Two New Species and a Revised Phylogeny of the Ellimmichthyiformes (Teleostei: Clupeomorpha)

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Sciences

in

Systematics and Evolution

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PREFACE

This thesis contains results of collaborative research that was prepared for publication in a scientific journal. Chapter 2 of the thesis has been accepted for publication in the Journal of Vertebrate Paleontology in co-authorship with my supervisor, Dr. Alison M. Murray:

Vernygora, O. V. and A. M. Murray. (In press) A new species of *Armigatus* (Clupeomorpha, Ellimmichthyiformes) from the Late Cretaceous of Morocco, and its phylogenetic relationships. Journal of Vertebrate Paleontology 36 (2).

I was responsible for the examination and description of the study material. Dr. Alison M. Murray provided supervisory and editiorial contribution to the manuscript composition.

Names for the new species described in chapters 2 and 3 of the present thesis are not validly published and will become valid only after they are published elsewhere according to the International Code of Zoological Nomenclature.

ABSTRACT

The Ellimmichthyiformes is an extinct order of clupeomorph fishes. This group includes fossil species from marine, estuarine, and freshwater sediments ranging in time from the Early Cretaceous to the Eocene. In spite of the long history of taxonomic studies on the Clupeomorpha, phylogenetic relationships within the group remain unresolved. Two new species of the Ellimmichthyiformes are described and included in the revised phylogenetic analysis of the order. The updated phylogenetic analysis recovered the Ellimmichthyiformes as a monophyletic group characterized by the medially united parietals, absence of the recessus lateralis, presence of the basipterygoid process, and epurals that are tightly fixed between the neural spines of the preural centra. The new phylogenetic hypothesis revealed patterns in the paleobiogeographic history of this group of fishes, suggesting that the ellimmichthyiforms may have originated in the tropical region of South America and were predominantly euryhaline fishes.

AKNOWLEDGEMENTS

I express my endless thanks and gratitude to everyone who has supported and encouraged my scientific endeavors throughout these years. First and foremost, I would like to thank my M.Sc. supervisor, Dr. Alison M. Murray for her wonderful mentorship and for providing me with an opportunity and funding to pursue my research interests. It has been an excellent graduate experience that bolstered my interest in fish paleontology and made me even more enthusiastic about continuing research!

I am sincerely grateful to the members of my examining committee, Drs. Philip J. Currie and Heather C. Proctor, for their effective feedback on my research. I am also thankful to the committee chair, Dr. Heather E. McDermid. I would also like to express my gratitude to Drs. Philip J. Currie and Eva Koppelhus for kindly taking me out on fieldwork at Dinosaur Provincial Park with their crew. Al Lindoe has been a great help to my research by making latex peels of my specimens and providing a great deal of valuable information and very positive attitude towards research and life in general, which is very much appreciated.

I would also like to thank everyone who collected and prepared specimens that I studied and described for my research project. Additional thanks go to the people from the Royal Tyrrell Museum, particularly, Dr. Donald B. Brinkman and Brandon Strilisky who provided me access to the specimens in the TMP collections.

I have been extremely fortunate to work with a great group of fellow students who welcomed me in the office and have been an excellent influence. I would like to acknowledge Thodoris Argyriou and Julien Divay who helped me start my studies and research at UALVP and continued to support me on my academic path. Special thanks go to Tiago R. Simões for his

enormous help with the theory and methods in phylogenetics; Paulina J. Huidobro for her support and advice; Katherine Bramble for her feedback on my work as well as countless discussions and conversations that helped me improve my research. I owe my thanks to other fellow graduate students and members of the University of Alberta Laboratory for Vertebrate Paleontology who contributed to the progress of my thesis and have been excellent role models throughout this time.

My undergraduate research supervisors, Dr. Sergey V. Mezhzherin and Vladislav V. Krakatitza provided a great start for my research work and encouraged me to pursue my academic interests beyond the undergraduate program. I could not have done it this far without their help.

Last but not least, I would like to thank my family – my parents, sister and her husband, and my aunts – for supporting me unconditionally in all of my decisions and always being there for me; I can never thank them enough for all their help.

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1.1 General introduction

The Clupeomorpha is a group of teleost fishes that includes the extant order Clupeiformes (herrings and allies) and the extinct order Ellimmichthyiformes. This diverse group includes over 360 extant species in 84 genera, and nearly 150 extinct species (Nelson, 2006; Lavoué et al., 2013). Members of this group occupy a wide range of ecological niches and are found in marine, freshwater and brackish environments. Moreover, some clupeomorphs are diadromous and undertake seasonal migrations between marine environments and rivers or estuaries. This remarkable tolerance of salinity in clupeomorphs allowed their successful dispersal worldwide. Ecomorphs and subspecies are known within many species that occupy waters with different salinity levels in the same geographic area. Examples include anadromous and marine ecomorphs of Pontic shad (*Alosa pontica* Bennett, 1835), Twaite shad (*Alosa fallax* (Lacepède, 1803)), Indian ilisha (*Ilisha melastoma* (Bloch and Schneider, 1801)), marine and brackish water subspecies of European anchovy (*Engraulis encrasicolus* (Linnaeus, 1758)) and others (Whitehead, 1985; Whitehead et al., 1988). While salinity does not pose a critical barrier to dispersal for clupeomorphs, these fishes are much more sensitive to temperature conditions and show a high level of endemism based on this environmental factor (Grant et al., 2010; Lavoué et al., 2013). Regional endemism is greatly emphasized in the tropic regions, where species richness is the highest; it is not as pronounced in the temperate and sub-Arctic regions. This pattern of distribution follows the latitudinal and longitudinal gradients in species richness (Fig. 1-1) – the majority of marine and euryhaline clupeomorph species (about 260 species) live in warm nearshore tropical waters. Among tropical environments, the Indo-West Pacific region has the highest species diversity, with more than 180 species of clupeomorphs represented there. Only about 60 species of clupeomorphs occur in the temperate and sub-Arctic regions (Whitehead, 1985; Lavoué et al, 2013).

It is hard to underestimate the economic significance of clupeomorphs as this group of fishes is one of the most heavily exploited by international fisheries. Clupeomorphs, and clupeoid fishes in particular, significantly outnumber other groups of commercial fishes. According to the Food and Agriculture Organization of the United Nations (FAO) statistics, in 2010 clupeoid fishes comprised almost 24% of the total world catch. Nineteen clupeoid species included in the top 59 fish species (catches of which exceeded 100 000 tons) contributed more than 19% of the total fish catch in 2010 with the most exploited clupeoid species being Japanese pilchard (*Sardinops melanostictus* (Jenyns, 1842)), South American pilchard (*S. sagax* (Jenyns, 1842)), Peruvian anchoveta (*Engraulis ringens* Jenyns, 1842), Atlantic herring (*Clupea harengus* Linnaeus, 1758), and European pilchard (*Sardina pilchardus* (Walbaum, 1792)) (FAO, 2012). In Canada, clupeiforms comprise about 20% of the total catches with the value exceeding 41.64 million dollars (Department of Fisheries and Ocean, 2011; FAO, 2012).

Despite the great abundance of clupeiforms and their economic significance, this group of fishes remains surprisingly understudied. Classification of the extinct as well as extant species is still problematic. The most recent studies on classification of the Clupeiformes are based on molecular data (Lavoué et al. 2007, 2013; Wilson et al., 2008; Bloom and Lovejoy, 2012) and largely overlook morphological characteristics. Yet, it is morphological traits that play a key role in identifying clupeiform species in the field. Classification keys for commercial fisheries usage are based primarily on the external characteristics that are easier to observe and investigate compared to molecular analyses that require laboratory settings.

Extensive morphologic studies, on the other hand, were conducted and published about 30 years ago by Grande (1985), Whitehead (1985), and Whitehead et al. (1988). Those studies represent the most complete and comprehensive morphologic works and classification keys to the clupeomorph fishes that are still widely used today. In the catalogues of clupeoid species (Whitehead, 1985; Whitehead et al., 1988) the authors noted that their work reflected the current state of the classification for the Clupeoidea group and was not a definitive statement, implying that further updates would be necessary as taxonomic changes are made in the future.

These two approaches (molecular and morphological) to the classification of the Clupeomorpha have produced different hypothesis of the phylogenetic relationships within the superorder contributing to the long-standing disputes over interrelationships within the Clupeomorpha. During the past few decades, new species of recent and fossil clupeomorph fishes have been described and added to the classification, changing the composition of some taxonomic groups and interrelationships within the group. However, a comprehensive study and up-to-date classification of clupeiform fishes is still missing, hampering both biological and fisheries studies.

1.2 Introduction to the history of Clupeomorpha systematics

The Clupeomorpha as a taxon was first recognized by Carl Linnaeus in the first edition of his *Systema Naturae* (1735). At that time, the group included a single genus, *Clupea*, with four species: European herring (*Clupea harengus*), anchovy (*Engraulis encrasicolus*), sprat (*Sprattus sprattus*), and shad (*Alosa alosa*). In the tenth edition of *Systema Naturae* (1758), Linnaeus added another six species to the genus: gizzard shad (*Clupanodon thrissa*), grenadier anchovy (*Coilia mystus*), and *Gasteropelecus sternicla*, the latter of which is currently recognized as an ostariophysan, as well as three *nomina dubia* (Lecointre and Nelson, 1996). Since that time the clade has greatly expanded and currently includes hundreds of species; however, interrelationships within the group remain a subject of debate.

Ever since the beginning of the Darwinian period in systematics, clupeomorphs were recognized as the most basal teleosts. In the major systematic works by Cope (1871), Gill (1872), and Woodward (1895), clupeomorphs were included in the order Isospondyli, the basal taxon among teleost fishes that also included elopomorphs, osteoglossomorphs, and any other primitive teleosts of uncertain affinities. The Clupeomorpha continued to be a 'wastebasket' taxon through the first half of the XX century. In the classifications by Goodrich (1909), Jordan (1923), Regan (1929), Svetovidov (1952), and others, the Clupeomorpha included clupeomorphs, gonorynchiforms, salmoniforms, esocoids, and other taxa. A clear diagnosis for the Clupeomorpha was yet to be defined.

Among the earliest works that aimed to clarify relationships within the Clupeomorpha, was Norman's synopsis (1957) where he assigned a family rank to this group of fishes further subdividing it into four subfamilies: Clupeinae, Chirocentrinae, Engraulinae, and Dussumieriinae. To define his family Clupeidae (equivalent now to Clupeomorpha), Norman used two diagnostic characteristics: (1) intracranial penetration by the swim bladder and (2) reduced lateral line system. Almost one decade later, Greenwood et al. (1966) published a major study of higher levels of all teleostean fishes in which they proposed a more rigorous diagnosis for the extant members of the Clupeomorpha, which included the following characters: reduced lateral line system, intracranial connection between the swim bladder and the inner ear; presence of the recessus lateralis, temporal foramina, pre-epiotic fossae, and the auditory fenestrae. They also recognized important features in the caudal skeletons of the clupeomorph fishes: fusion of the second hypural and the first ural centrum, separation of the first hypural from the first ural centrum, and fusion between the first uroneural and the first preural centrum. Based on these diagnostic features, Greenwood (1968) later concluded that the monotypic suborder Denticipitoidei, characterized by most of the major clupeomorph traits (presence of recessus lateralis, abdominal series of scutes, and otophysial connection between the inner ear and the swim bladder) but also having a complete lateral line system, unfused uroneural one and the first preural centrum, and the first hypural in close contact with the first ural centrum, is the sister-group to the Clupeoidei. The classification by Greenwood et al. (1966) was foundational for the further advances in Clupeomorpha systematics.

The next step in clupeomorph systematics was incorporating fossil taxa into the existing classification. Patterson and Rosen (1977) and Grande (1982, 1985) examined extinct clupeomorphs and subsequently revised the diagnosis for the group. According to Patterson and Rosen (1977), the subcohort Clupeomorpha is distinguished by the presence of the following features: (1) fusion of the second hypural and the first ural centrum; (2) supratemporal commissural sensory canal primitively passing through the parietals and supraoccipital; (3) otophysic connection between the swim bladder and the inner ear.

Grande (1982, 1985) conducted an extensive morphological study of the fossil as well as recent clupeomorphs. Similar to Patterson and Rosen (1977), Grande recognized Clupeomorpha by the presence of an otophysic connection between the swim bladder and the inner ear and the supratemporal commissural canal passing through the parietals and supraoccipital. In addition to those characters, Grande (1985) also used presence of one or more abdominal scutes as a distinguishing feature of the Clupeomorpha.

The classification system developed by Grande (1985) has become one of the most influential and widely accepted works in Clupeomorpha systematics and remains a core of the phylogenetic hypotheses for the superorder up to the present day. In his classification, Grande (1982) recognized Clupeomorpha as a distinct superorder of fishes with two divisions. Monotypic Division 1 contained a single species (*Ornategulum sardinoides* Forey, 1973; later (1985), Grande replaced this with *Erichalcis arcta* Forey, 1975), and the rest of the extinct and living members of the group were placed in Division 2. Grande's Division 2 contained two orders, Clupeiformes and Ellimmichthyiformes, as well as a single genus, *Armigatus*, that was left outside the designated orders. The order Clupeiformes includes clupeomorphs with the following set of characteristics: (1) presence of a recessus lateralis; (2) parietals completely separated by the supraoccipital; (3) loss of the 'beryciform' foramen in the anterior ceratohyal; and (4) reduced size/number of teeth. This order was further subdivided into two suborders – Denticipitoidei (includes two genera, *Denticeps* Clausen, 1959 and *Palaeodenticeps* Greenwood, 1960) and Clupeoidei (contains recent clupeomorphs in four families). The order Ellimmichthyiformes was first recognized by Grande (1982) and included the genera *Ellimmichthys* Jordan 1919 and *Diplomystus* Cope, 1877 in a single family Ellimmichthyidae, characterized by the presence of subrectangular dorsal scutes. Although this family was later found to be a junior synonym of Paraclupeidae Chang and Maisey, 2003, the order Ellimmichthyiformes is valid.

The classification of Grande (1985) is summarized in Fig. 1-2. Over the last three decades, the addition of numerous newly described species and remarkable advances in phylogenetics and molecular techniques has modified Grande's system. Reexamination of *Erichalcis arcta* specimens (Arratia 1997; Hermus and Wilson, 2001) has shown that this species belongs to the Euteleostei. According to Arratia (1997), *Erichalcis* is more closely related to salmonids than to clupeomorphs; therefore, Grande's Divison 1 is no longer valid.

Grande's Division 2 can now be synonymized with the Clupeomorpha that includes two sister groups – the orders Ellimmichthyiformes and Clupeiformes. Recent morphological studies by Chang and Maisey (2003), Zaragüeta-Bagils (2004), Alvarado-Ortega et al. (2008), and Murray and Wilson (2013) added new taxa to the Ellimmichthyiformes and suggested different phylogenetic hypotheses of the interrelationships within the order (Fig. 1-3). According to Chang and Maisey (2003), Forey (2004), and Murray and Wilson (2013), the Ellimmichthyiformes includes the genus *Armigatus*, which Grande (1985) previously left outside the two recognized orders of clupeomorphs. Other authors (Zaragüeta-Bagils, 2004; Alvarado-Ortega et al., 2008) suggest that *Armigatus* is not a member of the Ellimmichthyiformes, but rather a sister-group to the order. The question of the relationships of the genus *Armigatus* to other ellimmichthyiforms is further discussed in Chapter 2 of the thesis.

The sister group of the Ellimmichthyiformes, the Clupeiformes, has also undergone some changes over the past few decades. In Grande's classification, the order included two suborders – monotypic Denticipitoidei and Clupeoidei. The latter contained three superfamilies – Engrauloidea, Pristigasteroidea, and Clupeoidea. The superfamily Clupeoidea was subdivided into Chirocentridae and Clupeidae. These major groups defined by Grande are still recognized in the most recent morphological and molecular studies that divide the suborder Clupeoidei into four families: Engraulidae, Clupeidae, Pristigasteridae, and Chirocentridae (Di Dario, 2002; Lavoué et al., 2007; Li and Orti, 2007). Recently, a new family has been added to the suborder – the Sundasalangidae, but affinities of this group within the Clupeoidei are still uncertain (Siebert, 1997; Ishiguro et al., 2005).

Many questions still persist regarding the diagnosis of the Clupeomorpha. Most of the characters used to define the group are problematic because they are hard to assess or are not exclusive to the clupeomorphs. A cephalic sensory canal that passes through the parietal and/or supraoccipital bones also occurs in other groups of fishes, including characoids and osteoglossomorphs, however, none of the members of these groups shows other characteristics of the Clupeomorpha. Presence of the abdominal scutes is considered to be one of the most obvious and easy to recognize characteristics. However, abdominal scutes are also present in some members of *Notopterus* Lacepède, 1800, *Argyropelecus* Cocco, 1829 and extinct pycnodonts, but the morphology of their scutes is different from that of clupeomorphs. The main distinction between clupeomorph and non-clupeomorph scutes is that the former are made of single elements, while non-clupeomorph fishes usually have scutes that are composed of two or more elements. The only exception is *Chirocentrus* Cuvier, 1816 in which the scutes are secondarily separated on the midline (Grande, 1985). Although an otophysic connection between the swim bladder and the inner ear is unique to the clupeomorphs, it is extremely hard to assess in fossil taxa due to the flattened lateral preservation of the majority of the specimens. The problems with clupeomorph characters, and more specifically those used in phylogenetic analyses, are discussed in more detail in Chapter 3.

1.3 Focus and objectives of the thesis

The main focus of this research project is the extinct order Ellimmichthyiformes. This group was first established by Grande (1982) and initially included a single family Ellimmichthyidae with two genera – *Ellimmichthys* and *Diplomystus*. The latter taxon was previously placed in the order Clupeiformes, but was recognized by Grande (1982, 1985) as missing some derived characters of the clupeiforms (recessus lateralis, parietal bones completely separated by the supraoccipital, and loss of the ‘beryciform’ foramen) and subsequently moved to the Ellimmichthyiformes. Chang and Maisey (2003) also redescribed one of the clupeid species, *Ellimma branneri* (Jordan, 1910) and came to the conclusion that it belongs to the Ellimmichthyiformes rather than to the Clupeiformes. Since that time, the order has significantly expanded and currently includes about thirty species. Similar to the extant members of the Clupeiformes, extinct clupeomorphs had a wide geographic distribution with fossil records in Europe, North and South America, Asia, and Africa with the temporal range extending from the early Early Cretaceous to the Eocene. Extinct clupeomorphs also represent a wide range of ecological adaptations. This group of fishes includes taxa from freshwater, marine, and brackish environments. It is possible that some of the ellimmichthyiforms were diadromous fishes similar to the extant members of the Clupeiformes.

The main objectives of the present thesis are: (1) to provide descriptions of the new clupeomorph taxa from the late Cenomanian/early Turonian of Morocco and early/mid Albian of Northwest Territories, Canada, (2) to perform the most extensive and up-to-date phylogenetic analysis of the Ellimmichthyiformes, and (3) to assess characters used for the phylogenetic analysis of the order. The concluding chapter of the thesis also includes a glance at the patterns of biogeography and diversification of ellimmichthyiforms throughout their evolutionary history.

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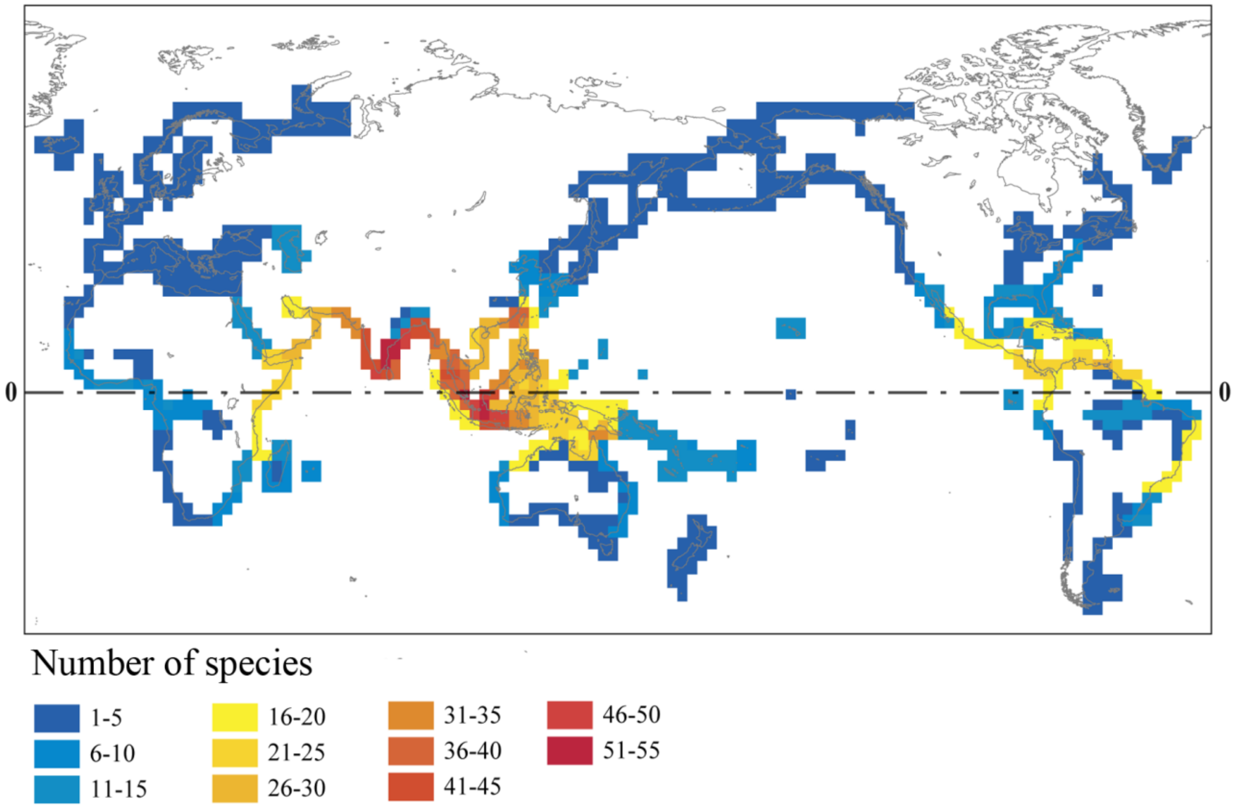

FIGURE 1-1. Distribution and species richness of the clupeoid fishes in the world. Cool colours represent low species diversity, and warm colours high diversity (modified from Lavoué et al., 2013)

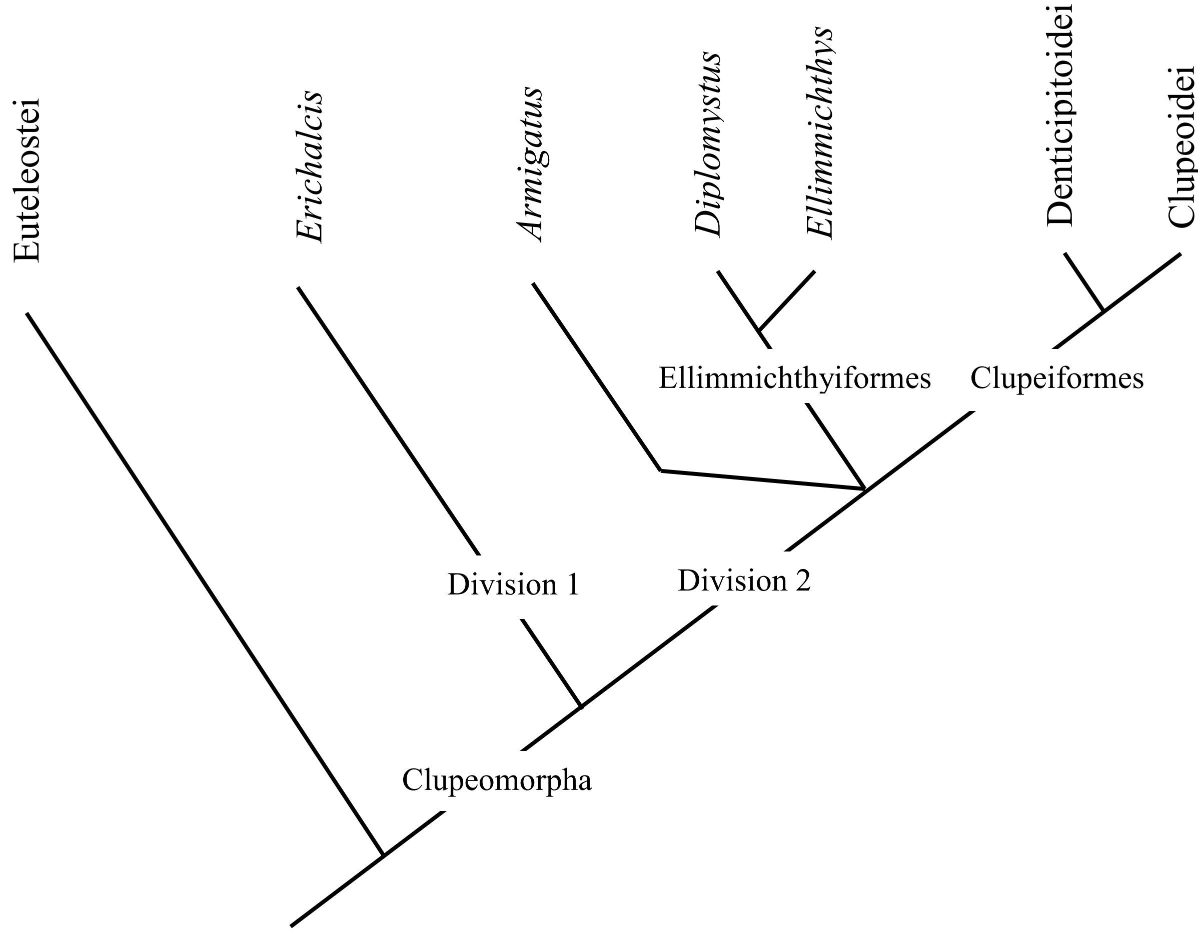

FIGURE 1-2. Hypothesis of phylogenetic relationships within the Clupeomorpha by Grande (1985).

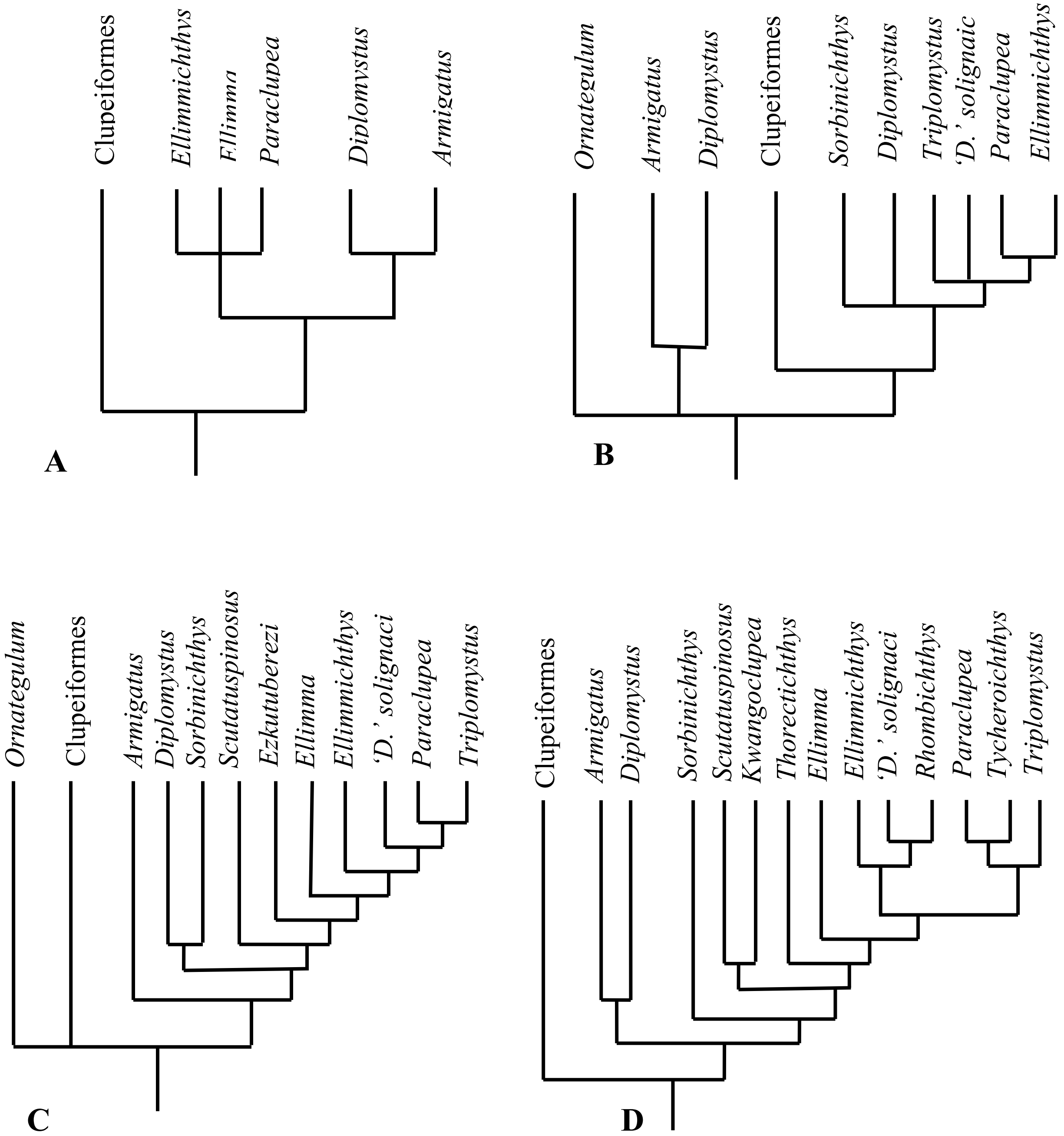

FIGURE 1-3. Phylogenetic hypotheses of the Ellimmichthyiformes by: **A** – Chang and Maisey (2003); **B** – Zaragüeta-Bagils (2004); **C** – Alvarado-Ortega et al. (2008); **D** – Murray and Wilson (2013)

Chapter 2: A new species of *Armigatus* (Clupeomorpha, Ellimmichthyiformes) from the Late Cretaceous of Morocco, and its phylogenetic relationships

2.1 Introduction

The Ellimmichthyiformes are an extinct order of the clupeomorph fishes. This group includes a number of fossil species from marine, estuarine, and freshwater sediments ranging in time from the Early Cretaceous to the Eocene. Members of the Ellimmichthyiformes have a worldwide distribution including localities in South and North America, Africa, Europe, and Asia. Recently, more new fossil clupeomorph species have been described from sites in Morocco, Mexico, Argentina, and Brazil (Figueiredo, 2009; Gallo et al., 2011; Murray and Wilson, 2013; Alvarado-Ortega, 2014). While these newly described specimens help our understanding of clupeomorph phylogeny, relationships of certain groups remain problematic.

The genus *Armigatus* Grande, 1982 has long been a subject of controversy regarding its relationship to the rest of the members of the order Ellimmichthyiformes. In the fundamental works on clupeomorph systematics, Grande (1982, 1985) placed *Armigatus* outside the Ellimmichthyiformes. Similarly, Zaragüeta-Bagils (2004) and Alvarado-Ortega et al. (2008) excluded the genus *Armigatus* from the order, while Chang and Maisey (2003), Forey (2004), Hay et al. (2007), and Murray and Wilson (2013) placed *Armigatus* within the Ellimmichthyiformes. *Armigatus* includes three species (*A.alticorpus* Forey et al., 2003*,* *A.brevissimus* (Blainville, 1818)*,* and *A.namourensis* Forey et al., 2003), all known from Upper Cretaceous (Cenomanian) deposits of Lebanon. Here, I provide a description of the new ellimmichthyiform from the marine Cenomanian/Turonian deposits of southeastern Morocco.

Results of morphological and phylogenetic analyses show that the specimens represent a new species that belongs in the genus *Armigatus*.

2.2 Geological settings

The fossil specimens were recovered from the Akrabou Formation in southeastern Morocco. This formation is known from the numerous discoveries of its diverse ichthyofauna described by Cavin and Dutheil (1999), Cavin et al. (2010), Martill et al. (2011), Murray and Wilson (2013, 2014), and others. The fish-bearing horizon lies near the top of the Gara es Sbaa hill, above a blocky limestone layer and is composed of a laminated limestone.

Part of the carbonate Moroccan Cretaceous North Saharan Platform, the Akrabou Formation was deposited during the incursion of the Tethys Sea and probably had a minor connection with the Atlantic Ocean to the east (Ettachfini and Andreu, 2004; Engel et al., 2012; Murray et al., 2013). Based on the presence of the ammonoid *Neolobites vibrayeanus* (Cavin et al., 2010) and a lithology (silica nodules) similar to a better studied section (Engel et al., 2012), the Akrabou Formation has been dated as late Cenomanian to early Turonian. Stable isotope analysis showed that the paleoenvironment of the locality was a normal marine setting with a temperature around $24.81^{o}C$ (Engel et al., 2012; Murray et al., 2013). A detailed stratigraphic section of the Agoult locality was previously published by Engel et al. (2012).

2.3 Material and Methods

Description of the new species is based on eight specimens housed in the collections of the University of Alberta, Laboratory for Vertebrate Paleontology (UALVP). One specimen is preserved as part and counterpart, while the others are each on a single slab. Most of the specimens preserved as natural moulds, from which latex peels were made. All specimens are adult fish as determined from the high degree of ossification and development of the skeletons. All fish are complete preserved in lateral view, well-articulated, and with no significant damage or displacement of the elements.

The original fossils as well as latex peels of several specimens were examined under a Wild M3 stereomicroscope. Drawings and reconstructions were made based on digital photographs of the specimens and interpretations of camera lucida drawings. Photographs for figures 2-2 and 2-3 were taken under UV light.

2.3.1 Comparative material

For the purposes of the taxonomic description and phylogenetic analysis, I analyzed the following specimens based on personal observations: *A. brevissimus* (Blainville, 1818): UALVP 5087,17620, 47258; *D. dentatus* (Cope, 1877): UALVP 17731, 21163, 22860; *Sorbinichthys africanus* Murray and Wilson, 2011: UALVP 51640 (holotype), 47186, 51641; *Thorectichthys marocensis* Murray and Wilson, 2013: UALVP 47178 (holotype), 51647, 51649, 51657, 51659; *T. rhadinus* Murray and Wilson, 2013: UALVP 51653 (holotype), 51664.

2.3.2 Phylogenetic analysis

The phylogenetic analysis was based on the existing character matrix used in earlier works on ellimmichthyiform phylogeny by Zaragüeta-Bagils (2004), Alvarado-Ortega et al. (2008), and Murray and Wilson (2013). A total of 31 taxa were used for the phylogenetic analyses including the species of Ellimmichthyiformes listed in Section 2.3.1, the new species of *Armigatus* described here, and five outgroup taxa, three chosen from the ellimmichthyiform sister group Clupeiformes (*Chirocentrus dorab* Forsskål, 1775, *Denticeps clupeoides* Clausen, 1959, *Odaxothrissa vittata* Regan, 1917), along with *Ornategulum sardinoides* Forey, 1973(which is thought to be a basal clupeomorph), and *Chanos chanos* (Forsskål, 1775), a member of the sister group to Clupeomorpha: Ostariophysi (Chanidae, Gonorhynchiformes).

The list of characters and states used is from Murray and Wilson (2013) and includes a total of 62 characters (Appendix 2-1). Morphological data for the new species were coded and added to the character matrix (Appendix 2-2). The phylogenetic analysis was done using TNT 1.1 (Goloboff et al., 2008) employing heuristic search methods with 1000 replicates and tree bisection and reconnection (TBR) swapping algorithm. The most parsimonious trees (MPTs) generated by the initial analysis were used to construct a strict consensus tree. Tree length, consistency (C.I.) and retention (R.I.) indices were calculated for the strict consensus tree in Mesquite v.2.75 (Maddison and Maddison, 2011).

2.4 Systematic Paleontology

Subdivision TELEOSTEI Müller, 1845

Cohort CLUPEOCEPHALA Patterson and Rosen, 1977

Superorder CLUPEOMORPHA Greenwood et al., 1966

Order ELLIMMICHTHYIFORMES Grande, 1982

Family ARMIGATIDAE Murray and Wilson 2013

ARMIGATUS Grande, 1982

ARMIGATUS OLIGODENTATUS, sp. nov.

(Figs. 2-1—2-3)

Family ?Paraclupeidae unnamed species: Murray, Wilson, Gibb and Chatterton, 2013

Holotype—UALVP 51679 – a complete fish

Paratypes—UALVP 47146, 47155 (a, b), 51602, 51622, 51623, 51680, 51681 – all complete fish

Etymology—From the Greek “oligo” meaning few and Latin “dentis” – teeth, in reference to the lack of teeth on the parasphenoid and endopterygoid bones, and presence of small teeth on the upper and lower jaws.

Locality—Agoult fossil locality, near Agoult, Morocco (Akrabou Formation), top of Gara es Sbaa Hill.

Age—Cenomanian/ early Turonian (Late Cretaceous)

Diagnosis—A member of the genus *Armigatus*, based on the incomplete series of heart-shaped predorsal scutes with smooth and rounded posterior margin. Distinguished from other members of the genus by a lack of teeth on the parasphenoid and endopterygoid. Skull roof bones are not ornamented. This is a small clupeomorph about 22 – 32 mm standard length (SL), with a relatively shallow body, only 28 – 36.4% of SL. There are about nine scutes in the predorsal series. Total number of abdominal scutes is 20 – 22 with 8 – 10 postpelvic. The dorsal fin has 11 – 13 fin rays and the anal fin is supported by 12 – 14 pterygiophores. There are 38 – 40 vertebrae of which only 13 – 14 are caudal.

2.5 Description

General body form—This small clupeomorph has a moderately deep body with a smooth dorsal outline, lacking an abrupt angle at the dorsal fin origin (Fig. 2-1). All specimens of the new species have a similar size, between 22 and 32 mm. All the specimens are preserved in lateral view, which suggests that the body of the fish was laterally compressed. The general body form and proportions (Table 2-1) are very similar to those of *Armigatus namourensis* (Forey et al. 2003).

The greatest body depth varies from 28 % to 36 % of standard length (SL), with the holotype (UALVP 51679) being 33%. The head length from the tip of the dentary to the posterior edge of the opercle is 32 % to 35 % of SL. The caudal fin is strongly forked, with the fin being roughly 25% of SL. There is a negative correlation between body depth and standard length in the species, with smaller individuals having slightly greater relative body depths than larger individuals, which is similar to the situation noted by Forey et al. (2003) for *Armigatus namourensis*.

The dorsal fin originates close to the midpoint of the body, with the predorsal length being 46 – 52 % of SL. The pelvic fin originates just behind the level of the origin of the dorsal fin with the prepelvic length 50–58% of SL. The anal fin is poorly preserved in most of the specimens but where it can be identified it originates at a level approximately half way between the dorsal fin insertion and the caudal fin, with the preanal length from 75% to 81.8% of SL.

Skull roof—The skull roof is not well-preserved in any of the specimens, and the bones of the posterior region are mostly crushed and displaced. Skulls are preserved in lateral view in all specimens and are elongate with the head length/head depth ratio ranging from 1.0 to 1.3 (1.0 in the holotype). As in *Thorectichthys rhadinus* (UALVP 51664, 51653) and species of *Armigatus*, the skull roof is not steeply inclined, but slopes gradually in a straight line from the anterior part of the frontal bones to the posterior end of the skull (Fig. 2-2). The frontals are long, narrow anteriorly between the orbits, and expand posteriorly where they are sutured with the parietals. The parietals are small and meet each other at the midline. Due to the poor preservation, it is hard to distinguish the parietals in most specimens and identify their shape. None of the bones of the skull roof is ornamented, which is unlike the condition seen in other species of *Armigatus*. There is no recessus lateralis, which is not expected in the ellimmichthyiforms anyway.

Orbital region—Circumorbital bones are not preserved in any specimen. The parasphenoid is well preserved in all specimens; it is long and narrow in lateral view. Unlike in the other species of *Armigatus* and *Diplomystus dentatus*, the parasphenoid is edentulous. The lateral ethmoid is preserved in all specimens and reaches the parasphenoid. The autosphenotic and orbitosphenoid are best preserved in the holotype (UALVP 51679) and UALVP 51623. The sphenotic is well-developed and located in the postero-dorsal portion of the orbit. Posteriorly it contacts the head of the hyomandibula.

The mesethmoid is crushed in most of the specimens, so that it is impossible to clarify its shape. The nasals are preserved in the holotype (UALVP 51679) as well as in UALVP 51622 and 51623 and appear to be small tubular bones.

Jaws—The upper jaw is poorly preserved in all specimens with only the premaxilla being clearly visible in the holotype (UALVP 51679). The premaxilla is small with an expanded anterior end and does not exclude the maxilla from the gape. The maxilla and supramaxillary bones are crushed in the holotype but can be identified in UALVP 51622 and 51681. There are two supramaxillae but details of the bones cannot be distinguished. It is most likely that the general shape and position of the supramaxillary bones are similar to those of other ellimmichthyiforms with the posterior supramaxilla being slightly larger than the first supramaxilla and having an anterior process overlying the anterior supramaxilla. The dentary is narrow at the symphysis and similar to that of other *Armigatus* spp. and *Thorectichthys rhadinus*. The anguloarticular is crushed in all specimens and details of the bone cannot be identified. Unlike in many ellimmichthyiforms, the mouth is not sharply upturned but rather it is terminal. Teeth on the upper jaw cannot be seen, but it is most likely that they were present in this fish, but are not preserved in the specimens or are obscured by a lamina. The dentary bears poorly developed teeth. A similar condition is seen in *Thorectichthys rhadinus* (UALVP 51653).

Hyopalatine bones and gill arches—The hyomandibula has a single head reaching slightly above the level of the dorsal tip of the preopercle. The shaft of the hyomandibula is the same width as the head and is not ornamented, unlike in *Armigatus namourensis* which is characterized by a long and narrow shaft with a prominent lateral ridge (Forey et al., 2003). The metapterygoid is crushed in most specimens, but the position of the quadrate suggests the metapterygoid has a similar shape and position to that of *Armigatus* and *Diplomystus*, being subrectangular and placed dorsally relative to the quadrate. The quadrate is subtriangular and appears to be larger than the metapterygoid. The palatine and ectopterygoid bones are not visible in any specimen. Traces of the endopterygoid are preserved in the holotype and UALVP 47146, 51622, 51623, and 51681. There are no teeth on the endopterygoid.

There are at least seven branchiostegal rays preserved in UALVP 51623 and 51681. The anterior and posterior ceratohyals can also be identified in UALVP 47146. Similar to the condition seen in *Rhombichthys intoccabilis* Khalloufi et al., 2010, the anterior ceratohyal is hourglass-shaped and has a narrow beryciform foramen (Fig. 2-2). The posterior ceratohyal is subtriangular and smaller than the anterior ceratohyal.

Opercular series—The opercle is large, about two times deeper than long, with a rounded posterior margin (Fig. 2-2). The subopercle appears to be mostly covered by the opercle. The preopercle is poorly preserved in all specimens, showing only impressions of the dorsal limb; the ventral limb of the preopercle is missing in most specimens. Most likely, the preopercle is L-shaped with smooth margins similar to those of *Diplomystus* and other species of *Armigatus*. The sensory canal on the preopercle is partially preserved in the holotype (UALVP 51679) and appears to be enclosed in bone, but the exact number of pores cannot be determined. The interopercle is covered by the preopercle and is not visible in any of the specimens.

Paired fins and girdles—The pectoral girdle is fairly well preserved in all specimens. In the holotype, the posttemporal, supracleithrum, cleithrum, scapula, and coracoid can be identified. A single postcleithrum is partially preserved in each of the holotype and UALVP 51623 and appears to be thin and pointed at the posteroventral end. The post-temporal is elongate and has a distinct comma-shaped appearance. The dorsal arm of the post-temporal is long and sharp, while the ventral arm appears as an anteroventral expansion of the bone.

The supracleithrum is best preserved in UALVP 51602. It is relatively long and narrow, similar in shape to that of *Armigatus namourensis* (Forey et al., 2003) and *Thorectichthys marocensis*, UALVP 47178 (Murray and Wilson, 2013; Fig.2-2). Ventrally, the supracleithrum contacts the well-developed S-shaped cleithrum. The cleithrum is narrow at its dorsal tip but gradually becomes broader as it smoothly follows the posterior margin of the opercle. The lower part of the cleithrum is convex anteriorly and reaches ventrally below the opercular series. The ventral tip of the cleithrum is pointed. The scapula and coracoid are partially preserved in each of the holotype and UALVP 51623. Details of these bones as well as radials cannot be determined. There are at least eight pectoral fin rays visible in the holotype, but the pectoral fins are best preserved in UALVP 51622, 51680, 51681, and 51623b with 11 – 13 fin rays preserved.

The pelvic girdle is poorly preserved in all specimens, so that it is only possible to determine the position of the fin, but not the actual number of the fin rays. The number of pelvic fin rays present varies from six to nine in the specimens with the pelvic fin best preserved (UALVP 41755, 51602, 51622, 51680).

Predorsal bones, dorsal and ventral scutes—Predorsal bones (supraneurals) are well preserved in the holotype as well as in UALVP 51623 and 51681. There are eight long and narrow predorsal bones in the holotype and UALVP 51623 and at least seven bones in UALVP 51681.

There are two series of scutes present: predorsal and abdominal. Predorsal scutes are poorly preserved in most specimens. There are nine predorsal scutes in the holotype and at least five scutes can be identified in front of the dorsal fin in UALVP 51681. The predorsal series of scutes is similar to that of other *Armigatus* species; it runs from the origin of the dorsal fin anteriorly but does not reach the occiput, which leaves a gap with no scutes just posterior to the skull. According to Grande (1982), this is a characteristic feature for the genus *Armigatus*. Additionally, the predorsal scutes have similar shapes and sizes to those of other *Armigatus* species– they are small and heart-shaped. Even though no ornamentation can be observed on the scutes, as is found in other species of *Armigatus*, this could be a result of poor preservation. There is no variation in the size of the predorsal scutes.

The abdominal series consists of a total of 20 – 22 robust scutes, of which 11 – 13 are prepelvic and 8 – 10 are postpelvic. The abdominal scutes have prominent spine-like lateral wings that reach up to about 15% of the body depth, significantly shorter than those of *Tycheroichthys* Hay et al. 2007 and *Triplomystus* Forey et al. 2003. The lateral wings of the abdominal scutes are narrow and contact one another only at their ventralmost extent.

Median fins—The triangular dorsal fin is positioned close to the midpoint of the body. It is made up of at least 11-13 principal rays and supported by 13 pterygiophores (UALVP 51679). The second dorsal fin ray is the longest – a condition also seen in other species of *Armigatus* (Forey et al., 2003). The anal fin is long, but poorly preserved in most of the specimens so that it is hard to determine the exact shape and number of fin rays. There are approximately 12 – 14 pterygiophores (12 pterygiophores in the holotype UALVP 51679) supporting the anal fin, which is less than in most Ellimmichthyiformes.

Vertebral column—There are 38 – 40 vertebrae including two ural centra. Of these, 14 – 15 are caudal centra. Throughout the anterior abdominal region the neural arches carry paired neural spines. Posterior to the 15/16th vertebra, the neural spines are unpaired, with the left and right halves being fused in the midline.

There are 18 pairs of pleural ribs (on most specimens the count is difficult to make due to the preservation). The anteriormost 10-11 pairs of ribs are inserted into pits on the lateral sides of abdominal centra, while the posterior ribs articulate with parapophyses. This condition is also found in many ellimmichthyiforms: *Triplomystus, Thorectichthys*, and *Tycheroichthys* (Forey et al., 2003; Hay et al., 2007; Murray and Wilson, 2013), in contrast to *Armigatus namourensis* in which all pleural ribs articulate with parapophyses (Forey et al., 2003).

Both epineurals and epipleurals can be identified in the holotype (UALVP 51679) and paratypes (UALVP 51623, 51681). The series of epineurals is not well-preserved and only few epineural bones associated with the vertebrae 10 through 26 (preural 10) can be identified. Epineurals have a length of approximately two centra. The epipleural series is visible from the abdominal centrum 17 to 26 (preural 10) with the longest epipleural having the length of 2.5 centra.

Caudal fin—The caudal fin is forked, but not as deeply as in *Triplomystus noorae* Forey et al., 2003*, Thorectichthys marocensis*, and *Diplomystus dentatus*, being more similar to that of *Armigatus namourensis*. It is about 25% of the total length of the fish. Details of the fin are best preserved in the holotype (Fig. 2-3).The first ural centrum is only slightly smaller than the first preural centrum.

The first preural centrum has a short and broad neural spine. The first ural centrum is fused with hypural 2, which is one of the diagnostic characteristics for clupeomorphs. Hypural 1 is autogenous and lies close to the first ural centrum, but is not fused to it.

There are six hypurals in total, five of which can be clearly identified on the holotype and the sixth hypural is overlapped by fin rays. There is no diastema between hypurals 2 and 3 (Fig. 2-3). There are two long and slender uroneurals that are of equal length. The first uroneural extends anteriorly to the midpoint of the first preural centrum and does not reach the second preural centrum.

Hypural 1 is broad at the posterior end while hypural 2 is long and narrow. Hypural 3 is similar in shape and size to the first hypural, while hypurals 4 and 5 appear to be triangular and smaller in size. There are 19 principal fin rays with ten rays in the upper lobe and nine in the lower. There are six to eight procurrent rays (UALVP 51680, 51679, 51681) in both upper and lower lobes of the fin.

2.6 Phylogenetic results

The initial analysis of 62 morphological characters generated six most parsimonious trees which were used to construct a strict consensus tree of length 225 steps and relatively low consistency and retention indices (C.I.=0.35; R.I.=0.57) suggesting significant amounts of homoplasy. Bootstrap analysis of the strict consensus tree showed that only four clades had support values over 50 percent (Fig. 2-4). In all six most parsimonious trees, the new species belongs to the clade that includes the three previously described species of *Armigatus*, and together they form the sister-group to the Paraclupeidae. Similar to the results obtained by Murray and Wilson (2013) and Alvarado-Ortega et al. (2008), Ellimmichthyiformes was recovered as a monophyletic group. The strict consensus tree (Fig. 2-4) contains two polytomies within the Ellimmichthyiformes: one basal polytomy among the species of *Diplomystus*, and a trichotomy within Paraclupeidae including *Ellimmichthys maceioensis* Malabarba et al., 2004, *'Diplomystus' solignaci* Guadant and Guadant, 1971, and *Rhombichthys intoccabilis*.

Both *Ellimmichthys* and *Diplomystus* were revealed as polyphyletic genera. It has been well-established by previous phylogenetic studies (Zaragüeta-Bagils, 2004; Alvarado-Ortega, 2008; Murray and Wilson, 2013) that *'Diplomystus' solignaci* does not belong to the genus *Diplomystus*, but is rather more closely related to *Rhombichthys intoccabilis* and *Ellimmichthys* *maceioensis*. In this study, I included three species of *Ellimmichthys* which helped to resolve a problem concerning relationship of the type species, *E.longicostatus* Cope, 1886, noted by Murray and Wilson (2013). As revealed by the analysis, *E.longicostatus* and *E.goodi* (Eastman, 1912) form a clade that is sister to the tribe Triplomystini Murray and Wilson (2013), while the third species of *Ellimmichthys*, *E.maceioensis*, appears in a polytomy with *'Diplomystus' solignaci* and *Rhombichthys intoccabilis*.

2.7 Discussion

The phylogenetic hypothesis presented here suggests that the new species belongs to the Armigatidae which was recovered as a sister group to the Paraclupeidae. In the resulting strict consensus tree, the new species is placed as a member of the genus *Armigatus* based on the two synapomorphies that distinguish members of this genus from the rest of the Ellimmichthyiformes: incomplete series of predorsal scutes, and heart-shaped predorsal scutes with smooth and rounded posterior margins. Forey (2004) recognized these characters as derived and autapomorphic for the genus. In contrast, the subrectangular shape of the predorsal scutes was used by Grande (1982, 1985) as a single character to group members of the Ellimmichthyiformes, and therefore he excluded *Armigatus* from that order. Initially, Grande (1982, 1985) included only two genera in the Ellimmichthyiformes, *Ellimmichthys* and *Diplomystus*, based on this scute shape character. However, *Paraclupea* Sun, 1956 was later reevaluated and added to the order with the family Ellimmichthyidae synonomized with Paraclupeidae, and the latter having nomenclatural priority (Chang and Grande, 1997). Description of new fossil clupeomorphs, in particular *Ellimma* Jordan, 1913 and *Scutatuspinosus* Silva Santos and Silva Corréa, 1985 that have subrectangular scutes only in the posterior part of the predorsal series, showed that the shape of the dorsal scutes as a diagnostic character of the Ellimmichthyiformes needed to be reevaluated. In recent phylogenetic studies (Zaragüeta-Bagils, 2004; Alvarado-Ortega et al., 2008, Murray and Wilson, 2013) this character was split into two: presence of subrectangular scutes in the anterior part of predorsal series and subrectangular scutes in the posterior part of predorsal series. The latter character alone was used by Alvarado-Ortega et al. (2008) to group members of the Ellimmichthyiformes.

Variation in the numbers and shapes of predorsal scutes is also observed in the extant members of the order Clupeiformes that include fishes with no predorsal scutes as well as those with complete or partial series of predorsal scutes. Interspecific variation in the shape of predorsal scutes occurs in two living species of *Hyperlophus* Ogilby, 1892 with the first dorsal scute in *H. vittatus* Castelnau, 1875 having an elongate oval shape while in *H. translucidus* McCulloch, 1917 it is broader than long and has a subrectangular shape (Yabumoto and Uyeno, 1982). Considering this variability in the pattern of the predorsal scute series, it is necessary to find characters other than those associated with the dorsal scutes to support monophyly of the Ellimmichthyiformes, as noted earlier by Chang and Maisey (2003).

Whether or not the dorsal scute morphology is apomorphic for *Armigatus* or Ellimmichthyiformes, the new species shares at least two derived characters with the Armigatidae (*Armigatus* and *Diplomystus*). These fish have no diastema between the second and third hypurals, and uroneural 2 reaches the distal end of the first uroneural. Therefore, placement within this family is confirmed.

The topology of the strict consensus tree showed a number of differences from the phylogenetic hypotheses published previously. As revealed by the analysis, the Ellimmichthyoidei are a paraphyletic group with the Sorbinichthyidae being the most basal clade of the Ellimmichthyiformes with the next most basal clade containing four species of *Diplomystus*. Members of the monogeneric family Sorbinichthyidae are characterized by the L-shaped cleithrum (22: 0), prominent shape of the dorsal process of the posttemporal (23:2), only five hypurals (26:2), large diastema with a concave ventral edge (32:2), fewer than 20 abdominal scutes (61:0), and ten or more predorsal bones (62:0).

The next most basal clade within Ellimmichthyiformes includes *Diplomystus* species (excluding *'D.'solignaci*). Relationships of this group within the Ellimmichthyiformes are uncertain. Forey (2004) grouped *Diplomystus* with *Sorbinichthys* Bannikov and Bacchia, 2000 and *Triplomystus*; Alvarado-Ortega et al. (2008) placed *Diplomystus* and *Sorbinichthys* in the family Sorbinichthyidae, and Murray and Wilson (2013) included *Diplomystus* with *Armigatus* in the family Armigatidae within the suborder Armigatoidei. In the present analysis, the sister-group relationship of *Diplomystus* and *Armigatus* was not supported, resulting in Armigatidae being a paraphyletic group. The following characteristics that were previously used to group *Armigatus* and *Diplomystus* together (Murray and Wilson, 2013), appeared to be homoplastic: absence of diastema between second and third hypurals (31:1), and distal ends of the first and second uroneurals reaching the same level (38:0). Chang and Maisey (2003) also recognized presence of teeth on the parasphenoid and endopterygoid as a shared characteristic for these two genera. However, not all members of *Armigatus* and *Diplomystus* have teeth on both the parasphenoid and endopterygoid bones; *D. shengliensis* Zhang et al., 1985 has no teeth on the parasphenoid (Chang and Maisey, 2003) and the parasphenoid and endopterygoid are edentulous in the new species (although it is possible that teeth were present on these bones, but were not preserved in the specimens). Absence of the endopterygoid teeth as well as poorly developed teeth on the upper and lower jaws, and small size of the individuals may suggest a different feeding behavior, most likely filter feeding. A similar pattern is observed in extant members of the Clupeiformes (*Alosa*, *Clupeoides*, *Sprattus*, etc.) with different species of the same genus having different degrees of tooth development based on their diet.

Paraclupeidae is recovered by the analysis as the sister-group to *Armigatus* and includes *'Diplomystus' solignaci*, *Ellimmichthys*, *Ezkutuberezi* Poyato-Ariza et al., 2000, *Kwangoclupea* (Casier, 1965), *Paraclupea, Rhombichthys*, *Scutatuspinosus*, *Thorectichthys*, *Triplomystus*, and *Tycheroichthys*. This family is supported by the following characteristics: fused halves of the neural arches of most abdominal vertebrae (18:1), irregular size of scutes in the predorsal series (52:1), and postpelvic abdominal scutes with a strong ventral spine (57:1).

The most basal clade within Paraclupeidae includes *Kwangoclupea dartevellei* (Casier, 1965) as sister group to the monogeneric subfamily Thorectichthyinae. These two groups share the presence of hypural 1 with a massive proximal end forming an upward process (29:0) and a prominent median spine on scutes in the posterior part of predorsal series (51:0).

The next most basal clade comprises *Scutatuspinosus itapagipensis* Silva Santos and Silva Corréa, 1985, *Ezkutuberezi carmenae* Poyato-Ariza et al., 2000, and an unresolved trichotomy formed by *Rhombichthys intoccabilis*, *Ellimmichthys maceioensis*, and *'Diplomystus' solignaci*. The latter polytomy corresponds to the subfamily Ellimmichthyinae Murray and Wilson (2013). However, in this study I included the type species of *Ellimmichthys*, *E. longicostatus*, that is recovered as a sister species to *E. goodi.* Therefore relationships among the species forming the unresolved trichotomy should be further studied and clarified.

Paraclupea chetungensis Sun, 1956 and *Tycheroichthys dunveganensis* Hay et al. 2007 were recovered as sister taxa. This group is supported by homoplastic characters: distal end of second uroneural not reaching the distal end of the first uroneural (38:1), epineurals located far from the spine of the second preural centrum leaving a gap between them (42:1), 16 – 19 predorsal scutes (54:1), and more than 32 abdominal scutes (61:2).

The next clade includes two sister groups *Ellimmichthys* (excluding *E. maceioensis*) and *Triplomystus*. This clade is supported by the following homoplasies: presence of epipleurals (21:1), first uroneural with a dorsal expansion of laminar bone (37:1), and first ural centrum with a neural arch (45:1). The small clade comprising two species of *Ellimmichthys* (*E. goodi* and *E. longicostatus*) is characterized by eight to eleven anal fin rays (24:0), second hypural with the distal end significantly broader than proximal end (30:0), large neural spine of the first preural centrum (44:0), and six to fourteen predorsal scutes (54:0). Genus *Triplomystus* is supported by first ural centrum significantly smaller than the preural centra (33:1), two uroneurals (34:1), and presence of the postdorsal scute series (60:1).

2.8 Conclusions

Results of the morphological description and phylogenetic analysis indicate that the new species of clupeomorph from the upper Cenomanian/lower Turonian deposits of Morocco belongs to the genus *Armigatus*. This is the first record of the genus from the western part of the Mediterranean region. Previously, *Armigatus* was only known from the Cenomanian localities of Lebanon and a single occurrence in the Cenomanian sediments of Portugal (Forey et al., 2003). Therefore, the new species of *Armigatus* extends the distribution of the genus to the west and south across the Tethys Sea. Western (Morocco) and eastern (Lebanon) regions of the Tethys share two ellimmichthyiform taxa, *Sorbinichthys* and Paraclupeidae. This pattern of distribution is consistent with the ideas proposed by Alvarado-Ortega et al. (2008) and Murray and Wilson (2013) that *Sorbinichthys* and *Armigatus* originated in the eastern Tethys during the Late

Cretaceous. *Diplomystus*, which was placed within Sorbinichthyidae by Alvarado-Ortega et al. (2008) and within Armigatidae by Murray and Wilson (2013), also probably arose in the eastern Tethys and reached North America and Asia by the Early Cenozoic.

Inclusion of this Moroccan species of *Armigatus* in the phylogenetic analysis supported placement of the genus within the Ellimmichthyiformes as was previously suggested by Chang and Maisey (2003), Forey (2004), Hay et al. (2007), and Murray and Wilson (2013). However, the phylogenetic hypothesis presented here raises questions about the monophyly of *Ellimmichthys*, Armigatidae, and the position of the Sorbinichthyidae within the Ellimmichthyiformes.

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TABLE 2-1. Meristics and measurements for the eight specimens of the clupeomorph species, *Armigatus oligodentatus*, sp. nov. Measurements are given in millimeters; proportions are given as percentages.

UALVP	51679 (holotype)	47146	47155	51602	51622	51680	51681	51623
Standard length (SL)	32	23	22	25	27	24	28	31
Total length	37	30	29	30	31	29	34	37
Head length	10	8	7	8	9	8	9	10
Head length/SL	31	35	32	32	33	33	32	32
Head depth	10	7	6.5	6	7	6.5	7	9
Head depth/SL	31	30	30	24	26	27	25	29
Greatest body depth	10	8	8	7	9	8	9	9
Body depth/SL	31	35	36	28	33	33	32	29
redorsal length	15	12	11	12	13	11	14	15
Predorsal length/SL	47	52	50	48	48	46	50	48
Prepelvic length	17	13	12	14	15	12	16	18
Prepelvic length/SL	53	57	55	56	56	50	57	58
Preanal length	24	?	18	19	21	?	22	24
Preanal length/SL	75	?	82	76	78	?	79	77
Longest dorsal ray length	5	3	3.5	3.5	3	4	?	5
Longest dorsal ray length/SL	16	13	16	14	11	17	?	16
Head length/head depth	1	1.1	1.1	1.3	1.3	1.2	1.3	1.1
Dorsal fin rays	?13	11	?10	11	13	?	11+	?12
Anal fin rays	?12	?	?	?	?	?	?14	?
Pectoral fin rays	8+	8+	?	8	11-13	11+	?12	?11
Pelvic fin rays	?	?	9	7	7-8	6	4+	?6
Caudal fin principal rays	19	19	19	19	?19	19	?19	19
Total vertebrae	39	38	38	37-38	38	38	38	?39
Caudal vertebrae (incl. u1+u2)	14	?	?	15	?	?	15	14
Predorsal bones	?8	?	?	?	?	?	7+	8
Abdominal scutes	18+	20	19	21	?19	18+	?21	?22
Prepelvic scutes	8+	13	?11	11	?10	8+	13	?11
Postpelvic scutes	?10	?7	8	10	?9	?10	?8	11
Predorsal scutes	?9	?	?	?	?	?9	5+	?
Pairs of ribs	?18	14+	13+	?19	15	?18	16+	18
Number of epurals	3	?3	?3	3	3	3	3	3

Number of uroneurals	2	2	2	2	2	2	2	2

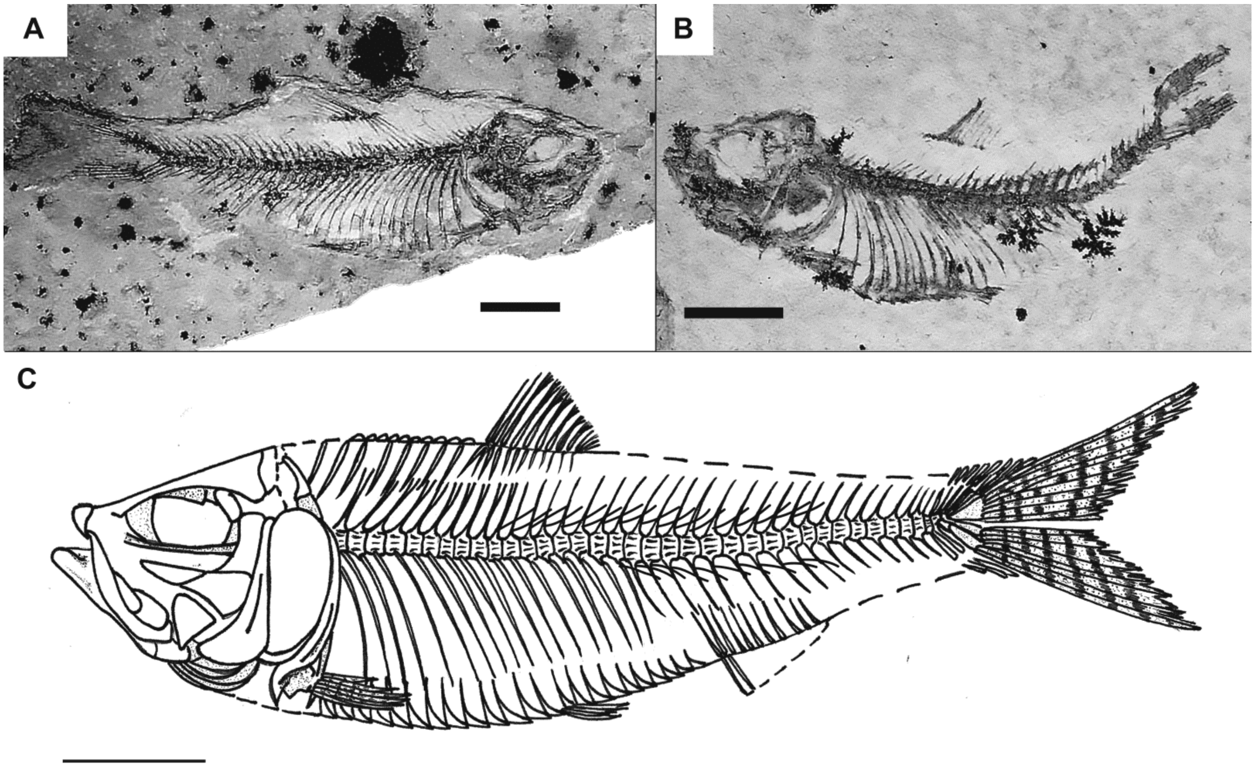

FIGURE 2-1. *Armigatus oligodentatus*, sp. nov. **A**, holotype, UALVP 51679; **B**, paratype, UALVP 51622; **C**, reconstruction of *Armigatus oligodentatus* sp. nov. based on the eight specimens. Scale bars = 5mm.

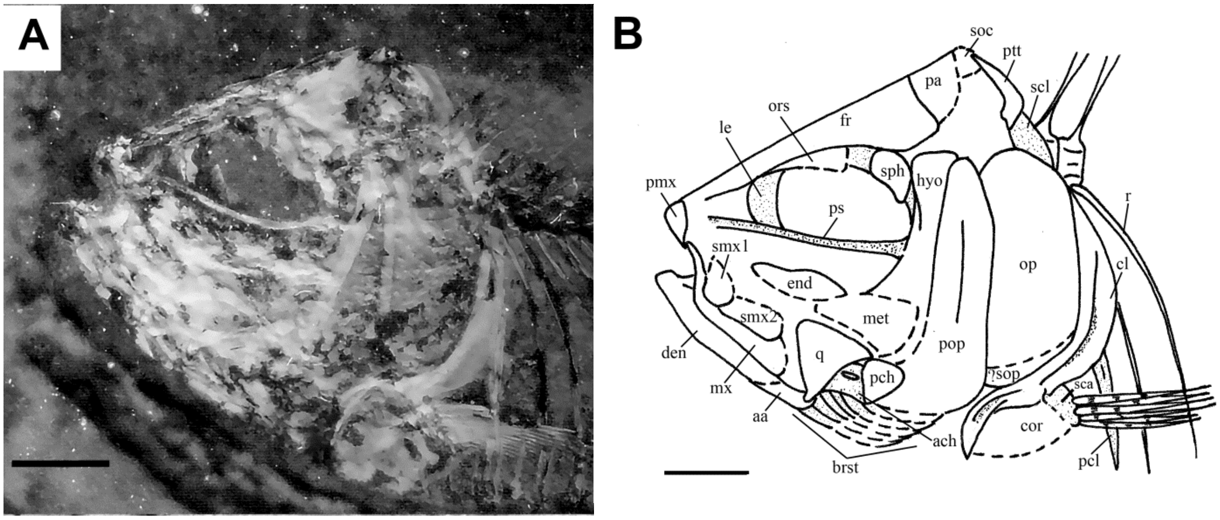

FIGURE 2-2. *Armigatus oligodentatus* sp. nov. **A**, head of a paratype, UALVP 51623 photographed under UV light; **B**, restoration of the head in left lateral view based on the holotype (UALVP 51679) and paratype (UALVP 51623). **Abbreviations**: **aa**, anguloarticular; **ach**, anterior ceratohyal; **brst**, branchiostegal rays; **cl**, cleithrum; **cor**, coracoid; **den**, dentary; **end**, endopterygoid; **fr**, frontal bones; **hyo**, hyomandibular; **sop**, subopercle; **le**, lateral ethmoid; **met**, metapterygoid; **mx**, maxilla; **op**, opercle; **ors**, orbitosphenoid; **pa**, parietal; **pch**, posterior ceratohyal; **pcl**, postcleithrum; **pmx**, premaxilla; **pop**, preopercula; **ps**, parasphenoid; **ptt**, posttemporal; **q**, quadrate; **r**, rib; **sca**, scapula; **scl**, supracleithrum; **soc**, supraoccipital; **sph**, sphenoid; **smx**, supramaxilla. Scale bars = 2 mm

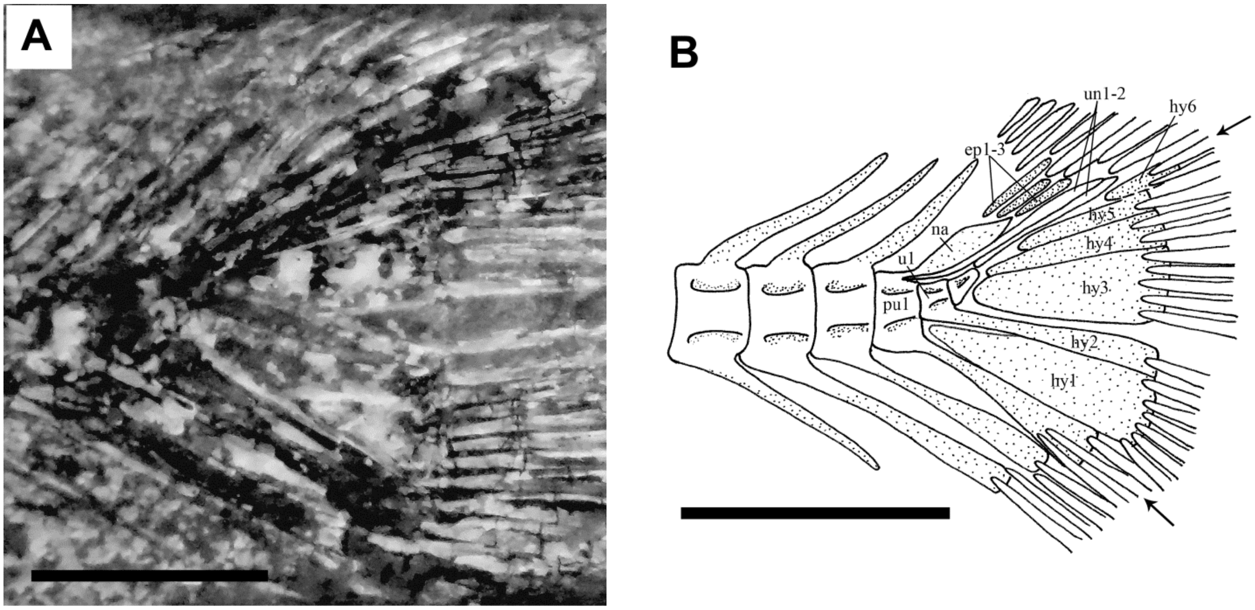

FIGURE 2-3. Caudal fin of *Armigatus oligodentatus*, sp. nov. **A**, caudal fin of the holotype, UALVP 51679 (image flipped horizontally) photographed under UV light; **B**, drawing of the caudal skeleton in left lateral view based on the holotype, UALVP 51679. **Abbreviations**: **ep 1-3**, epineurals 1-3; **hy**, hypurals; **na**, neural arch; **pu1,** first preural centrum; **u1**, first ural centrum; **un**, uroneural. Arrows point at the first principal caudal fin rays. Scale bars = 2 mm.

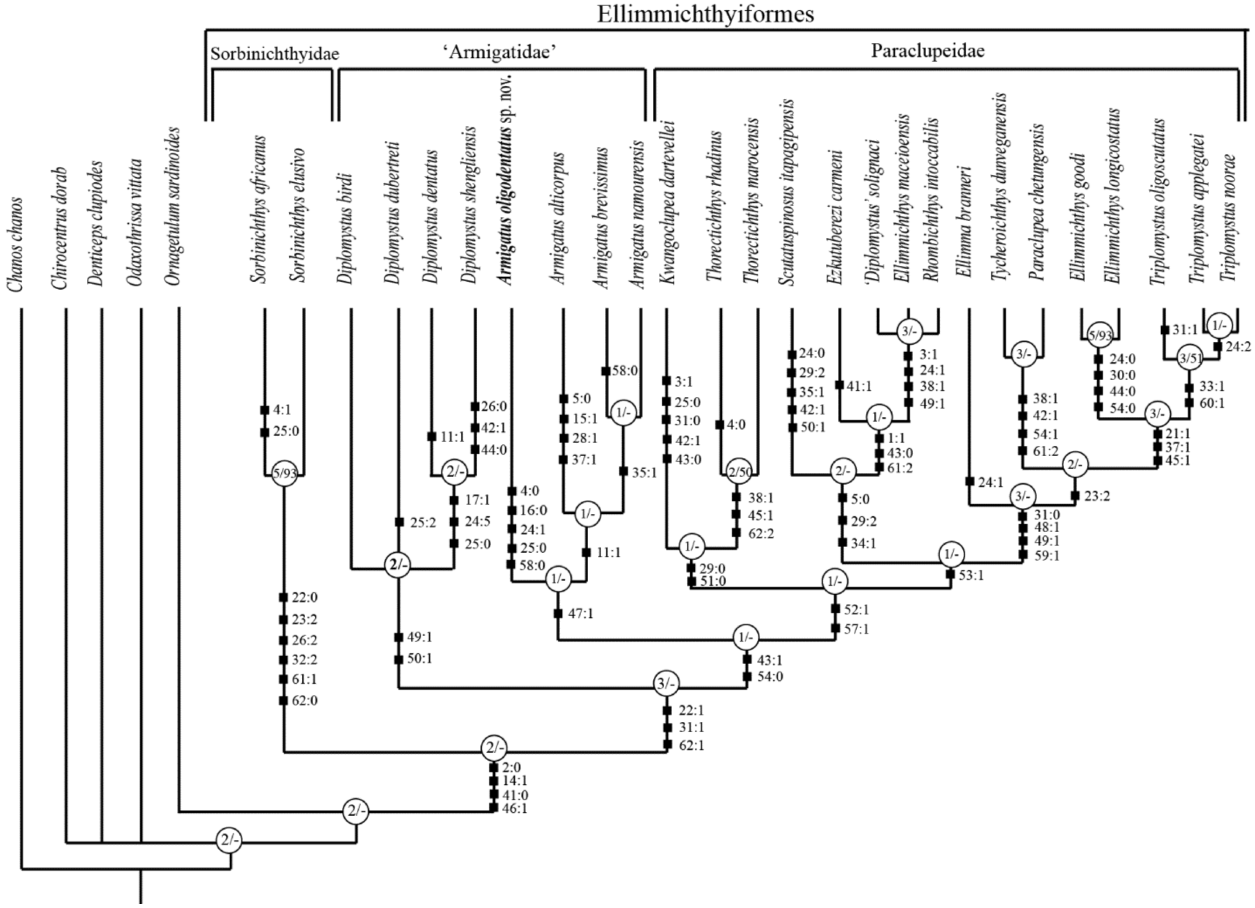

FIGURE 2-4. Strict consensus of the six most parsimonious trees retrieved in TNT 1.1 based on 62 morphological characters and 31 taxa including *Armigatus oligodentatus*, sp.nov. Characters supporting each node are listed along corresponding branches. Numbers in the circles at each node represent Bremer support/bootstrap values. Only bootstrap values higher than 50% are shown on the tree.

APPENDIX 2-1. Character state list used in the phylogenetic analysis based on Murray and Wilson (2013):

1. Anterior dorsal margin of body: [0] rounded and convex; [1] almost straight, forming a marked angle at the dorsal fin insertion.
2. Skull roof: [0] parietals bones contacting each other in the midline; [1] supraoccipital separates parietal bones.
3. Lateral profile of skull roof: [0] a straight line from anterior tip of frontal to back of skull, with no distinct angle apparent; [1] with distinct angle between anterior and posterior parts, normally in the region of the parietal.
4. Ornamentation of skull roof bones: [0] absent; [1] present.
5. Ornamentation of skull roof bones: [0] fine, more or less parallel grooves; [1] strong grooves with numerous fine, radiating ridges.
6. Posttemporal fossa: [0] absent; [1] present.
7. Cavity in the temporal region of the skull: [0] pre-epioccipital fossa (between parietal, epioccipital and pterotic bones); [1] pre-epioccipital fenestra (between the parietal, epioccipital and supraoccipital bones); [2] absence of cavity or fenestra.
8. Recessuslateralis: [0] absent; [1] present.
9. Supramaxillary bones: [0] two; [1] one or none.
10. 'Basipterygoid' process of parasphenoid: [0] absent; [1] present.
11. 'Osteoglossid' tooth patch on the parasphenoid: [0] absent; [1] present.
12. Supraorbital bone: [0] absent; [1] present.
13. Antorbital bone: [0] absent; [1] present.

14. Beryciform foramen within the anterior ceratohyal: [0] absent; [1] present.

15. Foramen in posterior ceratohyal: [0] absent; [1] present.

16. Teeth on endopterygoid: [0] absent; [1] present.

17. Total number of vertebrae excluding ural centra: [0] 30-40; [1] 41-43; [2] more than 50.

18. Halves of the neural arches of most abdominal vertebrae: [0] separate medially; [1] fused medially.

19. Pleural ribs: [0] all ribs articulate with parapophyses along the abdominal region; [1] anteriormost ribs articulate with deep pits on the lateral side of all abdominal centra and those located posteriorly articulate with well-developed parapophyses; [2] all ribs articulate with deep pits on the lateral side of all abdominal centra.

20. Epineurals and epipleurals in the caudal region: [0] absent; [1] present.

21. Epicentrals: [0] absent; [1] present.

22. Shape of cleithrum: [0] L-like (having a single angle in the bone); [1] S-like (having two angles).

23. Dorsal process of posttemporal: [0] slender and sharp; [1] sub-rectangular; [2] broad, wider at distal tip than at midpoint of bone.

24. Number of anal fin rays: [0] eight to eleven; [1] fourteen or fifteen; [2] seventeen or eighteen; [3] twenty; [4] twenty-two to thirty-two; [5] thirty-six to forty-one.

25. Number of dorsal fin rays: [0] eight to thirteen; [1] fourteen to nineteen; [2] twenty-one to twenty-five.

26. Number of hypurals: [0] seven; [1] six; [2] five.

27. Hypural 2: [0] autogenous; [1] fused to first ural centrum (diural terminology).

28. Length of hypural 1: [0] long, reaching ural centrum 1; [1] short, not reaching ural centrum 1.

29. Proximal end of hypural 1 (was originally termed “articulation of hypural 1): [0] massive and forming an upward process; [1] sharp; [2] massive but no upward process.

30. Shape of hypural 2: [0] Distal end distinctly broader than proximal end; [1] very thin and stick-like.

31. Diastema between second and third hypural: [0] third hypural not expanded posteriorly leaving a gap or notch between the second and third hypural; [1] third hypural expanded posteriorly, leaving no gap or notch between second and third hypural.

32. Shape of diastema between hypurals 2 and 3: [0] small triangular notch; [1] deep triangular cavity; [2] large concavity formed by hypural 3 having a concave ventral edge.

33. Size of first ural centrum (diural terminology): [0] roughly the same size (length and depth) as the preural centra; [1] much smaller than the preural centra.

34. Number of uroneurals: [0] three; [1] two; [2] one.

35. First uroneural: [0] extends anteriorly to reach second preural centrum; [1] does not reach second preural centrum.

36. Fusion of first uroneural and first ural centrum: [0] absent; [1] present.

37. First uroneural bearing a dorsal expansion of laminar bone: [0] absent; [1] present.

38. Distal end of second uroneural: [0] reaching the distal end of the first uroneural; [1] not reaching the distal end of the first uroneural.

39. Parhypural: [0] base/arch of bone fused with preural centrum 1; [1] autogenous.

40. Fusion of hypural two and first ural centrum: [0] absent; [1] present.

41. Number of epurals: [0] three; [1] two; [2] none, or those present are weakly ossified, perhaps cartilaginous.

42. Position of epurals: [0] epurals fill the space between the neural spines of pu1 and pu2; [1] epurals are located far from the spine of pu2, leaving an open space between them.

43. Caudal scutes: [0] absent; [1] present.

44. Neural spine of first preural centrum: [0] large or lanceolate; [1] short or sub-rectangular.

45. Neural arch of first ural centrum: [0] absent; [1] present.

46. Predorsal scutes: [0] absent; [1] present.

47. Predorsal scute series: [0] incomplete (absent in anterior part); [1] complete.

48. Subrectangular scutes (i.e., scutes significantly broader than long) in anterior part of predorsal series: [0] absent; [1] present.

49. Subrectangular scutes in posterior part of predorsal series: [0] absent; [1] present.

50. Series of spines on the posterior margin of the lateral wings of the predorsal scutes: [0] absent; [1] present.

51. Prominent median strong spine on posteriormost predorsal scutes: [0] absent; [1] present.

52. Size of scutes of predorsal series: [0] all scutes of same size; [1] irregular in size, size of scutes increasing posteriorly.

53. Surface of predorsal scutes: [0] smooth; [1] ornamented with radiating grooves.

54. Number of predorsal scutes: [0] six to fourteen; [1] sixteen to nineteen; [2] twenty to forty-one.

55. Abdominal scute series: [0] absent; [1] present.

56. Complete abdominal scute series between isthmus and anus (i.e., postpelvic scutes are present): [0] absent; [1] present.

57. Postpelvic abdominal scutes bearing very prominent and strong ventral spine: [0] absent; [1] present.

58. Size of lateral wings of abdominal scutes: [0] small; [1] large, extended upward and covering the abdominal cavity laterally for at least one quarter of the distance from ventral body edge to vertebral column.

59. Shape of lateral wing of abdominal series scutes: [0] spine-like, with large spaces between wings of scutes; [1] wide or spatula-like, with wings of adjacent scutes touching for most of their length.

60. Postdorsal scute series: [0] absent; [1] present.

61. Number of abdominal scutes (in some taxa they will not be equivalent to vertebral counts): [0] fewer than 20; [1] 22-30; [2] more than 32.

62 Number of predorsal bones: [0] 10 or more; [1] 7-9; [2] 6 or fewer.

APPENDIX 2-2. Data matrix used in the phylogenetic analysis based on the matrix of Murray and Wilson (2013) and Alvarado-Ortega et al. (2008).

	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	66
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12
Chanos chanos	0100-?20?0	01?0001001	1100110111	00-1-10110	100100----	----0----0	-0
Chirocentrus dorab	010??10100	0110002101	1014111111	0100-10011	100100----	----10--00	-?
Denticeps clupeoides	0100-02110	0010110021	1014021020	0102101101	100110----	----110000	0?
Odaxothrissa vittata	0100-10110	01100111?1	1012111111	0100-10011	000100----	----110100	00
Ornategulum sardinoides	0001100001	0111?12001	?0?0101121	??00001001	000100----	----0----0	-0
Armigatus alticorpus	000101??01	111?110000	?10?1111?0	0?00001000	0011?10000	000?110100	??
Armigatus brevissimus	000111?001	1?11??000?	?104111011	1-00100001	00?1010000	10??11?000	12
Armigatus namourensis	000111?001	11?1010001	0104111011	1-00100001	0011010000	1011110100	12
Armigatus oligodentatus	0000-??001	0??1000011	0101011011	10000000?1	0?11010??0	00?0110000	11
Diplomystus birdi	1?????????	??????0???	???41?????	1-001???01	00???11011	1??21???00	11
Diplomystus dentatus	001????001	1??1011??1	01?5011011	1-00100001	00?1011011	100211?100	21
Diplomystus dubertreti	0?11????0?	???1??0???	???42?????	??????????	????11011	???21????0	?1
Diplomystus shengliensis	0010-???01	0????11??1	??050010??	1-00000?01	0100?11011	10021??100	?1
Diplomystus solignaci	1?1???????	?????11???	???121?0?1	100???????	00?1?1??1?	????111100	21
Ellimma branneri	00011???01	0??1?10?1?	?1011110?1	0100000001	0011?11110	1110111110	11
Ellimmichthys goodi	1??031??00	?????0110	1110111000	0?00001000	0010111110	1112111110	??
Ellimmichthys longicostatus	1??11??00?	0???100110	1110111000	0?00001000	0110111110	1112111110	??
Ellimmichthys maceioensis	1?110???0?	??????0???	?1?11?102?	1-01000101	0101111010	1110111?0	21
Ezkutuberezi carmenae	100?0???0?	????00111	?1?42?1021	??0?0000?1	100101??00	111?111100	20
Kwangoclupea dartevellei	00111?0001	0?????0??1	???40?1001	0100000001	0101011000	010?1110-0	11
Paraclupea chetungensis	10011???01	0??1010???	?1?1111011	0100000101	0111010-10	1111111110	21
Rhombichthys intoccabilis	1011??0001	0101?10111	01012?1001	0-01000101	0000?11010	1110111110	21
Scutatuspinosus itapagipensis	00010???01	01?1100111	0100010021	1?01100000	0111011001	11101110-0	10
Sorbinichthys africanus	1?00-???01	010??10011	0024020001	0200000100	2-00011000	10?2110100	00
Sorbinichthys elusivo	1?01????0?	0???10011	?024120001	0200000100	2-0?011000	10?2110100	00
Thorectichthys marocensis	10010??001	0?01010111	0104111001	1-00000101	0011111000	0100111100	12
Thorectichthys rhadinus	0000-??001	0??1010111	0104111001	1-00000101	0011111000	0100111100	12
Triplomystus applegatei	10011????1	00????011?	?1121?1011	0011100101	0010111010	1110111111	22
Triplomystus noorae	1001110001	000??10111	1112211011	0011001001	0011?11010	1110111111	12
Triplomystus oligoscutatus	1001110001	000??10111	1114111011	1-11001001	0011?11010	1110111111	12
Tycheroichthys dunveganensis	1000-???01	000???0111	011411????	0101100101	1101011110	1101111110	21

Chapter 3: A basal clupeomorph from the Albian Loon River Formation (Northwest Territories, Canada)

3.1 Introduction

The extant members of the superorder Clupeomorpha (herrings and allies), all in the order Clupeiformes, are among the most diverse and abundant fish species, but little is known about their early evolutionary history. The majority of fossil members of this group are placed in the extinct order Ellimmichthyiformes. The earliest fossil record of the clupeomorph fishes is dated back to the early Early Cretaceous deposits of Europe, Asia, and South and North America. Already at that time clupeomorphs had a broad environmental distribution occurring in freshwater, marine, and brackish water settings. Their remarkable ecological plasticity allowed for a successful dispersal worldwide. The most diverse and abundant fossil material of this group of fishes is known from the Aptian – Albian deposits of Brazil and Late Cretaceous deposits of the Mediterranean region. These localities have yielded a great number of ellimmichthyiform taxa.

In Canada, the early fossil record of the Clupeomorpha is limited to only a few mid- to Late Cretaceous species: *Horseshoeichthys armaserratus* Newbrey et al., 2010 from the Maastrichtian Horseshoe Canyon Formation, *Tycheroichthys dunveganensis* Hay et al., 2007 from the Cenomanian Dunvengan Formation, and an enigmatic taxon *Erichalcis artca* first described by Forey (1975) from the early/mid Albian deposits of the Loon River Formation. Description of the last taxon was based on a number of specimens collected in 1972 that showed a perplexing combination of characters. Forey (1975) recognized *Erichalcis* as Clupeiformes *incertae sedis* mainly based on the presence of abdominal scutes; however, he noted that unlike other clupeomorphs the new taxon had enlarged modified scales along the lateral midline of the body and showed specialized features of the caudal skeleton – fusion of the upper hypurals, first preural centrum without a neural arch, and laminar flanges associated with the haemal spine of the second preural centrum and neural spines of the third and second preural centra. This perplexing combination of characters led Forey (1975) to the conclusion that *Erichalcis* represented a primitive clupeomorph and could not be classified as a member of either Denticipitoidei or Clupeoidei.

In his monograph on the classification of the clupeomorph fishes, Grande (1985) placed *Erichalcis* in his monotypic Division I as the sister group to all known recent and fossil clupeomorphs. He referred to a few specimens from the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) collections, including the holotype (UALVP 8606) showing enlarged lateral line scales, paratypes UALVP 8598 and UALVP 8629 with modified caudal skeletons, and UALVP 17535 showing a complete series of abdominal scutes (Grande, 1985, p. 257).

Subsequent re-examination of the holotype and a number of paratype specimens of *Erichalcis arcta* led Arratia (1997) to the conclusion that this taxon belongs to the Euteleostei and is more closely related to salmoniforms than to clupeomorphs. Later, Hermus et al. (2004) described another species of *Erichalcis, E. conspicua*, from the middle Albian Christopher Formation, Nunavut, Canada. Similar to the type species, *E.conspicua* has enlarged modified lateral mid-line scales diagnostic for the genus. These studies, however, did not investigate the clupeomorph part of *Erichalcis arcta sensu* Forey (1975).

In the present study, I describe the clupeomorph specimen that was originally part of the description of *Erichalcis arcta*. This work includes morphological and phylogenetic analyses of specimen UALVP 17535 that represents the oldest known clupeomorph from Canada.

3.2 Geological settings

The fossil fish material was recovered from the Loon River Formation at Hay River, Northwest Territories, (60°01’ N, 116°57’ W). This formation is part of the Fort St. John Group and is dominated by black marine shales and limestones. This locality has yielded a number of vertebrate taxa including a holostean, aspidorhynchiform, ananogmiid, euteleosts, and at least two genera of ichthyosaurs (Forey, 1975; Hermus et al., 2004; Maxwell and Caldwell, 2006).The Loon River Formation has been dated as early to middle Albian (Rudkin, 1964; Singh, 1971). The most recent biostratigraphic revision of the Loon River Formation indicates that the upper interval of the formation may be late Albian in age, based on the presence of the foraminiferan *Miliammina manitobensis* and age-indicative dinocysts (Hathway et al., 2013).

3.3 Material and Methods

Description of the new taxon is based on a single specimen preserved in part and counterpart in black laminated shales. The specimen is incomplete, with only the anterior part of the fish preserved. This is the only specimen from the original collection of the fossil fish material from the locality that is catalogued in the collections of the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) that shows the abdominal series of scutes. The specimen is catalogued under the register number 17535 with the prefix UALVP.

The morphological description is based on examination of the original specimen, as well as a latex peel of the part, using a Wild M3 stereomicroscope. All drawings and reconstruction of the specimen are based on digital photographs.

3.3.1 Comparative material

The following taxa of extinct and recent clupeomorphs were examined for the purpose of morphological analysis and comparative study: *Alosa sappidissima* (Wilson, 1811): Z-366; *Armigatus brevissimus* (Blainville, 1818): UALVP 5087, 17620, 47258; *Diplomystus dentatus* (Cope, 1877): UALVP 17731, 21163, 22860, TMP 1986.224.0081, 1986.224.0083 – 0086, 1986.224.0088 – 0091; *Dorosoma cepedianum* (Lesueur, 1818): Z-441; *Horseshoeichthys armaserratus* Newbrey et al., 2010: TMP 2001.045.0093l; *Sorbinichthys africanus* Murray and Wilson, 2011: UALVP 51640 (holotype), 47186, 51641; *Thorectichthys marocensis* Murray and Wilson, 2013: UALVP 47178 (holotype), 51647, 51649, 51657, 51659; *T. rhadinus* Murray and Wilson, 2013: UALVP 51653 (holotype), 51664.

Institutional abbreviations: UALVP , Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Alberta, Canada; TMP, Royal Tyrrell Museum, Drumheller, Alberta, Canada; Z, zooarchaeology collections of the Canadian Museum of Nature, Ottawa, Ontario, Canada.

3.3.2 Phylogenetic analysis

Cladistic analysis was performed using TNT 1.1 (Goloboff et al., 2008) employing a heuristic search method with 1000 replicates and tree bisection and reconnection (TBR) swapping algorithm. The most parsimonious trees (MPTs) retrieved by the initial analysis were used to construct a strict consensus tree. Mesquite v 3.03 (Maddison and Maddison, 2011) was used to construct a character matrix for the analysis and calculate tree length, and consistency (C.I.) and retention (R.I.) indices for the strict consensus tree. Ancestral state reconstruction was also carried out in Mesquite v 3.03 (Maddison and Maddison, 2011).

The character matrix used for the phylogenetic analysis includes a total of 13 taxa and 62 characters (Appendix 3-1). I used ten early Cretaceous ellimmichthyiform taxa along with two Early Cretaceous clupeiforms and gonorhynchiform *Chanos chanos* (Forsskål, 1775) (as a representative member of the Ostariophysi, sister group to the Clupeomorpha) for the purpose of out-group comparison.

Character descriptions and states were adopted from previously published works by Zaragüeta-Bagils (2004), Alvarado-Ortega et al. (2008), and Murray and Wilson (2013). The new taxon was scored based on the morphological description provided in this study and included to the character matrix (Appendix 3-2). All characters are unordered and equally weighted. Missing data for the characters are coded by question marks; inapplicable characters are coded by dashes.

3.3.3 Fossil taxa included in the phylogenetic analysis

Ellimma branneri (Jordan, 1910); *Ellimmichthys goodi* (Eastman, 1912), *E. longicostatus* (Cope, 1886), *E. maceoiensis* Malabarba et al., 2004; *Ezkutuberezi carmenae* Poyato-Ariza et al., 2000; *Paraclupea chetungensis* Sun, 1956; *Pseudoellimma gallae* De Figueiredo, 2009; *Ranulfoichthys dorsonudum* Alvarado-Ortega, 2014; *Santanaclupea silvasantosi* Maisey, 1993;

Scutatuspinosus itapagipensis Silva Santos and Silva Correa, 1985; *Triplomystus applegatei* Alvarado-Ortega and Ovalles-Damian, 2008.

3.4 Systematic Paleontology

Subdivision TELEOSTEI Müller, 1845

Cohort CLUPEOCEPHALA Patterson and Rosen, 1977

Superorder CLUPEOMORPHA Greenwood et al., 1966

Order ELLIMMICHTHYIFORMES Grande, 1982

Family SCUTATUSPINOSIDAE Santos and Silva Corréa, 1985, new rank

Genus FOREYCLUPEA, gen. nov.

Diagnosis—as for type and only known species.

Etymology – the genus is named in honor of Dr. Peter L. Forey in recognition of his great contribution to paleoichthyology and who first described this fossil fish material from the Loon River Formation; and from the Latin 'clupea' to indicate clupeomorph affinities of the new taxon.

Type and only known species—*Foreyclupea loonensis*, sp. nov.

FOREYICHTHYS LOONENSIS, sp. nov.

Fig. 3-1 – 3-3

Diagnosis— clupeomorph fish with a shallow torpedo-shaped body, reaching approximately 10 cm; different from other ellimmichthyiforms (except *Ranulfoichthys dorsonudum*) in having at least two broad postcleithra and lacking predorsal series of scutes;

distinguished from *R. dorsonudum* by the pelvic fin insertion anterior to the origin of the dorsal fin and abdominal scutes with spine-like ascending lateral wings with strengthening ridge at the posterior margin.

Etymology—the specific epithet is derived from the name of the formation where the specimen was found.

Holotype—UALVP 17535 (a, b) a single specimen in part and counterpart. The part showing the specimen in left lateral view (UALVP 17535a) preserves the complete head and anterior part of the body; the counterpart (UALVP 17535b) has only the postorbital part of the skull and the anterior part of the body preserved.

Locality—Loon River Formation, Hay River, Northwest Territories, Canada.

Age—Early/middle Albian (Early Cretaceous)

3.5 Description

General body form—This is a slender fish with a shallow body similar to that of several other Early Cretaceous clupeomorphs – *Scutatuspinosus itapagipensis*, *Ranulfoichthys dorsonudum*, and *Santanaclupea silvasantosi* (Santos and Correa, 1985; Maisey, 1993; Alvarado-Ortega, 2014). The dorsal margin of the body, although distorted, seems to run in a smooth and straight line from the back of the head to the origin of the dorsal fin (Fig. 3-1). The predorsal part of the trunk appears to be uniformly deep with the body depth equal to 19 mm. The posterior part of the fish, including the anal and caudal fins, is missing and thus the standard length (SL) of the fish cannot be determined. The total length of the preserved portion is 56 mm. I estimate the SL of this fish would have been about 100 mm, if the proportions of this fish were similar to those of the three other Early Cretaceous clupeomorphs mentioned above (Fig. 3-2).

The head is preserved in lateral view; it is relatively narrow, triangular and about 1.4 times longer than deep. The dorsal profile of the skull is a straight line from the tip of the snout to the back of the skull. Only the dorsal, pectoral, and pelvic fins are preserved in the specimen. The pelvic fin insertion is slightly farther anterior than the dorsal fin origin. Measurements and counts of the specimen are summarized in Table 3-1.

Skull roof—Skull bones are not well-preserved with many elements crushed, displaced or preserved only as impressions. The head, as is typical for clupeomorphs, is triangular in shape and relatively narrow with a pointed snout (Fig. 3-3).

The ethmoid region of the skull is partially preserved with only the mesethmoid and lateral ethmoid visible in the specimen. The mesethmoid is a well-ossified bone with a blunt and bilobed anterior end that contacts the maxillary and premaxillary bones; however, details of the articulation cannot be determined. Posteriorly, the mesethmoid has two elongated processes that suture with the frontal bones. A small tubular nasal bone is present but displaced below the mesethmoid.The lateral ethmoid is only partially visible in the specimen; it appears to be large, extending from the frontals to reach the parasphenoid.

The frontal bones are long, extending over the entire orbital and anterior part of the otic regions of the skull; they are narrow anteriorly and gradually expand posteriorly where they suture with the parietal and pterotic bones. The frontals contact each other in the midline leaving no frontal fontanelle; there is also no posttemporal fossa. In the posterior part, the frontal bones are ornamented with deep sinuous ridges similar to those in *Pseudoellimma gallae* (De Figueiredo, 2009; Fig. 3).

The supraorbital sensory canal runs through the frontal bones. It is visible in the posterior part of the left frontal where the sensory canal becomes bone-enclosed. At the suture between the frontal, parietal and pterotic bones, the supraorbital canal gives off at least two branches.

The pterotic is a relatively large, wedge-shaped bone that contains the bone-enclosed supratemporal sensory canal. There are no openings for a recessus lateralis in the pterotic. The parietals are relatively small trapezoid bones, located just above the posterior portion of the orbit. They are not separated by the supraoccipital and so contact each other in the midline (medioparietal condition). The suture between the parietals is not deeply sinuous as in *Ranulfoichthys dorsonudum* (Alvarado-Ortega, 2014). The right parietal is marked with a transverse groove for the supratemporal commissure that is one of the diagnostic characters of the Clupeomorpha (Grande, 1985). The parietal bones are ornamented with only a few sinuous ridges, much less pronounced than those of the frontals.

The supraoccipital is poorly preserved and only a low crest is distinguishable behind the parietals. The lateral surface of the braincase is distorted and it is impossible to determine details of the individual bones. The recessus lateralis is absent.

Orbital region and hyopalatine bones—Circumorbital bones are not preserved in the specimen; only impressions of infraorbitals 3 and 4 can be identified. Infraorbital 3 is located in the posteroventral part of the orbit and appears to be a relatively large and expanded bone with an open groove for the infraorbital sensory canal (Fig. 3-3). The sensory canal continues dorsally where only a partial impression of infraorbital 4 is visible. Partially preserved bone in the posterodorsal portion of the orbit is identified as the sphenotic. Presence of the antorbital and supraorbital bones cannot be confirmed.

The parasphenoid is narrow and edentulous. Its anterior and posterior ends are obscured and the presence of the basipterygoid process, which would be expected in basal clupeomorphs (Chang and Maisey, 2003; Zaragüeta-Bagils, 2004; Alvarado-Ortega et al., 2008), is uncertain.

The hyomandibula is large; it has a single head and the shaft appears to be the same width as the head. No other hyopalatine bones are preserved in the fossil; there is fragmentary bone material present in the area where the ecto- and endopterygoid bones would be expected, but details cannot be determined.

Jaws—The jaw bones are only partially preserved with most bones displaced or preserved only as impressions. The premaxilla, maxilla, and two supramaxillae comprise the upper jaw. The premaxilla is small and slightly curved. It is relatively short, less than one quarter the length of the maxilla. The premaxilla has a moderately expanded ascending anterior process and tapers posteriorly. The maxilla is a long and curved bone with a longitudinal ridge running at least half the length of the bone. It is very narrow anteriorly with a well-defined head that articulates with the premaxilla and mesethmoid; however, the details of articulation cannot be determined. From its anterior tip, the maxilla widens as it extends posteriorly to just under the anterior margin of the orbit.

There are two supramaxillae displaced dorsally above the maxilla (Fig. 3-3). The posterior supramaxilla is large with a long antero-dorsal process that projects over the smaller anterior supramaxilla. Both supramaxillary bones bear fine longitudinal ridges.

The lower jaw is missing; there is only a partial impression of the right dentary in the specimen suggesting that the mouth was most likely terminal or slightly upturned.
There is no evidence of teeth on any of the jaw bones, but this may be an artifact of preservation.

Opercular series and branchial arches—The opercle is large with a convex posteroventral margin; it is about twice as high as long. The opercular bone is thickened anteriorly where it contacts the preopercle; just posterior to the robust anterior ridge there are fine striations on the opercle. The subopercle is an elongate bone with a rounded ventral margin; the surface of the subopercle is smooth with no ridges or striations.

The preopercle is L-shaped with both limbs well-developed; the dorsal limb is slightly longer that the ventral limb. The surface of the bone is smooth without ornamentation. The preopercular sensory canal is enclosed in bone and runs close to the anterior margin of the preopercle giving off at least six secondary branches. The interopercle is elongated, with a prominent longitudinal groove close to the dorsal margin of the bone.

The ceratohyal elements are not preserved in the specimen. At least six branchiostegal rays are visible below the interopercle but the ‘clupeoid’ projections (McAllister, 1968) cannot be distinguished on them. The branchiostegals gradually become wider and more robust from the anterior to posterior direction.

Vertebral column—The vertebral column is obscured in the specimen and so the total number of the vertebrae as well as details of the individual vertebral centra cannot be determined (Fig. 3-1). Based on the number of ribs and neural spines visible, there are approximately 25 vertebrae present. Abdominal vertebrae are cylindrical, about 1.5 times longer than high. Neural spines associated with the abdominal vertebrae are paired. There are 22 or 23 pairs of pleural ribs. The ribs are very long and thin; the anterior ten ribs are curved while the posterior 12 or 13 ribs have a sinuous shape. It is hard to determine details of the rib articulation in the fossil, but it appears that the anterior-most ribs articulate in deep pits of the abdominal centra.

Intermuscular bones are well-developed in the specimen and present in three series: epineurals, epicentrals, and epipleurals. The epineurals and epicentrals are associated with all vertebral centra visible; they are thin and long reaching the length of approximately 2 centra. The epipleurals are shorter than the epineurals; their length is equal to 1.5 vertebral centra.

Paired fins and girdles—The pectoral girdle is partially preserved. The posttemporal is present but details of the bone cannot be accurately determined; it is relatively large compared to the posttemporal bones described previously for ellimmichthyiforms. The ventral arm of the posttemporal is expanded and ovoid, but very little can be inferred about the antero-dorsal process of the bone. Just below and posterior to the posttemporal, an elongated supracleithrum is visible; it has been displaced during preservation and appears as a flat and slightly curved bone.

The cleithrum is L-shaped, similar to that of *Ranulfoichthys dorsonudum* (Alvarado-Ortega, 2014) and *Pseudoellimma gallae* (De Figueiredo, 2009), but with a more slender and pointed dorsal limb (Fig. 3-3). The ventral limb of the cleithrum is poorly preserved but it appears to be broader then the dorsal limb. There are at least two flat, ovoid postcleithra in the specimen, preserved well behind the cleithrum, that have been displaced posteriorly during preservation. Both postcleithra are broad unlike the rod-like postcleithra described in some ellimmichthyiforms (*Armigatus*, *Diplomystus,* and *Sorbinichthys*) and most clupeiforms; the ventral postcleithrum is slightly elongated and pointed. The right coracoid is preserved overlying the left pectoral fin; it is a subtriangular bone with a convex dorsal margin. The scapula and radials are not preserved in the specimen. The pectoral fin is long, approximately equal to the length of seven abdominal vertebrae. There are 14 pectoral fin rays; the third and fourth rays are the longest in the series.

The pelvic fin is small and positioned anterior to the level of the origin of the dorsal fin (Fig. 3-1). The pelvic girdle is not preserved in the specimen. Both pelvic fins are visible in the specimen with a total 12 fin rays preserved; however, the left and right pelvic fins are clumped together and the number of rays in each fin is not clear. Based on the total fin ray counts, there are approximately 6 pelvic fin rays.

Median fins—Only the dorsal fin is preserved in the specimen; it originates approximately above vertebral centrum 20 or 21. The fin is almost complete but the last few fin rays are missing due to the partial preservation of the specimen. There are 11 dorsal fin rays visible; the first two or three fin rays are unbranched and the first fin ray is shorter than the second ray. Distal ends of the third and fourth dorsal fin rays are not preserved, making it impossible to determine whether they are branched. Posterior to the fourth ray, the dorsal fin rays are branched and gradually become shorter.

The dorsal fin is supported by at least 12 pterygiophores. The first pterygiophore is a large and complex element that appears to be made by the first three bones in the series which are connected by a lamina.The anterior ten pterygiophores are long and interdigitate with the neural spines.

Predorsal bones, dorsal and abdominal scutes—Predorsal bones are for the most part not preserved in the fossil and only the proximal ends of the bones can be identified. They are long, interdigitating with the neural spines of the anteriormost vertebrae and thin, without antero-posterior laminar expansions as in *Diplomystus* (Grande, 1982).The exact number of predorsal bones cannot be determined; there are two or three bones visible just in front of the dorsal fin in UALVP 17535a and at least three bones close to the occiput in the counterpart of the specimen, UALVP 17535b.

The dorsal margin of the body is largely obscured and presence of a dorsal series of scutes cannot be determined. However, in the areas that are clearly visible in the specimen, just behind the occiput and anterior to the dorsal fin origin, there is no evidence of dorsal scutes.

The abdominal series of scutes is well-preserved in the specimen (Fig. 3-1). There are approximately 19 ventral scutes with 13 preserved anterior to the pelvic fin insertion and six scutes posterior to the pelvic fin. Additional scutes likely would have been present in the living fish anterior to the anal fin, but the fossil does not preserve this region. Each abdominal scute has a median keel that partially overlaps the succeeding scute in an antero-posterior direction, and a spine-like ascending lateral arm. These lateral arms are relatively short and cover less than one third of the distance between the vertebral column and the ventral margin of the body; each lateral spine is marked with a thick posterior margin forming a strengthening ridge.

3.6 Phylogenetic results

In the present study, I performed a phylogenetic analysis of the Lower Cretaceous (Berriasian – Albian) clupeomorphs with a purpose of clarifying interrelationships and early diversification patterns within the group. I included 12 fossil clupeomorph taxa from Europe, Asia, South and North America that have been assigned to either Ellimmichthyiformes, Clupeiformes or left as Clupeomorpha *incertae sedis*. Some of the taxa used in the present study have never been included in the phylogenetic analysis of the Clupeomorpha before (*Pseudoellimma gallae* and *Ranulfoichthys dorsonudum*).

The analysis retrieved seven most parsimonious trees that were used to construct a strict consensus tree. The resulting strict consensus tree has a length of 132 steps, a consistency index (CI) of 0.523, and a retention index of 0.566 (Fig. 3-4). The bootstrap and Bremer support analyses revealed a weak support for most clades; only one clade (*Ellimmichthys longicostatus* + *E. goodi*) had a bootstrap support value higher than 50%. The consensus tree contains two polytomies: a very basal trichotomy includes two fossil taxa that have been described as clupeiforms (*Santanaclupea silvasantosi* and *Pseudoellimma gallae*) and a large group containing ellimmichthyiforms and clupeomorphs of uncertain affinities. Another polytomy within the ingroup includes *Ellimma branneri*, *Ellimmichthys maceioensis*, *Paraclupea chetungensis*, *Triplomystus applegatei* and a clade containing *Ellimmichthys longicostatus* and *E. goodi*.

Results of the analysis suggest that *Ellimmichthys* is a polyphyletic genus with *E.maceioensis* not forming a natural group with the type species, *E. longicostatus*. This agrees with the general pattern recovered by previous phylogenetic analyses that grouped *E. longicostatus* and *E. goodi* as sister-taxa (Zaragüeta-Bagils, 2004; Alvarado-Ortega et al., 2008) and revealed *E. maceoiensis* as being closely related to the Late Cretaceous ellimmichthyiforms *Diplomystus solignaci* and *Rhombichthys intoccabilis* (Murray and Wilson, 2013). However, none of the previous analyses included all three species of *Ellimmichthys* that would provide a better comparison with the present results.

The new species, *Foreyclupea loonensis*, was recovered as a member of a clade that also includes *Scutatuspinosus itapagipensis* and *Ranulfoichthys dorsonudum*. This is the first time this clade has been recovered in a phylogenetic analysis.

3.7 Discussion

Morphological examination of the specimen UALVP 17535 provides conclusive evidence that the new species, *Foreyclupea loonensis*, is a member of the superorder Clupeomorpha: the specimen shows a complete abdominal series of scutes and the supratemporal commissural sensory canal that passes through the parietals. The former character has been regarded by many authors as a diagnostic feature exclusive to clupeomorph fishes (Whitehead, 1963; Patterson, 1970; Grande, 1982, 1985; Arratia, 1997). Unfortunately, because the specimen is missing its posterior part, no conclusions can be made about the structure of the caudal skeleton. In clupeomorphs, the caudal skeleton is characterized by the autogenous hypural 1 and the second hypural fused to the first ural centrum. These features, although not exclusive to the Clupeomorpha, in combination with other clupeomorph traits provide a reliable diagnosis for the group.

Along with the general clupeomorph characteristics mentioned above, *Foreyclupea loonensis* shows a mosaic of primitive and derived features that make further classification of the new taxon within the Clupeomorpha problematic. The cranial skeleton of *F. loonensis* shows the following plesiomorphic conditions: parietals contacting each other in the midline and absence of the recessus lateralis.

The parietal bones contacting each other medially (medioparietal condition of the skull roof) is a common plesiomorphic condition present in most ellimmichthyiforms and many other groups of teleost fishes including ichthyodectiforms, osteoglossomorphs, elopiforms, salmoniforms and others (Grande, 1985; Arratia, 1997). Grande (1985) used this character to separate non-clupeiform clupeomorphs from more derived members of the order Clupeiformes that have parietals completely separated by the supraoccipital (lateroparietal condition). However, some members of the extinct order Ellimmichthyiformes have also been described as having the lateroparietal skull roof condition – *Ellimmichthys longicostatus* and *E. goodi*, as well as *Paraclupea chetungensis* that has parietal bones partially separated by the supraoccipital (Chang and Grande, 1997).

Presence of the recessus lateralis is a highly diagnostic character exclusive to all extant member of the Clupeomorpha (equivalent to the order Clupeiformes). The evolutionary pattern of this character distribution within the group corresponds to the subdivision of the Clupeomorpha into two orders: Clupeiformes that have a recessus lateralis and Ellimmichthyiformes without the recessus lateralis. In the fossil taxa, presence of a recessus lateralis can be inferred from the reduced size of the dermosphenotic that does not carry the infraorbital sensory canal (Forey, 1975; Grande, 1985) and perforation of the pterotic with the openings for the cephalic sensory canals (Patterson, 1970; Maisey, 1993; Di Dario, 2002). The dermosphenotic is missing in the studied specimen, but the preserved pterotic bone does not show any openings for the sensory canals; this may indicate that a recessus lateralis was primitively absent in the fish.

Foreyclupea loonensis also shows unfused neural spines of the abdominal vertebrae. This is a primitive condition that has been recognized in many teleost groups (Aratia, 1997). Among the clupeomorphs, paired neural spines are present in the basal Early Cretaceous fossil taxa

Ranulfoichthys dorsonudum, *Santanaclupea silvasantosi*, *Pseudoellimma gallae*, and members of the Late Cretaceous genus *Armigatus*.

The new species is distinguished from other ellimmichthyiforms by the following combination of derived characters: loss of the predorsal series of scutes, presence of at least two broad postcleithra, and position of the pelvic fin anterior to the origin of the dorsal fin. Some of these features also occur in *Scutatuspinosus* and *Ranulfoichthys*, basal clupeomorphs of unresolved affinities.

The above characteristics suggest that *Foreyclupea loonensis* is a new taxon of basal clupeomorph with close affinities to the known species of the ellimmichthyiforms. This conclusion is also supported by the results of the present phylogenetic analysis.

Based on the phylogenetic hypothesis presented here, the Early Cretaceous clupeomorphs form a natural group characterized by the ornamented skull roof bones (4:1), presence of the 'beryciform' foramen in the anterior ceratohyal (14:1), and a strong ventral spine on the postpelvic abdominal scutes (57:1).

The two fossil clupeiform taxa, Barremian *Pseudoellimma gallae* from the brackish deposits of the Coqueiro Seco Formation, Brazil and the middle/late Albian *Santanaclupea silvasantosi* from the black shales of the Santana Formation, Brazil, are distinguished from the ellimmichthyiforms by the parietals completely separated by the supraoccipital (2:1), presence of the recessus lateralis (8:1), and reduced size of the first ural centrum in *Pseudoellimma*. However, these early clupeomorphs also show some primitive characteristics also present in the ellimmichthyiforms – *Santanaclupea* has the 'beryciform' foramen in the anterior ceratohyal (this condition is unknown in *Pseudoellimma* due to the missing ceratohyal elements); *Pseudoellimma* shares the following characters with ellimmichthyiforms: long and lanceolate neural spine of the first preural centrum (44:0), subrectangular scutes in the posterior part of the predorsal series (49:1). Both taxa also primitively retain hypural 1 in contact with the first ural centrum (28:0); in derived clupeiforms, hypural 1 is separated from the first ural centrum by a gap (Grande, 1985; Chang and Maisey, 2003).

These basal clupeiforms (*Santanaclupea* + *Pseudoellimma*) form a polytomy with a large clade of fossil non-clupeiform clupeomorphs. Members of this clade are different from the clupeiforms in having parietals contacting each other in the midline (2:0), lacking a recessus lateralis (8:0), having the anteriormost pleural ribs articulate with deep pits on the lateral side of abdominal centra and those located posteriorly articulate with well-developed parapophyses (19:1), and the caudal fin supported by six hypurals (26:1). The first two characteristics (medioparietal condition of the skull roof and absence of recessus lateralis) have been attributed to the ellimmichthyiforms (Grande, 1985). Grande (1982, 1985) and Alvarado-Ortega et al. (2008) also recognized the presence of subrectangular predorsal scutes as a synapomorphy of the ellimmichthyiforms; however, this character was questioned by Chang and Maisey (2003) as being a reliable diagnostic feature of the order. The latter authors noted that due to the variability in the scute shape within the Ellimmichthyiformes, it is necessary to reevaluate the shape of the dorsal scutes as a single character supporting monophyly of the order. This large clade of non-clupeiform clupeomorphs includes two major groups: a clade containing the Neocomian (Valanginian – Barremian) *Scutatuspinosus itapagipensis* from Brazil, and the early/middle Albian *Ranulfoichthys dorsonudum* and *Foreyclupea loonensis* from Mexico and Canada respectively as a sister group to a clade of all ellimmichthyiform taxa included in the analysis: (*Ezkutuberezi carmeni* + (*Paraclupea chetungensis* + *Ellimma branneri* + *Ellimmichthys maceoiensis* + *Triplomystus applegatei* + (*Ellimmichthys longicostatus* + *Ellimmichthys goodi*)).

The clade (*Scutatuspinosus* + *Ranulfoichthys* + *Foreyclupea*) includes basal clupeomorphs of uncertain affinities; it is supported by plesiomorphic characters: torpedo-shaped body with a smooth and slightly rounded anterior dorsal margin of the body (1:0), abdominal scutes with short ascending lateral 'arms' (58:0), and a homoplastic character – absence of a diastema between hypurals 2 and 3 (31:1, this feature also occurs in the ellimmichthyiform genera *Armigatus* and *Diplomystus*). I adopt Scutatuspinosidae Silva Santos and Silva Correa, 1985 (new rank) as a name for this clade with the type species *Scutatuspinosus itapagipensis*.

Unlike any other ellimmichthyiform species, *Ranulfoichthys dorsonudum* and *Foreyclupea loonensis* do not have a predorsal series of scutes; however, a complete series of predorsal scutes is present in *Scutatuspinosus*, the most basal and the oldest member of the clade. This finding supports the idea that presence of a predorsal series of scutes is a primitive characteristic within the Clupeomorpha that is retained by some living members of the Clupeiformes. *Foreyclupea* and *Ranulfoichthys* share at least one more characteristic unique among the ellimmichthyiforms – presence of at least two expanded postcleithra. Grande (1985) regarded presence of two rod-shaped postcleithra as a diagnostic character for the Clupeidae; since then, long rodlike postcleithra have been described in some ellimmichthyiforms: *Armigatus* (Forey et al., 2003), *Diplomystus* (pers.obs. UALVP 17731, 21163, 22860)*, Thorectichthys* (Murray and Wilson, 2013), *Horseshoeichthys* (Newbrey et al., 2010), and *Tycheroichthys* (Hay et al., 2007). Grande (1985) also noted that in some clupeids postcleithra can be moderately to broadly expanded; however, this condition is not known in any ellimmichthyiform species.

Foreyclupea and *Ranulfoichthys* each share unique characteristics with *Scutatuspinosus*. Both, *Ranulfoichthys* and *Scutatuspinosus* have a unique morphology of the ascending lateral 'arms' of the abdominal scutes – each ventral scute has very short, broad and subrectangular lateral wings. This condition is different from the spine-like ascending processes of the abdominal scutes observed in the extinct and recent clupeomorphs (*Armigatus*, *Diplomystus*, *Sorbinichthys*, *Thorectichthys, Ellimmichthys*, Clupeidae, Pristigasteridae) or the long spatula-like ascending arms of abdominal scutes in ellimmichthyiform genera *Triplomystus, Tycheroichthys,* and *Rhombichthys*.

For *Foreyclupea* and *Scutatuspinosus*, position of the pelvic fin anterior to the level of the origin of the dorsal fin is recognized as a shared derived characteristic. This position of the pelvic fin is not common among the ellimmichthyiforms or recent clupeiforms and is considered to be a derived feature among teleost fishes. Chang and Maisey (2003) also noted that the pelvic fin is inserted in advance of the dorsal fin origin in *Ellimmichthys longicostatus*.

The third major group retrieved by the phylogenetic analysis contains all previously recognized Early Cretaceous ellimmichthyiform taxa that have been included in the analysis; it most closely corresponds to the family Paraclupeidae *sensu* Alvarado-Ortega et al. (2008) and Murray and Wilson (2013). Grouping of these taxa in the analysis is supported by the following characteristics: straight ascending dorsal margin of the body that forms a distinct angle at the insertion of the dorsal fin (1:1), fused neural arches and spines of abdominal vertebrae (18:1), S-shaped cleithrum (22:1), large lateral spines of the abdominal scutes (58:1), and an increased number of abdominal scutes (61:2). Within this group of ellimmichthyiforms, *Ezkutuberezi carmeni* from the Valanginian – Barremian of Spain appears as the most basal taxon; other ellimmichthyiform taxa were recovered in a sister group to *Ezkutuberezi* with relationships among the taxa being mostly unresolved. Only two species of *Ellimmichthys* (*E. longicosatus* and *E. goodi*) form a well-supported clade characterized by the broad distal end of hypural 2 (30:0), dorsal laminar expansion of the first uroneural (37:1), presence of the subrectangular scutes in the anterior part of the predorsal series (48:1), increased number of predorsal scutes (54:2), and a small number of anal fin rays (24:0).

Overall, the results of the phylogenetic analysis of the Early Cretaceous clupeomorphs suggest that the clupeiforms and ellimmichthyiforms diverged in the early Early Cretaceous and formed separate lineages as early as in the Barremian (with the clupeiform *Pseudoellimma gallae* from Brazil and ellimmichthyiforms *Ezkutuberezi carmeni* from Spain and *Scutatuspinosus itapagipensis* from Mexico). It is also worth noting that the oldest clupeomorphs described from the Berriasian - Barremian, are known predominantly from freshwater and estuarine environments; this includes the Neocomian (Valanginian – Barremian) *Scutatuspinosus itapagipensis* from the lacustrine sediments of Reconcavo Basin, Brazil, *Ellimmichthys longicostatus* (Cope, 1886) from the late Hauterivian – early Barremian estuarine deposits of the Marfim Formation, Brazil, *Ezkutuberezi carmeni* Poyato-Ariza et al., 2000, from the Valanginian – Barremian deltaic and lacustrine deposits of the Villaro Formation, Spain; and *Pseudoellimma gallae* from the Barremian brackish water deposits of the Coqueiro Seco Formation, Brazil. Evolutionary significance of this pattern is yet not clear but it may shed light on the origins of the diadromous behavior of the clupeomorphs as well as provide valuable information on the evolution of the osmoregulatory system in these fishes; therefore, description of the earliest members of the Clupeomorpha is crucial to our understanding of the complex evolutionary patterns of clupeomorph ecology and biogeography.

3.8 Summary

The evolutionary history of the Clupeomorpha remains an unresolved issue. The major questions persist on the clupeomorph origin, diversification between clupeiforms and ellimmichthyiforms, and biogeographic dynamics of these fishes. The early fossil record of clupeomorphs provides some valuable clues to these questions. *Foreyclupea loonensis* is the oldest clupeomorph species described from Canada. Based on the primitive cranial characteristics (parietals contacting each other in the midline and absence of the recessus lateralis), the new species is classified as a member of the Ellimmichthyiformes. *Foreyclupea loonensis* is a remarkable taxon in showing a number of derived characteristics (absence of dorsal scutes, pelvic fin insertion anterior to the origin of the dorsal fin, and presence of at least two broad postcleithra) that distinguish it from other ellimmichthyiforms. Together with other basal clupeomorphs from the Neocomian deposits of Brazil (*Scutatuspinosus*) and Albian of Mexico (*Ranulfoichthys*), the new species forms a clade of torpedo-bodied fishes. This clade supports Grande's (1985) idea of the evolutionary pattern of the predorsal series of scutes in the clupeomorphs – a complete series of predorsal scutes is an ancestral condition in clupeomorphs that precedes the loss of this feature in multiple lineages.

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TABLE 3—1. Counts and measurements of *Foreyclupea loonensis*, sp. et gen. nov. based on a single specimen UALVP 17535. All measurements are in mm.

UALVP Characteristic	13575
Standard length (SL)	?
Head length	21
Head depth	15
Greatest body depth	19
Predorsal length	42
Prepelvic length	40
Preanal length	?
Dorsal fin rays	?10
Pectoral fin rays	14
Pelvic fin rays	?6
Abdominal vertebrae	22-23
Predorsal bones	?
Abdominal scutes	?19
Pre-pelvic scutes	13
Post-pelvic scutes	6
Pre-dorsal scutes	-
Pairs of ribs	18

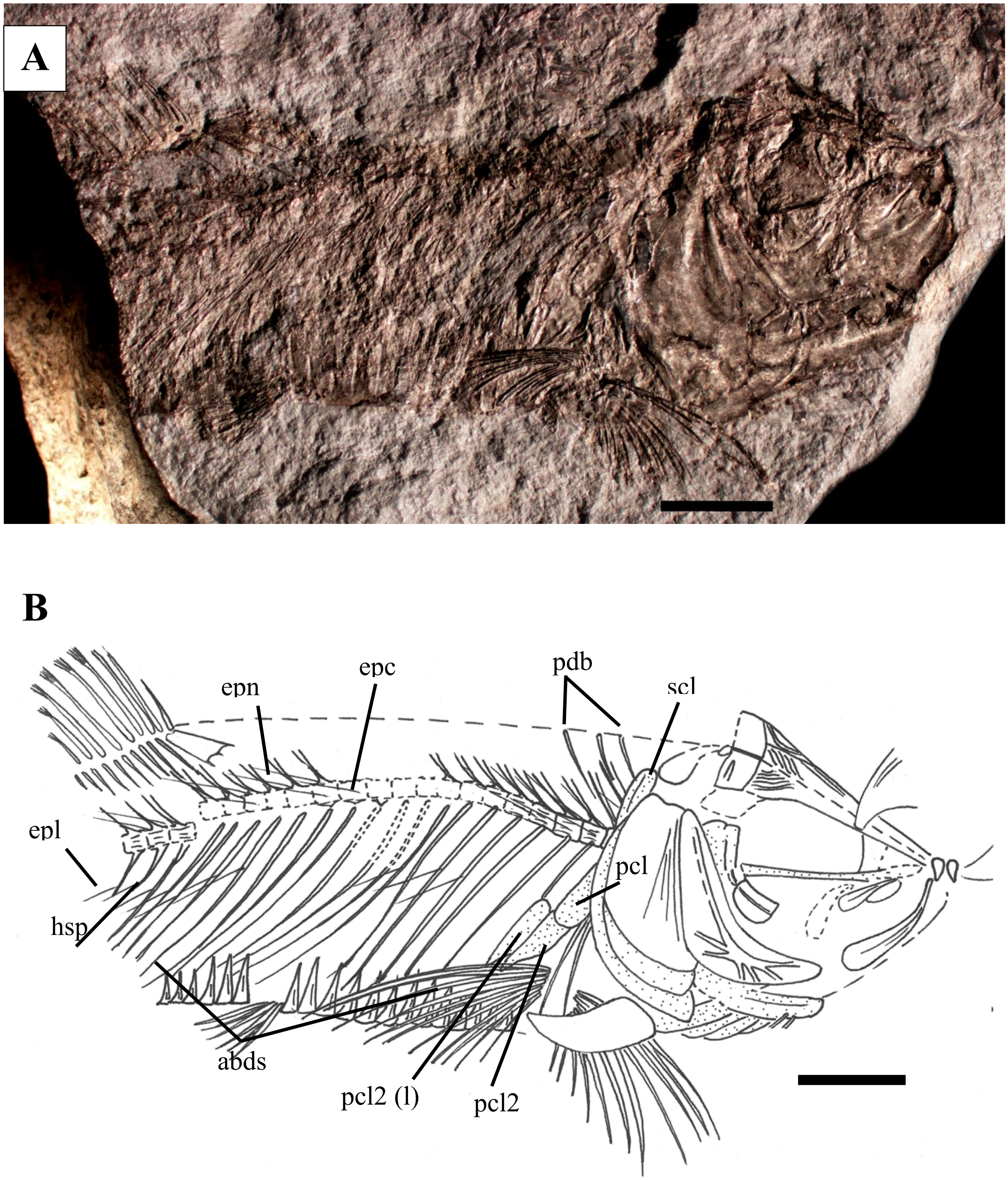


FIGURE 3-1. Foreyclupea loonensis sp. et gen. nov.; **A,** photograph of UALVP 17535; **B,** line drawing of the specimen UALVP 17535a. **Abbreviations: abds,** abdominal scutes; **epc,** epicentral; **epl,** epipleural; **epn,** epineural; **hsp,** haemal spine; **pcl** 1-2, postcleithra 1-2; **pcl2 (l),** left postcleithrum 2; **pdb,** predorsal bones; **scl,** supracleithrum. Scale bars = 5 mm.

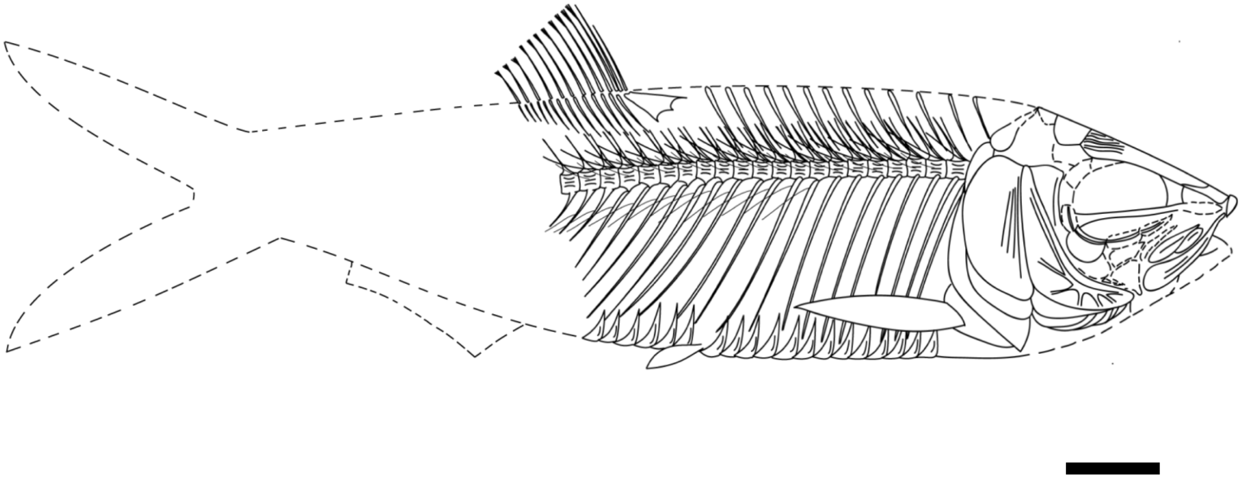
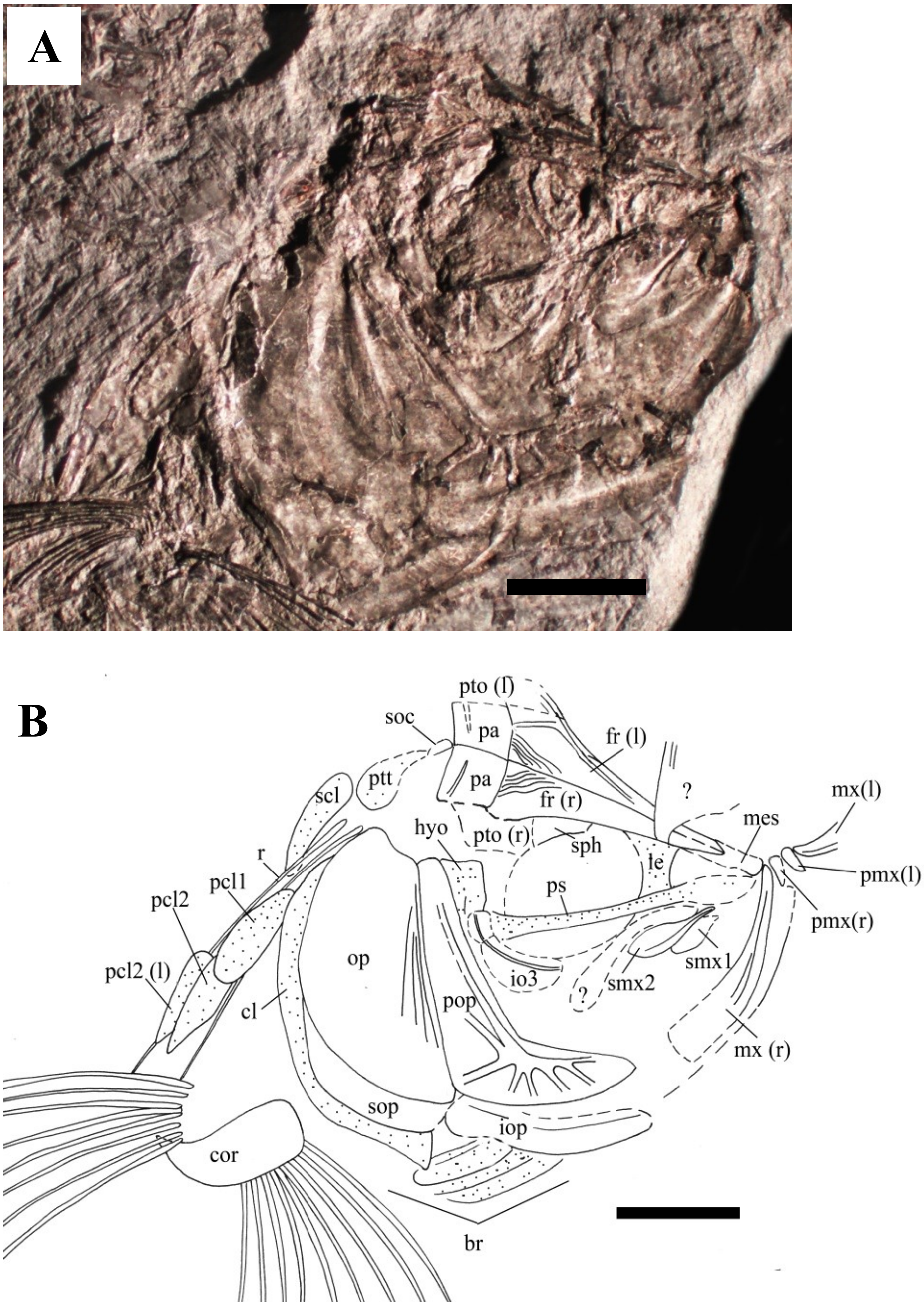


FIGURE 3-2. Reconstruction of *Foreyclupea loonensis*. Scale bar = 5 mm.


A
B
pto (l)
soc
pa
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fr (l)
ptt
scl
?
mx(l)
fr (r)
mes
hyo
pto (r)
sph
r
le
pmx(l)
pcl1
ps
pmx(r)
pcl2
smx1
op
io3
pcl2 (l)
cl
pop
?
smx2
mx (r)
sop
iop
cor
br

FIGURE 3-3 (previous page). *Foreyclupea loonensis:* **A**, photograph of the head of UALVP 17535; **B**, restoration of the head in right lateral view. **Abbreviations**: **br,** branchiostegal rays; **cl**, cleithrum; **cor**, coracoid; **fr**, frontal bones; **hyo**, hyomandibular; **io3**, infraorbital 3; **iop,** interopercle; **le**, lateral ethmoid; **mes,** mesethmoid; **mx**, maxilla; **op**, opercle; **pa**, parietal; **pcl 1-2**, postcleithra 1-2; **pmx**, premaxilla; **pop**, preopercula; **ps**, parasphenoid; **pto,** pterotic; **ptt**, posttemporal; **r**, rib; **scl**, supracleithrum; **soc**, supraoccipital; **sop**, subopercle; **sph**, sphenoid; **smx 1-2**, supramaxillae 1-2. Scale bar = 5 mm

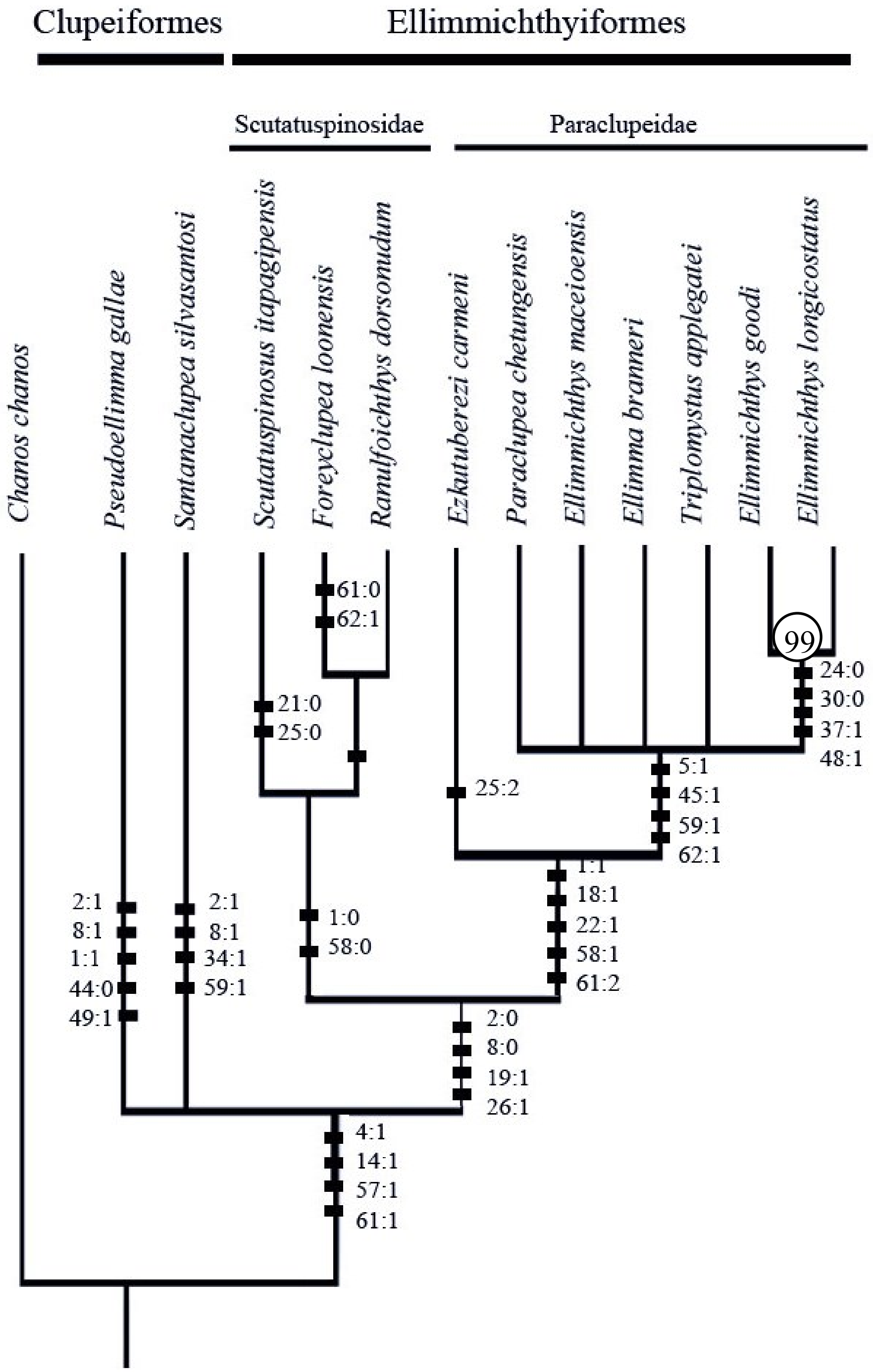

FIGURE 3-4. Strict consensus of the seven most parsimonious trees retrieved by the analysis of the Early Cretaceous clupeomorphs including *Foreyclupea loonensis* sp. et gen. nov. Characters supporting each node are listed along corresponding branches. Bootstrap support values higher than 50% are shown at the nodes.

APPENDIX 3-1. Character state list used in the phylogenetic analysis based on Murray and Wilson (2013):

1. Anterior dorsal margin of body: [0] rounded and convex; [1] almost straight, forming a marked angle at the dorsal fin insertion.
2. Skull roof: [0] parietals bones contacting each other in the midline; [1] supraoccipital separates parietal bones.
3. Lateral profile of skull roof: [0] a straight line from anterior tip of frontal to back of skull, with no distinct angle apparent; [1] with distinct angle between anterior and posterior parts, normally in the region of the parietal.
4. Ornamentation of skull roof bones: [0] absent; [1] present.
5. Ornamentation of skull roof bones: [0] fine, more or less parallel grooves; [1] strong grooves with numerous fine, radiating ridges.
6. Posttemporal fossa: [0] absent; [1] present.
7. Cavity in the temporal region of the skull: [0] pre-epioccipital fossa (between parietal, epioccipital and pterotic bones); [1] pre-epioccipital fenestra (between the parietal, epioccipital and supraoccipital bones); [2] absence of cavity or fenestra.
8. Recessuslateralis: [0] absent; [1] present.
9. Supramaxillary bones: [0] two; [1] one or none.
10. ‘Basipterygoid’ process of parasphenoid: [0] absent; [1] present.
11. ‘Osteoglossid’ tooth patch on the parasphenoid: [0] absent; [1] present.
12. Supraorbital bone: [0] absent; [1] present.
13. Antorbital bone: [0] absent; [1] present.

14. Beryciform foramen within the anterior ceratohyal: [0] absent; [1] present.

15. Foramen in posterior ceratohyal: [0] absent; [1] present.

16. Teeth on endopterygoid: [0] absent; [1] present.

17. Total number of vertebrae excluding ural centra: [0] 30-40; [1] 41-43; [2] more than 50.

18. Halves of the neural arches of most abdominal vertebrae: [0] separate medially; [1] fused medially.

19. Pleural ribs: [0] all ribs articulate with parapophyses along the abdominal region; [1] anteriormost ribs articulate with deep pits on the lateral side of all abdominal centra and those located posteriorly articulate with well-developed parapophyses; [2] all ribs articulate with deep pits on the lateral side of all abdominal centra.

20. Epineurals and epipleurals in the caudal region: [0] absent; [1] present.

21. Epicentrals: [0] absent; [1] present.

22. Shape of cleithrum: [0] L-like (having a single angle in the bone); [1] S-like (having two angles).

23. Dorsal process of posttemporal: [0] slender and sharp; [1] sub-rectangular; [2] broad, wider at distal tip than at midpoint of bone.

24. Number of anal fin rays: [0] eight to eleven; [1] fourteen or fifteen; [2] seventeen or eighteen; [3] twenty; [4] twenty-two to thirty-two; [5] thirty-six to forty-one.

25. Number of dorsal fin rays: [0] eight to thirteen; [1] fourteen to nineteen; [2] twenty-one to twenty-five.

26. Number of hypurals: [0] seven; [1] six; [2] five.

27. Hypural 2: [0] autogenous; [1] fused to first ural centrum (diural terminology).

28. Length of hypural 1: [0] long, reaching ural centrum 1; [1] short, not reaching ural centrum 1.

29. Proximal end of hypural 1 (was originally termed “articulation of hypural 1): [0] massive and forming an upward process; [1] sharp; [2] massive but no upward process.
30. Shape of hypural 2: [0] Distal end distinctly broader than proximal end; [1] very thin and stick-like.
31. Diastema between second and third hypural: [0] third hypural not expanded posteriorly leaving a gap or notch between the second and third hypural; [1] third hypural expanded posteriorly, leaving no gap or notch between second and third hypural.
32. Shape of diastema between hypurals 2 and 3: [0] small triangular notch; [1] deep triangular cavity; [2] large concavity formed by hypural 3 having a concave ventral edge.
33. Size of first ural centrum (diural terminology): [0] roughly the same size (length and depth) as the preural centra; [1] much smaller than the preural centra.
34. Number of uroneurals: [0] three; [1] two; [2] one.
35. First uroneural: [0] extends anteriorly to reach second preural centrum; [1] does not reach second preural centrum.
36. Fusion of first uroneural and first ural centrum: [0] absent; [1] present.
37. First uroneural bearing a dorsal expansion of laminar bone: [0] absent; [1] present.
38. Distal end of second uroneural: [0] reaching the distal end of the first uroneural; [1] not reaching the distal end of the first uroneural.
39. Parhypural: [0] base/arch of bone fused with preural centrum 1; [1] autogenous.
40. Fusion of hypural two and first ural centrum: [0] absent; [1] present.
41. Number of epurals: [0] three; [1] two; [2] none, or those present are weakly ossified, perhaps cartilaginous.

42. Position of epurals: [0] epurals fill the space between the neural spines of pu1 and pu2; [1] epurals are located far from the spine of pu2, leaving an open space between them.

43. Caudal scutes: [0] absent; [1] present.

44. Neural spine of first preural centrum: [0] large or lanceolate; [1] short or sub-rectangular.

45. Neural arch of first ural centrum: [0] absent; [1] present.

46. Predorsal scutes: [0] absent; [1] present.

47. Predorsal scute series: [0] incomplete (absent in anterior part); [1] complete.

48. Subrectangular scutes (i.e., scutes significantly broader than long) in anterior part of predorsal series: [0] absent; [1] present.

49. Subrectangular scutes in posterior part of predorsal series: [0] absent; [1] present.

50. Series of spines on the posterior margin of the lateral wings of the predorsal scutes: [0] absent; [1] present.

51. Prominent median strong spine on posteriormost predorsal scutes: [0] absent; [1] present.

52. Size of scutes of predorsal series: [0] all scutes of same size; [1] irregular in size, size of scutes increasing posteriorly.

53. Surface of predorsal scutes: [0] smooth; [1] ornamented with radiating grooves.

54. Number of predorsal scutes: [0] six to fourteen; [1] sixteen to nineteen; [2] twenty to forty-one.

55. Abdominal scute series: [0] absent; [1] present.

56. Complete abdominal scute series between isthmus and anus (i.e., postpelvic scutes are present): [0] absent; [1] present.

57. Postpelvic abdominal scutes bearing very prominent and strong ventral spine: [0] absent; [1] present.

58. Size of lateral wings of abdominal scutes: [0] small; [1] large, extended upward and covering the abdominal cavity laterally for at least one quarter of the distance from ventral body edge to vertebral column.

59. Shape of lateral wing of abdominal series scutes: [0] spine-like, with large spaces between wings of scutes; [1] wide or spatula-like, with wings of adjacent scutes touching for most of their length.

60. Postdorsal scute series: [0] absent; [1] present.

61. Number of abdominal scutes (in some taxa they will not be equivalent to vertebral counts): [0] fewer than 20; [1] 22-30; [2] more than 32.

62 Number of predorsal bones: [0] 10 or more; [1] 7-9; [2] 6 or fewer.

APPENDIX 3-2. Data matrix used in the phylogenetic analysis of the Early Cretaceous clupeomorphs (based on the data matrices of Murray and Wilson (2013) and Alvarado-Ortega et al. (2008)).

	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	66
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12
Chanos chanos	0100-?20?0	01?0001001	1100110111	00-1-10110	100100----	----0----0	-0
Ellimma branneri	00011???01	0??1?10?1?	?101111O?1	0100000001	0011?11110	1110111110	11
Ellimmichthys goodi	1??031??00	??????0110	1110111000	0?00001000	0010111110	1112111110	??
Ellimmichthys longicostatus	1??11??00?	0???100110	1110111000	0?00001000	0110111110	1112111110	??
Ellimmichthys maceioensis	1?110???0?	??????0???	?1?11?102?	1-01000101	0101111010	1110111?0	21
Ezkutuberezi carmenae	100?0???0?	????00111	?1?42?1021	??0?0000?1	100101??00	111?111100	20
Foreyclupea loonensis	00010??00?	01???01011	100?1?????	??????????	?????0----	----111000	01
Paraclupea chetungensis	10011???01	0??1010???	?1?1111011	0100000101	0111010-10	1111111110	21
Pseudoellimma gallae	11?101010?	0????00001	?0?1121001	00?0000001	???0?1??10	1?0?111000	10
Ranulfoichthys dorsonudum	00010??001	0111101011	?000111001	1-00000001	0011?0----	----111000	10
Santanaclupea silvasantosi	010101010?	0??1??000?	?0?0121001	00?1000001	???100----	----111010	1?
Scutatuspinosus itapagipensis	00010???01	01?1100111	0100010021	1?01100000	0111011001	11101110-0	10
Triplomystus applegatei	10011????1	00????011?	?1121?1011	0011100101	0010111010	1110111111	22

Chapter 4: Revised phylogenetic analysis of the Ellimmichthyiformes

4.1 Introduction

Phylogenetic relationships of subgroups within the Clupeomorpha have been addressed by many authors (e.g. Whitehead, 1963; Patterson, 1970; Forey, 1975; Grande, 1982; 1985; Chang and Maisey, 2003; Forey, 2004; Zaragüeta-Bagils, 2004; Alvarado-Ortega et al., 2008; Murray and Wilson, 2013); however, only a few of the studies published were based on parsimony analysis. Among the pre-cladistic studies of clupeomorph fishes, is Grande's (1982, 1985) revision of the recent and fossil members of the group. His work formed the basis for the subsequent phylogenetic studies of other authors. According to Grande's hypothesis (1982), the Clupeomorpha is subdivided into two divisions: monotypic Division 1 that originally included *Ornategulum sardinoides* Forey, 1973, but later Grande (1985) substituted this with *Erichalcis arcta* Forey, 1975 (this species has been proven to be a composite taxon and is discussed in more detail in Chapter 3 of the present thesis); and Division 2 comprising all other clupeomorphs. Within Division 2, three major groups were identified: two sister groups, Clupeiformes and Ellimmichthyiformes, as well as an unnamed group of unresolved affinities containing only *Armigatus brevissimus* (Blainville, 1818). The significance of Grande's studies (1982, 1985) is emphasized by an extensive morphological analysis of the clupeomorph taxa; and although those studies included only a limited number of ellimmichthyiforms, they established diagnostic characters for two major clupeomorph groups – monotypic Denticipitoidei and Clupeoidei comprising four families Engraulidae, Clupeidae, Pristigasteridae, and Chirocentridae – that are currently recognized and supported by molecular analyses (Di Dario, 2002; Lavoué et al., 2007;

Li and Orti, 2007). Anatomical features described by Grande (1982, 1985) were transformed by other researchers into characters for the cladistics analyses.

The Ellimmichthyiformes were originally diagnosed by a single character, the presence of subrectangular dorsal scutes with expanded lateral wings (Grande, 1985); however, reliability of this diagnostic feature was challenged by the subsequent descriptions and redescriptions of the fossil clupeomorph taxa. Chang and Maisey (2003) redescribed the Early Cretaceous *Ellimma branneri* (Jordan, 1910) and noted that in this taxon, subrectangular scutes are only present in the posterior part of the predorsal series while anterior scutes are longer than wide and do not have expanded lateral wings. In their cladistic analysis, which included 30 osteological characters and 11 taxa, the Ellimmichthyiformes comprised five genera (*Armigatus* Grande, 1982, *Diplomystus* Cope, 1877, *Ellimma* Jordan, 1913, *Paraclupea* Sun, 1956, and *Ellimmichthys* Jordan, 1919) and was defined by the following primitive characteristics: presence of the basipterygoid process of the parasphenoid, 'beryciform' foramen in the anterior ceratohyal, and presence of the dorsal scutes. Subrectangular shape of the dorsal scutes was not included in the list of characters.

Zaragüeta-Bagils (2004) provided a more extensive phylogenetic analysis of the ellimmichthyiforms and basal clupeiforms including 15 taxa and 56 characters, adding a number of osteological characters of the vertebral column and caudal skeleton, as well as characters describing the morphology of the dorsal scutes. The subrectangular shape of the predorsal scutes and details of scute ornamentation were also included in the list of characters. The phylogenetic analysis by Zaragüeta-Bagils (2004) recovered the Ellimmichthyiformes as a paraphyletic group.

Alvarado-Ortega et al. (2008) used a total of 24 taxa and 58 morphological characters in their cladistic analysis. Their updated character list included new meristic characters (vertebral and fin ray counts), a more detailed description of the skull roof ornamentation, and morphology of the dorsal scutes. The phylogenetic hypothesis by Alvarado-Ortega et al. (2008) supported monophyly of the Ellimmichthyiformes; however, these authors excluded the genus *Armigatus* from the order. According to their results, monophyly of the Ellimmichthyiformes is supported by the presence of subrectangular scutes in the posterior part of the predorsal series.

The most recent and inclusive cladistic analysis of the Ellimmichthyiformes was undertaken by Murray and Wilson (2013), and was based in part on the previously published works by Alvarado-Ortega et al. (2008), Zaragüeta-Bagils (2004), and Chang and Maisey (2003). The authors updated the character list modifying some of the existing characters and adding new characters for a total of 62 characters; their analysis included new ellimmichthyiform species described from Canada (*Horseshoeichthys armaserratus* Newbrey et al., 2010 and *Tycheroichthys dunveganensis* Hay et al., 2007), Morocco (*Sorbinichthys africanus* Murray and Wilson, 2011, *Thorectichthys marocensis* Murray and Wilson, 2013 and *T. rhadinus* Murray and Wilson, 2013), and Palestine (*Rhombichthys intoccabillis* Khalloufi et al., 2010). Murray and Wilson (2013) recovered two major clades within the monophyletic Ellimmichthyiformes. The first clade included *Armigatus* and *Diplomystus* (excluding *'Diplomystus' solignaci* Guadant and Guadant, 1971); the second clade contained all other ellimmichthyiforms. The two clades were designated a rank of suborder – Armigatoidei and Ellimmichthyoidei respectively. According to this analysis, the Ellimmichthyiformes are characterized by the medioparietal condition of the skull roof (parietals contacting each other on the midline), presence of the basipterygoid process of the parasphenoid, 'beryciform' foramen in the anterior ceratohyal, ornamentation of the skull roof, three epurals, and a predorsal series of scutes.

One of the main objectives of this research project is to provide an updated phylogenetic hypothesis of the relationships within the Ellimmichthyiformes using information available on the newly described species as well as those fossil clupeomorph species that have not yet been included in the cladistic analysis (De Figueiredo, 2009; Alvarado-Ortega, 2014). The existing list of characters used in the most recent phylogenetic studies of ellimmichthyiforms has been revised and updated to optimize character coding and add new characters to the list. Using the updated phylogenetic hypothesis, the following questions were addressed:

- Is *Armigatus* a member of the Ellimmichthyiformes?
- What are the main trends in the character evolution within the Ellimmichthyiformes?
- What were the biogeographic patterns of the group throughout the Cretaceous?

4.2 Methods

A total of 33 taxa were used in the phylogenetic analysis including three outgroup taxa and 30 fossil clupeomorph species. The outgroup included *Chanos chanos* (Forsskål, 1775), a member of the Ostariophysi (Gonorhynchiformes, Chanidae), which is the sister group to the Clupeomorpha, as well as two fossil clupeiform taxa – *Pseudoellimma gallae* De Figueiredo, 2009 and *Santanaclupea silvasantosi* Maisey, 1993*,* which represent a sister group to the Ellimmichthyiformes. A full list of taxa analyzed is provided in Table 4-1 along with information about each species's temporal and geographic distribution, habitat preference for the living species, and paleoecological settings at the sites of occurrence for the fossil taxa. Two new ellimmichthyiform species described in the previous chapters, *Armigatus oligodentatus* (Chapter 2) and *Foreyclupea loonensis* (Chapter 3) are also included in the analysis.

The character matrix was constructed in Mesquite v 3.03 (Maddison and Maddison, 2011) and includes a total of 61 characters revised and adopted in part from Zaragüeta-Bagils (2004), Alvarado-Ortega et al. (2008), and Murray and Wilson (2013) (Appendix 4-1 and 4-2).

All characters were treated as unordered and of equal weight. Cladistic analysis was conducted in TNT 1.1 (Goloboff et al., 2008) employing a Traditional (heuristic) search option with 1000 replicates and tree bisection and reconnection (TBR) swapping algorithm. The most parsimonious trees (MPTs) retrieved by the analysis were used to construct a strict consensus tree. Bremer support and bootstrap values for the strict consensus tree were calculated in TNT; the tree length, consistency and retention indices were calculated in Mesquite.

4.3 Characters: revised, new, and deleted from the character list

The most recent character matrix by Murray and Wilson (2013) was used in the present analysis as a starting point for the character revision and modification. The following discussion of the characters that have been modified or deleted from the character list with the reference numbers of the characters as they appear in the character list by Murray and Wilson (2013); references in parentheses indicate numbers of the corresponding characters in the previous phylogenetic analyses by other authors.

4.3.1 Characters with modified character states:

Characters 4 and 5: Ornamentation of the skull roof

(Zaragüeta-Bagils, 2004: char. 3 and 4; Alvarado-Ortega et al., 2008: char. 4 and 5)

Ornamentation of the skull roof is common in ellimmichthyiforms, but is rather limited in the clupeiforms. Among the ellimmichthyiforms, skull roof ornamentation has been described in some species of *Armigatus*, *Diplomystus*, *Triplomystus*, *Paraclupea*, *Ellimma*, *Sorbinichthys*, *Thorectichthys*, *Rhombichthys*, *Ellimmichthys*, and *Kwangoclupea.* This character is known to be affected by growth. In their redescription of *Ellimma branneri*, Chang and Maisey (2003) noted that the larger individuals have well-developed skull ornamentation covering the posterior part of the frontals, parietals, and the dorsal part of the supraoccipital with radiating ridges; however, in the smaller specimens, no ornamentation was observed. This observation has significant implications for using this character in phylogenetic studies – presence of the skull roof ornamentation should only be scored in the character matrix when the adult age of the studied specimens has been clearly established. In cases where material is fragmentary or poorly preserved and does not allow a reliable conclusion about the age of the specimen, I suggest that absence of the ornamentation of the skull roof bones should be coded as missing data. This way the negative impact of the incorrect character scoring can be minimized.

Zaragüeta-Bagils (2004), coded presence/absence of the ornamentation (character 3) as an independent character separate from the type of ornamentation (character 4). Alvarado-Ortega et al. (2008) expanded the presence/absence of ornamentation character by adding extra character states related to the location of the skull sculpturing (character 4: [0] absent; [1] present on the middle part of the frontals; [2] present on the posterior part of the frontal and parietal bones; [3] present on the posterior part of the frontal, parietal and pterotic bones; [4] present on the frontal, parietal, and supraoccipital bones). Considering the ontogeny-dependent nature of this character, it is nearly impossible to accurately assess distribution of the skull ornamentation without clearly establishing the developmental stage of the specimens. Murray and Wilson (2013) later simplified coding for this character and reverted to the original binary coding (character 4: [0] absent; [1] present) that allowed a clearer assessment of the taxa.

In my analysis, I follow Maddison's (1993) and Brazeau's (2011) suggestions for the construction of a compound character and chose to combine characters 4 and 5 in a single multistate character – Skull roof ornamentation: [0] absent; [1] present, fine parallel grooves; [2]

present, strong grooves with radiating ridges. I leave this character unordered and unweighted because there is no evidence for any particular direction of the character state change for this trait.

Characters 31 and 32: Diastema between second and third hypurals

(Chang and Maisey, 2003, char. 26; Zaragüeta-Bagils, 2004, char. 28; Alvarado-Ortega et al, 2008, char. 31)

The hypural diastema is defined by Schultze and Arratia (2013) as a 'space positioned between hypurals 2 and 3, or a notch positioned at the distal regions of hypurals 2 and 3'. This trait forms at the earliest stages of development and is easily observed in most specimens. Presence/absence of the gap or notch between hypurals 2 and 3, as well as its shape, are useful taxonomic characters that are often employed in systematic studies of various groups of teleosts (Springer and Fraser, 1976; Konstantinidis and Johnson, 2012; Schultze and Arratia, 2013).

In ellimmichthyiforms, the hypural diastema is present in *Ellimmichthys* (excluding *E. maceioensis* Malabarba et al., 2004), *Ellimma*, *Paraclupea*, *Sorbinichthys*, *Triplomystus* (excluding *T. applegatei* Alvarado-Ortega and Ovalles-Damian, 2008), *Tycheroichthys*, *Rhombichthys*, and *Thorectichthys*. According to the phylogenetic hypothesis by Murray and Wilson (2013), absence of the hypural diastema is one of the characteristics uniting *Armigatus* and *Diplomystus*. In these fishes, the posterior end of hypural 3 is expanded, leaving no notch or gap between hypurals 2 and 3. Alvarado-Ortega et al. (2008) and Alvarado-Ortega (2014) also indicated the absence of a hypural diastema in the Early Cretaceous clupeomorphs *Scutatuspinosus itapagipensis* Silva Santos and Silva Corréa, 1985 and *Ranulfoichthys dorsonudum* Alvarado-Ortega, 2014.

The original coding of this feature by Chang and Maisey (2003) included a single binary character (character 26) defining presence of the hypural diastema as ‘third hypural not expanded posteriorly, leaving a gap or notch between second and third hypurals’ and absence of diastema as ‘third hypural expanded posteriorly, leaving no gap or notch between second and third hypurals’. These character state definitions were simplified to ‘present/absent’ in the phylogenetic analysis by Zaragüeta-Bagils (2004) and Alvarado-Ortega et al. (2008), but this way of coding does not encompass all the variation observed in this feature of the caudal skeleton. Murray and Wilson (2013) reverted to the original character state definitions by Chang and Maisey (2003) and added another character describing the shape of the hypural diastema (character 32): [0] small triangular notch; [1] deep triangular cavity; [2] deep concavity formed by hypural 3 having a concave ventral edge. These character states are easily distinguishable and highly characteristic of some taxa (character state 2 is one of the diagnostic features of *Sorbinichthys*).

Similar to the previous character, I unite two characters describing presence/absence and shape of the hypural diastema in a single multistate character: Diastema between hypurals 2 and 3: [0] absent; [1] present, small triangular notch; [2] present, deep triangular cavity; [3] present, deep concavity formed by hypural 3 having a concave ventral edge. This optimization of the character construction eliminates the problem of scoring the shape of the diastema as missing data for the taxa without this trait.

Characters 48 and 49: Subrectangular predorsal scutes.

(Zaragüeta-Bagils, 2004, ch. 47; Alvarado-Ortega et. al 2008, ch. 46 and 47)

Scutes are modified scales that are present along the ventral and/or dorsal margins of the body in clupeomorphs. In clupeiforms, predorsal scutes are limited to only a few species of the genera † *Knightia*, *Nematalosa*, *Hyperlophus*, *Ethmidium*, *Gosiutichthys*, and *Clupanodon* (Grande, 1982; Whitehead, 1985; Nelson, 2006); however, predorsal scutes are well-developed in most ellimmichthyiforms and can have complex structure with surface sculpturing as well as marginal spines and projections. The most common condition among ellimmichthyiforms is the presence of a complete series of predorsal scutes from the occiput to the origin of the dorsal fin; however, there are modifications to this condition. In *Armigatus*, the predorsal series is incomplete, leaving an unscuted gap posterior to the back of the skull, and in *Triplomystus* the dorsal scute series continues behind the dorsal fin forming a postdorsal series of scutes that is unique to the members of this genus.

Ellimmichthyiforms also show variation in the dorsal scute shape: subrectangular as in *Diplomystus* and partially in *Ellimmichthys*; heart-shaped to ovoid in *Armigatus, Kwangoclupea,* and partially in *Thorectichthys* and some paraclupeids; and subrhomboid scutes in *Sorbinichthys* (Grande, 1982; Chang and Grande, 1997; Bannikov and Bacchia, 2000; Forey et al., 2003; Murray and Wilson, 2011, 2013). Despite this variation in shape, only presence or absence of subrectangular scutes has been used as a character in phylogenetic analyses. This is mostly due to the fact that presence of subrectangular scutes was originally used by Grande (1985) as a single diagnostic character of the Ellimmichthyiformes. At the time that Grande established the order Ellimmichthyiformes (Grande, 1982), it contained only two genera, *Ellimmichthys* and *Diplomystus*, both of which have subrectangular scutes of the predorsal series; *Armigatus*, with its incomplete predorsal series of heart-shaped scutes, was not included in the order. As new ellimmichthyiforms have been described, the need for the revision of this character became apparent. Chang and Maisey (2003), in their redescription of *Ellimma branneri* and *Diplomystus schengliensis*, noted that the shape of the predorsal scutes is clearly variable among the ellimmichthyiforms, and Grande's diagnosis of the order based on this character needed to be revised. Chang and Maisey (2003) did not use this character in their phylogenetic analysis. Zaragüeta-Bagils (2004) first included the presence of subrectangular scutes of the predorsal series in his phylogenetic analysis. This character was later elaborated by Alvarado-Ortega et al. (2008) and was split into two characters to recognize presence/absence of subrectangular scutes in the anterior and posterior parts of the predorsal series separately. Murray and Wilson (2013) followed this character coding in their analysis.

Variation in the shape of the predorsal scutes has been described in the ellimmichthyiforms *Ellimma branneri* and *Scutatuspinosus itapagipensis* as well as in living species of *Hyperlophus* (Yabumoto and Uyeno, 1982; Chang and Maisey, 2003; Alvarado-Ortega et al., 2008). Herein, I add character states to each character describing the shape of the scutes in the anterior and posterior parts of the predorsal series to account for the observed variation:

44) Shape of scutes in the anterior part of predorsal series: [0] subrectangular; [1] heart-shaped or ovoid; [2] subrhomboid.

45) Shape of scutes in the posterior part of predorsal series: [0] subrectangular; [1] heart-shaped or ovoid; [2] subrhomboid.

4.3.2 Meristic characters:

Meristic characters have been regarded by some authors (e.g., Thiele, 1993; Swiderski et al., 1998) as undesirable to use in a phylogenetic analysis, while others consider meristic data to provide valuable phylogenetic information (e.g., Wiens, 1995; Wiens and Servedio, 1998;

Lawing et al., 2008). I have identified a group of characters used in the phylogenetic assessment of the Ellimmichthyiformes that are based on meristic data:

9) Supramaxillary bones: two [0]; one or none [1] (Zaragüeta-Bagils, 2004: ch. 10; Alvarado-Ortega et al., 2008: ch. 9).

17) Total number of vertebrae excluding ural centra: [0] 30 – 40; [1] 41 – 43; [2] more than 50. (Alvarado-Ortega et al 2008, ch. 17)

24) Number of anal fin rays: [0] eight to eleven; [1] fourteen or fifteen; [2] seventeen or eighteen; [3] twenty; [4] twenty-two to thirty-two; [5] thirty-six to forty-one. (Alvarado-Ortega et al., 2008, ch. 24)

25) Number of dorsal fin rays: [0] eight to thirteen; [1] fourteen to nineteen; [2] twenty-one to twenty-five. (Alvarado-Ortega et al., 2008, ch. 25)

26) Number of hypurals: [0] seven; [1] six; [2] five.

(Chang and Maisey, 2003, ch. 21; Zaragüeta-Bagils, 2004, ch. 23; Alvarado-Ortega et al 2008, ch. 26)

34) Number of uroneurals: [0] three; [1] two; [2] one. (Zaragüeta-Bagils, 2004, ch. 29; Alvarado-Ortega et al 2008, ch. 29)

41) Number of epurals: [0] three; [1] two; [2] none, or those present are weakly ossified, perhaps cartilaginous. (Chang and Maisey, 2003, ch. 23; Zaragüeta-Bagils, 2004, ch. 37; Alvarado-Ortega et al., 2008, ch. 40)

54) Number of predorsal scutes: [0] six to fourteen; [1] sixteen to nineteen; [2] twenty to forty-one. (Zaragüeta-Bagils, 2004, ch. 52; Alvarado-Ortega et al., 2008, ch. 52)

61) Number of abdominal scutes: [0] fewer than 20; [1] 22 – 30; [2] more than 32.

62) Number of predorsal bones: [0] 10 or more; [1] 7 – 9; [2] 6 or fewer.

An intrinsic problem associated with using quantitative characters in a phylogenetic analysis relates to defining character states. Considering the natural variation in continuous as well as discrete characters, delimiting non-overlapping character states for such features across taxa can be extremely difficult and, in some cases, even impossible. Whenever meristic data is being incorporated into a character matrix for a phylogenetic analysis, a few methods are available to help deal with these types of characters. The most commonly used methods include: arbitrary character state delimitation based on the observed distribution of the character values in different taxa, step-matrix gap-weighting (Thiele, 1993; Wiens, 2001), generalized frequency coding (Smith and Gutberlet, 2001), and numerous other methods that, like the last two methods mentioned, are based on the principle of converting meristic or continuous data into a finite number of character states separated by the ‘natural gaps’ (Simon, 1983; Archie, 1985; Thiele, 1993; Swiderski et al., 1998; Wiens, 2001; Bardin et al., 2014). Unfortunately, an overview of these methods is beyond the scope of this chapter, but references cited provide ample information on the topic.

In paleontology, meristic and continuous data are predominantly arbitrarily divided up into discrete character states, without employing any statistical methods to evaluate character distribution. This is a consequence of usually having only a small number of specimens or even partial fossil material available for study. As a result of such crude character state delimitation, it is a common practice to adjust character states in order to accommodate new taxa included in a phylogenetic analysis.

Although meristic characters have been regarded as those being more prone to homoplasy than other types of characters (Wiens and Servedio, 1998; Lawing et al., 2008), prior studies on teleost phylogeny (Patterson, 1977; Arratia, 1997) suggest that meristic characters can be a reliable source of phylogenetic information. Within the broad group of meristic characters, however, two groups can be established according to the level of variation observed for the character. The first group contains highly conserved characters that have a high degree of fixed count values among different groups of teleosts and provide a strong phylogenetic signal. Such characters include the number of supramaxillary bones (char. 9), hypurals (char. 26), uroneurals (char. 34), epurals (char. 41), and predorsal bones (char. 62).

The second group of characters includes more variable meristic traits, such as numbers of fin rays, vertebrae, and scutes (characters 17, 24, 25, 54, 61). These characters show significant levels of variation and perform better at the lower taxonomic levels (genus and species); however, at a higher taxonomic level they may increase the amount of homoplasy on a tree.

In order to test the performance of the meristic characters in the phylogenetic analysis of the Ellimmichthyiformes, two additional iterations were performed: one, excluding all meristic characters, and another excluding only the second group of more variable count traits.

4.3.3 Characters deleted from the list

The following characters have been recognized as difficult to score consistently or that are redundant and have been removed from the character list:

3) Lateral profile of the skull roof: [0] a straight line from anterior tip of frontal to back of skull, with no distinct angle apparent; [1] with distinct angle between anterior and posterior parts, normally in the region of the parietals (Zaragüeta-Bagils, 2004, ch. 2; Alvarado-Ortega et al., 2008, ch. 3; Murray and Wilson, 2013, ch. 3).

This character has been interpreted and scored differently by different authors. Zaragüeta-Bagils (2004) and Alvarado-Ortega et al. (2008) defined this character as ‘depth of the supraoccipital crest'; however, scoring of this character has been inconsistent due to the different interpretations of this feature. Alvarado-Ortega et al. (2008) specified that the supraoccipital crest should be considered high (condition equivalent to the character state [1] of character 3 in the list of Murray and Wilson (2013)) when the laminar projection of the supraoccipital forms an angle less than 180 degrees with the dorsal profile of the skull roof bones. This feature is often misinterpreted due to the taphonomic deformations of the skull roof.

40) Fusion of hypural two and first ural centrum: [0] absent; [1] present.

(Zaragüeta-Bagils, 2004, ch. 24; Alvarado-Ortega et. al 2008, ch. 39; Murray and Wilson, 2013, ch. 40)

This character is identical to character 27 (Alvarado-Ortega et al., 2008; Murray and Wilson, 2013) which is worded in a slightly different way. In order to avoid double weighting of this particular feature and keep all the characters equally weighted, character 40 has been removed from the list. In this way, fusion between hypural two and the first ural centrum is only scored once as character 25 of the new character list.

4.4 Results

4.4.1 All characters included

The parsimony analysis using all 61 characters recovered a single most parsimonious tree (MPT) of 192 steps and with consistency (C.I.) and retention (R.I.) indices equal 0.42 and 0.67, respectively. In the recovered tree (Fig.4-1), the two outgroup clupeiform taxa included in the analysis, *Pseudoellimma gallae* and *Santanaclupea silvasantosi*, form a monophyletic group with a sister-group relationship to the rest of the clupeomorph species. A problematic taxon *Ornategulum sardinoides* appears at the base of the large clade that is the sister group to the outgroup *Pseudoellimma* + *Santanaclupea*. The uncertain affinities of *Ornategulum* within the Clupeomorpha have previously been noted by many authors (Forey, 1973; Grande, 1982, 1985; Zaragüeta-Bagils, 2004; Murray and Wilson, 2013); according to the results of the present cladistic analysis, *Ornategulum sardinoides* can be included in the Ellimmichthyiformes as the most basal member of this extinct order.

The Early Cretaceous clupeomorphs *Scutatuspinosus itapagipensis*, *Ranulfoichthys dorsonudum*, and *Foreyclupea loonensis* form the next basalmost clade of the ellimmichthyiforms. Out of these taxa, only *S. itapagipensis* has previously been included in the phylogenetic analyses by Alvarado-Ortega et al. (2008) and Murray and Wilson (2013); however, in those analyses this taxon was placed among more derived ellimmichthyiforms. The next clade recovered is formed by the two species of *Sorbinichthys*, and then the next taxon going up the tree is *Kwangoclupea dartvellei* .

Armigatus and *Diplomystus* (excluding *'D.' solignaci*) form the next clade, equivalent to the family Armigatidae Murray and Wilson, 2013, but with the addition of the Late Cretaceous (Santonian – Maastrichtian) ellimmichthyiform from Canada, *Horseshoeichthys armaserratus*. *Horseshoeichthys* was recovered as the sister taxon to the four species of *Diplomystus* (*D.birdi*, *D.dubertreti*, *D. shengliensis*, and *D. dentatus*). The two species of *Thorectichthys* form the next clade up on the tree followed by *'Diplomystus' solignaci* and *Rhombichthys intoccabilis*.

Within the more derived ellimmichthyiforms, *Paraclupea chetungensis*, *Ellimma branneri*, and two species of *Ellimmichthys* (*E. goodi* and *E. longicostatus*) form a clade of successive taxa. The sister group to this clade includes *Ezkutuberezi carmenae* as the basalmost taxon and two sister clades – monophyletic genus *Triplomystus* and a clade comprising *Tycheroichthys dunveganensis* and *Ellimmichthys maceioensis*.

Results of the bootstrap and Bremer support analyses did not show strong support for the clades recovered. The bootstrap support above 50% was indicated for only five clades (Fig. 4-1). The major clades of the Ellimmichthyiformes and their synapomorphies are shown in Fig. 4-2.

4.4.2 Meristic characters excluded

To test performance of the meristic characters and their overall effect on the tree topology, I ran two separate analyses: (1) excluding all meristic characters; (2) excluding only highly variable meristic variables (fin ray, vertebral, and scute counts), as discussed earlier in the chapter.

4.4.2.1 All meristic characters excluded

When all ten meristic characters were excluded from the analysis, two MPTs were recovered. The strict consensus of these trees has 204 steps, C.I. = 0.41 and R.I. = 0.64 (Fig. 4-3 A). The overall topology at the base of the tree remained the same as in the reference tree (Fig. 4-2). Relationships among the three species of *Armigatus* (*A. alticorpus*, *A. namourensis*, and *A. brevissimus*) were unresolved with the three species of the genus forming a polytomy (Fig. 4-3 A, node 1). In the *Diplomystus* group, *D. shengliensis* was recovered as the most basal member with *Horseshoeichthys armaserratus* placed within the *Diplomystus* group (Fig. 4-3 A, node 2). Another three species of *Diplomystus* (*D. dentatus*, *D. dubertreti*, and *D. birdi*) appeared in a polytomy (Fig. 4-3 A, node 3)

Relationships among the derived ellimmichthyiforms, however, were not as well-resolved as in the reference tree, with a major polytomy formed among paraclupeids (Fig. 4-3 A, node 4): *Ezkutuberezi carmenae* + *Triplomystus* + (*Ellimmichthys maceioensis* + *Tycheroichthys dunveganensis*) + (*Paraclupea chetungensis* + (*Ellimma branneri* + (*Ellimmichthys goodi* + *Ellimmichthys longicostatus*))). The three species of *Triplomystus* were also recovered in a polytomy (Fig. 4-3 A, node 5).

4.4.2.2. ‘Highly variable’ meristic characters excluded

In the second iteration of the analysis, only ‘highly variable’ meristic characters (characters 17, 24, 25, 54, 61) were excluded while more conserved meristic traits were returned to the matrix. The analysis retrieved a single MPT with 196 steps, C.I. = 0.42 and R.I. = 0.67 (Fig. 4-3 B).

Topology of the resulting tree was different from that of the reference tree only in the arrangement of species within the *Armigatus* and *Diplomystus* groups. In the *Armigatus* group, *A. alticorpus* was recovered as a sister taxon to *A. brevissimus* plus *A. namourensis* (Fig. 4-3 B, node 1). In the *Diplomystus* group, similar to the results of the first iteration of the analysis with all meristic characters excluded, *Horseshoeichthys armaserratus* was recovered as a member of *Diplomystus* with *D. shengliensis* placed at the base of the group (Fig. 4-3 B, node 2).

The results of the test with removal of the meristic characters show that their inclusion in this analysis does not have a critical effect on the overall tree topology with the major groups (the orders Clupeiformes and Ellimmichthyiformes, and the four family groups – Scutatuspinosidae, Sorbinichthyidae, Armigatidae, and Paraclupeidae) recovered even when all of the meristic traits were removed from the data matrix. The group of conserved meristic characters (number of supramaxillae, hypurals, epurals, uroneurals, and supraneurals) was the most effective at resolving relationships at the subfamily level within the Paraclupeidae. The group of characters with higher natural variation (fin ray, vertebral, and scute counts) only affected relationships at the species level. Remarkably, *Horseshoeichthys armaserratus*, for which most of the meristic data are missing, was more deeply placed within the *Diplomystus* group when these types of characters were excluded.

4.5 Discussion

The overall results of the present phylogenetic analysis of the fossil clupeomorphs support the bipartite division of the Clupeomorpha into the Clupeiformes and Ellimmichthyiformes (Fig. 4-2). The two Early Cretaceous taxa from Brazil, *Pseudoellimma* and *Santanaclupea*, form a monophyletic clade of the fossil clupeiforms with a sister-group relationship to the clade comprising all ellimmichthyiforms included in the analysis. Fossil clupeiforms, like their living relatives, are characterized by the following combination of derived characters: the parietal bones completely separated by the supraoccipital (2:1), presence of the recessus lateralis (6:1), loss of the 'basipterygoid' process of the parasphenoid (8:0), first ural centrum significantly smaller than the preural centra (31:1), and presence of two epurals (38:1). However, the early clupeiforms also retain a number of primitive characters – ornamentation of the skull roof (3:1), 'beryciform' foramen in the anterior ceratohyal (12:1), unfused neural spines of the most of the abdominal vertebrae (16:0), and hypural one with a massive upward process at the proximal end (27:0).

The sister group to the fossil clupeiforms is a large clade that includes all ellimmichthyiforms and *Ornategulum*, which is here included in that order; all these taxa share the following primitive and derived characters: parietals contacting each other on the midline (2:0; except *Ellimmichthys longicostatus* and *E. goodi* in which Chang and Grande (1997) reported parietal bones separated by the supraoccipital), absence of recessus lateralis (6:0), presence of the basipterygoid process of the parasphenoid (8:1), and three epurals (38:0). The first two features have been previously regarded as characteristics of the ellimmichthyiforms (Grande, 1985; Chang and Maisey, 2003); therefore, the problematic taxon, *Ornategulum sardinoides*, appears as the most basal member of the group. *Ornategulum* was originally described by Forey (1973) as Clupeomorpha *insertae sedis* due to the lack of diagnostic features that would allow a more accurate classification. Placement of this taxon within the Clupeomorpha was justified primarily based on the caudal skeleton featuring a complete neural spine of the second preural centrum, a free first hypural not articulating with the first ural centrum, and second hypural fused to the first ural centrum. Forey (1973) also noted that *Ornategulum* and *Diplomystus* share a number of cranial characteristics including medioparietal skull roof condition, presence of the basipterygoid process and endopterygoid dentition; but he recognized *Ornategulum* as a more advanced taxon based on the loss of the parasphenoid dentition. This combination of characters, however, was not sufficient to place *O. sardinoides* in either the Clupeiformes or the Ellimmichthyiformes. Grande (1982) placed *Ornategulum* in Division 1 of the Clupeomorpha as the sister group to Divison 2 comprising ellimmichthyiforms plus clupeiforms. Later (Grande, 1985), *Ornategulum* was removed from the Clupeomorpha in the absence of reliable evidence that this taxon belongs to the superorder; however, disputes over the clupeomorph affinities of *O. sardinoides* persist to the present day. The obvious problem with classifying *Ornategulum* as a member of the Clupeomorpha is the absence of any scute development. Interestingly, another clupeomorph taxon lacking both dorsal and ventral scutes, *Nardoclupea grandei* Taverne, 2002, has been described from the Late Cretaceous (Campanian – Maastrichtian) of Nardo, Italy. *Nardoclupea*, however, shows some derived clupeomorph characteristics including presence of the recessus lateralis and parietals completely separated by the supraoccipital. Taverne (2002) tentatively classified *Nardoclupea* as a member of the Dussumieriidae (round herrings), mostly based on the structure of the caudal skeleton. However, it does not show a single W-shaped pelvic scute, which is a unique feature shared by the dussumierids. Presence of at least one abdominal scute is regarded as a diagnostic character exclusive to the clupeomorphs (Patterson, 1970; Grande, 1985; Arratia, 1997); therefore, classification of scuteless taxa within the Clupeomorpha is problematic.

The next most basal clade of the Ellimmichthyiformes includes three Early Cretaceous species, *Ranulfoichthys dorsonudum*, *Scutatuspinosus itapagipensis*, and *Foreyclupea loonensis*. *Scutatuspinosus* is the type species of the subfamily Scutatuspinosinae Silva Santos and Silva Correa, 1985. Here, the clade containing *Scutatuspinosus* and two other basal clupeomorphs, *Foreyclupea* and *Ranulfoichthys*, is given familial status as Scutatuspinosidae (Fig. 4-3, node C). These torpedo-bodied clupeomorphs are distinguished from other ellimmichthyiforms by the presence of a foramen in the posterior ceratohyal (13:1; this condition is not known in *Foreyclupea loonensis* due to the missing ceratohyal elements) and short lateral wings of the ventral scutes (55:0). This clade of basal clupeomorphs is remarkable because it includes one of the oldest clupeomorphs described (Neocomian *Scutatuspinosus* from Brazil) as well as the oldest clupeomorph from Canada (Albian *Foreyclupea* from the Northwest Territories). Considering the earlier mentioned occurrence of the clupeiform *Pseudoellimma gallae* in the Barremian sediments of Brazil, these findings suggest that the two major lineages of clupeomorphs (ellimmichthyiforms and clupeiforms) diverged prior to that time. Another intriguing fact about this basal clade of ellimmichthyiforms is the loss of the dorsal scute series in *Ranulfoichthys* and *Foreyclupea*; this condition is not typical for the ellimmichthyiform fishes that are commonly referred to as 'double-armored' herrings. The loss of the dorsal scutes has been regarded as a derived characteristic of the clupeiforms; however, occurrence of this feature in the basal ellimmichthyiforms suggests that this condition has evolved multiple times within different lineages of the Clupeomorpha.

The monogeneric family Sorbinichthyidae (Fig. 4-3, node D) comprises two Late Cretaceous species, *Sorbinichthys africanus* from Morocco and *S. elusivo* from Lebanon. This group is very distinct among other ellimmichthyiforms and is characterized by a number of apomorphies: broad, spatula-shaped dorsal process of the posttemporal (21:2), extensive diastema between hypurals two and three (30:3), distinct subrhomboid shape of the dorsal scutes (44:2 and 45:2), and the posteriormost predorsal scutes with anteroposteriorly inclined lateral processes (61:1). The phylogenetic position of *Sorbinichthys* within the Ellimmichthyiformes has changed from being a basal clade with unresolved relationships with other ellimmichthyiforms (Zaragüeta-Bagils, 2004), or as having a sister-group relationship with *Diplomystus* (Alvarado-Ortega et al., 2008), to its placement within the suborder of more advanced ellimmichthyiforms, the Ellimmichthyoidei (Murray and Wilson, 2013). In the reference tree (Fig.4-3), Sorbinichthyidae is placed close to the base of the Ellimmichthyiformes, outside of the suborder Ellimmichthyoidei Murray and Wilson, 2013.

The rest of the ellimmichthyiforms are grouped into two major clades that most closely correspond to the families Armigatidae and Paraclupeidae *sensu* Murray and Wilson (2013). These fishes are united by the presence of the S-shaped cleithrum (20:1).

The present analysis recovered *Armigatus* as a sister group to a clade containing *Horseshoeichthys armaserratus* and the four species of *Diplomystus*. The sister-group relationship of *Armigatus* and *Diplomystus* was previously described in the phylogenetic hypothesis by Murray and Wilson (2013) who proposed a family rank Armigatidae for the clade (Fig. 4-2, node E). This clade is supported by the following combination of characteristics: shape of the proximal end of the first hypural (27:1), third hypural expanded posteriorly leaving no gap between second and third hypurals (29:0), and a uniform size of the scutes of the predorsal series (48:0). The phylogenetic analysis by Murray and Wilson (2013) originally included *Horseshoeichthys armaserratus*, but this species was identified as a 'wild-card' taxon and removed from the analysis in order to resolve a near-basal polytomy. Although *Horseshoeichthys* is known only from a single partially preserved specimen, the grouping of this Late Cretaceous (Santonian – Maastrichtian) ellimmichthyiform from freshwater deposits of Canada with the species of *Diplomystus* is not surprising; *H. armaserratus* and *D. dentatus* from the Eocene freshwater deposits of the Green River Formation (Wyoming, USA) share an overall similarity of the head and body shape as well as dentition and shape of the maxilla as described by Newbrey et al. (2010).

Monophyly of *Armigatus* is supported by the presence of an incomplete predorsal series of scutes (43:0). Forey (2004) recognized the heart-shaped scutes forming an incomplete predorsal series as a derived and autopomorphic feature of the genus. Taking into account newly described ellimmichthyiform taxa lacking predorsal scutes (*Ranulfoichthys dorsonudum* and *Foreyclupea loonensis*), it can be inferred that ellimmichthyiforms showed some variation in the degree of the development of the dorsal series of scutes with a complete series being a predominant form. The trend is reversed among the living clupeiforms with only a few species retaining a complete or partial series of dorsal scutes and most clupeiform fishes lacking scutes along the dorsal margin of the body.

The sister group to the Armigatidae is a large clade that contains the rest of the ellimmichthyiforms and is similar in species composition to the family Paraclupeidae *sensu* Murray and Wilson, 2013 (excluding subfamily Scutatuspinosinae). This group (Fig. 4-2, node F) is characterized by the dorsal margin of the body forming a distinct angle at the base of the dorsal fin (1:1), presence of a neural arch on the first ural centrum (41:1), and ornamentation of the dorsal scutes (49:1, this character is not observed in *Tycheroichthys dunveganensis*, but this may be a result of preservation (Hay et al., 2007)).

The monotypic subfamily Thorectichthyinae Murray and Wilson, 2013 is the most basal clade of the Paraclupeidae (Fig. 4-2, node G). The two species of *Thorectichthys* are characterized by a short second uroneural that does not reach the distal end of the first uroneural (35:1); this feature is also present in more derived paraclupeids: *Triplomystus noorae, T. applegatei, T. oligoscutatus*, *Tycheroichthys dunveganensis*, and *Paraclupea chetungensis*.

The next two branches at the base of the Paraclupeidae clade support a single species each, *'Diplomystus' solignaci* and *Rhombichthys intoccabillis*. These species have also been recovered as members of the family Paraclupeidae by Alvarado-Ortega et al. (2008) and Murray and Wilson (2013); however, their phylogenetic hypotheses did not include all the same taxa of paraclupeids making it impossible to compare placement of the taxa in question within the Paraclupeidae. In the present phylogenetic hypothesis, *'D.' solignaci* and *R. intoccabillis* are identified as paraclupeids without further assigning them to separate subfamilies; both taxa share with the rest of the derived paraclupeids presence of the subrectangular scutes in the posterior part of the predorsal series (45:0; this condition is also present in *Diplomystus*; but unlike in paraclupeids, predorsal scutes in *Diplomystus* are all the same size and shape). *Rhombichthys intoccabillis*, also shares some characteristics with the rest of the derived paraclupeids: presence of the strong median spine on the posterior margin of the last few predorsal scutes (47:1) and wide, spatula-like shape of the ascending lateral wings of the abdominal scutes (55:1).

The more derived paraclupeids are subdivided into two clades, subfamilies Paraclupeinae (Fig. 4-3, node H) Chang and Chou, 1977 and Triplomistinae Murray and Wilson, 2013, new rank. The Paraclupeinae includes exclusively Early Cretaceous taxa: *Paraclupea chetungensis*, *Ellimma branneri*, and two species of *Ellimmichthys*, *E. longicostatus* and *E. goodi*. These species share the presence of distinct skull roof sculpturing, the parietals and frontals strongly ornamented with radiating ridges (3:2), and a deep hypural diastema between the second and third hypurals (29:2; also observed in *Tycheroichthys dunveganensis*). *Ellimma branneri* along with *Ellimmichthys longicostatus* and *E. goodi* are placed in a tribe Ellimmichthyini (Fig. 4-3, node J).

The Triplomystinae comprises *Ezkutuberezi carmenae* as the most basal taxon and two sister groups, monophyletic *Triplomystus* and a clade containing *Tycheroichthys dunveganensis* and *Ellimmichthys maceioensis*. This clade, however, has weak support and is characterized by the plesiomorphic characters: number of anal fin rays and shape of the proximal end of the first hypural (27:1 or 2). Results of the present analysis suggest that *E. maceioensis* does not form a monophyletic group with the type species of *Ellimmichthys* (*E. longicostatus*) and probably is not a member of that genus.

A revised classification, modifying that of Murray and Wilson (2013) is as follows:

Superorder Clupeomorpha

Order Clupeiformes

Order Ellimmichthyiformes Grande, 1985

unranked

Ornategulum sardinoides

Family Scutatuspinosidae Silva Santos & Silva Corréa, 1985, new rank

Scutatuspinosus itapagipensis

Ranulfoichthys dorsonudum

Foreyclupea loonensis

Family Sorbinichthyidae Bannikov and Bacchia, 2000

Sorbinichthys elusivo, S. africanus

unranked

Kwangoclupea dartvellei

Suborder Armigatoidei Murray and Wilson, 2013

Family Armigatidae Murray and Wilson 2013

Armigatus oligodentatus, *A. brevissimus*, *A. alticorpus*, *A. namourensis*

Diplomystus dubertreti, D. birdi, D. dentatus, D. shengliensis

Horseshoeichthys armaserratus

Suborder Ellimmichthyoidei Grande, 1985

Family Thorectichthyidae Murray and Wilson 2013, new rank

Thorectichthys marocnesis, T. rhadinus

unranked

'Diplomystus' solignaci

unranked

Rhombichthys intoccabilis

Family Paraclupeidae Chang and Chou, 1977

  Subfamily Paraclupeinae Chang and Chou, 1977

    Tribe Ellimmichthyini Grande, 1982, new rank

      Ellimma branneri

      Ellimmichthys goodi, E. logicostatus

    unranked

    Paraclupea chetungensis

  Subfamily Triplomystinae Murray and Wilson 2013, new rank

      Ezkutuberezi carmenae

      Tycheroichthys dunveganensis

      'Ellimmichthys' maceioensis

      Triplomystus oligoscutatus, T. applegatei, T. noorae

4.6 Conclusions

Overall results of the updated phylogenetic analysis of the ellimmichthyiforms and some fossil clupeiforms suggest that the order Ellimmichthyiformes is a monophyletic group and includes the genus *Armigatus* as well as a problematic taxon *Ornategulum sardinoides*. The four major family groups within the Ellimmichthyiformes were recovered: Scutatuspinosidae, Sorbinichthyidae, Armigatidae, and Paraclupeidae. According to this phylogenetic hypothesis, *Diplomystus* and *Ellimmichthys* are not monophyletic with *'D.' solignaci* and *'E.' maceioensis* falling out of their corresponding generic groups. The early fossil record of clupeiforms (*Pseudoellimma gallae*) and ellimmichthyiforms (*Scutatuspinosus itapagipensis*) suggests that the two lineages of the clupeomorphs diverged by the middle of the early Early Cretaceous (Barremian). The Ellimmichthyiformes were a diverse group with a wide geographical range and probably reached their highest diversity during the Late Cretaceous in the eastern Tethys region. The paleobiogeographic patterns of the Ellimmichthyiformes are discussed in more details in Chapter 5 of this thesis.

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TABLE 4-1. Taxa included in the revised phylogenetic analysis

Species	**Geographic distribution/Occurrence**	**Geological Age**	**Environment**
Chanos chanos	Indo-Pacific	Extant	Euryhaline
Armigatus brevissimus	Lebanon	Late Cretaceous (Cenomanian)	Marine
Armigatus namourensis	Lebanon	Late Cretaceous (Cenomanian)	Marine
Armigatus alticorpus	Lebanon	Late Cretaceous	Marine
*Armigatus oligodentatus**	Morocco	Late Cretaceous (Cenomanian/ Turonian)	Marine
Diplomystus birdi	Hakel, Lebanon	Late Cretaceous (Cenomanian)	Marine
Diplomystus dentatus	Wyoming, USA	Early Eocene	Freshwater
Diplomystus dubertreti	Sahel Alma, Lebanon	Late Cretaceous (Cenomanian)	Marine
Diplomystus shengliensis	eastern China	Middle Eocene	Freshwater
‘Diplomystus’ solignaci	Tunisia	Late Cretaceous (Senonian)	Marine
Ellimma branneri	Brazil	Early Cretaceous (Aptian – Albian)	Brackish and Marine
Ellimmichthyes goodi	Equatorial Guinea, Central Africa	Early Cretaceous (Aptian - Albian)	Freshwater
Ellimmichthyes maceioensis	Maceio Formation, Brazil	Aptian — early Albian	Lagoon with marine and freshwater incursion
Ellimmichthys longicostatus	Bahia, Brazil	Early Cretaceous (Hauterivian–Barremian)	Estuarine
*Foreyclupea loonensis**	North Western Territories, Canada	Early Cretaceous (Albian)	Marine
Ezkutuberezi carmenae	Basque Country, Spain	Early Cretaceous (Valanginian - Barremian)	Deltic and Lacustrine
Horseshoeichthys armigserratus	Alberta, Canada	Late Cretaceous (Santonian — Maastrichtian)	Freshwater
Kwangoclupea dartevellei	Congo, Africa	Late Cretaceous (Cenomanian)	Marine
Ornategulum sardinoides	Hakel, Lebanon	Late Cretaceous (Cenomanian)	Marine
Paraclupea chetungensis	Chawan Formation, China	Early Cretaceous	Freshwater
Pseudoellimma gallae	Alagoas, Brazil	Early Cretaceous (Barremian)	Brackish waters
Ranulfoichthys dorsonudum	Puebla, Mexico	Early Cretaceous (Albian)	Marine

TABLE 4—1 (continued)

Species	**Geographic distribution/Occurrence**	**Temporal range**	**Environment**
Rhombichthys intoccabillis	Ein Yabrud, Palestine	Late Cretaceous (Cenomanian)	Marine
Santanaclupea silvasantosi	Santana Formation, Brazil	Early Cretaceous (Albian)	Marine
Scutatuspinosus itapagipensis	Bahia, Brazil	Early Cretaceous (Neocomian)	Lacustrine
Sorbinichthys africanus	Akrabou Formation, Morocco	Late Cretaceous (Cenomanian/Turonian)	Marine
Sorbinichthys elusivo	Namoura, Lebanon	Late Cretaceous (Cenomanian)	Marine
Thorectichthys marocensis	Akrabou Formation, Morocco	Late Cretaceous (Cenomanian/Turonian)	Marine
Thorectichthys rhadinus	Akrabou Formation, Morocco	Late Cretaceous (Cenomanian/Turonian)	Marine
Triplomystus applegatei	Chiapas, Mexico	Early Cretaceous (Aptian/Albian)	Estuarine
Triplomystus oligoscutatus	Namoura, Lebanon	Late Cretaceous (Cenomanian)	Marine
Triplomystus noorae	Namoura, Lebanon	Late Cretaceous (Cenomanian)	Marine
Tycheroichthys dunveganensis	Dunvegan Formation, Canada	Late Cretaceous (Cenomanian)	Marine

* Names of the new species described in the chapters of this thesis have not been published yet

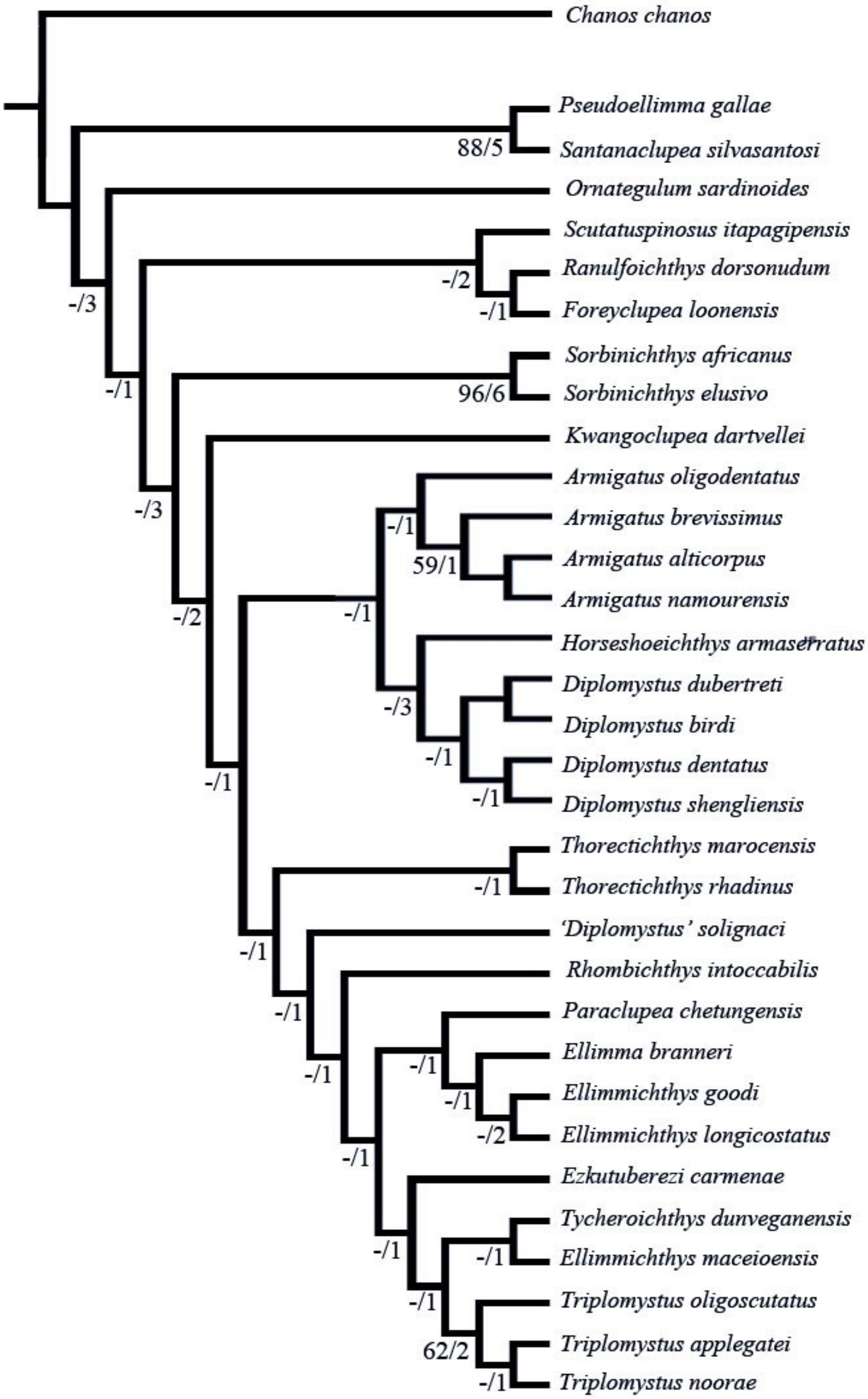

FIGURE 4-1. A single most parsimonious tree retrieved by the analysis including 33 taxa and 61 characters. Numbers below branches indicate bootstrap/Bremer support values (only bootstrap values >50% are shown).

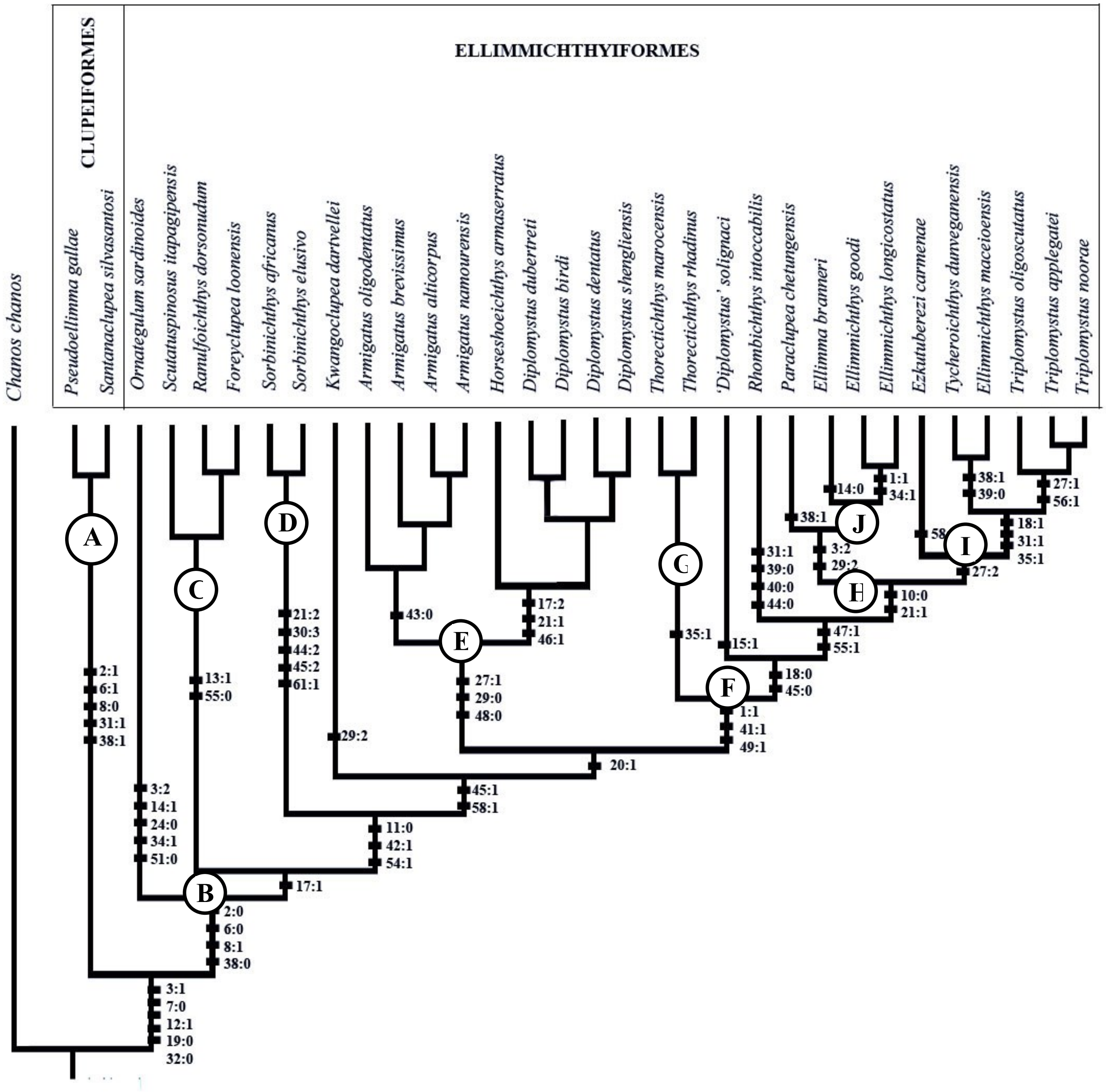

FIGURE 4-2. Phylogenetic hypothesis of the Ellimmichthyiformes with synapomorphies for the major groups indicated along branches and the major groups labeled at the nodes: A – Clupeiformes; B – Ellimmichthyiformes; C – Scutatuspinosidae; D – Sorbinichthyidae; E – Armigatidae; F – Paraclupeidae; G – Thorectichthyinae; H – Paraclupeinae; I – Triplomystinae; J - Ellimmichthyini.

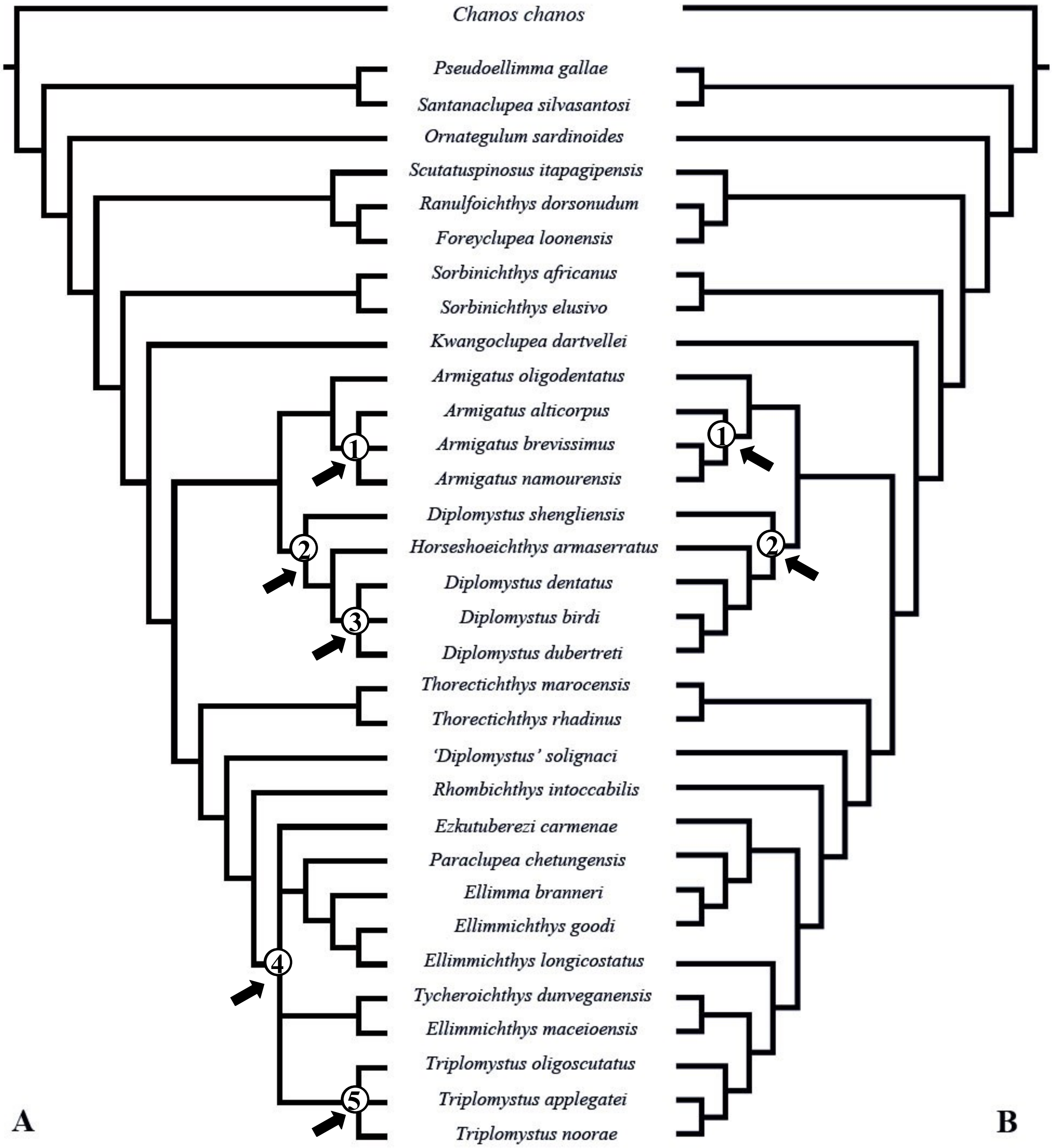
Chanos chanos
Pseudoellimma gallae
Santanaclupea silvasantosi
Ornategulum sardinoides
Scutatuspinosus itapagipensis
Ranulfoichthys dorsonudum
Foreyclupea loonensis
Sorbinichthys africanus
Sorbinichthys elusivo
Kwangoclupea dartvellei
Armigatus oligodentatus
Armigatus alticorpus
Armigatus brevissimus
Armigatus namourensis
Diplomystus shengliensis
Horseshoeichthys armaserratus
Diplomystus dentatus
Diplomystus birdi
Diplomystus dubertreti
Thorectichthys marocensis
Thorectichthys rhadinus
'Diplomystus' solignaci
Rhombichthys intoccabilis
Ezkutuberezi carmenae
Paraclupea chetungensis
Ellimma branneri
Ellimmichthys goodi
Ellimmichthys longicostatus
Tycheroichthys dunveganensis
Ellimmichthys maceioensis
Triplomystus oligoscutatus
Triplomystus applegatei
Triplomystus noorae
1
2
3
4
5
1
2
A
B

FIGURE 4-3 (previous page)**.** Results of the meristic characters removal from the matrix: **A**, Strict consensus of the two MPTs recovered after all meristic characters have been removed from the matrix; **B**, single MPT recovered after only characters with higher levels of variation have been removed. Arrows point at the nodes on the trees that have different resolution than on the reference tree; nodes are labeled as described in the text.

APPENDIX 4-1. Complete list of characters used in the analysis

The final data matrix included the 61 characters listed below with references to the previous phylogenetic analyses. New characters (59 – 61) are listed at the end along with the explanatory notes:

1. Anterior dorsal margin of body: [0] rounded and convex; [1] almost straight, forming a marked angle at the dorsal fin insertion. (Zaragüeta-Bagils, 2004: char.56; Alvarado-Ortega et al., 2008: char.1; Murray and Wilson, 2013: char.1).
2. Skull roof: [0] parietal bones contacting each other in the midline; [1] supraoccipital separates parietal bones (Zaragüeta-Bagils, 2004: char.1; Alvarado-Ortega et al., 2008: char.2; Murray and Wilson, 2013: char.2).
3. Modified: Ornamentation of skull roof: [0] absent; [1] present - fine, more or less parallel ridges; [2] present - strong grooves with numerous fine, radiating ridges (Zaragüeta-Bagils, 2004: chars. 3 and 4; Alvarado-Ortega et al., 2008: chars. 4 and 5; Murray and Wilson, 2013: chars. 4 and 5).
4. Posttemporal fossa: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 6; Alvarado-Ortega et al., 2008: char.6; Murray and Wilson, 2013: char.6).
5. Cavity in the temporal region of the skull: pre-epioccipital fossa (between parietal, epioccipital and pterotic bones) [0]; pre-epioccipital fenestra (between the parietal, epioccipital and supraoccipital bones) [1]; absence of cavity or fenestra [2] (Zaragüeta-Bagils, 2004: char.7; Alvarado-Ortega et al., 2008: char.7; Murray and Wilson, 2013: char.7).
6. Recessus lateralis: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 8; Alvarado-Ortega et al., 2008: char.8; Murray and Wilson, 2013: char.8).

7. Supramaxillary bones: two [0]; one or none [1] (Zaragüeta-Bagils, 2004: char. 10; Alvarado-Ortega et al., 2008: char. 9; Murray and Wilson, 2013: char. 9).

8. 'Basipterygoid' process of parasphenoid: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 11; Alvarado-Ortega et al., 2008: char. 10; Murray and Wilson, 2013: char. 10).

9. 'Osteoglossoid' tooth patch on the parasphenoid: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 12; Alvarado-Ortega et al., 2008: char.11; Murray and Wilson, 2013: char. 11).

10. Supraorbital bone: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 13; Alvarado-Ortega et al., 2008: char. 12; Murray and Wilson, 2013: char. 12).

11. Antorbital bone: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 16; Alvarado-Ortega et al., 2008: char. 13; Murray and Wilson, 2013: char. 13).

12. Beryciform foramen within the anterior ceratohyal: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 14; Alvarado-Ortega et al., 2008: char. 14; Murray and Wilson, 2013: char. 14).

13. Foramen in posterior ceratohyal: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 15; Alvarado-Ortega et al., 2008: char. 15; Murray and Wilson, 2013: char. 15).

14. Teeth on endopterygoid: absent [0]; present [1] (Chang and Maisey, 2003: char. 9; Alvarado-Ortega et al., 2008: char.16; Murray and Wilson, 2013: char.16).

15. Modified: Total number of vertebrae excluding ural centra: [0] 30-40; [1] 41-50; [2] more than 50 (Alvarado-Ortega et al., 2008: char.17; Murray and Wilson, 2013: char.17). The character states have been adjusted to accommodate data from the new species added to the analysis. The original character states were: 30 – 40 [0]; 41 – 43 [1]; more than 50 [2]. I expanded range for the character state [1] to include *Ranulfoichthys dorsonudum* that has 46 – 47 vertebral centra.

16. Halves of the neural arches of most abdominal vertebrae: separate medially [0]; fused medially [1] (Zaragüeta-Bagils, 2004: char. 17; Alvarado-Ortega et al., 2008: char.18; Murray and Wilson, 2013: char.18).

17. Pleural ribs: all ribs articulate with parapophyses along the abdominal region [0]; anteriormost ribs articulate in deep pits on the lateral side of all abdominal centra and those located posteriorly articulate with well-developed parapophyses [1]; all ribs articulate in deep pits on the lateral side of all abdominal centra [2] (Zaragüeta-Bagils, 2004: char. 18; Alvarado-Ortega et al., 2008: char.19; Murray and Wilson, 2013: char.19).

18. Epineurals and epipleurals in the caudal region: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 19; Alvarado-Ortega et al., 2008: char.20; Murray and Wilson, 2013: char.20).

19. Epicentrals: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 20; Alvarado-Ortega et al., 2008: char.21; Murray and Wilson, 2013: char.21).

20. Shape of cleithrum: L-like (having a single angle in the bone) [0]; S-like (having two angles) [1] (Alvarado-Ortega et al., 2008: char.22; Murray and Wilson, 2013: char.22).

21. Dorsal process of posttemporal: slender and sharp [0]; sub-rectangular [1]; broad, wider at distal tip than at midpoint of bone [2] (Zaragüeta-Bagils, 2004: char. 22; Alvarado-Ortega et al., 2008: char.23; Murray and Wilson, 2013: char.23).

22. Modified: Number of anal fin rays: eight to eleven [0]; twelve to sixteen [1]; seventeen to nineteen [2]; twenty or twenty-one [3]; twenty-two to thirty-two [4]; thirty-six to forty-one [5] (Alvarado-Ortega et al., 2008: char.24; Murray and Wilson, 2013: char.24). The character states were adjusted to accommodate data from the new taxa. The original character state [1] was fourteen to fifteen anal fin rays. I expanded this range to fit data available for *Pseudoellimma gallae*.

23. Number of dorsal fin rays: eight to thirteen [0]; fourteen to twenty [1]; twenty-one to twenty-six [2] (Alvarado-Ortega et al., 2008: char.25; Murray and Wilson, 2013: char.25). The character states were modified to fit the new taxa included in the analysis.
24. Number of hypurals: seven [0]; six [1]; five [2] (Zaragüeta-Bagils, 2004: char. 23; Alvarado-Ortega et al., 2008: char.26; Murray and Wilson, 2013: char.26).
25. Hypural 2: autogenous [0]; fused to first ural centrum [1] (Zaragüeta-Bagils, 2004: char. 24; Alvarado-Ortega et al., 2008: char.27; Murray and Wilson, 2013: char.27).
26. Length of hypural 1: long, reaching ural centrum 1 [0]; short, not reaching ural centrum 1 [1] (Zaragüeta-Bagils, 2004: char. 25; Alvarado-Ortega et al., 2008: char.28; Murray and Wilson, 2013: char.28).
27. Proximal end of hypural 1: massive and forming an upward process [0]; sharp [1]; massive but no upward process [2] (Zaragüeta-Bagils, 2004: char. 26; Alvarado-Ortega et al., 2008: char.29; Murray and Wilson, 2013: char.29).
28. Shape of hypural 2: distal end distinctly broader than proximal end [0]; very thin and stick-like [1] (Zaragüeta-Bagils, 2004: char. 26; Alvarado-Ortega et al., 2008: char.30; Murray and Wilson, 2013: char.30).
29. Modified: Diastema between second and third hypural: third hypural expanded posteriorly leaving no gap or notch between the second and third hypurals [0]; third hypural expanded posteriorly, leaving a small triangular notch between second and third hypural [1]; third hypural expanded posteriorly, leaving a deep triangular notch between second and third hypural [2]; third hypural expanded posteriorly and has a concave ventral edge forming a large concavity between second and third hypurals [3](Zaragüeta-Bagils, 2004: char. 28; Alvarado-Ortega et al., 2008: char.31; Murray and Wilson, 2013: chars.31 and 32). As

described earlier in the chapter, I combined characters 31 and 32 to construct a single multistate character.

30. Size of first ural centrum (diural terminology): roughly the same size (length and depth) as the preural centra [0]; much smaller than the preural centra [1] (Zaragüeta-Bagils, 2004: char. 30; Alvarado-Ortega et al., 2008: char.32; Murray and Wilson, 2013: char.33).
31. Number of uroneurals: three [0]; two [1]; one [2] (Zaragüeta-Bagils, 2004: char. 29; Alvarado-Ortega et al., 2008: char.33; Murray and Wilson, 2013: char.34).
32. First uroneural: extends anteriorly to reach second preural centrum [0]; does not reach second preural centrum [1] (Zaragüeta-Bagils, 2004: char. 30; Alvarado-Ortega et al., 2008: char.34; Murray and Wilson, 2013: char.35).
33. Fusion of first uroneural and first ural centrum: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 32; Alvarado-Ortega et al., 2008: char.35; Murray and Wilson, 2013: char.36).
34. First uroneural bearing a dorsal expansion of laminar bone: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char.33; Alvarado-Ortega et al., 2008: char.36; Murray and Wilson, 2013: char.37).
35. Distal end of second uroneural: reaching the distal end of the first uroneural [0]; not reaching the distal end of the first uroneural [1] (Zaragüeta-Bagils, 2004: char. 34; Alvarado-Ortega et al., 2008: char.37; Murray and Wilson, 2013: char.38).
36. Parhypural: base/arch of bone fused with preural centrum 1 [0]; autogenous [1] (Zaragüeta-Bagils, 2004: char. 35; Alvarado-Ortega et al., 2008: char.38; Murray and Wilson, 2013: char.39).

37. Number of epurals: three [0]; two [1]; none, or those present are weakly ossified, perhaps cartilaginous [2] (Zaragüeta-Bagils, 2004: char. 37; Alvarado-Ortega et al., 2008: char.40; Murray and Wilson, 2013: char.41).

38. Position of epurals: epurals fill the space between the neural spines of pu1 and pu2 [0]; epurals are located far from the spine of pu2, leaving an open space between them [1] (Zaragüeta-Bagils, 2004: char.38; Alvarado-Ortega et al., 2008: char.41; Murray and Wilson, 2013: char.42).

39. Caudal scutes: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 39; Alvarado-Ortega et al., 2008: char.42; Murray and Wilson, 2013: char.43).

40. Neural spine of first preural centrum: large or lanceolate [0]; short or sub-rectangular [1] (Zaragüeta-Bagils, 2004: char. 40; Alvarado-Ortega et al., 2008: char.43; Murray and Wilson, 2013: char.44).

41. Neural arch of first ural centrum: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char.42; Alvarado-Ortega et al., 2008: char.44; Murray and Wilson, 2013: char.45).

42. Predorsal scutes: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char.45; Alvarado-Ortega et al., 2008: char.45; Murray and Wilson, 2013: char.46).

43. Predorsal scute series: incomplete (absent in anterior part) [0]; complete [1] (Alvarado-Ortega et al., 2008: char.45; Murray and Wilson, 2013: char.47).

44. Modified: Shape of scutes in anterior part of predorsal series: subrectangular [0]; heart-shaped or ovoid [1]; rhomboid [2] (Zaragüeta-Bagils, 2004: char. 47; Alvarado-Ortega et al., 2008: char.46; Murray and Wilson, 2013: char.48). The original character definition was: Subrectangular scutes in anterior part of predorsal series [0] absent; [1] present. I added

descriptive character states to recognize different scute morphologies observed in the ellimmichthyiforms (heart-shaped to ovoid [1] and subrhomboid [2]).

45. Modified: Shape of scutes in posterior part of predorsal series: [0] subrectangular; [1] heart-shaped or ovoid; [2] rhomboid (Zaragüeta-Bagils, 2004: char.47; Alvarado-Ortega et al., 2008: char.47; Murray and Wilson, 2013: char.49). Similar to the previous character, the descriptive character states have been added to recognize different scute morphologies observed in the ellimmichthyiform taxa.
46. Series of spines on the posterior margin of the lateral wings of the predorsal scutes: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 48; Alvarado-Ortega et al., 2008: char.48; Murray and Wilson, 2013: char.50).
47. Prominent median strong spine on posteriormost predorsal scutes: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char.49; Alvarado-Ortega et al., 2008: char.49; Murray and Wilson, 2013: char.51).
48. Size of scutes of predorsal series: all scutes of same size [0]; irregular in size, size of scutes increasing posteriorly [1]. (Zaragüeta-Bagils, 2004: char. 50; Alvarado-Ortega et al., 2008: char.50; Murray and Wilson, 2013: char.52).
49. Surface of predorsal scutes: smooth [0]; ornamented with radiating grooves [1] (Zaragüeta-Bagils, 2004: char. 51; Alvarado-Ortega et al., 2008: char.51; Murray and Wilson, 2013: char.53).
50. Number of predorsal scutes: six to fourteen [0]; sixteen to nineteen [1]; twenty to forty-one [2] (Alvarado-Ortega et al., 2008: char.52; Murray and Wilson, 2013: char.54).
51. Abdominal scute series: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char.52; Alvarado-Ortega et al., 2008: char.53; Murray and Wilson, 2013: char.55).

52. Complete abdominal scute series between isthmus and anus (postpelvic scutes are present): absent [0]; present [1] (Zaragüeta-Bagils, 2004: char.53; Alvarado-Ortega et al., 2008: char.54; Murray and Wilson, 2013: char.56).

53. Postpelvic abdominal scutes bearing very prominent and strong ventral spine: absent [0]; present [1] (Zaragüeta-Bagils, 2004: char. 54; Alvarado-Ortega et al., 2008: char.55; Murray and Wilson, 2013: char.57).

54. Size of lateral wings of abdominal scutes: small [0]; large, extended upward and covering the abdominal cavity laterally for at least one quarter of the distance from ventral body edge to vertebral column [1] (Alvarado-Ortega et al., 2008: char.56; Murray and Wilson, 2013: char.58).

55. Shape of lateral wing of abdominal series scutes: spine-like, with large spaces between wings of scutes [0]; wide or spatula-like, with wings of adjacent scutes touching for most of their length [1] (Zaragüeta-Bagils, 2004: char.55; Alvarado-Ortega et al., 2008: char.57; Murray and Wilson, 2013: char.59).

56. Postdorsal scute series: absent [0]; present [1] (Alvarado-Ortega et al., 2008: char.58; Murray and Wilson, 2013: char.60).

57. Number of abdominal scutes: fewer than twenty [0]; twenty-two to thirty [1]; more than thirty-two [2] (Murray and Wilson, 2013: char.61).

58. Number of predorsal bones: ten or more [0]; seven to nine [1]; six or fewer [2] (Murray and Wilson, 2013: char.62).

59. New character: Predorsal bones (supraneurals) forming a fan-shaped structure with at least one anteriormost predorsal bone inclined anterodorsally to meet proximal end of the next supraneural: [0] absent; [1] present. This feature has only been observed in the confirmed

species of the genus *Diplomystus*. In *'D.' solignaci* all supraneurals are inclined anteroventrally with the proximal ends not coming together in a single point.

60. New character: Position of the pelvic fin anterior to the origin of the dorsal fin: [0] absent; [1] present. The anterior shift in the position of the pelvic fin relative to the dorsal fin origin is generally regarded as a derived feature among teleost fishes (Rosen, 1982; Tanaka, 2011; Tanaka et al., 2015). Rosen (1982) recognized four distinct stages of the anterior shift of the pelvic fins, with the most primitive condition being the pelvic fin positioned near the anus; the second stage is characterized by the pelvic fin positioned roughly at the midpoint between the anus and pectoral fins; at the third stage, the pelvic fin is just behind the pectoral fin, and at the most derived stage four, the pelvic fin is positioned under the pectoral fin. In fishes with the dorsal fin positioned roughly at the midpoint between the head and the caudal fin, the position of the pelvic fin can be evaluated relative to the origin of the dorsal fin – in derived taxa, the pelvic fin insertion shifts anterior to the dorsal fin origin. Most clupeomorphs (living and extinct) have an abdominal pelvic fin inserted posterior to the origin of the dorsal fin; however, in some fossil taxa included in this analysis, the pelvic fin is shifted forward to become positioned further anterior than the dorsal fin origin.
61. New character: Lateral projections of the most posterior predorsal scutes inclined anteroposteriorly: [0] absent; [1] present. Murray and Wilson (2011) have described this feature in *Sorbinichthys africanus* and noted that this feature is also present in the type species of the genus, *S. elusivo*, although not mentioned in the original description by Bannikov and Bacchia (2000).

APPENDIX 4-2. Data matrix used in the phylogenetic analysis based on the revised and updated character list.

	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1
Chanos chanos	010?20?001	?000100111	0011011110	1-10111001	00--------	0----0-000	0
Ornategulum sardinoides	0020000101	11?12001?0	?010112100	0001000001	00--------	0----0-000	0
Armigatus alticorpus	0011??0111	1?110000?1	0?1111?000	0001000011	?10110000?	110100??00	0
Armigatus brevissimus	0021?0011?	11??000??1	041110110?	0100000?1	01011010??	11?0001200	0
Armigatus namourensis	0021?00111	?101000101	0411101100	0100000011	0101101011	1101001200	0
Armigatus oligodentatus	000??0010?	?100001101	0101101100	00000?0?11	0101000?0	1100001100	0
Diplomystus birdi	1?????????	????0?????	?41????00	01???000??	?110011??2	1???001110	0
Diplomystus dentatus	001??0011?	?1011??101	?501101100	0100000?1	0110011002	11?1002110	0
Diplomystus dubertreti	0?1???0???	?1??0?????	?42????00	??????????	?11001???2	1????0?110	0
Diplomystus shengliensis	001???010?	??11??1??	050010??00	0000?00100	?110011002	1??100?110	0
'Diplomystus' solignaci	1?????????	???11?????	?121?0?100	??????00?1	?1??0?????	1111002100	0
Ellimma branneri	002???010?	?1?10?1??1	011110?120	0000000011	?111001110	1111101100	0
Ellimmichthys goodi	1?21??00??	???011011	1011100020	0001000010	1111001112	111110??00	0
Ellimmichthys longicostatus	1?2??00?0?	??10011011	1011100020	0001000110	1111001112	111110??01	0
Ellimmichthys maceioensis	1?1???0???	????0????1	?11?102?00	1000100101	1111001110	1111?02100	0
Ezkutuberezi carmenae	101???0???	???00111?1	?42?102100	?0000?1001	01?100111?	1111002000	0
Foreyclupea loonensis	001??00?01	???0?01110	1?1???????	??????????	?0--------	1110001?01	0
Horseshoeichthys armaserratus	000?100??0	0????02?0?	1?????????	??????????	?1??010?0?	1???0????0	0
Kwangoclupea dartevellei	001?00010?	????0??1??	?40?100120	0000000101	011110010?	1110-01100	0
Paraclupea chetungensis	101???010?	?1010????1	?111101120	0000100111	0101001111	1111102100	0
Pseudoellimma gallae	011111000?	???0000100	0112100111	0000?011?0	11???01?0?	1110003100	0
Ranulfoichthys dorsonudum	001?000?01	1110001100	1011100100	0000000011	00--------	1110004200	0
Rhombichthys intoccabilis	101?000101	01?1011101	012?100100	1000100000	?110001110	1111102100	0
Santanaclupea silvasantosi	0111110?01	?100000000	?012100111	000100?1?0	?0--------	111010?100	0
Scutatuspinosus itapagipensis	001???0101	?110011101	0001002100	1100000111	0111211110	1110-01001	0
Sorbinichthys africanus	1?0???0101	0??1001100	2402000130	0000102-00	01122010?2	1101000000	1
Sorbinichthys elusivo	1?1???0?0?	???10011?0	2412000130	0000102-0?	01122010?2	1101000000	1
Thorectichthys marocensis	101??0010?	0101011101	0411100100	0000100011	1111100100	1111001200	0
Thorectichthys rhadinus	000??0010?	?101011101	0411100100	0000100011	1111100100	1111001200	0
Triplomystus applegatei	101????100	???011??1	121?101100	1100100010	1110001110	1111112200	0
Triplomystus noorae	1011000100	0??1011111	1221101 1??	1001100011	?110001110	1111111200	0
Triplomystus oligoscutatus	1011000100	0??1011111	1411101 1??	1001000011	?110001110	1111111200	0
Tycheroichthys dunveganensis	100???0100	0???011101	1411???20	1100101101	0110001101	1111102100	0

Chapter 5: Conclusions and Future Research

5.1 General conclusions

The main objective of this thesis is to provide descriptions of new fossil ellimmichthyiform fishes from the Early Cretaceous (early-middle Albian; Chapter 3) of Canada and the Late Cretaceous (Cenomanian/Turonian; Chapter 2) of Morocco. The information provided by these new species allows an update of the phylogeny of the order Ellimmichthyiformes (Chapter 4). Descriptions of the two new ellimmichthyiform taxa, *Armigatus oligodentatus* (Chapter 2) and *Foreyclupea loonensis* (Chapter 3) contribute to our understanding of the diversity of the fossil clupeomorphs with some valuable clues about their ecology and character evolution within the group.

Armigatus oligodentatus from the Late Cretaceous marine deposits of Morocco is the smallest known member of the genus and has a reduced dentition, which indicates that this species was presumably an obligate planktivore unlike larger species of *Armigatus* (*A. brevissimus* and *A. namourensis*) that had a well-developed dentition and were likely piscivorous. Interspecific variation in body size and dentition development, as well as in morphology and number of gill rakers, is common among genera of living clupeomorphs with different ecology (Whitehead, 1985; Whitehead et al., 1988); therefore, it is important to recognize this pattern among the extinct members of the Ellimmichthyiformes.

Foreyclupea loonensis from the Lower Cretaceous (Albian) Loon River Formation (Northwest Territories, Canada) is remarkable for its temporal and geographic occurrence as well as for a mosaic combination of characters. It is the oldest clupeomorph taxon from Canada that also occurs farther to the north than any other known species of the Ellimmichthyiformes. Similar to other ellimmichthyiforms, *F. loonensis* is lacking a recessus lateralis and has medially united parietals; but unlike other members of the order, this basal ellimmichthyiform does not have dorsal scutes.

Foreyclupea loonensis and *Ranulfoichthys dorsonudum*, another basal ellimmichthyiform lacking the predorsal series of scutes, provide valuable information about the morphological diversity that existed within the Ellimmichthyiformes. The ellimmichthyiform fishes are often referred to as 'double-armored' herrings for the presence of the dorsal series of scutes in addition to the abdominal scutes present in all living taxa (Grande, 1985; Nelson, 2006). The loss of predorsal scutes in the recent clupeomorphs is regarded as a derived feature with only a few living genera retaining this primitive feature; however, the fossil record of the Early Cretaceous clupeomorphs suggests that the dorsal armour in ellimmichthyiforms showed different degrees of development, similar to the condition observed in the living clupeiformes. *Scutatuspinosus itapagipensis* from the Neocomian sediments of Brazil is one of the oldest clupeomorphs known and shows a complete dorsal series of scutes. In the phylogenetic analysis presented in this thesis, *S. itapagipensis* forms a monophyletic group with other Early Cretaceous (Albian) ellimmichthyiforms, *Ranulfoichthys dorsonudum* and *Foreyclupea loonensis*, that, however, do not have a predorsal series of scutes. Among the earliest clupeiforms, the Barremian *Pseudoellimma gallae* shows development of the predorsal scutes (preservation of the specimen, however, makes it impossible to determine whether the dorsal scutes series was complete or incomplete) and the Albian *Santanaclupea silvasantosi* does not have a dorsal series of scutes. It is most parsimonious to suggest that presence of the dorsal scutes is the ancestral condition for both clupeiforms and ellimmichthyiforms, because it is observed in the oldest known members of each group; however, loss of the dorsal scutes occurred independently within the clupeiform and ellimmichthyiform lineages after they had diverged. In the Ellimmichthyiformes, a diversity of the dorsal scute series morphology continued to evolve throughout the Cretaceous with the incomplete series of predorsal scutes observed in *Armigatus* and an extended dorsal series of scutes in *Triplomystus* that continues behind the dorsal fin forming a postdorsal series.

Morphology of the scutes themselves also shows a great variation of shape and sculpturing development. In *Armigatus*, *Diplomystus*, *Kwangoclupea*, and *Thorectichthys*, dorsal scutes are smooth with varied shape from ovoid and heart-shaped in *Armigatus* to the subrectangular scutes with a serrated posterior margin in *Diplomystus*. In paraclupeids and *Sorbinichthys elusivo*, dorsal scutes are generally well-ornamented and often present in a heterogeneous series gradually increasing in size towards the posterior end of the series. The revision of this character presented in this thesis shows that a single type of predorsal scute series morphology should not be used as a defining feature for the entire order Ellimmichthyiformes.

5.2 Problematic characters used for the Ellimmichthyiformes diagnosis

In the updated phylogenetic hypothesis (Chapter 4), the order Ellimmichthyiformes was recovered as a monophyletic group characterized by a combination of primitive characters, including the medially united parietals, absence of the recessus lateralis, presence of the basipterygoid process of the parasphenoid, and epurals that are tightly located between the neural spines of the first and second preural centra. Each of these characters alone, however, is not exclusive to the Ellimmichthyiformes and entails problems for the accurate classification of the fossil taxa:

- The parietals contacting in the midline is not characteristic of all ellimmichthyiform taxa. In *Ellimmichthys longicostatus* and *E. goodi* the parietals are completely separated by the supraoccipital, and in *Paraclupea chetungensis* the parietal bones are only partially separated (Chang and Grande, 1997). Bannikov and Bacchia (2000) noted that in *Sorbinichthys elusivo* the parietals may also be separated by the supraoccipital, although this is not readily evident in the specimens of *S. africanus* examined.
- Presence of the recessus lateralis is regarded as a synapomorphy of the Clupeiformes (Grande, 1985). It is primitively absent in the extinct members of the order Ellimmichthyiformes. An accurate assessment of this character requires a three-dimensional preservation of the braincase that is extremely rare in the fossil clupeomorph taxa. In most cases, presence or absence of the recessus lateralis is determined from indirect evidence, size and position of the dermosphenotic and openings in the pterotic bone (Grande, 1985; Maisey, 1993; De Figueiredo, 2009), that is not always precise and can obscure results of the phylogenetic analysis.
- Presence of the basipterygoid process of the parasphenoid within the Clupeomorpha is known only in the ellimmichthyiforms; however, this is a primitive feature also present in some osteoglossoids, mormyroids, platyctids, and alepocephalids (Arratia and Schultze, 1991; Johnson and Patterson, 1996; Alvarado-Ortega et al., 2008).
- Determining homology of the epurals and therefore their position in the caudal skeleton is problematic as indicated by Schultze and Arratia (1989, 2013). They noted that ontogenetic data are required in order to establish homology between epural

elements in different groups of fishes. This presents the major problem for the study of fossil taxa for which ontogenetic data are not normally available.

The arguments listed above suggest that diagnosis of the Ellimmichthyiformes in the updated phylogenetic hypothesis, although based on more phylogenetically ‘robust’ characters than the dorsal scute morphology, still relies heavily on the problematic characters extremely hard to assess in the fossil taxa.

5.3 Paleobiogeographic implications

The revised phylogenetic hypothesis of the Ellimmichthyiformes presented in this thesis is based on the most inclusive cladistic analysis of most of the known ellimmichthyiform taxa. Addition of the basalmost clupeomorph taxa revealed new patterns in the paleobiogeographic history of this group of fishes (Figs. 5-1 and 5-2).

Of the four major family groups identified in the updated phylogeny of the Ellimmichthyiformes, the most basal group, Scutatuspinosidae, unites the Early Cretaceous species from the marine and freshwater environments of South and North America. The oldest member of the group, *Scutatuspinosus itapagipensis*, is known from Neocomian lacustrine deposits of northeast Brazil, while the other two taxa, *Ranulfoichthys dorsonudum* and *Foreyclupea loonensis*, were described from Albian marine sediments of Mexico and the Northwest Territories in Canada, respectively. This temporal and geographical pattern suggests that the group probably originated in the tropical region of South America in the early Early Cretaceous and dispersed northward reaching the northernmost limits of the known ellimmichthyiform distribution at a paleolatitude of about 70°N by the early/middle Albian. Previously, the most northerly record (65°N paleolatitude) of the ellimmichthyiforms, *Horseshoeichthys armaserratus*, was described from the Maastrichtian Horseshoe Canyon Formation of Alberta, Canada.

The Paraclupeidae is the most diverse group of the ellimmichthyiforms. Paraclupeid fishes had a wide geographic and temporal range with the earliest fossil record of the members of the group described from the early Early Cretaceous (Valanginian – Barremian) deposits of Europe (*Ezkutuberezi carmenae*) and South America (*Ellimmichthys longicostatus*), and the greatest species diversity recorded from the Late Cretaceous deposits of the eastern Tethys (Fig. 5-2). It is hard to establish a common paleobiogeographic pattern for the entire group considering its high species diversity and obviously incomplete fossil record; however, certain conclusions can be made about the biogeographic history of some clades of paraclupeids.

Two sister groups, monophyletic *Triplomystus* and a small clade containing *'Ellimmichthys' maceioensis* and *Tycheroichthys dunveganensis*, have their earliest members described from the Aptian-Albian estuarine deposits of Mexico (*Triplomystus applegatei*) and lagoonal deposits with a fluctuating salinity regime of Brazil (*'E.' maceioensis*). By the Late Cretaceous (Cenomanian), these paraclupeids dispersed far north to reach paleolatitudes of 65^{o}N (*Tycheroichthys dunveganensis*) and east to the eastern Tethys region (*Triplomystus noorae* and *T. oligoscutatus*) (Forey et al., 2003; Hay et al., 2007). This dispersal pattern suggests high ecological plasticity of paraclupeids capable of adapting to a wide range of salinity levels and temperature conditions. The tribe Ellimmichthyini, which unites the Early Cretaceous paraclupeid fishes that occurred in Brazil (*Ellimmichthys longicostatus* and *Ellimma branneri*) and Equatorial Guinea (*Ellimmichtys goodi*), indicates the dispersal of these fishes through the marine connection that existed between South America and Africa. The eastern Tethys region had the highest diversity of paraclupeids, and ellimmichthyiforms overall, which occurred during the Late Cretaceous (Cenomanian – Senonian), with the ellimmichthyiforms widely distributed in the region from Lebanon and Palestine as well as localities in Morocco and Europe. Another paraclupeid species, *Paraclupea chetungensis*, is known from the Early Cretaceous deposits of China and suggests a long distance dispersal of the paraclupeids that occurred during the early Early Cretaceous.

Another group of Ellimmichthyiformes, the Armigatidae (which includes the genera *Armigatus* and *Diplomystus* plus a single taxon *Horseshoeichthys armaserratus*) is known from the Late Cretaceous (Cenomanian – Turonian) and Eocene localities of Lebanon, Morocco, North America, and China (Chang and Maisey, 2003; Forey et al., 2003; Newbrey et al., 2010). Of this group, species of the genus *Armigatus* were restricted to the marine environments of the eastern Tethys region, contributing to the overall diversity of the ellimmichthyiforms in that region during the Late Cretaceous. The *Diplomystus* group had a much wider geographic and temporal range, with a fossil record known from the eastern Tethys (Cenomanian *Diplomystus birdi* and *D. dubertreti*), North America (Maastrichtian *H. armaserratus* and Eocene *D. dentatus*), and China (Eocene *D. shengliensis*). The dispersal pattern within this group suggests that both *Armigatus* and *Diplomystus* originated in the eastern Tethys region in the early Late Cretaceous with the subsequent dispersal of *Diplomystus* to the west where these fishes entered fresh waters. Interestingly, freshwater members of the genus *Diplomystus* are the only known ellimmichthyiforms to have survived the Cretaceous – Paleogene extinction event; this is congruent with the extinction model for the marine and freshwater faunas proposed by Robertson et al. (2013) that suggests that freshwater communities were subjected to a significantly lesser degree of extinction due to the overall better ability of the inland freshwater communities to adapt to the rapidly changing environmental conditions.

The monogeneric family Sorbinichthyidae had a restricted geographical distribution limited to the eastern Tethys. Members of this ellimmichthyiform group are known only from the Upper Cretaceous (Cenomanian – Turonian) sediments of Lebanon and Morocco, co-occurring with the other ellimmichthyiforms: *Armigatus*, *Diplomystus*, *Thorectichthys*, and *Triplomystus* (Bannikov and Bacchia, 2000; Forey et al., 2003; Murray and Wilson, 2011, 2013).

The phylogenetic hypothesis of the Ellimmichthyiformes presented in this thesis provides some intriguing clues about the possible centre of origin of this group of clupeomorph fishes (Fig. 5-1). The earliest fossil record of the Clupeomorpha is dated back to the lower Lower Cretaceous (Berriasian - Barremian) deposits of South America (*Scutatuspinosus itapagipensis, Ellimmichthys longicostatus,* and *Pseudoellimma gallae*). By the mid-Cretaceous (Aptian – Albian), the diversity of the clupeomorphs in the tropical region of South America increases (*Triplomystus applegatei*, *Ellimma branneri*, *Ellimmichthys maceioensis, Santanaclupea silvasantosi*) along with the new occurrences of the ellimmichthyiforms to the north (*Ranulfoichthys dorsonudum* from Mexico and *Foreyclupea loonensis* from Canada), east (*Ellimmichthys goodi* from Equatorial Guinea), and west (*Paraclupea chetungensis* from China) relative to the earliest sites of occurrence in northeast Brazil. This pattern suggests an extensive long-distance dispersal of the clupeomorphs that happened during the Early Cretaceous. According to this hypothesis, occurrence of *Ezkutuberezi carmenae* in the Valanginian – Barremian deposits of Spain suggests that the long-distance dispersal of the ellimmichthyiforms happened very early in the Cretaceous. This rapid and effective dispersal of the clupeomorphs worldwide can be explained by their extremely high ecological plasticity allowing clupeomorphs to adapt to a wide range of temperatures and salinity levels. It is reasonable to suggest that the earliest clupeomorphs were euryhaline fishes capable of surviving at varying salinity levels. This idea is supported by the fact that the oldest clupeomorph taxa (*Ellimmichthys longicostatus, Scutatuspinosus itapagipensis, Ezkutuberezi carmenae,* and *Pseudoellimma gallae*) are known from the estuarine, deltaic, and lacustrine settings characterized by fluctuating salinity levels.

5.4 Future research

Despite the recent progress in the systematics of the Ellimmichthyiformes and the Clupeomorpha in general, numerous questions regarding the evolutionary history of the group persist. Some of these questions that are directly related to the study undertaken in this thesis and are of particular interest for the systematics of the recent and fossil clupeomorphs include:

- Phylogenetic position of *'Diplomystus' solignaci* and *'Ellimmichthys' maceioensis* within the Ellimmichthyiformes. These taxa have been repeatedly recovered as not forming monophyletic groups with the other members of the corresponding genera. All previous phylogenetic studies recovered *'D.' solignaci* as being more closely related to the paraclupeids than to the other species of *Diplomystus* (Zaragüeta-Bagils, 2004; Alvarado-Ortega et al., 2008; Murray and Wilson, 2013). Murray and Wilson (2013) also included *Ellimmichthys maceioensis* in their phylogenetic analysis that recovered this taxon as a sister group to the clade comprising *'D.' solignaci* and *Rhombichthys intoccabillis*. In the present phylogenetic hypothesis, *E. maceioensis* was recovered as a sister taxon to *Tycheroichthys dunveganensis*, and *'D.' solignaci* is placed more basal within the Paraclupeidae.
- Centre of origin and diversification of the Ellimmichthyiformes. At the present stage of Ellimmichthyiformes classification, the phylogenetic hypotheses do not provide sufficient information for a reliable conclusion about the centre of the origin and

diversification of this group. The hypothesis of the Ellimmichthyiformes centre of origin proposed in this thesis is preliminary and additional data on the early clupeomorphs are required to either support or refute this suggested idea of the centre of origin of the Ellimmichthyiformes.

- In-depth study of the scute development in clupeomorphs. Understanding mechanisms underlying scute development in the recent taxa can provide important information for the classification and phylogenetic studies of the recent as well as fossil clupeomorph taxa. As mentioned earlier in the chapter and throughout this thesis, morphology of the scute armour in ellimmichthyiforms plays a significant role in phylogenetic studies of this extinct group of fishes; therefore, molecular and developmental studies of the living clupeomorphs, especially those taxa with the dorsal series of scutes present, may shed light on the significance of the scute armour for reconstructing the phylogeny of the clupeomorph fishes.

These questions can be answered by including more fossil taxa into the phylogenetic analysis of the group as well as by using information available from the morphological and molecular studies of the living clupeomorphs. Combining data on the living and fossil clupeomorphs will provide a more comprehensive picture of the evolutionary history of the Clupeomorpha.

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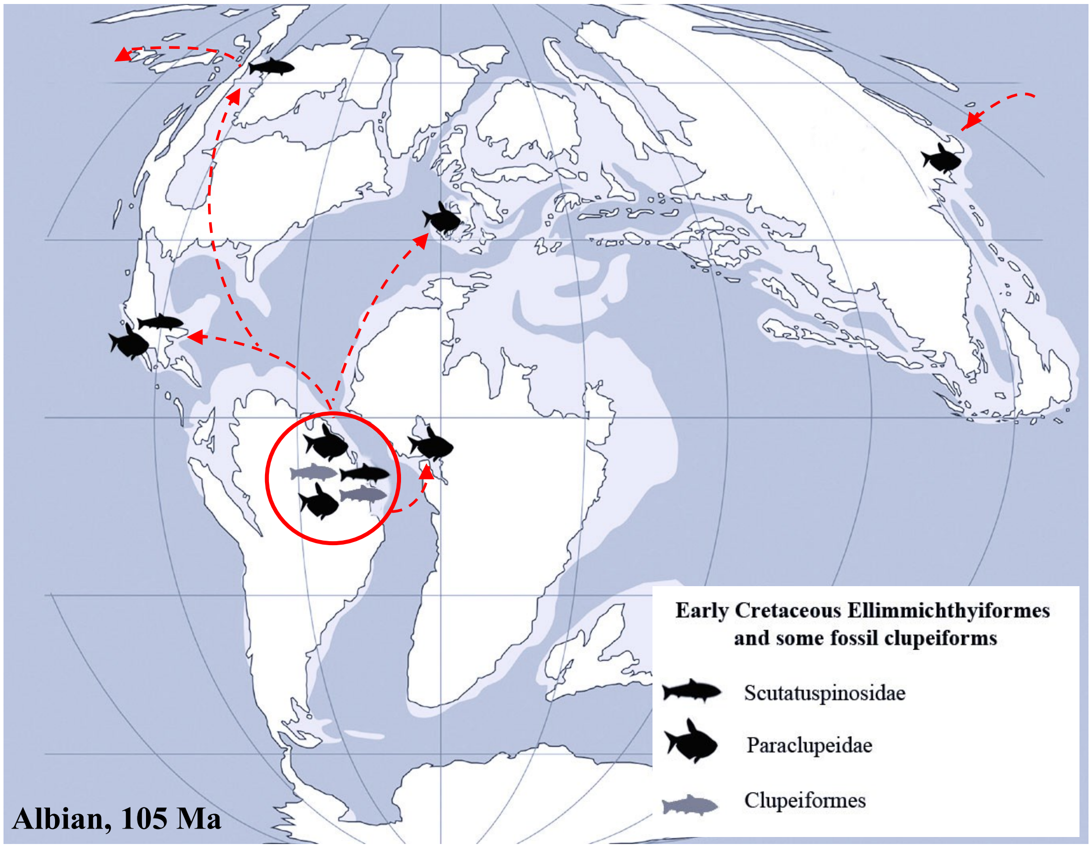

FIGURE 5-1. Distribution of the Ellimmichthyiformes and some fossil clupeomorphs in the Early Cretaceous. Red circle indicates a hypothesized centre of origin of the Ellimmichthyiformes with arrows showing general directions of dispersal (actual routs of dispersal are unknown). Map modified from Blakey, 2010.

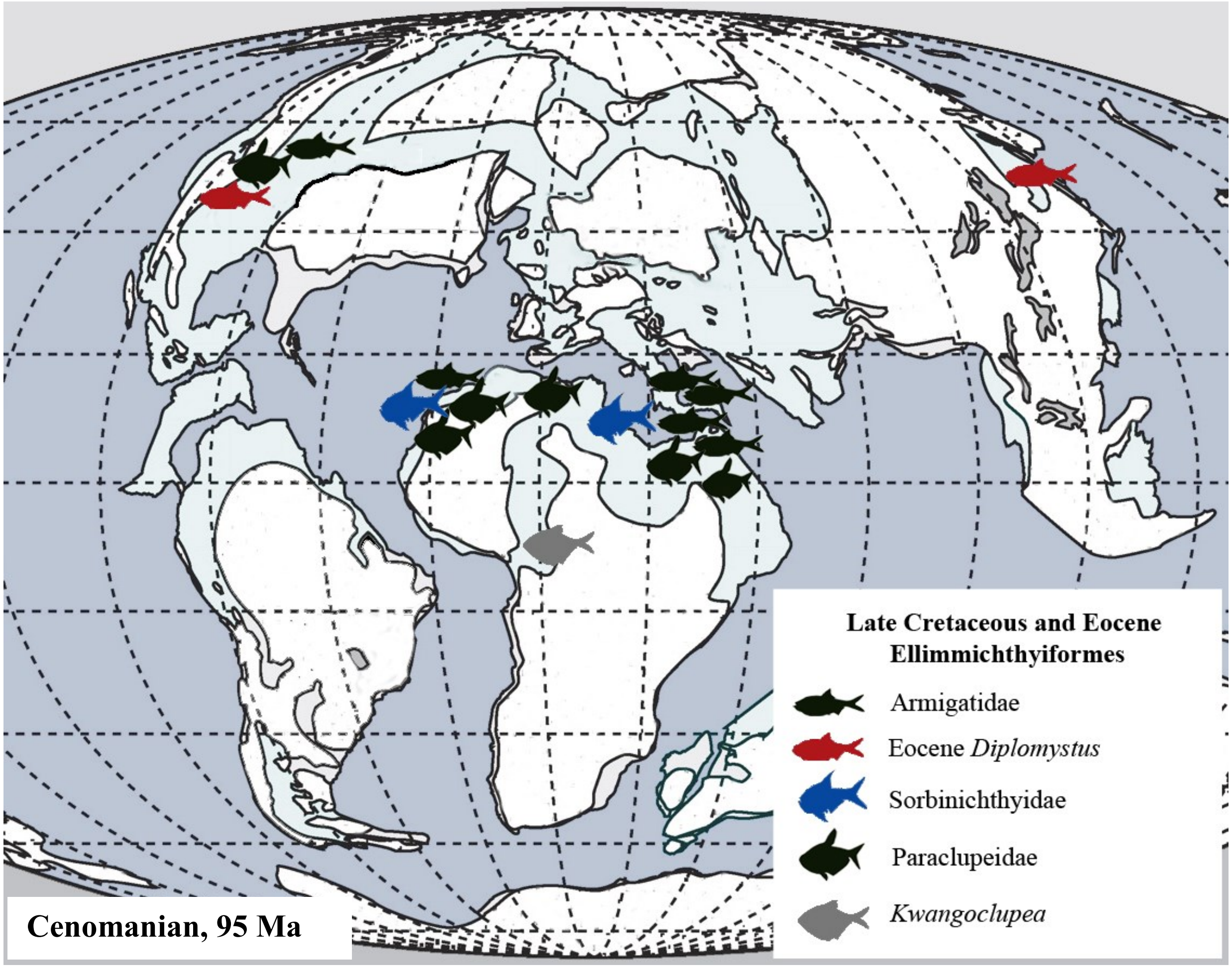

FIGURE 5-2. Distribution of the Ellimmichthyiformes during the Late Cretaceous and Eocene. Map modified from Blakey, 2010.

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