moderate ganoine ornamentation on skull roof bones
171(0) fringing fulcra absent
192(4) caudal outline is not cleft
196 (3) scale shape round and rhombic
200(1) posterior edges of rhombic scales are straight

Node 30 (Aesopichthyidae + (*Cyranorhis Wendyichthys dicksoni Wendyichthys lautreci + Beagiascus Lineagruan + Elonichthys + (Coccocephalus + Spinofacia)*

31(1) coronoid process present
60(2) postparietal short and rectangular

Node 31 Aesopichthyidae

B=28

13(2) height of posterior part of maxilla is high
19(2) posterior plate of maxilla is high and rounded
107(1) preoperculum anterodorsal region is subvertical or vertical
157(0) pectoral fin is lobe based
169(1) deep body form
178(1) rear of dorsal fin close to caudal fin
180(1) sigmoidal dorsal fin shape
185(0) scutes or basal fulcra between pelvic and anal fins absent
186(1) anal fin ends close to caudal fin

Aesopichthys erinaceus

17(3) maxilla preoperculum ornamentation is ridges and tubercles of ganoine
58(1) parietal not in contact with supraorbital
83(2) cheek fit is thick peripheral gaps
89(2) jugal/infraorbital three not in contact with suborbital

91(3) infraorbital bones ventral to orbit-is only the infrarobital 3/posteroventral infraorbital 95(2) suborbital fit is loose with gaps
110(1) preoperculum contacts posterior margin of maxilla
119(1) both axes of operculum approximately equal
128(1) fewer than 12branchiostegal rays per side
177(1) dorsal fin base is a scaled lobe
179(1) dorsal fin originates at same level as anal fin
183(1) pelvic fin absent
198(0) peg and socket articulation broad

Proceramala montanensis

65(1) extrascapular rows in two separate rows
93(3) suborbital number is more than six
94(2) suborbital bone arranged in two rows
126(1) branchiostegal rays not below mandible
153(1) preopercular canal to postorbital corner
205(1) enlarged postcleithral scales present
206(1) flank scales deep

Node 32 *Cyranorhis Wendyichthys dicksoni Wendyichthys lautreci + Beagiascus Lineagruan judithi Lineagruan snowyi + (Coccocephalus + Spinofacia)*

B=2

2(1), 3(2), 4(4), 7(2), 9(2) dealing with the absence of premaxillary bones
17(1) maxilla preoperculum ornamentation is mainly vertical ridges of ganoine
123(3) sigmoidal subopercular upper suture
130(1) extralateral gular present
131(1) extralateral gular begins at anterior most tip of median gular
148(1) supratemporal commissure not across midline
175(1) number of body scales to dorsal ridge scales is one to one

Cyranorhis bergeraci

12(1) anterior end of maxilla is orbital
17(2) max pop ornamentation is mainly tuberculations
34(1) dentary and maxillary teeth not in two series
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
86(1) lachrymal rhombic in shape
123(1) diagonal subopercular upper suture
124(0) horizontal subopercular lower suture
133(1) posterior and anterior margins of lateral gular angled
134(0) lateral gular similar in size to branchiostegal rays
162(1) dorsal end of cleithrum broad and round

Wendyichthys dicksoni

5(2) premaxilla nasal process absent because premaxilla absent
17(3) max pop ornamentation is ridges and tubercles of ganoine
34(1) dentary and maxillary teeth not in two series
43(1) median rostral that anterior and posterior margins with equal widths
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
135(0) short parasphenoid
143(0) supraorbital canal trajectory into postparietal
159(0) presupracleithrum absent
160(0) postcleithrum present
167(1) clavicle contact short
205(1) enlarged postcleithral scales present

Wendyichthys lautreci

5(2) premaxilla nasal process absent because premaxilla absent
16(0) marginal teeth orientation is vertical
21(1) slightly developed process posteroventral process of the maxilla
75(1) dermosphenotic number is one bone
159(0) presupracleithrum absent
160(0) postcleithrum present
174(1) many predorsal scutes/dorsal ridge scales
186(1) anal fin ends close to caudal fin
206(1) flank scales deep

Node 33 *Beagiascus Lineagruan*
B=62

2(0) premaxilla present
3(1) premaxilla separate and distinct bone
4(3) premaxilla not part of complex bone
6(0) premaxillae abutting medially
7(0) premaxilla not part of orbit
8(0) posterior margin of premaxilla contacts lachrymal bone
9(0) premaxilla not in contact with nasal bone
10(1) premaxillary teeth absent in midline
65(1) extrascapular rows two separate rows
73(1) dermosphenotic relative size-almost equal length of dermopterotic/supratemporotabular and dermosphenotic
78(0) dermopterotic/supratemporotabular not in contact with operculum
105(1) supraopercular bone present
114(2) antopercular bones extend to bottom of operculum
115(3) antopercular bone width tapers ventrally
116(2) antopercular bones extremely thin
122(0) operculum not in contact with lateral extrascapulars
131(2) extralateral gular begins at midpoint of median gular
205(1) enlarged postcleithral scales present

Beagiascus pulcherrimus

8(1) premaxilla contacts ventrally lachrymal bones
13(2) height of posterior part of maxilla is high
16(2) marginal teeth orientation is posteriad
17(0) maxilla pop ornamentation is circumferential ridges
78(2)dermopterotic/supratemporotabular ventroposteriorly in contact with operculum
93(3) suborbital number is more than six
115(2) antopercular bones widen ventrally
116(1) antopercular bones as thick as adjacent bones
123(0) horizontal subopercular upper suture
124(0) horizontal subopercular lower suture

Lineagruan judithi

16(0) marginal teeth orientation is vertical
19(2) posterior plate of maxilla is high and rounded
72(2) dermosphenotic not in contact with nasal
98(3) sclerotic plate number is three
107(1) preoperculum anterodorsal region is subvertical or vertical
108(1) preopercular angle is narrower than 90°
128(1) fewer than 12 branchiostegal rays per side
166(0) clavicle length is short

Lineagruan snowyi

14(0) ventral margin of maxilla is straight
93(2) suborbital number is four to six
114(3) antopercular bones extend to bottom of suboperculum
173(0) basal fulcra anterior to dorsal fin absent
174(3) predorsal scutes/dorsal ridge scales absent
175(0) body scales to dorsal ridge scales- not applicable because ridge scales absent
176(3) dorsal ridge scales absent

Node 34 *Coccocephalus + Spinofacia*

B=16

36(1) ganoine ornamentation on skull roof bones-moderate
dermosphenotoic present as one bone
77(1)dermopterotic/supratemporotabular not in contact with parietal

Coccocephalus

13(0) height of posterior part of maxilla is low
16(2) marginal teeth orientation is posteriad
71(3) dermosphenotic elongate in shape
143(0) supraorbital canal into Postparietal

Spinofacia

14(0) ventral margin of maxilla is straight

Node 35 *Mansfieldiscus + (Elonichthys + Pteroniscul**us)***

114(5) antopercular bones located on the ventral half of the operculum
115(2) antopercular bones widen ventrally
116(1) antopercular bones as thick as adjacent bones

Mansfieldiscus sweeti

14(0) ventral margin of maxilla is straight
16(1) marginal teeth oriented forward
21(1) slightly developed posteroventral process of maxilla
40(2) median and complex rostral bones
41(1) 2 rostral bones, dorsal and ventral, ventral part of complex bone
60(2) postparietal short and rectangular
77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal bone
78(2)dermopterotic/supratemporotabular ventroposteriorly in contact with operculum
89(1) jugal/infraorbital 3 contacts suborbital posterodorsally

Node 36 *Elonichthys + Pteroniscul**us***

79(1) ventral protuberance of dermopterotic/supratemporotabular absent
113(0) gap between operculum and skull roof bones present
122(0) operculum not in contact with lateral extrascapulars

'Elonichthys' palatinus

51(0) rear of nasal bones preorbital
60(0) postparietal long and rectangular
72(2) dermosphenotic not in contact with nasal bone
74(3) dermosphenotic not in contact with dermohyal because dermohyal absent
77(0) dermopterotic/supratemporotabular not in contact with parietal bone
86(2) lachrymal is inverted L in shape
91(1) 2 infraorbital bones ventral to orbit
104(0) dermohyal absent
123(2) concave subopercular upper suture

127(1) first branchiostegal ray deeper than second branchiostegal ray
160(1) postcleithrum absent

Pteronisculus stensioei

34(1) dentary and maxillary teeth not in two series
43(1) median rostral bone with equal lengths anteriorly and posteriorly
71(2) dermosphenotic rectangular
75(2) dermosphenotic present as two bones-dorsal and ventral dermosphenotics
103(0) postspiracular present
114(1) antopercular bones do not extend down to bottom of operculum
115(3) anteoperculuar bones taper in width ventrally
146(0) otic canal into three bones
148(1) supratemporal commissure not across midline
151(1) horizontal pit line present
153(1) preopercular canal to postorbital corner
157(0) pectoral fin is lobe based

Node 37 *Beishanichthys* through deep bodied

13(2) height of posterior part of maxilla is high
128(1) fewer than 12 branchiostegal rays per side-

Node 38 *Beishanichthys* through *Rhadinichthys*

4(0) complex premaxilla present as ventral-rostro-premaxillo-lachrymal
40(2) rostral condition of median and complex rostral bones
41(1) rostral condition-2 bones, dorsal and ventral, ventral part of complex bone
43(0) median rostral bone widens anteriorly
184(0) pelvic fin with long base

Node 39 *Beishanichthys* through *Kalops*

58(0) parietal contacts supraorbital
68(1) supraorbital bones present without canal
69(0) supraorbitals single series
72(2) dermosphenotic contact not in contact with nasal

Node 40 *Beishanichthys* + *Palaeoniscum*

B=2

51(0) rear of nasal bones preorbital
73(3) dermopterotic/supratemporotabular more than two times larger than dermosphenotic

Palaeoniscum freieslebeni

12(1) max anterior end-orbital
13(1) maxilla, height of posterior part-medium
74(3) dermosphenotic not in contact with dermohyal because no dermohyal
75(2) dermosphenotic two bones, a dorsal and ventral dermosphenotic
93(2) suborbital number is four to six
104(0) dermohyal-absent
121(2) operculum about same height as suboperculum
122(0) operculum not in contact with lateral extrascapulars
123(3) sigmoidal subopercular upper suture
146(0) otic canal into three bones

Beishanichthys brevicaudalis

14(0) ventral margin of maxilla is straight
15(1) maxillary teeth only on anterior part of bone
21(0) maxilla posteroventral process absent
60(2) postparietal shape short and rectangular

77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal bone
107(1) preoperculum anterodorsal region is subvertical or vertical
108(1) preopercular angle is narrower than 90°
143(1) supraorbital canal into parietal
170(0) basal fulcra between dorsal and caudal fins absent
171(0) fringing fulcra absent
174(1) many predorsal scutes/dorsal ridge scales
178(1) rear of dorsal fin close to caudal
180(4) dorsal fin shape is long and low
184(1) pelvic fin with short base
186(1) anal fin ends close to caudal fin
190(4) abbreviated heterocercal caudal fin shape
192(4) caudal outline is not cleft
200(1) posterior edges of rhombic scales are straight

Node 41 (New Brunswick + (*Gonatodus* + *Kalops*)

4(2) complex premaxilla present as ventral rostro-premaxilla
8(0) posterior margin of premaxilla contacts lachrymal bone

New Brunswick fish

10(1) premaxillary teeth absent in midline
69(2) supraorbital is a single bone
94(3) suborbitals arranged in many rows
114(2) antopercular bones extend to bottom of operculum
115(2) antopercular width-widens ventrally
116(1) antopercular thickness-same as adjacent bones
174(1) many predorsal scutes/dorsal ridge scales
201(1) ventral edges of scales are serrated

Node 42 *Gonatodus* +*Kalops*
B=1

9(0) premaxilla not in contact with nasal bone
60(2) postparietal short and rectangular
127(1) first branchiostegal ray is deeper than second branchiostegal ray
157(0) pectoral fin is lobe based

Gonatodus punctatus

34(1) dentary and maxillary teeth are not in two series
37(0) preparietal relative length is short
78(0) dermopterotic/supratemporotabular not in contact with operculum
104(2) dermohyal in single series
107(1) preoperculum anterodorsal region is subvertical or vertical
123(0) horizontal subopercular upper suture
160(1) postcleithrum absent
186(1) anal fin ends close to caudal fin
192(0) caudal outline is cleft equilobate

Node 43 *Kalops monophrys* + *Kalops diophrys*
B=86

3(1) premaxilla separate and distinct bone
4(3) premaxilla not part of complex bone
40(3) 2 median rostral bones
41(2) 2 rostral bones, dorsal and ventral, both separate and distinct
51(0) rear of nasal bones preorbital
79(1) ventral protuberance off of dermopterotic/supratemporotabular absent
94(2) suborbitals arranged in two rows
98(3) sclerotic plate number is three
113(0) gap between operculum and skull roof bones present
121(0) opercular three times deeper than suboperculum or more
140(1) ethmoid commissure through median ventral rostral

143(1) supraorbital canal into parietal bone
148(1) supratemporal commissure not across midline
184(1) pelvic fin with short base

Kalops diophrys

65(2) extrascapular rows two rows and shared median bone
69(1) supraorbital bones in a double series
73(1) dermosphenotic almost equal in size to dermopterotic/supratemporotabular
103(0) postspiracular present
134(0) lateral gular similar in size to branchiostegal ray
205(1) enlarged postcleithral scales present

Kalops monophrys

95(0) suborbital fit absent
174(2) predorsal scutes/dorsal ridge scales are complete to occiput

Node 44 *Rhadinichthys Cycloptychius Novogonatodus*

B=4

12(1) anterior end of maxilla is orbital
123(2) concave subopercular upper suture

Cycloptychius concentricus

73(1) almost equal length of dermopterotic/supratemporotabular and dermosphenotic
121(2) operculum about the same height as suboperculum
124(4) convex supobercular lower suture
179(0) dorsal fin originates behind anal fin
180(1) dorsal fin shape is sigmoidal

Novogonatodus kasantsevae

19(2) posterior plate of maxilla is high and rounded
107(1) preoperculum anterodorsal region is subvertical or vertical
124(0) horizontal subopercular lower suture
160(1) postcleithrum absent
162(1) dorsal end of cleithrum broad and round
169(2) round body form

Rhadinichthys canobiensis

13(1) height of posterior part of maxilla is medium
59(1) postparietal with pointed anterolateral process
179(1) dorsal fin originates at same level as anal fin

Node 45 Ambylpteridae through deep bodied

15(1) maxillary teeth only on anterior part of bone
34(1) dentary and maxillary teeth not in two series
95(2) suborbital fit is loose with gaps
108(1) preopercular angle narrower than 90°

Node 46 Ambylpteridae

B=11

21(1) slightly developed posteroventral process of maxilla
75(2) two dermosphenotic bones a dorsal and ventral bone
113(0) gap between operculum and skull roof bones present

Amblypterus latus

36(1) moderate ganoine ornamentation on skull roof bones
95(0) suborbital fit absent
122(0) operculum not in contact with lateral extrascapulars

123(2) concave subopercular upper suture
160(1) postcleithrum absent
200(1) posterior edges of rhombic scales are straight

Paramblypterus decorus

14(0) ventral margin of maxilla is straight
48(1) nasal number is two bones on each side
65(1) extrascapular rows are two separate rows
69(2) supraorbital is single bone
73(1) length of dermosphenotic almost equal to dermopterotic/supratemporotabular
77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal bone
93(3) suborbital number is more than six
94(3) suborbital bones arranged in many rows
104(2) dermohyal is one series
184(0) pelvic fin with long base
205(1) enlarged postcleithral scales present

Node 47 *Canobius elegantulus* + (Aeduellidae + Haplolepidae) + deep bodied

19(2) posterior plate of maxilla is high and rounded
107(1) preoperculum anterodorsal region is subvertical or vertical
110(1) preoperculum contacts posterior margin of maxilla

Canobius elegantulus

13(1) height of posterior part of maxilla is medium
58(1) parietal not in contact with supraorbital
74(3) dermosphenotic not in contact with dermohyal because dermohyal absent
104(0) dermohyal absent
119(1) both axes of operculum are approximately equal
179(1) dorsal fin originates at same level as anal fin

Node 48 (Aeduellidae + Haplolepidae) + deep bodied

21(0) maxilla posteroventral process absent
71(3) dermosphenotic is elongate
73(4) dermosphenotic longer than dermopterotic/supratemporotabular

Node 49 Aeduellidae + Haplolepidae
B=7

36(1) moderate ganoine ornamentation on skull roof bones
51(0) rear of nasal bones preorbital
60(2) Postparietal short and rectangular
97(1), 98(1) dealing with absence of sclerotic ring
126(1) branchiostegals rays not below mandible
143(1) supraorbital canal into parietal

Node 50 Aeduellidae
B=7

110(0) preoperculum contacts dorsal and posterior margins of the maxilla
157(0) pectoral fin is lobe based
160(1) postcleithrum absent

Bourbonnella jocelynae

14(0) ventral margin of maxilla straight
71(1) dermosphenotic T-shaped
73(1) dermosphenotic almost equal in size to dermopterotic/supratemporotabular
77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal bone
171(0) fringing fulcra absent
207(1) ventrolateral flanks scales narrow

Node 51 *Aeduella blainvilli* + *Bourbonnella guilloti*
B=67

60(0) Postparietal long and rectangular
104(0) dermohyal absent
121(2) operculum about the same height as suboperculum

Aeduella blainvillei

112(1) preoperculum widest midbone
122(0) operculum not in contact with lateral extrascapulars
123(3) sigmoidal subopercular upper suture
143(3) supraorbital canal into dermopterotic/supratemporotabular

Bourbonnella guilloti

124(0) horizontal subopercular lower suture

Node 52 Haplolepidae
B=85

55(1) pineal opening in parietal area
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
95(1) suborbital fit is sutured
96(1) maxilla not in contact with suborbitals
106(0) preoperculum without distinct regions
108(2) preopercular angle-n/a, preoperculum without distinct regions
112(1) preoperculum widest midbone
164(1) dorsal arm of cleithrum is stout and wide
182(1) number of dorsal fin rays is 10 or less
206(1) flank scales deep

Haplolepis corrugata

13(0) height of posterior part of maxilla is low
19(0) posterior plate of maxilla not differentiated
111(2) preoperculum anteriorly in contact with infraorbitals, extensively
121(1) operculum two times deeper than suboperculum
162(1) dorsal end of cleithrum is broad and round

Node 53 *Microhaplolepis* + *Parahaplolepis*
B=70

14(0) ventral margin of maxilla straight
63(2), 76(2), 80(1) dealing with fusion of postparietal bone and dermopterotic/supratemporotabular
104(0) dermohyal absent
179(1) dorsal fin originates at same level as anal
186(1) anal fin ends close to caudal fin
192(4) caudal outline not cleft
207(1) ventrolateral flank scales narrow

Microhaplolepis ovoidea

19(3) posterior plate of maxilla is high and triangular
113(0) gap between operculum and skull roof bones-present

Parahaplolepis tuberculata

38(1) snout shape is a sharp bump
100(0) quadratojugal present
101(1) large quadratojugal
110(0) preoperculum contacts dorsal and posterior margins of the maxilla
119(1) both axes of operculum approximately equal
122(0) operculum not in contact with lateral extrascapulars

Node 54 "Deep Bodied" *Paramesolepis* *Cheirodopsis* + Platysomids + Amphicentrids *Ebenaqua*
B=14

19(3) posterior plate of maxilla high and triangular

92(0), 93(0), 94(0), 95(0), 96(0) dealing with absence of suborbital bones
111(2) preoperculum anteriorly in contact with infraorbitals, extensively
123(2) concave subopercular upper suture
169(1) deep body form
178(1) rear of dorsal fin close to caudal fin
186(1) anal fin ends close to caudal fin

Paramesolepis tuberculata

4(0) complex premaxilla present as a ventral-rostro-premaxillo-lachrymal
8(0) premaxilla contacts posteriorly lachrymal bone
40(2) rostral present as median and complex bone
41(1) rostral condition is 2 bones, a dorsal and ventral bone, ventral part of complex bone
75(2) two bones dermosphenotic, adorsal and ventral bone
106(0) preoperculum without distinct regions
108(2) preopercular angle-n/a, no distinct regions
112(2) preoperculum width is even
119(1) both axes of operculum approximately equal
146(0) otic canal into 3 bones

Node 55 *Cheirodopsis* + Platysomids + Amphicentrids *Ebenaqua*

B=4

14(0) maxilla ventral margin straight
73(1) dermosphenotic almost equal to dermopterotic/supratemporotabular
175(0) body scales to dorsal ridge scales n/a because dorsal ridge scales absent
176(3) dorsal ridge scales absent

Cheirodopsis geikiei

206(1) flank scales deep

Node 56 Platysomids + Amphicentrids *Ebenaqua*

B=5

60(2) Postparietal short and rectangular
66(2) extrascapular number is four
71(2) dermosphenotic rectangular in shape
104(0) dermohyal absent

Platysomus superbus

15(3) maxillary teeth not on oral rim of maxilla
16(3) marginal teeth absent
22(3) maxillary teeth absent
34(2) dentary and maxillary teeth absent on oral rim
78(0) dermopterotic/supratemporotabular contact of-not in contact with operculum
85(1) lachrymal is a separate and distinct bone
178(0) rear of dorsal fin far from caudal fin
186(0) anal fin ends far from caudal fin
205(1) enlarged postcleithral scales present

Node 57 *Platysomus striatus* to *Platysomus swaffordae*

B=3

51(0) rear of nasal bones preorbital
74(3) dermosphenotic contact-not in contact with dermohyal because dermohyal absent
79(1) ventral protuberance of dermopterotic/supratemporotabularabsent
192(0) caudal outline is cleft equilobate

Platysomus striatus

19(2) posterior plate of maxilla is high and rounded
73(2) dermopterotic/supratemporotabular longer than dermosphenotic
112(3) preoperculum cinched in middle

123(0) horizontal subopercular upper suture
124(0) horizontal subopercular lower suture

Node 58 *Platysomus parvulus* to *swaffordae*

B=3

14(1) ventral margin of maxilla is curved
160(1) postcleithrum absent
169(3) angulate body form
176(2) dorsal ridge scales are peg like

Platysomus parvulus

20(1) maxilla posterior end-orbital
174(1) predorsal scutes/dorsal ridge scales-many
178(0) dorsal fin length-rear far from caudal fin
186(0) anal fin base-anal ends far from caudal fin

Node 59 *Amphicentrum jurgeni* to *Platysomus swaffordae*

B=14

106(0) preoperculum without distinct regions
179(1) dorsal fin originates at same level as anal
183(1), 184(3) dealing with absence of pelvic fin

Amphicentrum jurgenai

73(2) dermopterotic/supratemporotabular longer than dermosphenotic

Node 60 *Amphicentrum granulosum* to *Platysomus swaffordae*

B=7

3(1) premaxilla separate and distinct
4(3) complex premaxilla not part of complex bone
8(0) premaxilla relation of contact posteriorly lachrymal bone
85(1) lachrymal separate and distinct bone

Amphicentrum granulosum

21(1) slightly developed posteroventral process of maxilla
51(1) rear of nasal bones midorbital
62(2), 65(3), **149(2), dealing with absence of extrascapular bones**
152(1) vertical preopercular pit line absent
176(3) dorsal ridge scales absent
189(0) caudal fin without hinge line

Node 61 *Ebenaqua Platysomus gibbosus Platysomus schultzei Platysomus swaffordae*

B=44

19(2) posterior plate of maxilla is high and rounded
20(1/2) maxilla posterior end has slightly developed process/strong process
107(2) preoperculum anterodorsal region-not applicable, no differentiated regions
110(2) preoperculum not in contact with maxilla
113(0) gap between operculum and skull roof-bones present
124(4) convex subopercular lower suture
126(2), 127(2) dealing with absence of branchiostegal rays
171(0) fringing fulcra absent
174(2) predorsal scutes/dorsal ridge scales are complete to occiput
175(2) number of body scales to dorsal ridge scales is more than 1 body scale row to dorsal ridge scale

Node 62 *Ebenaqua + Platysomus gibbosus*

B=18

72(2) dermosphenotic not in contact with nasals

78(0) dermopterotic/supratemporotabular not in contact with operculum
103(0) postspiracular present
183(0) Pelvic fin present

Ebenaqua ritchiei

13(1) height of posterior part of maxilla is medium
17(1) maxilla pop ornamentation is mainly vertical ridges
19(0) posterior plate of maxilla not differentiated
79(0) ventral protuberance of dermopterotic/supratemporotabular present
125(2) branchiostegal plate present
157(0) pectoral fin is lobe based

Platysomus gibbosus

89(0) jugal/infraorbital 3 contacts suborbital posteriorly
92(1) suborbital bones present
93(1) 1 to 3 suborbital bones
94(1) suborbital bone(s) arranged in one row
95(1) suborbital fit is sutured
96(1) maxilla not in contact with suborbital(s)
111(1) preoperculum anteriorly in contact with suborbital bone(s)
169(1) deep body form

Node 63 *Platysomus schultzei* + *Platysomus swaffordae*

B=27

60(0) Postparietal long and rectangular
111(5) preoperculum anteriorly contacts platysomid quadratojugal/suborbital
169(2) round body form

Platysomus schultzei

13(1) height of posterior part of maxilla is medium
17(1) maxilla pop ornamentation is mainly vertical ridges
51(1) rear of nasal bones midorbital
62(1) postparietal not in contact with lateral extrascapulars
65(3) extrascapular rows absent
125(1) branchiostegal rays absent
200(0) posterior edges of rhombic scales are serrated

Platysomus swaffordae

160(0) postcleithrum-present
174(1) many predorsal scutes/dorsal ridges scales present
207(3) ventrolateral flank scales shorter

Appendix 4—Character supporting the nodes of the Bayesian tree with all taxa included (Figure 11). Characters resulted from tracing all characters across the tree in Mesquite using ancenstral state reconstruction and parsimony reconstruction methods.

Actinopterygii
P=81

21(0) posteroventral process of maxilla absent
26(1) splenial absent
28(0) prearticular anterior end is far from symphysis
33(1) acrodin caps on teeth present
34(1) dentary and maxillary teeth not organized in two series
155(0) mandibular canal through dentary
156(1) mandibular canal not through posterior infradentary
202(1) ganoine present

Polypterus bichir
17(4) maxilla preopercular ornamentation absent on these bones
23(1) maxilla is a complex bone with infraorbitals
36(2) ganoine ornamentation on skull roof is little or absent
58(2) parietal not in contact with suprarobital because supraorbitals absent
101(0) small quadratojugal
110(1) preoperculum contacts posterior margin of maxilla
122(0) operculum not in contact with lateral extrascapulars
169(4) blade-like body form
174(0) few predorsal scutes/ridge scales
175(1) number of body scales to dorsal ridge scales is one to one
176(0) dorsal ridge scales without a spine or spike
177(2) dorsal fin base with guard scales
178(2) dorsal fin merged with caudal
182(2) dorsal fin rays are in dorsal finlets
186(1) anal fin ends close to caudal fin
187(1) scutes and basal fulcra between anal and caudal fins present

Actinopteri
P=57
48(2) single nasal bone on each side of head
125(0) brachiostegal rays present
126(01) branchiostegal rays-between mandibles or not between mandibles
127(0) first branchiostegal ray as deep as second
128(1) fewer than 12 branchiostegal rays per side
134(2) lateral gular size, lateral gular absent
157(1) pectoral fin not lobed

Chondrostei
P=100
2(1), 3(2), 4(4), 5(2), 6(2), 7(2), 8(4), 9(2),10(2) dealing with absence of premaxillary bones
11(1), 12(4), 13(3), 14(2), 15(4), 16(3), 18(2), 19(4), 20(3), 21(3), **23(2)** dealing with the absence of a maxilla
34(2) dentary and maxillary teeth absent on oral rim
136(1) buccohypophysial foramen absent
192(0) caudal outline is cleft equilobate
206(2) flank scales absent
207(4) ventrolateral flank scales absent
209(1) rhombic scale limited to caudal region

Chondrosteus acipenseroides
60(2) postparietal short and rectangular
88(1) postorbital notch in jugal/infraorbital 3 present

89(4) Jugal/infraorbital 3 contacts suborbital ventrally
166(0) clavicle length is short

Acipenseriformes

P=100

68(1) supraorbital bones present without canal
118(1) operculum absent
196(4) shape of scales are round based and rhombic

Acipenser brevirostrum

101(0) small quadratojugal size
138(0) parasphenoid not sutured to vomer
168(0) interclavicle present
171(1) fringing fulcra present
174(2) predorsal scutes/dorsal ridge scales are complete to occiput
176(0) dorsal ridge scales without a spine or spike
185(1) scutes and/or basal fulcra between pelvic and anal fins present
192(1) caudal outline is strongly inequilobate

Polydon spathula

28(1) anterior end of prearticular near symphysis
47(1), 49(2), 50(3) dealing with absence of nasal bones
55(1) pineal opening in parietal area
100(1) quadratojugal absent
137(1) posterior ascending process absent
148(1) supratemporal commissure not across midline
167(1) clavicle contact short
201(2) ventral edges of scales not applicable, rhombic ganoid scales absent
208(1) stellate bones in snout are present

Holostei

P=75

3(1) premaxilla is separate and distinct
24(1) supramaxilla present
85(1) lachrymal is a separate and distinct bone
91(2) more than 2 infraorbital bones ventral to orbit
110(2) preoperculum not in contact with maxilla
158(1) anteriormost pectoral lepidotrichia segmented only distally
184(2) Pelvic fin with reduced base
190(4) caudal fin shape is abbreviated heterocercal

Amiiformes

P=93

37(0) preparietal relative length is short
60(1) postparietal is squared
100(1) quadratojugal absent
117(1) interoperculum present
129(0) median gular present
180(4) dorsal fin long and low
196(2) scale shape is rounded
200(2) posterior edges of rhombic scales is not applicable, no ganoid scales
201(2) ventral edges of scales is not applicable, no ganoid scales
202(0) ganoine absent
209(2) rhombic scale limits, none, rhombic scales absent

Amia calva

9(0) premaxilla not in contact with nasal
15(2) maxillary teeth only on maxillary body, not the anterior articulary region
27(1) surangular present
31(1) coronoid process present
58(2) parietal not in contact with suprarorbitals because no supraorbitals present
113(0) gap between operculum and skull roof bones present
122(0) operculum not in contact with lateral extrascapulars
146(2) otic canal into one bone
178(1) rear of dorsal fin close to caudal
193(0) epichordal fin rays of caudal fin present

194(0) epichordal fin rays of caudal fin short

Solnhofenamia elongata

13(1) height of posterior part of maxilla is medium
19(3) posterior plate of maxilla is high and triangular
22(1) maxillary teeth are pleurodont
50(3) notched nasals absent
86(5) lachrymal is rectangular
91(1) 2 infraorbital bones ventral to orbit
96(1) maxilla not in contact with suborbitals
98(2) two sclerotic plates
128(0) 12 or more branchiostegal rays per side
136(1) buccohypophysial foramen absent
162(1) dorsal end of cleithrum broad and round

Node 8 Lepisosteiformes

P=93

20(2) posterior end of maxilla is preorbital
30(1) dentition on coronoids is narrow marginal tooth rows
38(2) elongated snout
77(0) dermopterotic/supratemporotabular not in contact with parietal bone
137(1) posterior ascending process absent
182(1) number of dorsal fin rays is 10 or less
205(1) enlarged postcleithral scales present

Lepisosteus osseus

27(1) surangular present
31(1) coronoid process present
74(2) dermosphenotic not in contact with dermohyal
121(0) operculum three times deeper than suboperculum or more
122(0) operculumnot in contact with lateral extrascapulars
127(1) first branchiostegal ray deeper than second
160(1) postcleithrum absent
165(1), 166(2) dealing with the absence of the clavicle
178(1) rear of dorsal fin close to caudal
180(5) dorsal fin shape is short rounded

Obaichthys decoratus

15(1) maxillary teeth only on anterior part of maxilla
96(1) maxilla not in contact with suborbitals
113(0) gap between operculum and skull roof bones present
119(0) opercular shape-first axis longer than second
136(1) buccohypophysial foramen absent
162(1) dorsal end of cleithrum broad and round
171(1) fringing fulcra present
198(0) peg and socket articulation broad

Palaeonisci

P=72

13(2) height of posterior part of maxilla is high
14(1) ventral margin of maxilla is curved
17(0) maxilla preopercular ornamentation is circumferential ridges of ganoine
19(1) posterior plate of maxilla is a moderate rectangular plate
36(0) dense ganoine ornamentation on skull roof
43(2) median rostral narrows anteriorly
49(1) nasal bones with notches
50(0) nasals notched on medial and/or lateral borders
58(2) parietal contact not in contact with supraorbitals because supraorbital absent
60(1) postparietal squared
72(1) dermosphenotic contacts nasal
74(2) dermosphenotic not in contact with dermohyal
86(5) lachrymal rectangular
89(0) jugal/infraorbital 3 contacts suborbital bones posteriorly
95(1) suborbital fit is sutured
96(2) maxilla contacts suborbital
98(1) sclerotic plate number is four
100(1) quadratojugal absent

104(1) dermohyal present as single bone
108(0) preopercular angle is wider than 90°
119(0) first axis of operculum longer than second
124(1) diagonal subopercular lower suture
129(0) median gular present
134(1) lateral gular larger than branchiostegal rays
142(1) supraorbital canal between medial and lateral nasal openings
171(1) fringing fulcra present
173(1) basal fulcra or scutes anterior to dorsal fin present
174(0) few predorsal scutes/ridge scales
175(2) body scales to dorsal ridge scales arranged with more than 1 body scale row to dorsal ridge scale
176(0) dorsal ridge scales without a spine or spike
185(1) scutes or basal fulcra between pelvic and anal present
187(1) scutes and basal fulcra between anal and caudal fins present
189(1) caudal fin with hinge line
192(1) caudal outline is strongly inequilobate
200(0) posterior edges of rhombic scales are serrated

Aeduellidae + Haplolepidae
P=99

19(2) posterior plate of maxilla is high and rounded
36(1) moderate ganoine ornamentation on skull roof bones
37(0) preparietal relative length is short
51(0) rear of nasal bones preorbital
60(2) postparietal shape is short and rectangular
66(1) extrascapular number is two
71(3) dermosphenotic shape is elongate
77(0)dermopterotic/supratemporotabular not in contact with parietal bone
89(1) jugal/infraorbital 3 contacts suborbital bone(s) posterodorsally
97(1), 98(4) dealing with absence of sclerotic ring
126(1) branchiostegal rays not between the mandibles
143(1) supraorbital canal into parietal

Aeduellidae
P=85

157(0) pectoral fin is lobe based
160(1) postcleithrum absent
200(1) posterior edges of rhombic scales are straight

Bourbonnella jocelynae

14(0) ventral margin of maxilla is straight
71(1) dermosphenotic T-shaped
77(1) anterior 1/3 of dermopterotic bone in contact with parietal
171(0) fringing fulcra absent
207(1) ventrolateral flanks scales are narrow

Aeduella blainvillei + Bourbonnella guilloti
P=98

60(0) postparietal shape is long and rectangular
104(0) dermohyal absent

Aeduella blainvillei

112(1) preoperculum widest midbone
122(0) operculum not in contact with lateral extrascapulars
123(3) sigmoidal subopercular upper suture
143(3) supraorbital canal into dermopterotic

Bourbonnella guilloti

124(0) horizontal subopercular lower suture

Haplolepidae
P=100

55(1) pineal opening in parietal area
79(1) ventral protuberance of dermopterotic absent
96(1) maxilla not in contact with suborbital
106(0) preoperculum without distinct regions

112(1) preoperculum widest midbone

164(1) dorsal arm of cleithrum is stout and wide

182(1) number of dorsal fin rays is 10 or less

206(1) flank scales deep

Haplolepis corrugata

13(0) height of posterior part of maxilla is low

19(0) posterior plate of maxilla not differentiated

111(2) preoperculum anteriorly in contact with infraorbitals, extensively

162(1) dorsal end of cleithrum broad and round

Microhaplolepis + Parahaplolepis

P=100

14(0) ventral margin of maxilla is straight

63(2), 76(2), 80(1) dealing with fusion of postparietal to dermopterotic/supratemporotabular

104(0) dermohyal absent

179(1) dorsal fin originates at same level as anal

186(1) anal fin ends close to caudal

192(4) caudal fin is not cleft

207(1) ventrolateral flank scales narrow

Microhaplolepis ovoidea

19(3) high triangular posterior plateof maxilla

113(0) gap between operculum and skull roof bones present

Parahaplolepis tuberculata

38(1) snout shape is sharp bump

100(0) quadratojugal present

101(1) large quadratojugal

119(1) both axes of operculum approximately equal in size

122(0) operculum not in contact with lateral extrascapulars

200(1) posterior edges of rhombic scales are straight

Aesopichthyidae

P=99

19(2) posterior plate of maxilla is high and rounded

21(2) maxilla with strong posteroventral process

60(2) parietal/postparietal shape-short and rectangular

71(1) dermosphenotic T-shaped

75(2) two bones dermosphenotic, dorsal and ventral bone

157(0) pectoral fin is lobe based

159(1) presupracleithrum present

160(1) postcleithrum absent

169(1) deep body form

178(1) rear of dorsal fin close to caudal

180(1) dorsal fin shape is sigmoidal

185(0) scutes or basal fulcra between P2 and anal absent

186(1) anal fin ends close to caudal fin

Aesopichthys erinaceus

17(3) maxilla preoperculum ornamentation is ridges and tubercles of ganoine

45(1) rostral notch present

58(1) parietal not in contact with supraorbital

73(2)dermopterotic/supratemporotabular longer than dermosphenotic

83(2) cheek fit is thick peripheral gaps

89(2) jugal/infraorbital 3 not in contact with suborbital

91(3) infraorbital bones ventral to orbit is only infraorbital 3/posteroventral infraorbital

95(2) suborbital fit is loose with gaps

110(1) preoperculum contacts posterior margin of maxilla

119(1) both axes of operculum approximately equal

124(2) concave subopercular lower suture

127(1) first branchiostegal ray deeper than second

177(1) dorsal fin base is a scaled lobe
179(1) dorsal fin originates at same level as anal
183(1) pelvic fin absent
198(0) peg and socket articulation broad
207(1) ventrolateral flank scales narrow

Proceramala montanensis

16(1) marginal teeth orientation is forward
65(1) two separate extrascapular rows
93(3) suborbital number is more than six
94(2) suborbital bones arranged in two rows
123(2) concave subopercular upper suture
126(1) branchiostegal rays not below mandible
128(0) 12 or more branchiostegal rays per side
153(1) preopercular canal to postorbital corner
205(1) enlarged postcleithral scales present
206(1) flank scales deep

***Paramblypterus* + (*Amblypterus* + *Guntherichthys*)**

P=53

7(1) premaxilla part of orbit
21(1) slightly developed posteroventral process of maxilla
37(0) preparietal relative length short
75(2) two bones dermosphenotic, dorsal and ventral bone
100(0) quadratojugal present
101(0) small quadratojugal
113(0) gap between operculum and skull roof bones-present

Paramblypterus decorus

14(0) ventral margin of maxilla is straight
48(1) nasal number is two bones on each side
65(1) two separate extrascapular rows
69(2) supraorbital present as single bone
77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal bone
93(3) suborbital number is more than six
94(3) suborbital bones arranged in many rows
104(2) dermohyal in a series
184(0) pelvic fin with long base
205(1) enlarged postcleithral scales present

Amblypterus latus* + *Guntherichthys

P=58

36(1) moderate ganoine ornamentation on skull roof bones
123(2) concave subopercular upper suture
160(1) postcleithrum absent
200(1) posterior edges of rhombic scales are straight

Amblypterus latus

162(1) dorsal end of cleithrum broad and round

Guntherichthys lehiensis

13(1) medium height of posterior part of maxilla
21(2) maxilla with strong posteroventral process
124(4) convex subopercular lower suture
159(1) presupracleithrum present
171(0) fringing fulcra absent
196 (3) scale shape round and rhombic

"Deep bodied" clade *Platysomus parvulus* through *P. swaffordae*,

P=63

19(2) posterior plate of maxilla is high and rounded
51(0) rear of nasal bones preorbital
60(2) postparietal shape is short and rectangular
74(3) dermosphenotic not in contact with dermohyal because dermohyal absent
89(3), 92(0), 93(0), 94(0), 95(0), 96(0) dealing with the absence of suborbital bones
104(0) dermohyal absent
110(1) preoperculum contacts posterior margin of maxilla

111(2) preoperculum anterior contact-infraorbitals, extensive
123(2) subopercular upper suture-concave
160(1) postcleithrum absent
169(3) angulate body form
176(2) dorsal ridge scales are peg like
192(0) cleft equilobate caudal outline

Platysomus parvulus

20(1) posterior end of maxilla is orbital
72(2) dermosphenotic not in contact with nasal bone

***Amphicentrum jurgenai* through (*Platysomus swaffordae*)**

P=71

106(0) preoperculum-without distinct regions
178(1) rear of dorsal fin close to caudal
179(1) dorsal fin originates at same level as anal fin
183(1), 184(3), dealing with absence of pelvic fin absent
186(1) anal fin base ends close to caudal

Amphicentrum jurgenai

4(1) complex premaxilla is a premaxillo-lachrymal
73(2)dermopterotic/supratemporotabular longer than dermosphenotic
86(3) lachrymal shape vertical pillar

Amphicentrum granulosum* through *Platysomus swaffordae

P=68

3(1) premaxilla separate and distinct
8(0) premaxilla contacts posteriorly lachrymal bone
85(1) lachrymal separate and distinct bone

Amphicentrum granulosum

21(1) slightly developed posteroventral process of maxilla
51(1) rear of nasal bones-midorbital
62(2), 65(3), **149(2) dealing with absence of extrascapular bones**
152(1) vertical preopercular pit line absent
77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal
86(4) triangular shaped lachrymal
175(0) number of body scales to dorsal ridge scales not applicable because dorsal ridge scales absent
176(3) dorsal ridge scales absent
189(0) caudal fin without hinge line

(Ebenaqua+Platysomus gibbosus) + (Platysomus schultzei Platysomus swaffordae)

P=72

19(2) high rounded maxilla posterior plate
20(1/2) maxilla posterior process is slightly developed or strong
107(2) preoperculum anterodorsal region-not applicable because not differentiated
110(2) preoperculum not in contact with maxilla
113(0) gap between operculum and skull roof-bones present
124(4) subopercular lower suture convex
126(2), 127(2) dealing with absence of branchiostegal rays
171(0) fringing fulcra absent

Ebenaqua + Platysomus gibbosus

P=73

72(2) dermosphenotic not in contact with nasals
78(0)dermopterotic/supratemporotabular not in contact with operculum
103(0) postspiracular present
183(0) pelvic fin present

Ebenaqua ritchiei

13(1) medium height of posterior part of maxilla
17(1) maxilla pop ornamentation is mainly vertical ridges
19(0) maxilla posterior plate not differentiated

77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal
79(0) ventral protuberance of dermopterotic/supratemporotabular present
125(2) branchiostegal plate present
157(0) pectoral fin is lobe based

Platysomus gibbosus

86(4) triangular shaped lachrymal
89(0) jugal/infraorbital 3 contacts suborbital posteriorly
92(1) suborbital bones present
93(1) suborbital number present as 1 to 3 bones
94(1) suborbitals arranged in one row
95(1) suborbital fit is sutured
96(1) maxilla not in contact with suborbitals
111(1) preoperculum anteriorly contacts suborbitals
169(1) deep body form

Platysomus schultzei + Platysomus swaffordae
P=78

60(0) Postparietal long rectangular
111(5) preoperculum anteriorly in contact with platysomid quadratojugal/suborbital
169(2) round body form

Platysomus schultzei

13(1) medium height of posterior part of maxilla
17(1) maxilla pop ornamentation of mainly vertical ridges
51(1) rear of nasal bones midorbital
62(1) postparietal not in contact with lateral extrascapulars
65(3) extrascapular rows absent
125(1) branchiostegal rays absent

Platysomus swaffordae

160(0) postcleithrum present
207(3) ventrolateral flank scales shorter

[*Beagiascus pulcherrimus* + [*Lineagruan judithi* + *Lineagruan snowyi*]] + [[*Coccocephalus* + *Spinofacia*] + [*Wendyichthys lautreci* + [*Cyranorhis* + *Wendyichthys dicksoni*]]
P=99

21(2) maxilla with strong posteroventral process
34(0) dentary and maxillary teeth in two series
60(2) postparietal short and rectangular
71(1) dermosphenotic T-shaped
85(1) lachrymal is a separate and distinct bone
86(2) lachrymal is inverted L shaped
107(0) preoperculum anterodorsal region is subhorizontal
123(3) sigmoidal subopercular upper suture
124(4) subopercular lower suture convex
128(0) 12 or more branchiostegal rays per side
130(1) extralateral gular present
143(1) supraorbital canal into parietal
175(1) body scales to dorsal ridge scales are one to one
207(1) ventrolateral flank scales narrow

[*Beagiascus pulcherrimus* + [*Lineagruan judithi* + *Lineagruan snowyi*]
P=100

65(1) extrascapular rows two separate rows
75(2) two bones dermosphenotic, dorsal and ventral bone
105(1) supraopercular bone present
114(2) antopercular bones extend to bottom of operculum
122(0) operculum not in contact with lateral extrascapulars
146(0) otic canal in 3 bones
160(1) postcleithrum absent
205(1) enlarged postcleithral scales present

Beagiascus pulcherrimus

16(2) marginal teeth orientation is posteriad
49(0) nasal bones without notches

93(3) suborbital number is more than six
123(0) horizontal subopercular upper suture
124(0) horizontal subopercular lower suture

Lineagruan judithi + Lineagruan snowyi
P=82

177(2) dorsal fin base with guard scales

Lineagruan judithi

19(2) high rounded posterior plate of maxilla
107(1) preoperculum anterodorsal region is subvertical or vertical
108(1) preopercular angle is narrower than 90°
128(1) fewer than 12 branchiostegal rays per side
166(0) clavicle length is short

Lineagruan snowyi

14(0) ventral margin of maxilla is straight
93(2) suborbital number is four to six
114(3) antopercular bones extend to bottom of suboperculum
173(0) basal fulcra anterior to dorsal fin absent
174(3), 175(0), 176(3) dealing with absence of dorsal ridge scales

[*Coccocephalus + Spinofacia*] + [*Wendyichthys lautreci* + [*Cyranorhis + Wendyichthys dicksoni*]
P=96

73(2)dermopterotic/supratemporotabular longer than dermosphenotic

[*Wendyichthys lautreci* + [*Cyranorhis + Wendyichthys dicksoni*]
P=99

38(3) snout shape is notched 45(1) rostral notch present

Wendyichthys lautreci

21(1) slightly developed posteroventral process of maxilla
174(1) many predorsal scutes/dorsal ridge scales
186(1) anal fin ends close to caudal fin
206(1) flank scales are deep

[*Cyranorhis + Wendyichthys dicksoni*]
P=99

34(1) dentary and maxillary teeth not organized in two series
75(2) two bones dermosphenotic, dorsal and ventral bone
146(0) otic canal in 3 bones
177(2) dorsal fin base with guard scales

Cyranorhis bergeraci

12(1) anterior end of maxilla is orbital
123(1) diagonal subopercular upper suture
124(0) horizontal subopercular lower suture
133(1) posterior and anterior margins of lateral gular angled
134(0) lateral gular is similar in size to branchiostegal rays
160(1) postcleithrum absent
162(1) dorsal end of cleithrum is broad and round

Wendyichthys dicksoni

135(0) short parasphenoid
143(0) supraorbital canal into postparietal
167(1) clavicle contact short
205(1) enlarged postcleithral scales present

Coccocephalus + Spinofacia
P=98

36(1) moderate ganoine ornamentation on skull roof bones
77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal

Coccocephalus

13(0) height of posterior part of maxilla is low
71(3) dermosphenotic shape is elongate
143(0) supraorbital canal into postparietal

Spinofacia

14(0) ventral margin of maxilla is straight

(*Rhadinichthys* + (*Cycloptychius* + *Novogonatodus*)) + (*Palaeoniscum* + (*Beishanichthys* + (*Gonatodus* + New Brunswick fish)))

P=92

4(0) a complex premaxilla present as a ventral-rostro-premaxillo-lachrymal
7(1) premaxilla is part of orbit
21(2) maxilla with strong posteroventral process
40(2) median and complex rostral bones present
41(1) 2 rostral bones, a dorsal and ventral bone, ventral part of complex bone
43(0) median rostral bone widens anteriorly
140(4) ethmoid commissure through paired complex bone
184(0) pelvic fin with long base

Rhadinichthys + (*Cycloptychius* + *Novogonatodus*)

P=94

34(0) dentary and maxillary teeth in two series
38(1) snout shape is a sharp bump
71(1) dermosphenotic T-shaped
86(3) lachrymal shape is a vertical pillar
123(2) concave subopercular upper suture

Rhadinichthys canobiensis

13(1) height of posterior part of maxilla is medium
59(1) postparietal with pointed anterolateral process
73(2)dermopterotic/supratemporotabular longer than dermosphenotic
179(1) dorsal fin originates at same level as anal

Cycloptychius concentricus

121(2) operculum is about the same height as suboperculum
179(0) dorsal fin originates behind anal

Novogonatodus kasantsevae

19(2) posterior plate of maxilla is high and rounded
160(1) postcleithrum absent
162(1) dorsal end of cleithrum is broad and round
169(2) round body form

Palaeoniscum through New Brunswick fish

P=99

58(0) parietal contacts supraorbital
68(1) supraorbital bones present without canal
69(0) supraorbitals single series
72(2) dermosphenotic contact not in contact with nasal
73(3) dermosphenotic relative size-dermopterotic/supratemporotabular more than two times longer than dermosphenotic

Palaeoniscum freieslebeni

13(1) height of posterior part of maxilla is medium
74(3) dermosphenotic not in contact with dermoyhal because no dermohyal present
75(2) dermosphenotic is two bones, a dorsal and ventral dermosphenotic
104(0) dermohyal absent
121(2) operculum about same height as suboperculum
122(0) operculum not in contact with lateral extrascapulars
123(3) sigmoidal subopercular upper suture
146(0) otic canal in three bones

Beishanichthys + [*Gonatodus* + New Brunswick fish]

P=55

151(1) horizontal pit line present
186(1) anal fin ends close to caudal fin

Beishanichthys brevicaudalis

14(0) ventral margin of maxilla is straight

15(1) maxillary teeth present only on anterior part of maxilla
21(0) posteroventral process of maxilla absent
100(0) quadratojugal present
101(1) large quadratojugal
108(1) preopercular angle is narrower than 90°
143(1) supraorbital canal into parietal
170(0) basal fulcra between dorsal and caudal fins absent
171(0) fringing fulcra absent
178(1) rear of dorsal fin close to caudal fin
180(4) dorsal fin long and low
184(1) pelvic fin with short base
190(4) caudal fin shape is abbreviated heterocercal
200(1) posterior edges of rhombic scales are straight

Gonatodus **+ New Brunswick fish**
P=99

4(2) complex premaxilla present as of a ventral rostro-premaxilla
7(0) premaxilla not part of orbit
8(0) posterior margin of premaxilla contacts lachrymal bone
73(2)dermopterotic/supratemporotabular longer than dermosphenotic
124(0) horizontal subopercular lower suture

Gonatodus punctatus

9(0) premaxilla not in contact with nasal bone
13(0) height of posterior part of maxilla is low
37(0) preparietal relative length is short
104(2) dermohyal in a series
123(0) horizontal subopercular upper suture
127(1) first branchiostegal ray deeper than second
157(0) pectoral fin is lobe based
160(1) postcleithrum absent

New Brunswick fish

10(1) premaxillary teeth absent in midline
34(0) dentary and maxillary teeth in two series
69(2) supraorbital present as single bone
85(1) lachrymal is a separate and distinct bone
93(3) more than 6 suborbital bones present
94(3) suborbital bones arranged in many rows
114(2) antopercular bones extend to bottom of operculum
115(2) antopercular bone widen ventrally
116(1) antopercular bones as thick as as adjacent bones
159(1) presupracleithrum present
201(1) ventral edges of scales are serrated

Mesopoma **+** ***Boreosomus*** **+ Redfieldiidae**
P=100

4(1) complex premaxilla is a premaxillo-lachrymal
7(1) premaxilla is part of orbit
13(1) height of posterior part of maxilla is medium
21(1) slightly developed posteroventral process of maxilla
38(1) snout shape is a sharp bump
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
89(1) jugal/infraorbital 3 contacts suborbital posterodorsally
96(1) maxilla not in contact with suborbital
113(0) gap between operculum and skull roof bones present

Mesopoma planti

86(3) lachrymal shape is a vertical pillar
100(0) quadratojugal present
101(0) small quadratojugal
107(0) preoperculum anterodorsal region is subhorizontal
200(1) posterior edges of rhombic scales-straight

Mesopoma carricki **+ [*Boreosomus* + Redfieldiidae]**
P=68

73(4) dermosphenotic longer than dermopterotic/supratemporotabular
77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal

Mesopoma carricki

21(2) maxilla with strong posteroventral process
179(1) dorsal fin originates at same level as anal fin

Boreosomus **+ Redfieldiidae**
P=96

51(0) rear of nasal bones preorbital
72(2) dermosphenotic not in contact with nasal
192(0) caudal outline is cleft equilobate

Boreosomus piveteaau

37(0) preparietal relative length is short
60(0) postparietal long and rectangular
75(2) dermosphenotic number is 2, dorsal and ventral dermosphenotic bones
89(4) Jugal/infraorbital 3 contacts suborbital ventrally
93(2) suborbital number is four to six
157(0) pectoral fin is lobe based
173(0) basal fulcra anterior to dorsal fin absent
185(0) scutes or basal fulcra between pelvic and anal fin absent
200(1) posterior edges of rhombic scales are straight

Redfieldiidae
P=100

12(1) maxilla anterior end is orbital
13(2) height of posterior part of maxilla is high
46(1) tuberculated snout present
73(2)dermopterotic/supratemporotabular longer than dermosphenotic
111(2) preoperculum anteriorly in contact with infraorbitals, extensively
113(1) gap between operculum and skull roof bones absent
125(2) branchiostegal rays present as 1/branchiostegal plate
126(1) branchiostegal rays not below mandible
143(1) supraorbital canal into parietal

Dictyopyge **sp.**

19(3) high triangular posterior plate of maxilla
74(3) dermosphenotic not in contact with dermohyal because dermohyal absent
77(2) more than 1/3 of the dermopterotic/supratemporotabular bone contacts parietal
91(1) number of infraorbital bones ventral to orbit is two
104(0) dermohyal absent
108(1) preopercular angle is narrower than 90°
119(2) second axis of operculum longer than first
122(1) operculum in contact with lateral extrascapular
189(0) caudal fin without hinge line

Redfieldius gracilis

60(3) postparietal rounded
63(1) three postparietals bones, one per side and a median bone
66(1) extrascapular number is two
89(2) jugal/infraorbital 3 not in contact with suborbital
107(0) preoperculum anterodorsal region is subhorizontal
112(2) preoperculuar width is even
153(2) preopercular canal to postotic region
174(2) predorsal scutes/dorsal ridge scales are complete to occiput
175(1) body scales to dorsal ridge scales are one to one
176(0) dorsal ridge scales without a spine or spike

179(1) dorsal fin originates at same level as anal

Canobius elegantulus

4(1) complex premaxilla is a premaxillo-lachrymal
7(1) premaxilla is part of orbit
13(1) height of posterior part of maxilla is medium
15(1) maxillary teeth present only on anterior part of maxilla
19(2) posterior plate of maxilla is high and rounded
21(2) maxilla with strong posteroventral process
43(1) median rostral that anterior and posterior margins with equal widths
58(1) parietal not in contact with supraorbital
66(1) extrascapular number is two
73(2)dermopterotic/supratemporotabular longer than dermosphenotic
74(3) dermosphenotic not in contact with dermohyal because dermohyal is absent
86(1) lachrymal is rhombic
95(2) suborbital fit is loose with gaps
104(0) dermohyal absent
108(1) preopercular angle is narrower than 90°
110(1) preoperculum contacts posterior margin of maxilla
119(1) both axes of operculum approximately equal in size
121(2) operculum is about the same height as suboperculum
174(2) predorsal scutes/dorsal ridge scales are complete to occiput
179(1) dorsal fin originates at same level as anal fin

Cheirodopsis geikiei

14(0) ventral margin of maxilla is straight
19(3) high triangular posterior plate of maxilla
38(5) snout shape is beak shaped
43(1) median rostral that anterior and posterior margins with equal widths
66(1) extrascapular number is two
71(3) dermosphenotic shape is elongate
89(3), 92(0), 93(0), 94(0), 95(0), 96(0) dealing with absence of suborbital bones
108(1) preopercular angle is narrower than 90°
110(1) preoperculum contacts posterior margin of maxilla
111(2) preoperculum anteriorly in contact with infraorbitals, extensively
121(3) suboperculum deeper than operculum
123(2) concave subopercular upper suture
169(1) deep body form
174(3), 175(0), 176(3) dealing with absence of dorsal ridge scales
178(1) rear of dorsal fin close to caudal fin
186(1) anal fin l ends close to caudal fin
206(1) flank scales deep

***Osorioichthys through* Cheirolepididae**
P=83

4(1) complex premaxilla is a premaxillo-lachrymal
27(1) surangular present
60(0) postparietal long and rectangular
71(1) dermosphenotic T-shaped
75(2) two bones dermosphenotic, dorsal and ventral bone
77(0)dermopterotic/supratemporotabular not in contact with parietal bone
107(0) preoperculum anterodorsal region is subhorizontal
122(0) operculum not in contact with lateral extrascapulars
128(0) 12 or more branchiostegal rays per side
146(0) otic canal in 3 bones
159(1) presupracleithrum present

Osorioichthys marginis

15(1) maxillary teeth present only on anterior part of maxilla
19(2) posterior plate of maxilla is high and rounded

61(1) postparietal almost equal in size to parietal
86(1) lachrymal is rhombic
119(2) second axis of operculum is longer than first
121(2) operculum about the same height as suboperculum
127(1) first branchiostegal ray deeper than second
152(1) vertical preopercular pit line absent
153(1) preopercular canal to postorbital corner
157(0) pectoral fin is lobe based

***Moythomasia* through Cheirolepididae**
P=54

34(0) dentary and maxillary teeth in two series
123(2) concave subopercular upper suture

Moythomasia nitida

59(1) postparietal with pointed anterolateral process
124(3) sigmoidal subobpercular lower suture
151(1) horizontal pit line present
174(2) predorsal scutes/dorsal ridge scales are complete to occiput
177(3) dorsal fin base with smaller scales

***Woodichthys* through Cheirolepididae**
P=93

38(1) snout shape is a sharp bump
89(3), 92(0), 93(0), 94(0), 95(0), 96(0) dealing with absence of suborbital bones
111(2) preoperculum anteriorly in contact with infraorbitals, extensively
113(0) gap between operculum and skull roof bones present

Woodichthys bearsdeni

36(1) ganoine ornamentation on skull roof bones moderate
60(2) postparietal short and rectangular
77(2) more than 1/3 of the dermopterotic/supratemporotabular bone contacts parietal
122(1) operculum in contact with lateral extrascapular
124(2) concave subopercular lower suture
143(1) supraorbital canal into parietal
153(1) preopercular canal to postorbital corner
159(0) presupracleithrum absent
175(0) number of body scales to dorsal ridge scales not applicable because dorsal ridge scales absent
176(3) dorsal ridge scales absent

Tegeolepis clarki

4(23) complex premaxilla present as of a ventral rostro-premaxilla or absent as complex bone
8(1) premaxilla contacts ventral margin lachrymal bone
9(0) premaxilla not in contact with nasal bone
12(1) maxilla anterior end is orbital
13(0) height of posterior part of maxilla is low
16(2) marginal teeth orientation is posteriad
21(1) slightly developed posteroventral process of maxilla
38(2) elongated snout
49(0) nasal bones without notches
50(2) nasals not notched
74(3) dermosphenotic not in contact with dermohyal because dermohyal absent
85(1) lachrymal is a separate and distinct bone
86(4) triangular shaped lachrymal
89(2) jugal/infraorbital three not in contact with suborbitals
91(1) two infraorbital bones ventral to orbit
104(0) dermohyal absent
132(1), 133(2), 134(2) dealing with absence of lateral gular

(Gogosardinia + Mimia) + [Cuneognathus + [Stegotrachelus + Limnomis]]

P=50

124(0) horizontal subopercular lower suture
174(2) predorsal scutes/dorsal ridge scales are complete to occiput

Gogosardinia + Mimia

P=100

43(2) median rostral bone narrows anteriorly
59(1) postparietal with pointed anterolateral process
61(1) Postparietal relative size almost equal to f/p
119(1) opercular shape both axes approximately equal

Gogosardinia coatesi

52(0) postrostral bones present
53(4) postrostral number four
54(2) postrostral number more than 2 bones
123(3) sigmoidal subopercular upper suture
124(4) subopercular lower suture convex
134(0) lateral gular similar in size to branchiostegal ray
143(1) supraorbital canal into parietal
151(1) horizontal pit line present
207(1) ventrolateral flank scales narrow

Mimipiscis toombsi

121(2) operculum about same height as suboperculum
127(1) first branchiostegal ray deeper than second
133(0) lateral gular similar in size to branchiostegal ray

Cuneognathus + [Stegotrachelus + Limnomis]

P=84

60(1) Postparietal squared
79(1) ventral protuberance of dermopterotic/supratemporotabular absent

Cuneognathus gardineri

21(1) slightly developed posteroventral process of maxilla
77(1) anterior 1/3 of dermopterotic/supratemporotabular bone contacts parietal
123(0) horizontal subopercular upper suture
186(1) anal fin l ends close to caudal fin
207(1) ventrolateral flank scales narrow

Limnomis delaneyi + Stegotrachelus finlayi

P=72

14(0) ventral margin of maxilla is straight
121(0) operculum three times deeper than suboperculum or more

Stegotrachelus finlayi

38(0) snout shape is blunt rounded
68(3) supraorbital bones absent
114(5) antopercular bone(s) extend(s) to ventral half of operculum
115(2) antopercular bone(s) widen(s) ventrally
116(1) antopercular bones as thick as adjacent bones

Limnomis delaneyi

6(1) premaxillae separated medially
16(2) marginal teeth orientation is posteriad
42(1) median rostral contributes to jaw margin
44(1) teeth on rostral present
73(4) dermosphenotic larger than dermopterotic/supratemporotabular
90(1) three infraorbital bones, counting lachrymal
124(1) diagonal subopercular lower suture
171(0) fringing fulcra absent
184(2) pelvic fin with reduced base
189(0) caudal fin without hinge line

[Cheirolepididae + *Kentuckia*] + [*Donnrosenia schaefferi* + *Howqualepis rostridens*]

P=75

73(4) dermosphenotic longer than dermopterotic/supratemporotabular
82(0) spiracle angular shaped
158(0) anteriormost pectoral lepidotrichia segmented proximally
167(1) clavicle contact short
184(0) pelvic fin with long base
192(0) caudal outline is cleft equilobate

Cheirolepididae + *Kentuckia*

P=100

4(0) a complex premaxilla present as a ventral-rostro-premaxillo-lachrymal
38(0) snout shape is blunt rounded
40(2) median and complex rostral bones present
41(1) 2 rostral bones, a dorsal and ventral bone, ventral part of complex bone
115(2) antopercular bone(s) widen(s) ventrally
123(1) diagonal subopercular upper suture
142(0) supraorbital canal runs anterior to nasal openings
159(0) presupracleithrum absent

Kentuckia

113(1) gap between operculum and skull roof bones absent
153(1) preopercular canal to postorbital corner
168(0) interclavicle present

Cheirolepididae

P=100

9(0) premaxilla not in contact with nasal bone
13(2) height of posterior part of maxilla is high
37(0) preparietal relative length is short
52(0) postrostral bones present
58(1) parietal not in contact with supraorbital
68(1) supraorbital bones present without canal
75(1) dermosphenotoic present as one bone
110(3) preoperculum contacts dorsal margin of maxilla

Cheirolepis trailli

114(2) antopercular bones extend to bottom of operculum
134(0) lateral gular similar in size to branchiostegal rays
145(1) supraorbital and infraorbital canals not in contact rostrally
170(0) basal fulcra between dorsal and caudal fins absent

Cheirolepis canadensis + *C. schultzei*

P=99

49(0) nasal bones without notches
51(0) rear of nasal bones preorbital
146(1) otic canal trajectory in 2 bones

Cheirolepis schultzei

21(1) slightly developed posteroventral process of the maxilla
77(1) anterior 1/3 of dermopterotic/supratemporotabular bone in contact with parietal bone
106(0) preoperculum without distinct regions
112(3) preoperculum cinched in middle
159(1) presupracleithrum present

Donnrosenia schaefferi + *Howqualepis rostridens*

P=61

77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal
122(1) operculum in contact with lateral extrascapular

Donnrosenia schaefferi

9(0) premaxilla not in contact with nasal
61(1) postparietal almost equal in size to parietal

72(0) dermosphenotic contact absent
78(0)dermopterotic/supratemporotabular not in contact with the operculum
115(3) antopercular bone(s) taper(s) ventrally
194(0) epichordal fin rays of caudal fin short
198(0) peg and socket articulation broad
207(1) ventrolateral flank scales narrow

Howqualepis rostridens

21(1) slightly developed posteroventral process of maxilla
32(1) parasymphysial teeth on dentary present
42(1) median rostral contributes to jaw margin
44(1) teeth present on rostral
66(0) extrascapular number three
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
127(1) first branchiostegal ray deeper than second ray

Dialipina salgueiroensis

3(1) premaxilla is separate and distinct
13(0) height of posterior part of maxilla is low
17(1) maxilla pop ornamentation is mainly vertical ridges
19(0) posterior plate of maxilla not differentiated
33(0) acrodin caps on teeth absent
34(0) dentary and maxillary teeth in two series
37(0) preparietal relative length is short
43(0) median rostral bone widens anteriorly
49(0) nasal bones without notches
50(2) nasals not notched
52(0) postrostral bones present
53(2) postrostral number is one
54(0) median postrostral
59(1) postparietal with pointed anterolateral process
71(1) dermosphenotic T-shaped
74(3) dermosphenotic not in contact with dermohyal because dermohyal absent
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
82(1) spiracle shape is round
104(0) dermohyal absent
112(2) preoperculuar width is even
118(1), 119(3), 120(2), 121(4), 122(2) dealing with the absence of an operculum
129(1) Median gular absent
135(0) short parasphenoid
143(1) supraorbital canal into parietal
157(0) pectoral fin is lobe based
162(1) dorsal end of cleithrum is broad and round
163(1) posterior process of cleithrum absent
179(1) dorsal fin originates at same level as anal fin
181(0) two dorsal fins
184(0) pelvic fin with long base
189(0) caudal fin without hinge line
190(1) triphycercal caudal fin
193(0) epichordal fin rays of caudal fin present
194(1) epichordal fin rays of caudal fin elongated

Guildayichthyiformes

P=100

3(1) premaxilla is separate and distinct
8(0) posterior margin of premaxilla contacts lachrymal bone
9(0) premaxilla not in contact with nasal bone
13(0) height of posterior part of maxilla is low
14(0) ventral margin of maxilla is straight
15(1) maxillary teeth only on anterior part of bone
17(1) maxilla pop ornamentation is mainly vertical ridges
19(0) posterior plate of maxilla not differentiated
25(1) adductor mandibulae fossa on most of mandible
38(4) sharp snout shape
40(5) paired and median rostral bones
41(4) paired and median rostral bones

52(0) postrostral bones present
53(2) postrostral number is one
54(0) median postrostral
67(1) dermal supraoccipital present
68(1) supraorbital bones present without canal
74(3) dermosphenotic not in contact with dermohyal because dermohyal absent
75(2) two bones dermosphenotic, dorsal and ventral bone
78(0)dermopterotic/supratemporotabular not in contact with the operculum
85(1) lachrymal is a separate and distinct bone
93(3) more than 6 suborbital bones present
98(0) many sclerotic plates
103(0) postspiracular present
104(0) dermohyal absent
106(0) preoperculum without distinct regions
107(2) preoperculum anterodorsal region not differentiatied, not applicable
108(2) preopercular angle-n/a no distinct regions
109(1) two preopercular bones
110(2) preoperculum not in contact with maxilla
112(2) preoperculuar width is even
117(1) interoperculum present
121(5), 123(5), 124(5) dealing with absence of a suboperculum
122(0) operculum not in contact with lateral extrascapulars
152(1) vertical preopercular pit line absent
153(2) preopercular canal to postotic region
157(0) pectoral fin is lobe based
159(1) presupracleithrum present
162(1) dorsal end of cleithrum is broad and round
165(1), 166(2), 167(3) dealing with absence of a clavicle
169(2) round body form
174(2) predorsal scutes/dorsal ridge scales are complete to occiput
176(1) dorsal ridge scales are spine shaped
177(1) dorsal fin with a scaled lobe
178(1) rear of dorsal fin close to caudal
180(4) dorsal fin long and low
184(2) pelvic fin with reduced base
186(1) anal fin base ends close to caudal
190(4) abbreviated heterocercal caudal fin
191(1) caudal fin rays webbed
192(4) caudal fin is not cleft
206(1) flank scales deep

Guildayichthys carnegiei

43(0) median rostral bone widens anteriorly
57(1) two pairs of parietals
126(1) branchiostegal rays not below mandible

Discoserra pectinodon

60(2) postparietal bones short and rectangular
61(1) postparietal bone almost equal in size to parietal
72(2) dermosphenotic not in contact with nasal
91(3) only infraorbital 3/posteroventral infraorbital ventral to the orbit
95(2) suborbital fit is loose with gaps
148(1) supratemporal commissure not across midline
189(0) caudal fin without hinge line
194(0) epichordal fin rays of caudal fin short
198(0) peg and socket articulation broad

Elonichthys Mansfieldiscus Pteronisculus
P=62

3(1) premaxilla is a separate and distinct bone
8(0) posterior margin of premaxilla contacts lachrymal bone
9(0) premaxilla not in contact with nasal bone
13(1) medium height of posterior part of maxilla
21(2) maxilla with strong posteroventral process
107(0) preoperculum anterodorsal region is subhorizontal

114(5) antopercular bone(s) extend(s) to ventral half of operculum
115(2) antopercular bone widens ventrally
116(1) antopercular bones as thick as adjacent bones
128(0) 12 or more branchiostegal rays per side
152(1) vertical preopercular pit line absent
159(1) presupracleithrum present

'Elonichthys' palatinus

51(0) rear of nasal bones preorbital
60(0) postparietal long and rectangular
72(2) dermosphenotic not in contact with nasal bone
74(3) dermosphenotic not in contact with dermohyal because dermohyal absent
77(0)dermopterotic/supratemporotabular not in contact with parietal bone
86(2) lachrymal is inverted L shaped
91(1) number of infraorbital bones ventral to orbit is two
104(0) dermohyal absent
123(2) concave subopercular upper suture
127(1) first branchiostegal ray deeper than second
160(1) postcleithrum absent

Mansfieldiscus sweeti

8(1) premaxilla contacts ventrally lachrymal bone
14(0) ventral margin of maxilla is straight
16(1) marginal teeth orientation is forward
21(1) slightly developed posteroventral process of maxilla
40(2) median and complex rostral bones present
41(1) 2 rostral bones, a dorsal and ventral bone, ventral part of complex bone
60(2) postparietal short and rectangular
66(1) extrascapular number is two
77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal
78(2)dermopterotic/supratemporotabular ventroposteriorly in contact with operculum
89(1) jugal/infraorbital 3 contacts suborbital posterodorsally

Pteronisculus stensioei

17(3) maxilla preoperculum ornamentation is ridges and tubercles of ganoine
43(1) median rostral bone with anterior and posterior margins of equal lengths
73(2)dermopterotic/supratemporotabular longer than dermosphenotic
75(2) two bones dermosphenotic, dorsal and ventral bone
100(0) quadratojugal present
101(0) small quadratojugal
103(0) postspiracular present
114(1) antopercular bone(s) do not extend down to bottom of operculum
115(3) antopercular bone width-anteoperculuar bone(s) taper(s) ventrally
146(0) otic canal in 3 bones
148(1) supratemporal commissure not across midline
151(1) horizontal pit line present
153(1) preopercular canal postorbital corner
157(0) pectoral fin is lobe based
166(2) clavicle length, not applicable, clavicles absent

Tarrasiidae + *Kalops*
P=82

3(1) premaxilla is separate and distinct
8(0) premaxilla posteriorly in contact with lachrymal bone
9(0) premaxilla not in contact with nasal bone
40(3) median rostral bones
41(2) 2 rostral bones, dorsal and ventral, both separate and distinct
58(0) parietal contacts supraorbital
68(1) supraorbital bones present without canal
69(01) suprarobitals present as single bone or double series
72(2) dermosphenotic not in contact with nasal

79(1) ventral protuberance of dermopterotic/supratemporotabular absent
85(1) lachrymal is a separate and distinct bone
93(3) more than 6 suborbital bones present
157(0) pectoral fin is lobe based
162(1) dorsal end of cleithrum is broad and round

Kalops monphrys* + *Kalops diophrys
P=95

86(1) lachrymal is rhombic
121(0) operculum three times deeper than suboperculum or more
143(1) supraorbital canal into parietal bone
148(1) supratemporal commissure not across midline

Kalops diophrys

65(2) extrascapular rows-two rows share median bone
103(0) postspiracular present
134(0) lateral gular similar in size to branchiostegal ray
205(1) enlarged postcleithral scales present

Kalops monophrys

66(0) extrascapular number three
73(2)dermopterotic/supratemporotabular longer than dermosphenotic
93(2) suborbital number is four to six
95(0) suborbital fit is absent
124(2) concave subopercular lower suture
174(2) predorsal scutes/dorsal ridge scales are complete to occiput

Tarrasiidae
P=99

48(01) number of nasal bones either numerous or two on each side
71(1) dermosphenotic T-shaped
75(2) two bones dermosphenotic, dorsal and ventral bone
169(4) blade like body form
170(0) basal fulcra between dorsal and caudal fins absent
171(0) fringing fulcra absent
173(0) basal fulcra anterior to dorsal fin absent
174(3), 175(0), 176(3) dealing with absence of dorsal ridge scales
178(2) dorsal fin merged with caudal
180(4) dorsal fin long and low
183(1), 184(3), dealing with absence of pelvic fin absent
185(0) scutes or basal fulcra between pelvic and anal fin absent
186(2) anal fin base merged with caudal fin
189(0) caudal fin without hinge line
190(3) hypocercal caudal fin shape
192(3) caudal outline pointed
193(0) epichordal fin rays of caudal fin present
194(1) epichordal fin rays of caudal fin elongated
195(1) micromeric scales

Paratarrasius hibbardi

14(0) ventral margin of maxilla is straight
65(1) two separate extrascapular rows
78(0)dermopterotic/supratemporotabular not in contact with the operculum
83(1) thin overlapping cheek fit
104(2) dermohyal in a series
114(1) antopercular bones do not extend to bottom of operculum
115(3) antopercular width tapers ventrally
116(1) antopercular as thick as adjacent bones
119(1) both axes of operculum approximately equal in size
143(3) supraorbital canal into dermopterotic/supratemporotabular
144(1) supraorbital canal in contact with otic
146(0) otic canal in three bones
205(1) enlarged postcleithral scales present

Tarrasius problematicus

19(2) posterior plate of maxilla is high and rounded
49(0) nasal bones without notches

50(2) nasals not notched
66(1) extrascapular number is two
89(3), 92(0), 93(0), 94(0), 95(0), 96(0) dealing with absence of suborbital bones
106(0) preoperculum without distinct regions
110(1) preoperculum contacts posterior margin of maxilla
111(2) preoperculum anteriorly in contact with infraorbitals, extensively
124(0) horizontal subopercular lower suture
160(1) postcleithrum absent

Melanecta

4(1) complex premaxilla is a premaxillo-lachrymal
6(1) premaxillae separated medially
7(1) premaxilla is part of orbit
10(1) premaxillary teeth absent in midline
13(1) height of posterior part of maxilla is medium
16(1) marginal teeth orientation is forward
21(1) slightly developed posteroventral process of maxilla
34(0) dentary and maxillary teeth in two series
37(0) preparietal relative length is short
38(1) snout shape is a sharp bump
42(1) median rostral contributes to jaw margin
44(1) teeth on rostral present
51(0) rear of nasal bone preorbital
77(0)dermopterotic/supratemporotabular not in contact with parietal bone
107(0) preoperculum anterodorsal region is subhorizontal
143(1) supraorbital canal into parietal
158(1) anteriormost pectoral lepidotrichia segmented only distally
160(1) postcleithrum absent
174(1) many predorsal scutes/dorsal ridge scales

Paramesolepis tuberculata

4(0) a complex premaxilla present as a ventral-rostro-premaxillo-lachrymal
8(0) premaxilla contacts posteriorly lachrymal bone
15(1) maxillary teeth present only on anterior part of maxilla
19(3) high triangular posterior plate of maxilla
37(0) preparietal relative length is short
40(2) rostral bones present as median and complex bone
41(1) 2 rostral bones-dorsal and ventral, ventral part of complex bone
66(1) extrascapular number is two
71(3) dermosphenotic shape is elongate
73(4) dermosphenotic longer than dermopterotic/supratemporotabular
75(2) dermosphenotic present as two bones, dorsal and ventral
77(0)dermopterotic/supratemporotabular not in contact with parietal bone
86(3) lachrymal shape is a vertical pillar
89(3), 92(0), 93(0), 94(0), 95(0), 96(0) dealing with absence of suborbital bones
106(0) preoperculum without distinct regions
108(2) preopercular angle-n/a no distinct regions
110(1) preoperculum contacts posterior margin of maxilla
111(2) preoperculum anteriorly in contact with infraorbitals, extensively
112(2) preoperculum width is even
119(1) both axes of operculum approximately equal in size
121(3) suboperculum deeper than operculum
123(2) concave subopercular upper suture
140(4) ethmoid commissure through paired complex bone
146(0) otic canal in 3 bones
169(1) deep body form
174(2) predorsal scutes/dorsal ridge scales are complete to occiput
178(1) rear of dorsal fin close to caudal fin
186(1) anal fin l ends close to caudal fin

Platysomus striatus

4(1) complex premaxilla is a premaxillo-lachrymal
14(0) ventral margin of maxilla is straight
15(1) maxillary teeth present only on anterior part of maxilla
19(2) maxilla posterior plate is high and rounded
38(4) snout shape is sharp
51(0) rear of nasal bones preorbital
60(2) postparietal short and rectangular
72(2) dermosphenotic not in contact with nasal
73(2)dermopterotic/supratemporotabular longer than dermosphenotic
74(3) dermosphenotic not in contact with dermohyal because dermohyal absent
77(1) anterior 1/3 of dermopterotic/supratemporotabular contacts parietal
79(1) ventral protuberance of dermopterotic/supratemporotabular absent
86(3) lachrymal shape is a vertical pillar
89(3), 92(0), 93(0), 94(0), 95(0), 96(0) dealing with absence of suborbital bones
104(0) dermohyal absent
108(1) preopercular angle is narrower than 90°
110(1) preoperculum contacts posterior margin of maxilla
111(2) preoperculum anteriorly in contact with infraorbitals, extensively
112(3) preoperculum cinched in middle
121(2) operculum is about the same height as suboperculum
123(0) horizontal subopercular upper suture
124(0) horizontal subopercular lower suture
169(1) deep body form
174(3), 175(0),176(3) dealing with absence of dorsal ridge scales
178(1) rear of dorsal fin close to caudal fin
180(1) dorsal fin shape is sigmoidal
186(1) anal fin l ends close to caudal fin
192(0) caudal outline is cleft equilobate
198(0) peg and socket articulation broad
200(1) posterior edges of rhombic scales are straight

Platysomus superbus

14(0) ventral margin of maxilla is straight
15(3) maxillary teeth not on oral rim of maxilla
16(3) marginal teeth absent
19(3) high triangular posterior plate of maxilla
22(3) maxillary teeth absent
34(2) dentary and maxillary teeth absent on oral rim
38(4) snout shape is sharp
60(2) postparietal bones short and rectangular
78(0) dermopterotic contact of-not in contact with operculum
85(1) lachrymal-separate and distinct bone
86(3) lachrymal shape vertical pillar
89(3), 92(0), 93(0), 94(0), 95(0), 96(0) dealing with absence of suborbital bones
104(0) dermohyal-absent
108(1) preopercular angle is narrower than 90°
110(1) preoperculum contacts posterior margin of maxilla
111(2) preoperculum anteriorly in contact with infraorbitals; extensive
121(3) suboperculum deeper than operculum
123(2) concave subopercular upper suture
169(1) deep body form
174(3), 175(0), 176(3) dealing with absence of dorsal ridge scales
180(2) dorsal fin shape is long and acuminate
205(1) enlarged postcleithral scales present