JURASSIC FISHES OF GONDWANA

Adriana LÓPEZ-ARBARELLO[1], Oliver W. M. RAUHUT[2] and Katrin MOSER[3]

Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany.
E-mails: [1]a.lopez-arbarello@lrz.uni-muenchen.de, [2]o.rauhut@lrz.uni-muenchen.de, [3]k.moser@lrz.uni-muenchen.de

ABSTRACT

The Jurassic is an important period for understanding the origin of modern fish faunas, since it saw the first radiation - and in some cases the origin - of most modern groups. In chondrichthyans, neoselachian sharks and rays diversified during this time. In actinopterygians, the neopterygians, and among them the teleosts, experienced an important radiation, which led to the appearance of several of the modern teleosts groups. In the sarcopterygians, dipnoans and actinistians approached their current forms. However, the Jurassic fossil record of fishes is strongly biased towards the Northern Hemisphere. The only notable Early Jurassic fish fauna from Gondwana is that of the Kota Formation of India. For the Middle Jurassic, the most important Gondwanan fish faunas are those of the Aalenian-Bathonian Stanleyville Beds of the Democratic Republic of Congo, in which a distinct freshwater and a marine fauna are found. In the Late Jurassic, the Gondwanan record is slightly better, with important marine faunas being known from the Oxfordian Quebrada del Profeta in Chile and the Tithonian Vaca Muerta Formation of Argentina. Freshwater faunas have been described from the Tithonian Talbragar Beds of eastern Australia and the Tithonian Cañadón Calcáreo Formation of Argentina. The taxonomic composition of the known marine actinopterygian faunas of Gondwana is in general agreement with faunas of the Northern Hemisphere. However, the Jurassic fish record from Gondwana is highly incomplete both stratigraphically and geographically, and most faunas are in need of revision, further hampering an interpretation of Jurassic fish evolution in the Southern Hemisphere.

Keywords: *Jurassic, Gondwana, Chondrichthyes, Osteichthyes, Fossil record.*

RESUMEN: *Peces jurásicos de Gondwana.* El Período Jurásico es muy importante para entender el origen de las ictiofaunas modernas, dado que evidenció la primera radiación - y en algunos casos el origen - de la mayoría de los grupos modernos. Así, los condrictios neoselacios se diversificaron durante este periodo. Los actinopterigios neopterigios, y entre ellos los teleósteos, experimentaron una importante radiación que llevó a la aparición de varios de los grupos de teleósteos modernos. Entre los sarcopterigios, dipnoos y celacantos se aproximaron a sus formas actuales. No obstante, el registro fósil está fuertemente sesgado hacia el Hemisferio Norte. La única ictiofauna destacable del Jurásico Temprano de Gondwana proviene de la Formación Kota, India. Para el Jurásico Medio, las ictiofaunas gondwánicas más importantes provienen de las Stanleyille Beds (Aaleniano-Bayociano), República Democrática de Congo, donde se distinguen una ictiofauna dulceacuícola y otra marina. En el Jurásico Tardío el registro de peces gondwánicos es mejor, con importantes faunas marinas en la Quebrada del Profeta (Oxfordiano), Chile, y la Formación Vaca Muerta (Titoniano), Argentina. Ictiofaunas dulceacuícolas han sido descriptas de las Talbragar Beds (Titoniano), Australia, y la Formación Cañadón Calcáreo (Titoniano), Argentina. La composición taxonómica de las faunas de actinopterigios marinos de Gondwana se asemeja a la de faunas contemporáneas del Hemisferio Norte. No obstante, el registro de peces jurásicos de Gondwana es muy incompleto tanto estratigráfica como geográficamente y la mayoría de estas ictiofaunas necesitan una revisión profunda, lo cual dificulta aún más la interpretación de la evolución de los peces jurásicos en el Hemisferio Sur.

Palabras clave: *Jurásico, Gondwana, Chondrichthyes, Osteichthyes, Registro fósil.*

INTRODUCTION

More than half of the Recent vertebrate taxa known to date are "fishes" - more accurately chondrichthyans (cartilaginous fishes), actinopterygians (ray-finned fishes), dipnoans (lungfishes), and actinistians (coelacanths) - and this is likely to remain so, since the vast majority of unknown Recent species are probably marine taxa. Among these groups, modern fish faunas are vastly dominated by neoselachian sharks and rays and teleostean actinopterygians, which account for mo-re than 95% of Recent fishes (Nelson 2006).

In the long evolutionary history of jawed fishes, from the Early Devonian to now, many new groups appeared, flourished and diminished or disappeared. However, the Permian-Triassic extinction event finally set the stage for the evolution of modern fish faunas, and both neoselachians and teleosts first appeared during the Triassic in the fossil record (Arratia 2004, Maisey *et al.* 2004). However, in this time, they represent only one of many groups that appeared or diversified in this period. Thus, although many typical Jurassic groups have their oldest records during the Triassic, most of them were still rather poorly represented at that time (Benton 2005). Many of the groups that appeared or radiated in the Triassic flourished only briefly, and a large number of taxa and lineages died out at the Triassic-Jurassic boundary, *e.g.* the perleidiforms. Those clades that survived were the groups that were to dominate Mesozoic fish faunas, and they included the early representatives of the lineages leading towards our modern groups of fishes. These clades experienced their first great radiation during the Jurassic. Teleosts, for example, became ever more important components of Jurassic fish faunas, and several important Recent lineages first appeared in the later stages of this period (Arratia 2004). Thus, this period is of greatest importance for our understanding of the origin and early evolution of modern fish biodiversity.

However, our understanding of Jurassic fishes mainly rests on a relatively small number of exceptional *lagerstätten*, such as the Posidonia Shale or the lithographic limestones of Solnhofen, most of which are situated in the Northern Hemisphere. Gondwanan fish faunas are less well understood and have contributed only to a limited degree to our understanding of Jurassic fish evolution. Thus, in the current contribution, we will give a short overview of the Jurassic fossil record of fishes and their evolutionary history during this time, but with a special emphasis on our current knowledge of Jurassic fishes from the southern continents.

Institutional abbreviations

MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina, **NHM**, Natural History Museum, London, UK, **NMB**, National Museum Bloemfontein, South Africa, **P**, Museo "Profesor Dr. Juan A. Olsacher", Zapala, Neuquén, Argentina, **RMCA**, Royal Museum for Central Africa.

JURASSIC FISHES

Before trying to understand the composition of the Jurassic ichthyofaunas of Gondwana and their history, it is necessary to know which groups of fishes lived during that time in general and, as far as possible, to understand the evolutionary history of each group. In this section, following the systematic classification, we will have a closer, though still brief look at the Gondwanan history of the groups of fishes that lived during the Jurassic. They rapidly flourished during that time, producing the rich and highly diversified fish faunas of the Cretaceous, and giving rise to the modern fish faunas, mainly constituted by teleosts.

CHONDRICHTHYES

Several chondrichthyan lineages survived the Permo-Triassic extinction, but most of them disappeared by the end of the Triassic (*e.g.* cladoselachids, eugenodontiforms, symmoriids, xenacanths, ctenacanthids, phoebodontids, Cappetta 1987, Stahl 1999a, Maisey *et al.* 2004). Only the chimaeriform holocephalians and the hybodont and neoselachian elasmobranchs survived into the Jurassic, and only relatively few chimaeroid taxa and the neoselachians lived into the Cenozoic.

Holocephali

Chimaeriformes: Holocephalians were numerous and highly diversified during the Palaeozoic, but only one among seven currently accepted lineages survived into the Mesozoic (Stahl 1999a). Eighteen chimaeriform genera, classified in three suborders (Squalorajoidei, Myriacanthoidei, and Chimaeroidei) are known from Jurassic sediments in the Northern Hemisphere (Table 1), but no chimaeriform has yet been reported from the Jurassic of Gondwana (López-Arbarello 2004). However, the record in Gondwana of some possible Palaeozoic chimaeriforms and several Cretaceous and Tertiary remains suggest that they might have been present during the Jurassic along the coasts of this supercontinent (Table 2). Chimaeriforms have always been strictly marine fishes. Recent chimaeriforms have their greatest diversity in the deep temperate waters of shelves and slopes, generally at depths of up to 3000 m, with most species occurring between 200 and 2000 m (Didier 2002). Jurassic chimaeriforms are known from palaeoarchipelagos and costal palaeoenvironments. They were large predators, morphologically similar to the modern chimaeriforms. As the modern forms, they were durophagous fishes, probably predating on benthic organisms mainly, but also on other fishes.

Elasmobranchii

Hybodontiformes: Though great improvements have been made in the last decades, hybodontiforms are still a relatively poorly understood group of sharks, and it is still unclear weather they represent a natural, monophyletic group. However, hybodonts share several features that are currently considered apomorphic characters, such as the heterodont dentition (combining piercing anterior teeth and flat, crushing posterior teeth), fin spines with longitudinal furrows and denticles on the posterior surface, and cephalic spines (more detailed information in Maisey *et al.* 2004). Hybodonts diversified and were the dominant sharks during the Triassic and Jurassic, and they are considered to be the extinct sister group of neoselachians (modern sharks and batoids, Maisey *et al.* 2004). They declined during the Cretaceous and most hybodonts disappeared before the Maastrichtian (only one species known in the Maastrichtian, Kriwet and Benton 2004). They include a wide variety of dentitions, indicating many different feeding habits, very large forms (several meters) as well as some that were only a few centimeters long, and although many of them were marine fishes, they are also represented in non-marine sediments, indicating at least a tolerance to brackish and even

TABLE 1: Jurassic record of Chimaeriformes (Holocephali).

Suborder	Family	Genus	Provenance	Age
Squalorajoidei	Squalorajidae	*Squaloraja*	Great Britain, Italy, Luxembourg	Early Jurassic
Myriacanthoidei	Myriacanthidae	*Agkistracanthus*	Switzerland, Austria, Great Britain, France	Late Triassic-Early Jurassic
		Myriacanthus	Great Britain, France, Belgium, Luxemburg, Germany, Russia	Late Triassic-Late Jurassic
		Acanthorhina	Germany	Early Jurassic
		Alethodontus	Germany	
		Holonodon	Belgium, Luxemburg	
		Metopacanthus	Great Britain, Germany	
		Recurvacanthus	Great Britain	
	Chimaeropsidae	*Chimaeropsis*	Belgium, Germany	Early and Late Jurassic
Chimaeroidei	Callorhynchidae	*Bathytheristes*	Germany	Early Jurassic
		Eomanodon	Great Britain	
		Brachymylus	Great Britain, Germany, Russia	Early and Middle, Jurassic
		Callorhinchus	Germany, Russia	Middle Jurassic
		Pachymylus	Great Britain	
		Ganodus	Great Britain	
	Rhinochimaeridae	*Ischyodus* *Elasmodectes*	Great Britain, Germany, France, Komi Republic, Russia	Middle and Late Jurassic
		Harriotta	Great Britain, Russia France, Canada	Late Jurassic

Data from Stahl (1999a, b, 2004), Delsate *et al.* (2002), Popov and Beznosov (2006), Popov and Shapovalov (2007).

TABLE 2: Mesozoic record of Chimaeriformes (Holocephali) in Gondwana.

Age	Taxon	Provenance
Palaeozoic	?Chimaeriformes	Bolivia
Early Cretaceous	*Ptyktoptychion tayyo*	Australia
	Edaphodon eyrensis	Australia
Late Cretaceous	*Edaphodon sweeti*	Australia
	Ischyodus thurmanni	New Zealand
	Elasmodectes zangerli	Anctartica
	Ischyodus dolloi	Antarctica
	Chimaera sp.	Antarctica
	Elasmodectes-like	Chile

Data from Stahl (1999a, b, 2004).

fresh waters (Maisey *et al.* 2004). Jurassic hybodonts are mainly known from North America, Europe, Asia, and Africa. However, in Gondwana, apart from several African records of hybodonts in Somalia (Murray 2000), the Democratic Republic of Congo (DRC) (Saint-Seine and Casier 1962), Tanzania (Arratia *et al.* 2002), and Ethiopia (Godwin *et al.* 1999), hybodonts are only known in the Late Jurassic-Early Cretaceous Tacuarembó Formation in Uruguay (Perea *et al.* 2001) (Table 3). Nevertheless, they are present in Triassic sediments of Africa and Australia, as well as in Cretaceous rocks of Africa and South America (Murray 2000, López-Arbarello 2004).

Neoselachii: The clade Neoselachii includes all modern and Recent sharks and rays. The oldest neoselachian remains are known from the Early Triassic (Cuny 1998, Underwood 2006). These earliest neoselachian taxa apparently represent extinct lineages, and modern neoselachian lineages can only be traced back to the Early or Middle Jurassic (Maisey *et al.* 2004, Fig. 1). Early Mesozoic neoselachians were small, but already highly diversified in marine habitats, apparently colonizing fresh waters only in the Cretaceous (Maisey *et al.* 2004, Underwood 2006). Most Mesozoic neoselachian remains consist of isolated teeth, and articulated remains are very rare and limited to a few especially well-preserved faunas (*Lagerstätte*). However, most of these fossil teeth can be identified to the species level, giving a reliable testimony of neoselachian history (Underwood 2006). Curiously, the known fossil record of neoselachians (mainly represented by isolated teeth) agrees better with the phylogenies based on molecular data than those based on whole-body morphological data (Maisey *et al.* 2004, Underwood 2006). Despite a remarkable increase of our knowledge of the early neoselachian fossil record during the last twenty years, the Jurassic record of the group remains poor and Jurassic neoselachians are mainly known from Europe only (Underwood 2006). The record of Jurassic neoselachians in the Southern Hemisphere is extremely poor (Table 4) and very little can be said about the history of this group in the Jurassic of Gondwana. The single, though very important record of a neoselachian in the Jurassic of South America is the partial skeleton of a batoid from the Tithonian Vaca Muerta Formation of the Neuquén Basin in Argentina (Fig. 2, Cione 1999). After this first finding, only two other rays have been reported from the Jurassic of Gondwana, in the Tithonian Mugher Mudstone Formation of Ethiopia (Godwin *et al.* 1999) and the Tithonian Upper Saurian Beds of the Tendaguru Beds in Tanzania (Arratia *et al.* 2002).

SARCOPTERYGII

Most sarcopterygian lineages vanished at the end of the Palaeozoic, and only the actinistians, dipnoans and tetrapods survived into the Mesozoic and Cenozoic. These three groups are not closely related with each other, and their respective earliest records go back to the Devonian. The sarcopterygian fishes were very diverse during the Palaeozoic and are comparably much more poorly represented during the Mesozoic and, especially, during the Cenozoic, and have only a few Recent representatives.

Actinistia

Actinistian fishes appear in the Middle

Devonian (Givetian, Friedman and Coates 2006) and have a rather continuous fossil record until the Late Cretaceous (Coniacian-Santonian, Forey 1991), when they were thought to go extinct until the discovery of the first specimen of the Recent *Latimeria chalumnae* in 1938 (Benno *et al.* 2006). Actinistians are currently classified in two major groups, the 'Diplocercidiformes' (paraphyletic) and the Coelacanthiformes (monophyletic) (Schultze 2004). The fishes classified in 'Diplocercidiformes' are mainly Palaeozoic, with only a few Early Triassic genera. The more derived coelacanthiformes are classified in two suborders, the 'Coelacanthoidei' (paraphyletic) and the Latimeroidei (monophyletic) (Schultze 2004).

Coelacanthiformes: In contrast to the dipnoans, the Jurassic coelacanthiforms are mostly preserved as complete specimens and, thus, their morphology and interrelationships are well known. Only one of the genera classified in the 'Coelacanthoidei' lived during the Jurassic (*i.e. Coccoderma* from the Late Jurassic of Europe, Schultze 2004). Among the Latimeroidei, eight genera (Table 5) are represented in the Jurassic. Five of them are classified in the extinct fresh water family Mawsoniidae, and the remaining three, together with the unique Recent genus *Latimeria*, conform the marine family Latimeriidae (Schultze 2004). The two families represent monophyletic groups (Cloutier 1991, Forey 1991, 1998). Most of these Jurassic coelacanths are known from central Europe (Lower and Upper Jurassic of England and Germany). One genus, *Diplurus*, is known from North America, and only two genera are known from Gondwana (*Indocoelacanthus* Jain, 1974, from the Early Jurassic of India, and Lualabaea Saint-Seine, 1955, from the Middle Jurassic of Africa). One coelacanth has been reported from the Jurassic of South America. The specimen consist of an imperfectly preserved skull from the Quebrada Vaquillas Altas (Sinemurian) in Chile, which was identified in the family Mawsoniidae and might represent a new genus, closely related to the North American *Diplurus* (Arratia and Schultze 1999a). *Bunoderma baini* from the Late Jurassic (Tithonian) Vaca Muerta Formation, Neuquén Basin, Argentina, was first described as a coelacanth, but the fish was reinterpreted as a primitive teleost by Cione and Pereira (1990).

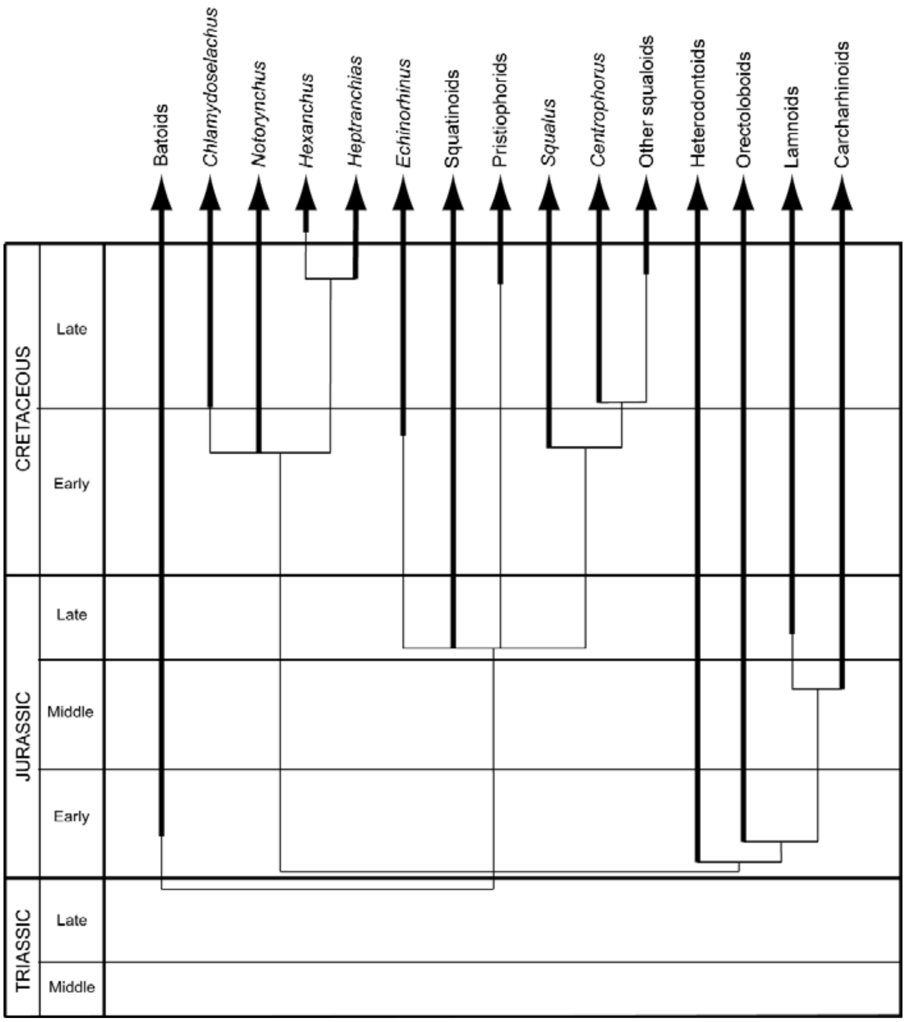

Figure 1: Hypothesis of phylogenetic relationships of the main neoselachian lineages. Based on Maisey *et al.* (2004).

Dipnoi

The history of dipnoans goes back to the Early Devonian, and the group has an excellent fossil record during the rest of the Palaeozoic, including some magnificently three dimensionally preserved specimens (Marshall 1986). The Mesozoic record of dipnoans is, instead, fragmentary. Schultze (2004: 469) gave a complete list of the known skull roofs of Mesozoic dipnoans (note that *Mioceratodus* is known from the Tertiary, Kemp 1998). All of them are of Triassic age and, with a few exceptions, the post-Triassic fossil dipnoans are mostly known from tooth plates only. This notable shift in the preservation of fossil dipnoans through time is directly related to an observed evolutionary trend from heavily ossified skeletons with dermal bones sometimes covered by cosmine in the Devonian dipnoans, to the much more weakly ossified skeletons with thin dermal skull bones embedded in the skin of the Mesozoic and Cenozoic dipnoans (Cavin *et al.* 2007). In parallel, tooth plates became stronger through increasing mineralization with petrodentine (Cavin *et al.* 2007).

Figure 2: Indeterminate bathoid (P 2564) from the Tithonian Vaca Muerta Formation of the Neuquén Basin, Argentina (modified from Cione 1999). Scale bar equals 2 cm.

Ceratodontoidei: During the Palaeozoic and Triassic, dipnoans had a worldwide distribution, but they are already restricted to the Southern Hemisphere at the beginning of the Cenozoic. Although they are still widely distributed, the Jurassic record of dipnoans is relatively poor, and only ceratodontoid dipnoans are represented in the Jurassic (Marshall 1986, Schultze 2004). In particular, Jurassic dipnoans are almost unknown in Gondwana, although the group has a good fossil record in the Triassic and Cretaceous of the Southern Hemisphere. They are only represented in the Late Jurassic of Africa with *Asiatoceratodus tiguidensis* in the Mugher Mudstone Formation, Ethiopia (Goodwin *et al.* 1999), the Taouratine Formation (Early Oxfordian-Late Tithonian) of Algeria (Martin 1984, Kemp 1998), and the Tacuarembó Formation (Late Jurassic-Early Cretaceous, Perea *et al.* 2001) of Uruguay, South America, where they occur together with other, still undescribed ceratodontoid tooth plates (Soto *et al.* 2007).

ACTINOPTERYGII

The oldest articulated remains undoubtedly referred to the Actinopterygii are found in the Middle Devonian, and actinopterygians are rare among the Devonian fishes (Friedman and Blom 2006). Actinopterygians evolved rapidly during the Carboniferous and Permian, and several atinopterygian lineages went to extinction at the Permo-Triassic boundary. The actinopterygian faunas recovered very rapidly during the Triassic, especially diversifying in shallow marine and brackish environments, giving rise to the very rich and diverse actinopterygian faunas of the Jurassic.

Basal Actinopterygians

The term "basal actinopterygians" is informally used to refer to a non-monophyletic group of all non-neopterygian actinopterygians. Several different lineages are thus grouped under this term. Most of these lineages are exclusively or mostly represented in the Palaeozoic or Triassic. Only three of these lineages range through the Jurassic (polypteriforms, ptycholepids, and chondrosteans *sensu stricto*), and only two of them are represented in the Jurassic of Gondwana (Fig. 3, Table 6). Polypteriforms are considered to be among the most primitive actinopterygian fishes, though their fossil record only starts in the Cretaceous. Ptycholepids are a relatively small group of early Mesozoic (Triassic - ?Middle Jurassic) fishes of still uncertain relationships. The family includes the Triassic *Boreosomus*, the Late Triassic-Early Jurassic *Ptycholepis*, and two Middle Jurassic Chinese genera, *Yuchoulepis* and *Chungkingichthys* (Su 1974). No ptycholepids have been reported from the Jurassic of Gondwana. However, *Ameghinichthys* from the Late Jurassic of Longing Gap, Antarctica, is probably related to these fishes (Arratia *et al.* 2004). Other fishes probably related to the ptycholepids, though placed in the family Acrolepidae, are known from the Early Triassic of Australia, and the Late Triassic of the Cuyo and the Bermejo basins in Argentina (López-Arbarello *et al.* 2006), so that the presence of this group in the Jurassic of Gondwana would not be too surprising. Given that Ptycholepids are well-represented in the northern Tethyan margin in the Early Jurassic (López-Arbarello and Rauhut 2006), their absence in Gondwana might reflect the fact that no good fish localities are yet known from the southern Tethyan margin at that time, especially from northern Africa.

Chondrostei: The name Chondrostei has been restricted to the clade including the Triassic fish *Birgeria* and the modern Acipenseriformes and their fossil relatives (Grande and Bemis 1996). The Acipenseriformes, fossil and Recent, are so far restricted to the Northern Hemisphere and have their oldest record, *Eochondrosteus*, in the Late Permian Fangshankou Formation in the Subei County, Gansu Province, China (Lu *et al.* 2005). This Lazarus taxon is unknown for about 80 Ma until its next record, *Chondrosteus*, in the Early Jurassic of Lyme Regis, England. The group had an important diversification during the Late Jurassic (4 genera: 5 species) and a few new genera and species (3 genera: 3 species) originated in the Upper Cretaceous. However, chondrostean diversity decreased during the Middle Cretaceous with the disappearance of the two basal fossil groups, Chondrosteidae and Peipiaosteidae. Nowadays Chondrosteans are represented by only twenty-seven species (2 polyodontid, 25 acipenserids) (López-Arbarello *et al.* 2002). Apart from *Birgeria*, many 'palaeonisciform' taxa might meet the character definition of Chondrostei, but the early history of the group is still very poorly understood. Among the possible chondrosteans lineages are the coccolepids (López-Arbarello *et al.* 2002). Coccolepid fishes are known from Late Jurassic and Early Cretaceous sediments in Europe, Asia, and North America in the Northern Hemisphere, and are also represented in Gondwana (South America and Australia, Hilton *et al.* 2004). The South American coccolepids come from the Almada Fauna (see below) of the Cañadón Calcáreo Formation and have been identified as *Coccolepis groeberi* (Fig. 4). The same species was also reported from the Lower Cretaceous La Cantera Formation in western Argentina. The fishes in the Alamada Fauna do not belong to *Coccolepis*, but represent a new coccolepid genus (López-Arbarello *et al.* 2002). The fishes from the La Cantera Formation are not coccolepids, they might represent a basal, non-acipenseriform chondrostean (López-Arbarello *et al.* 2002). The only other possible chondrostean reported from the Jurassic of Gondwana is *Coccolepis australis* from the Talbragar Fish Beds of Australia (Woodward 1895).

TABLE 3: Jurassic record of hybodontiform sharks in Gondwana.

Age	Taxon	Provenance
Late Triassic or Early Jurassic	*Hybodus cf. minor*	Lugh Series, Somalia
Early Jurassic	*?Polyacrodus* *Lissodus indicus*	Kota Formation, India
Middle Jurassic	*Hybodus songaensis*	Songa limestones, DRC
Late Jurassic	*Hybodus sp.* *Lonchidion sp.*	Tendaguru, Tanzania
	Hybodus sp. *Priohybodus arambourgi*	Mugher Mudstone Formation, Ethiopia
	Hybodus sp. *Priohybodus sp.*	Lugh Series, Somalia
Late Jurassic or Early Cretaceous	*Priohybodus*	Tacuarembó Formation, Uruguay

Data from Saint-Seine (1955), Goodwin *et al.* (1999), Murray (2000), Perea *et al.* (2001), Arratia *et al.* (2002), Prasad *et al.* (2004).

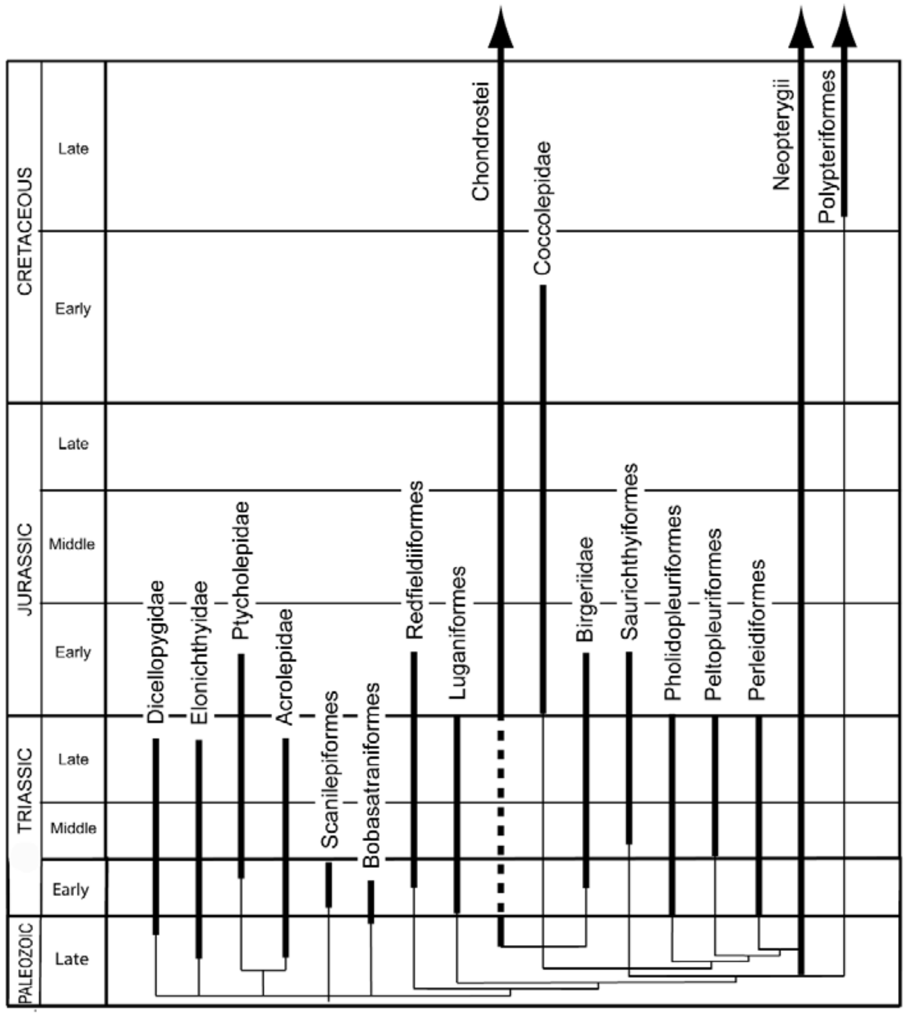

Figure 3: Hypothesis of phylogenetic relationships of the main non-neopterygian lineages of the Actinopterygii. Based on Gardiner and Schaeffer (1989), Tintori and Sassi (1992), Cloutier and Arratia (2004), Gardiner *et al.* (2005), Hurley *et al.* (2007).

Non-teleostean Neopterygians

A very important step in the evolution of the actinopterygians is the origin of the Neopterygii, with the acquisition of a better control of the movements of both dorsal and anal fins, and the consequent improvement in their swimming capabilities. The Neopterygii appear in the fossil record during the Permian, but their first and rapid radiation occurred during the Triassic, producing a very interesting variety of fishes with very different feeding specializations and habitat preferences. The phylogenetic relationships of the main neopterygian lineages are still very poorly understood (Fig. 5). Among the

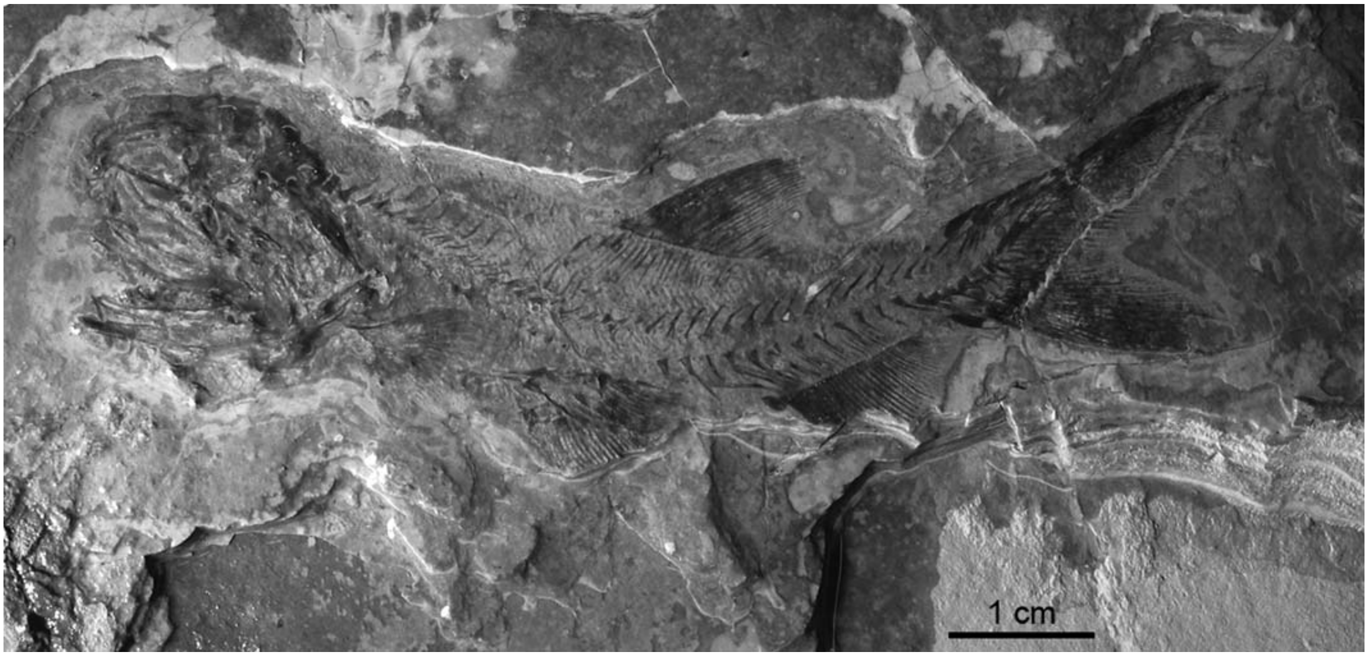

Figure 4: *"Coccolepis" groeberi* (MPEF-PV 1732) from the Almada Fauna of the ?Tithonian Cañadón Calcáreo Formation of Chubut, Patagonia, Argentina.

Jurassic neopterygians there are many still poorly understood taxa that cannot be placed in a particular group. Several of these fishes are known from Gondwana (Table 6). Among them are the halecostome *Atacamichthys* from the Oxfordian of Chile (Arratia and Schultze 1987), the archaeomaenid *Archaeomaene* and *Madariscus, Aetheolepis*, and *Aphnelepis* (Fig. 6) from the Late Jurassic Talbragar Fish Beds in Australia (Woodward 1895), the possible archaeomaenid *Oreochima ellioti* from sedimentary intercalations in the Middle Jurassic Kirkpatric basalts (Aalenian, K-Ar about 179 Ma, Kyle *et al.* 1981) of the Transantarctic Mountains in Antarctica (Schaeffer 1972), *Paradapedium egertoni* and *Tetragonolepis oldhami* from the Early Jurassic Kota Formation of India (Prasad *et al.* 2004), and the halecostome *Songanella callida* from the marine sediments of the Middle Jurassic Stanleyville beds at Songa, Zaire (Saint-Seine and Casier 1962, see Colin 1994 for the age of the Stanleyville Beds). Several poorly known fish remains, including neopterygians, are known from the Early Jurassic (Toarcian) of Tunisia, from Late Triassic or Early Jurassic sediments in the Lugh Series in northern Somalia, and the also Late Triassic or Early Jurassic Adigrat Sandstone in Ethiopia (Murray 2000). Finally, Cione and Pereira (1990) classified ?*Platysomus pehuenchensis* and ?*Platysomus cajoensis* from the Tithonian Vaca Muerta Formation of Argentina as Halecostomi *incertae sedis*. The authors considered the two species as *nomina dubia* (see comments below concerning the use by these authors of the term *nomen nudum*). However, Cione and Pereira (1990) were not able to examine the type material, which was considered lost at that time. However, the holotype of ?*Platysomus pehuenchensis* MCNAM-PV 118 was later found in the collections of the Museo de Ciencias Naturales y Antropológicas "J.C. Moyano" (Mendoza, Argentina, see Cerdeño 2005) and the taxonomic status of this species should be revised. The holotype of ?*Platysomus cajoensis* remains lost (Cerdeño 2005).

Semionotiformes: Following the few available phylogenetic analyses of semionotiform fishes (Olsen and McCune 1991, Brito 1997, Cavin and Suteethorn 2006) we include the Lepisosteidae, Semionotidae, and Macrosemiidae in the Semionotiformes. *Acentrophorus*, from the Permian of Germany, has been regarded as the first semionotiform, but its referral to this group is questionable. The first unquestionable semionotiforms come from the Early Triassic of central Europe, *i.e.* *Semionotus alsaticus* from the Zwischenschichten at the limit between the Middle and Upper Buntsandstein in Alsace, France (López-Arbarello 2008). Represented by the Semionotidae, the semionotiforms have a very good fossil record in the Triassic of Europe, and they are well diversified and widely distributed in the Jurassic and Cretaceous of Europe, North America, China, India, Africa, South America, and Australia. Only one semionotiform family, the Lepisosteidae, survived into the Cenozoic and is represented today with two genera, *Lepisosteus*

TABLE 4: Jurassic record of neoselachians in Gondwana.

Late Jurassic	
Undescribed batoid	Vaca Muerta Formation, Argentina
Sphenodus sp. *Engaibatis schultzei*	Tendaguru, Tanzania
Orthacodus sp.	Lugh Series, Somalia
"Rhinobatos" sp.	Mugher Mudstone Formation, Ethiopia

Data from Cione (1999), Goodwin *et al.* (1999), Murray (2000), Arratia *et al.* (2002).

(four species) and *Atractosteus* (three species), which are restricted to fresh water environments in eastern North America and Central America. The Lepisosteidae had a wider distribution in the past, with the oldest members being known from the Lower Cretaceous of South America and Africa, and a good fossil record during the Late Cretaceous and Tertiary of Africa, South America, Madagascar, India, Europe, and North America (Brito 2006). The Macrosemiidae is a relatively small group of small fishes known from the Late Triassic to the Early Cretaceous of Europe and the Early Cretaceous of Mexico (Bartram 1977, González-Rodríguez and Reynoso 2004). The only macrosemiids reported from the Jurassic of Godwana are *Macrosemius maeseni* and *Songanella callida* from the Middle Jurassic marine levels of the Stanleyville Beds at Songa, Africa (Saint-Saine and Casier 1962, Table 6). However, the first of these species has been reinterpreted as a more primitive, non-neopterygian actinopterygian, and tentatively referred to the genus *Tanaocrossus*, which is known from the Late Triassic of North America, by Bartram (1977). Similarly, Bartram (1977) excluded *Songanella* from the Macrosemiidae, though he did not comment on the possible systematic position of this genus. *Uarbrichthys lauts*, from the Late Jurassic of Talbragar in Australia has been consider to be the sister taxon of the Macrosemiidae.

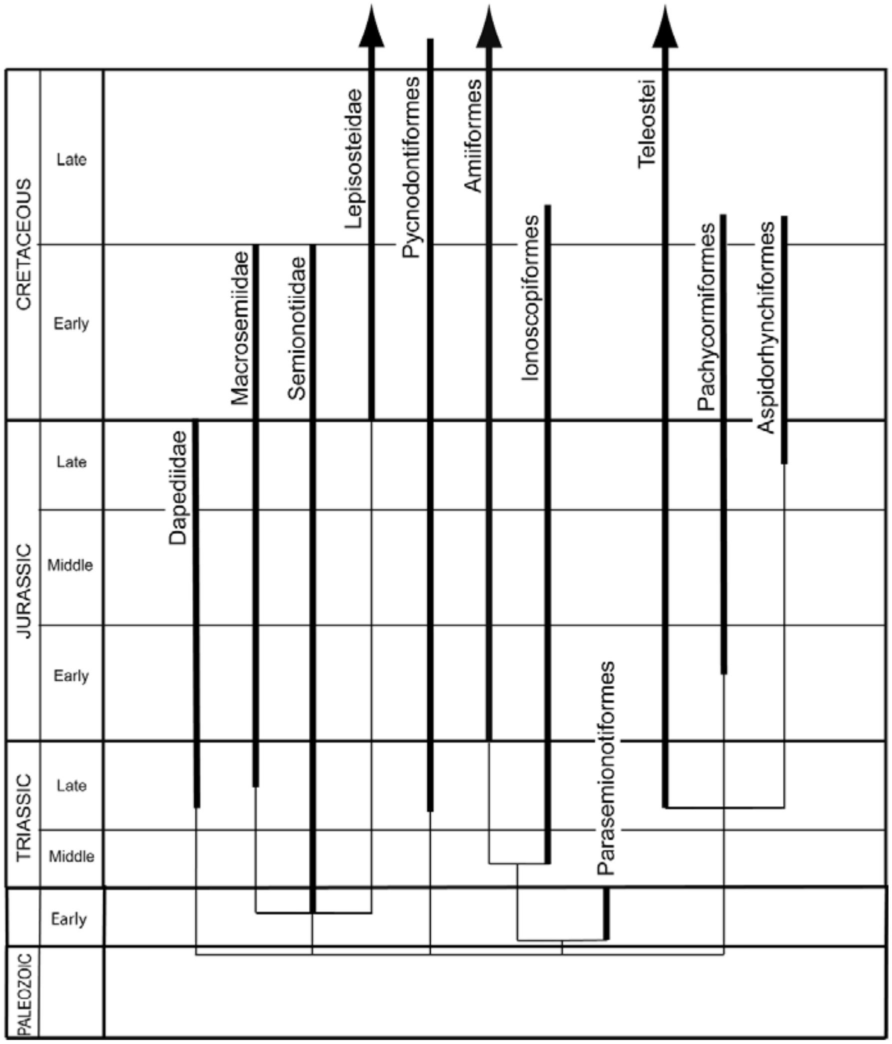

Figure 5: Hypothesis of phylogenetic relationships of the main neopterygian lineages. Based on Brito (1997), Grande and Bemis (1998) and Cavin and Suteethorn (2006).

Although semionotids are among the most common fishes in the Jurassic of the Northern Hemisphere, their fossil record is relatively poor in the Jurassic of Gondwana (Table 6). The oldest reliable records of semionotids in Gondwana are known from the Early Jurassic (see below). In Africa, scales of *Lepidotes* have been reported from the Late Triassic-Early Jurassic Adigrat Sandstones and the Late Jurassic Mugher Mudstone in Ethiopia (Goodwin *et al.* 1999). *Semionotus capensis* Woodward, 1888 (Fig. 7) is certainly the best-represented semionotid from the Jurassic of Gondwana. Several articulated specimens of this species are known from the Early Jurassic Clarens Formation, Karoo supergroup, in South Africa. *Lepidotes congolensis* is known from numerous disarticulated bones from the Middle Jurassic Stanleyville Beds of the Lualaba Series in DRC, Africa (Hussakof 1917, Saint-Seine 1955). The Late Jurassic (Tithonian) Upper Saurian Beds of Tendaguru produced several semionotid specimens, which were identified by Arratia and Schultze (1999b) as *Lepidotes tendaguruensis*.

Lepidotes deccanensis (Fig. 8) is the only valid among five species of *Lepidotes* that have been described from the Early Jurassic Kota Formation in India (Jain 1983). In northern Madagascar, semionotids are represented by very abundant disarticulated material, mainly jaw fragments and scales, in the Ambondromamy assemblage of the Bathonian Isalo IIIb Formation in the Mahajanga Basin (Flynn *et al.* 2006).

In South America, semionotids are known from the Pastos Bons Formation of the Paranaíba Basin in Brazil, with an undescribed species referred to *Semionotus* and *Lepidotes piauhyensis* (Gallo and Brito 2004, Gallo 2005). The age of the Pastos Bons Formation is controversial, being dated as Late Jurassic (Góes and Feijó 1994, Brito and Gallo 2002) or Early Cretaceous (Santos 1974, Lima and Campos 1980, Rossetti and Truckenbrodt 1999). In Chile, semionotids are

Figure 6: *Aphnelepis australis* (NHM P.12412) from the Late Jurassic at Talbragar, New South Wales, Australia. Photograph by Phil Hurst (NHM).

represented by poorly preserved material tentatively identified as ?*Lepidotes* indet. or *Lepidotes* sp. from different Jurassic outcrops ranging from Early Callovian to Oxfordian age (Arratia and Schultze 1999a). Semionotids have also been reported from the Tithonian Vaca Muerta Formation in Argentina (Cione *et al.* 1987), but these fossils have never been studied in detail. Furthermore, more than one semionotid taxon is represented by one articulated postcranium and several isolated bones and scales in the Late Jurassic-Early Cretaceous Tacuarembó Formation in Uruguay (Perea and Martínez 2003, ALA pers. obs.).

Apart from the macrosemiiform *Uarbrichthys*, a partial squamation identified as a semionotiform is the only other record of the group in the Jurassic of Australia (Bathonian-Callovian Walloon Coal Measures, Thies and Turner 2002).

Halecomorphi: The Halecomorphi is a well-defined neopterygian clade that includes three orders: Parasemionotiformes, Ionoscopiformes, and Amiiformes (Grande and Bemis 1998). The Parasemionotiformes include several Triassic genera from northwestern Madagascar (Lehman 1952, Beltan 1996), eastern Greenland (Stensiö 1932), and southern China (Tong *et al.* 2006). The Ionoscopiformes include the Early Cretaceous genus *Oshunia* from the Santana Formation in northeastern Brazil, and the families Ophiopsidae and Ionoscopidae. The Ionoscopidae are restricted to the Kimmeridgian-Tithonian of Europe. The Ophiopsidae include numerous species from the Middle Triassic through the Early Cretaceous. In the Jurassic of Gondwana, the group is represented by *Ophiopsis lepersonnei* from the marine sediments of the Stanleyville beds at Songa, Zaire (Saint-Seine and Casier 1962, Table 6). The Amiiformes are certainly the best-studied halecomorph clade, including the only Recent halecomorph taxon, *Amia calva*, which inhabits fresh waters of eastern North America (Grande and Bemis 1998). Four families, classified in two superfamilies, are included in the Amiiformes: Caturidae and Liodesmidae (in the Caturoidea), and Sinamiidae and Amiidae (in the Amioidea). However, most studies on amiiform fishes are focused on a few well-known genera, and the systematic of these fishes, especially the caturoids, is still very problematic (Patterson 1973, Lambers 1995). Most amiiforms are known from the Northern Hemisphere, with their oldest uncontroversial record in the Early Jurassic of England (Grande and Bemis 1998). However, the group is well represented by the Calamopleurini tribe of the Amiidae in the Cretaceous of Africa and South America. Earlier re-cords of amiiforms in Gondwana (Table 6) are in need of revision. These records include *Eugnathus* in the Late Triassic or Early Jurassic of the Lugh Series of Somalia, specimens referred to *Caturus* in the Middle Jurassic marine sediments of the Stanleyville beds at Songa, Zaire (Saint-Seine and Casier 1962), and caturidlike halecomorphs in the Tithonian Vaca Muerta Formation of Argentina (Cione *et al.* 1987). Catervariolus passaui and *C. hornemani* (Fig. 9A, Catervariolidae), *Lombardina decorata* (Lombardinidae), and *Signeuxella preumonti* (Signeuxellidae) from the Middle Jurassic Stanleyville Beds, Lualaba Series, DRC, were described and classified in separate families within the Amioidea by Saint-Seine (1955). Patterson (1973) classified the Catervarioliidae as teleosts and the Lombardinidae and Signeuxellidae as halecostomes of uncertain relationships. Arratia (2004: table 1)

TABLE 5: Jurassic coelacanth taxa.

Continent	Taxon	Provenance
Europe	*Trachymetopon liassicum* (Mawsoniidae)	Early Jurassic, Germany
	Holophagus gulo (Latimeriidae)	Sinemurian, England
	Undina (?) barroviensis	Kimmeridgian, France
	Undina cirinensis	Kimmeridgian-Tithonian, England, Germany
	Undina grandis	Tithonian, Germany
	Coccoderma substriolatum (Luagiidae)	
	Coccoderma bavaricum (Luagiidae)	
	Coccoderma gigas (Luagiidae)	
	Coccoderma suevicum (Luagiidae)	
	Macropoma willemoesi (Latimeriidae)	
	Undina acutidens (Latimeriidae)	
	Undina penicillata (Latimeriidae)	
	Libys lerichei (Mawsoniidae)	
North America	*Diplurus longicaudatus* (Mawsoniidae)	Hettangian-Sinemurian, USA
Gondwana	*Indocoelacanthus* (Mawsoniidae)	Early Jurassic, India
	Lualabaea lerichei and Lualabaea henryi (Mawsoniidae)	Middle Jurassic, DRC, Africa

Data from Schultze (2004).

listed these three genera from the Stanleyville beds as teleosts. However, none of the latter two authors studied the material first hand, and, thus, the systematic position of these genera should be revised.

Pycnodontiformes: Pycnodontiforms are a monophyletic and both morphologically and ecologically very distinct group of neopterygians. The oldest pycnodontiforms are known from the Late Triassic (Norian) of Italy and Austria (Tintori 1981). They are well represented throughout the Mesozoic and have their youngest records in the early Cenozoic (Eocene, *e.g.* Longbottom 1984, Bellwood 1996). During the Jurassic, the pycnodontiforms experienced a very important diversification, reached an almost worldwide distribution and became one of the most common components of marine Late Jurassic assemblages. However, as is the case with most other actinopterygians groups, their record in the Jurassic of Gondwana is very poor and limited to isolated dentitions or very incomplete specimens. The group is only represented in the Late Jurassic of Africa and South America. In Africa, pycnodontiforms are recorded from the Late Jurassic Mugher Mudstone Formation in Ethiopia by a fragment of a toothed vomer identified in the genus *Pycnodus* (Goodwin *et al.* 1999). In South America, indeterminate pycnodontiforms and specimens representing the genus *Gyrodus* have been reported from several localities in the Oxfordian of Chile (Table 6, Martill *et al.* 1998, Arratia and Schultze 1999a, Kriwet 2000).

Teleosts

There is currently no agreement about the definition of Teleostei, regarding the inclusion of fossil forms (*e.g.* Patterson 1973, de Pinna 1996, Brito 1997, 1999, Arratia 2004). Among others, the pycnodontiforms, pachycormiforms, and aspidorhynchiforms have been classified in Teleostei by several authors (*e.g.* Patterson 1973). Here we follow the most recent classification of Teleosts by Arratia (2004). Thus, pachycormiforms, and aspidorhynchiforms are stem-group teleosts and belong to a more inclusive clade named Teleosteomorpha (Arratia 2004). The "true" teleosts or Teleostei *sensu stricto* (Arratia 2004, Fig. 10) include several taxa that lie on the stem-line of modern groups and which are usually referred to as basal teleosts, and the Teleocephala (comprising living teleosts and their fossil relatives). Dapedids and pycnodontiforms where classified as Telesteomorpha by Arratia (2004). However, Patterson (1973) excluded these groups from

Figure 7: *Semionotus capensis* (NMB 1502) from the Sinemurian-Pliensbachian Clarens Formation, Stormberg Group, Karoo Supergroup, South Africa.

TABLE 6: Jurassic actinopterygian taxa from Gondwana.

Actinopterygii incertae sedis	*Ameghinichthys*	Late Jurassic of Longing Gap, Antarctica
	Tanaocrossu maeseni	Middle Jurassic, Songa limestones, DRC
	Songanella callida	
Chondrostei incertae sedis	*"Coccolepis" groeberi*	Late Jurassic Cañadón Calcáreo Formation, Argentina
	"Coccolepis" australis	Late Jurassic Talbragar Fish Beds, Australia
Neopterygii incertae sedis	*Paradapedium egertoni,*	Early Jurassic Kota Formation, India
	Tetragonolepis oldhami	
Halecostomi incertae sedis	*Lombardina decorata*	Middle Jurassic Stanleyville Beds, DRC
	Signeuxella preumonti	
	Atacamichthys	Oxfordian of Quebrada del Profeta, Chile
	Aphnelepis australis - Aetheolepis mirabilis -	
	Archaeomaene tenuis - Madarisucus robustus -	Late Jurassic, Talbragar Fish Beds, Australia
	Oreochima ellioti	
Semionotiformes	*Semionotus capensis* (Semionotidae)	
	Lepidotes deccanensis (Semionotidae)	Late Jurassic, Transantarctic Mountains, Antarctica
	Lepidotes congolensis (Semionotidae)	Early Jurassic Clarence Formation, Karoo Series, South Africa
	Lepidotes tendaguruensis (Semionotidae)	Early Jurassic, Kota Formation, India
	Semionotus sp., Lepidotes piauhyensis (Semionotidae)	Middle Jurassic Stanleyville Beds, DRC
	Uarbrichthys latus (macrosemiiform)	Tithonian, Upper Saurian Beds, Tendaguru
Pycnodontiformes	*Gyrodus* sp.	?Late Jurassic Pastos Bons Formation, Brazil
	Pycnodus sp.	Late Jurassic, Talbragar Fish Beds, Australia
Ionoscopiformes	?*Ionoscopus*-type teeth	Oxfordian of Quebrada del Profeta and Quebrada San Pedro, Chile
	Ophiopsis lepersonnei	Late Jurassic Mugher Mudstone Fm., Ethiopia
Amiiformes	*Eugnathus* sp.	Early Jurassic, Kota Formation, India
	?*Caturus*-type teeth	Middle Jurassic, Songa limestones, DRC
	Caturus sp.	Late Triassic or Early Jurassic Lugh Series of Somalia
Pachycormiformes	*Leedsichthys notocetes*	Early Jurassic, Kota Formation, India
	Notodectes argentinus	Middle Jurassic, Songa limestones, DRC
Aspidorhynchiformes	*Vinctifer* sp.	Callovian-Oxfordian, Quehuita Formation, Chile
	Belonostomus sp.	Tithonian Vaca Muerta Formation, Argentina
Teleostei	Proleptolepid indet.	Kimmeridgian-Tithonian, Ameghino Fm., Antarctica
	Leptolepis	Tithonian Vaca Muerta Formation, Argentina
	Ligulella fourmarieri - Pholidophorus aequatorialis -	Sinemurian of Quebrada La Carreta, Chile
	Paraclupavus caheni	Toarcian of Tunisia
	Catervariolus passaui - Catervariolus hornemani	Middle Jurassic, Songa limestones, DRC
	Pleuropholis jamotti - Pleuropholis lannoyi -	
	Parapleuropholis olbrechtsi - Parapleuropholis koreni	Middle Jurassic Stanleyville Beds, DRC
	Austropleuropholis lombardi - Ligulella sluysi -	
	Majokia brasseuri	
	?*Pholidophorus domeykanus - Bobbichthys opercularis -*	
	Domeykos profetaensis - Protoclupea atacamensis	Oxfordian of Quebrada del Profeta, Chile
	Protoclupea chilensis - Protoclupea sp. *- Varasichthys*	
	ariasi - Chongichthys dentatus	
	Antarctithrissops australis	Kimmeridgian-Tithonian, Ameghino Fm., Antarctica
	Cavenderichthys talbragarensis	Late Jurassic Talbragar Beds, Australia
	Luisiella inexcutata - Tharrhias feruglioi	?Tithonian Cañadón Calcáreo Fm., Argentina
	Bunoderma baini	Tithonian Vaca Muerta Formation, Argentina
	Pachyrhizodontoidei indet.	Tithonian of Termas del Flaco, Chile
	Gondwanapleuropholis longimaxillaris	?Late Jurassic Pastos Bons Formation, Brazil

Data from Woodward (1888, 1895), Hussakof (1917), Saint-Seine (1955), Saint-Seine and Casier (1962), Schaeffer (1972), Jain (1973, 1983), Cione and Pereira (1987, 1990), Arratia and Schultze (1999a, b), Goodwin *et al.* (1999), Murray (2000), Perea *et al.* (2001), Brito and Gallo (2002), Arratia *et al.* (2004), Prasad *et al.* (2004), Gallo (2005), Bean (2006).

his Teleostei [here Teleostei *sensu lato*, *i.e.* (Teleostemorpha (Teleostei s*ensu stricto*))]. According to Patterson (1973), dapedids are semionotiforms and pycnodontiforms have a basal position among neopterygians. Arratia did not include the semionotiforms and other groups of basal neopterygians, to which the dapediids and pycnodontiforms might be more closely related than to the teleosts, in her various analyses of teleosts phylogenetic relationships (*e.g.* Arratia 1999, 2000, 2001, Arratia and Thies 2001). Therefore, we do not include the dapediids and pycnodontiforms in the Teleosteomor-

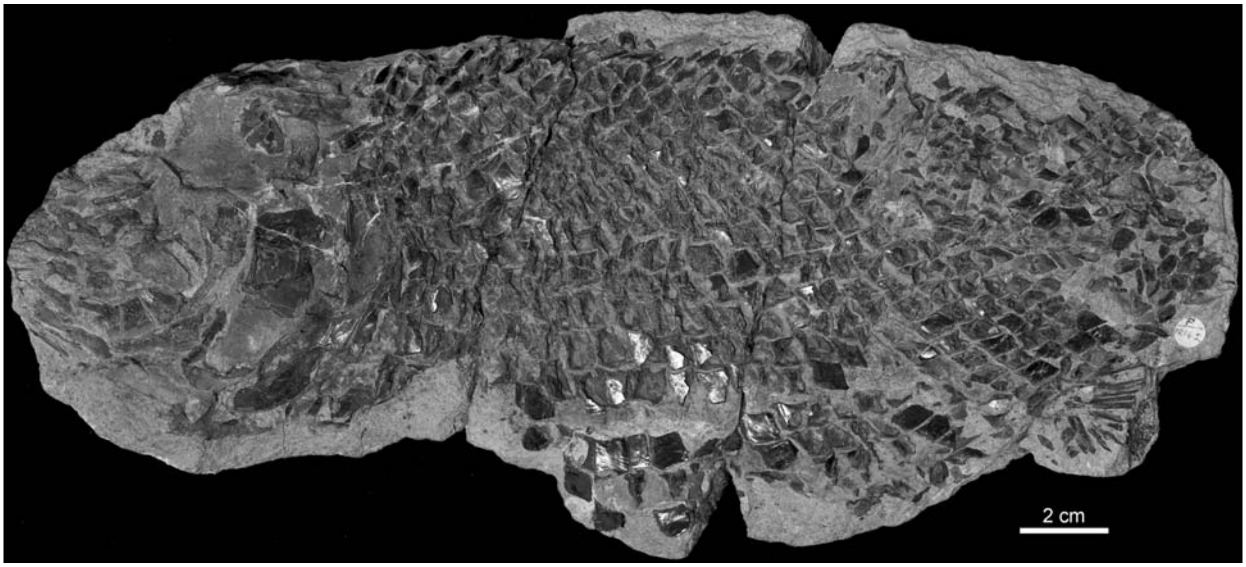

Figure 8: *Lepidotes deccanensis* (NHM P.12142) from the Early Jurassic Kota Formation, Deccan, India. Photograph by Phil Hurst (NHM).

pha and consider them as basal halecostomes, which is a non-monophyletic group that includes all halecostomes that are neither halecomorphs nor teleosteomorphs. In contrast, the close phylogenetic relationship among pachycormiforms, aspidorhynchiforms, and teleosts *sensu stricto* is well supported and generally accepted (Patterson 1973, Brito 1997, 1999, Arratia 2004).

Teleosteomorpha - Pachycormiformes: The pachycormiforms are very well represented by several genera, including excellently preserved specimens, in the Jurassic of the Northern Hemisphere, especially in Europe. The Cretaceous fossil record of the group is comparatively poor, but the group is apparently widespread in Gondwana by that time, including indeterminate records in South America (Arratia and Cione 1996), and some isolated teeth referred to *Protosphyraena* (a genus otherwise known from North America, Germany, Russia, and Japan) and a partially preserved skull described as a new endemic genus *Australo-pachycormus* from Australia (Kear 2007). Pachycormiforms are also, though poorly, represented in the Jurassic of Gondwana. Indeterminate pachycormiform remains have been reported from the Oxfordian of Quebrada del Profeta in Chile (Arratia and Schultze 1999a). In the Tithonian Vaca Muerta Formation in Argentina, *Notodectes argentinus* Dolgopol de Sáez, 1949, originally identified as an ichthyodectid might rather represent a pachycormid, according to Cione and Pereira (1990). *Leedsichthys notocetes* is known from the Quehuita Formation (Callovian-Oxfordian) of Chile (Martill *et al.* 1999), the genus is otherwise only known from the Middle to Late Jurassic of England and France (Liston 2004, López-Arbarello 2004).

Teleosteomorpha - Aspidorhynchiformes: Another monophyletic group, easily distinguishable morphologically, are the Aspidorhynchiformes. These fishes have a very long rostrum, formed by the elongated premaxillae and, though not as pronounced, also the mandible. Only four genera, classified in a single family Aspidorhynchidae, are included in the Aspidorhynchiformes (Brito 1997, Bartholomai 2004): *Aspidorhynchus*, ranging from the Middle Jurassic (Bathonian) to the earliest Cretaceous (Berriasian), *Belonostomus*, which is known from the Late Jurassic (Kimmeridgian) and probably reaches the earliest Tertiary, *Vinctifer,* ranging from the Late Jurassic (late Kimmeridgian-early Tithonian) to the Late Cretaceous (Campanian), and *Richmondichthys*, from the Early Cretaceous of Australia. *Aspidorhynchus* and *Belonostomus* are mainly known from the Northern Hemisphere (Brito 1997). *Aspidorhynchus* is known from Europe, the Oxfordian of Cuba (Jagua Formation), and the Late Jurassic of Antarctica (Richter and Thomson 1989, Brito 1997). *Belonostomus* is well represented in the Late Jurassic and Cretaceous of Europe and North America, and it has also been reported in the Tithonian Vaca Muerta Formation (Cione *et al.* 1987) and the Late Cretaceous Coli Toro Formation (Casamiquela 1984) in Argentina, and the Late Cretaceous Quiriquina Formation of Chile (Brito and Suárez 2003). In contrast to the previous genera, *Vinctifer* is almost entirely restricted to the Gondwanan continents, the only exception being the record of *Vinctifer comptoni* in the Albian Morelos Formation of Tepexi de Rodriguez in Mexico (Brito 1997). Despite the wide distribution of the aspidorhynchiforms, mainly represented by *Vinctifer*, in the Cretaceous of Gondwana, the Jurassic record of this group in this supercontinent is limited to the record of *Belonostomus* in the Vaca Muerta Formation mentioned above, and an occurrence of *Vinctifer* in the late Kimmeridgian-early Tithonian, Longing Member, Ameghino Formation, Antarctica (Arratia *et al.* 2004, Table 6).

Teleostei sensu stricto (basal teleosts + Teleoce-

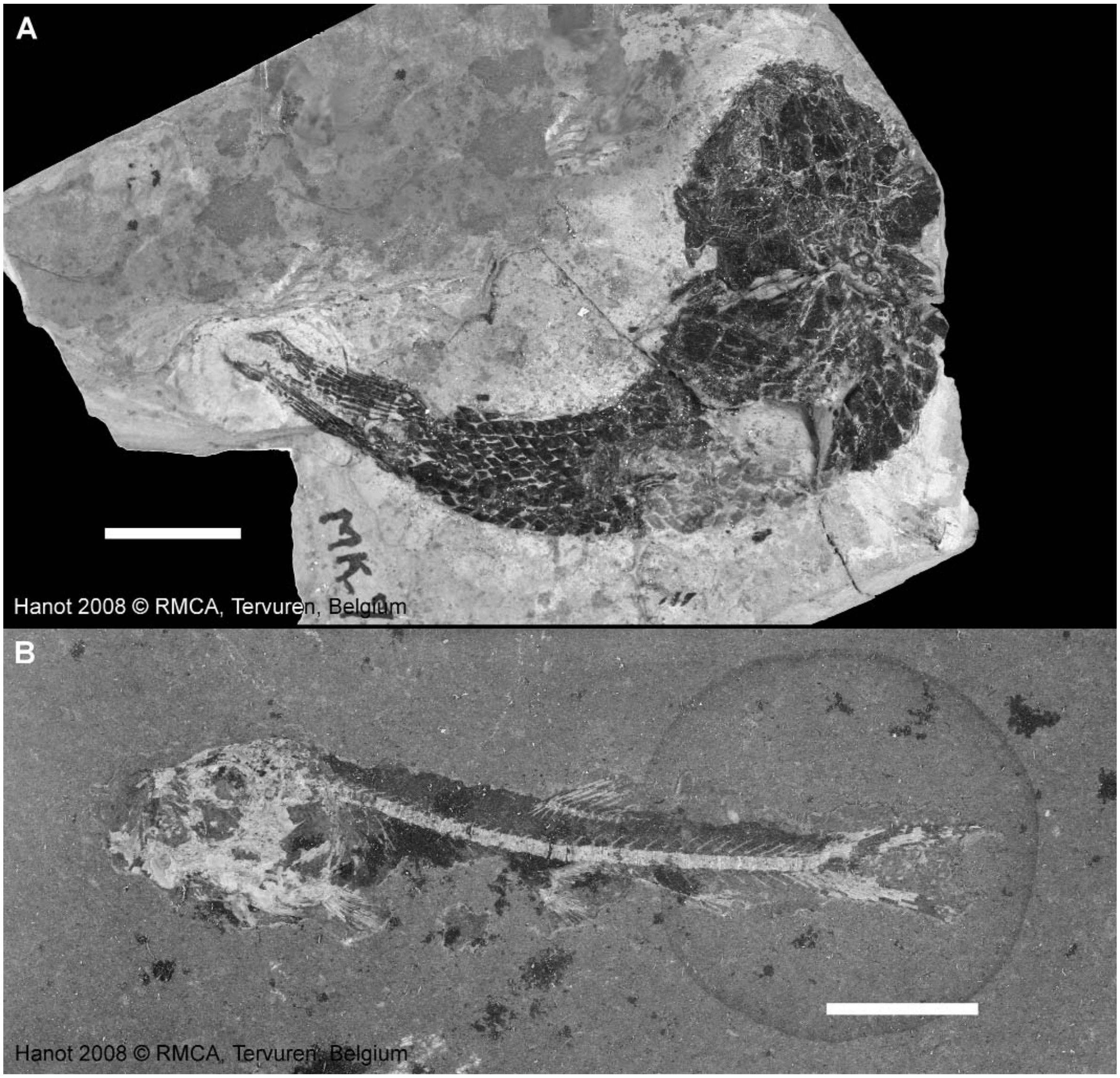

Figure 9: A) *Catervariolus hornemani* (RMCA RG 7486, paratype), B) *Paraclupavus caheni* (RMCA RG 8717a, paratype). Scale bars represent 1 cm. None of the pictures for the RMCA specimens can be reproduced or transmitted in any form or by any means without the permission in writing to the RMCA (isabelle.gerard@africamuseum.be).

phala): A very important find in Chile are the oldest pachyrhizodontoid remains in the Tithonian of Termas del Flaco (Arratia and Schultze 1999a). Pachyrhizodontoids are basal clupeocephalans, even likely primitive Euteleostei and, thus, already represent the modern teleosts (Cavin 2001, Taverne and Gayet 2005). Pachyrhizodonotids and clupeocephalans in general, are only known with certainty since the Early Cretaceous. The Chilean material referred to Pachyrhizodontoidei would thus represent not only the oldest record of this group, but also the oldest Clupeocephala. The Teleocephala (elopomorphs, osteoglossomorphs, and more advanced teleosts) have their oldest records in the Late Jurassic of the Northern Hemisphere, appearing in Gondwana only in the Cretaceous. However, among the stem-Teleocephala are several Gondwanan Jurassic taxa (Table 6, Fig. 10).

According to Arratia (2004), the Pholidophoriformes are among the most primitive teleosts, although, as currently defined, the group is not monophyletic and needs urgent revision. Pholidophoriforms are known from the Middle Triassic to the Early Cretaceous (Early Aptian, Traquair 1911, Taverne 1981) and are especially well represented in central Europe. Pholidophorids have been reported from the Early Triassic of Gosford, Australia, and the Late Triassic of Tanzania and Argentina (López-Arbarello 2004). However, the Argentinean material identified as *?Pholidophorus dentatus*, from the Potrerillos Formation, and *?Pholidophorus vallejensis*, from the Cacheuta Formation, are represented by undiagnosable material, which cannot be referred to the Pholidophoriformes, but probably rather represent more primitive, non-neopterygian actinopterygians (ALA pers. obs.). In the Jurassic, the group is only represented by *Pholidophorus aequatorialis* in the marine Middle Jurassic Stanleyville Beds at Songa, DRC (Table 6, Saint-Seine 1955, Saint-Seine and Casier 1962). According to Arratia and Schultze

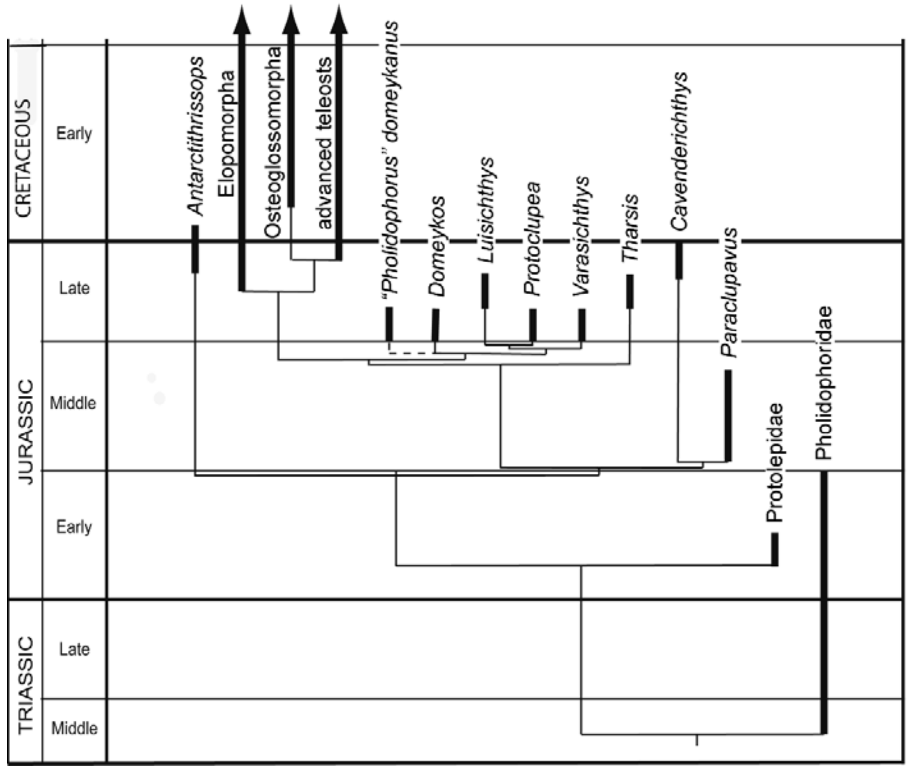

Figure 10: Phylogenetic hypothesis showing the relationships of some basal teleosts from Gondwana. Based on Taverne (2001), Arratia (2004), Arratia *et al.* (2004).

(1999a), *Pholidophorus domeykanus* from the Oxfordian of Quebrada del Profeta in Chile, is not a pholidophoriform, but probably represents a member of the Varasichthyidae (see below). Similarly, *Pholidophorus argentinus* from the Tithonian Vaca Muerta Formation in Chile is considered a *nomen dubium* (Arratia and Cione 1996).

Another group of primitive teleosts are the pleuropholids, although their phylogenetic relationships within the Teleostei are still unclear. These small fishes, easily distinguishable because of the presence of a single row of extremely deepened ganoid scales covering almost the whole side of the body, have been found in marine and freshwater environments from the Late Jurassic to the Early Cretaceous of Europe and Gondwana (Chiappe *et al.* 1998). The Jurassic records of this group in Gondwana (Table 6) are *Pleuropholis jamotti, Pleuropholis lannoyi, Parapleuropholis olbrechtsi, Parapleuropholis koreni*, and *Austropleuropholis lombardi* from the Middle Jurassic Stanleyville Beds of the Lualaba Series, DRC (Saint-Seine 1955), and *Gondwanapleuropholis longimaxillaris* from the Late Jurassic or Early Cretaceous Pastos Bons Formation in Brazil (Brito and Gallo 2002). Younger Gondwanan records are limited to the Early Cretaceous of Lebanon (Janensch 1925) and the Lagarcito Formation of Argentina (Chiappe *et al.* 1998). *Ligulella sluysi*, *Ligulella fourmarieri*, and *Majokia brasseuri* also from the continental Stanleyville Beds of the Lualaba Series (Saint-Seine 1955, Saint-Seine and Casier 1962), are teleosts of uncertain relationships, though Schaeffer and Patterson (1984: table 3, page 75) classified *Ligulella* from the marine Stanleyville Beds at Songa as a pleuropholid.

Among the Gondwanan Jurassic teleosts, the Chilean taxa are by far the best understood (Arratia 2004 and numerous articles cited therein). The indeterminate proleptolepids of the Sinemurian of the Quebrada La Carreta (Arratia and Schultze 1999a) represent the oldest record of Teleostei in the Jurassic of Gondwana, though it should be noted that teleosts were already present in the Late Triassic of Tanzania (Gardiner 1960, Nybelin 1974). The most important fauna of teleosts is, however, that from the Oxfordian of Quebrada del Profeta, including *Bobbichthys opercularis, Chongichthys dentatus*, two forms of distinct, though indeterminate teleosts, and the varasichthyids *Domeykos profetaensis, Varasichthys ariasi, Protoclupea atacamensis, Protoclupea chilensis, Protoclupea* sp., and probably also ?*Pholidophorus domeykanus* (Arratia and Schultze 1999a and references therein). Though still insufficiently studied, the teleosts of the lacustrine Almada Fauna from the ?Tithonian Cañadón Calcáreo Formation in the province of Chubut, Argentina, are potentially very important. Two freshwater teleosts taxa are currently recognized in this unit: *Tharrhias feruglioi* (Fig. 11) and *Luisiella inexcutata* (Cione and Pereira 1987). The only other freshwater teleost known from the Jurassic of Gondwana is the leptolepid *Cavenderichthys talbragarensis* from the Late Jurassic Talbragar Beds in Australia (Woodward 1895). The marine teleost *Paraclupavus caheni* (Fig. 9B) from the Middle Jurassic Stanleyville Beds at Songa, DRC, has been shown to form a monophyletic group with *Cavenderichthys* (Taverne 2001).

The ichthyodectiform *Antarctithrissops australis* from the Tithonian Longing Member of the Ameghino Formation in Antarctica (Arratia *et al.* 2004) constitutes a very important find. The Ichthyodectiformes are a monophyletic group of basal teleosts known from the Middle Jurassic to the Cretaceous only. *Antarctithrissops* is the oldest record of an ichthyodectiform in the Southern Hemisphere, and the first Jurassic record of the group in Gondwana (Arratia *et al.* 2004). Several teleost species have been named from the Tithonian Vaca Muerta Formation of Argentina. However, the validity of most of these species has been questioned by Cione and Pereira (1990). These authors do not make formal taxonomic decisions using the rules and ter-

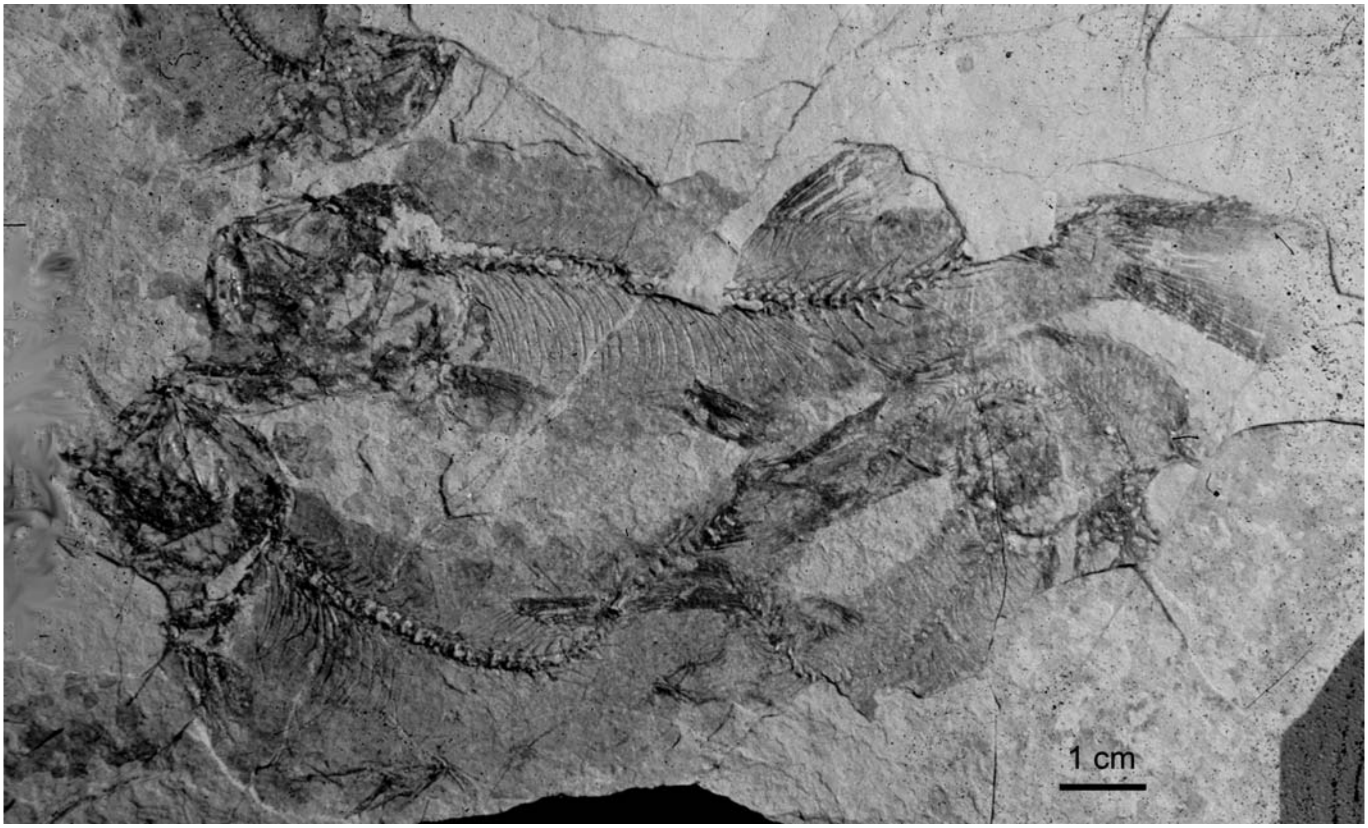

Figure 11: *"Tharrhias" feruglioi* (MPEF, unnumbered) from the Almada Fauna of the ?Tithonian Cañadón Calcáreo Formation of Chubut, Patagonia, Argentina.

minology accepted in the International Code of Zoological Nomenclature (ICZN 1985, 1999). However, it is clear from their statements that, in their opinion, *Pholidophorus argentinus, Leptolepis australis, Leptolepis argentinus, Leptolepis patagonicus*, which they indicated as *nomina vana*, and *Leptolepis dubius*?, indicated by the authors as not recognizable, are *nonima dubia* and, thus, these names do not represent valid taxa. It should be noted that the term *nomen vanum* has been used in two different senses, neither of which is recognized in the ICZN (1985, 2000, for recommendations on the use of the term *nomen vanum* see Chorn and Whetstone 1978). In the sense used by Cione and Pereira (1990), the taxa indicated as *nomina vana* represent nomina dubia (ICZN 1985, 2000). As mentioned above (see Coelancanthiformes) *Bunoderma baini* Dolgopol de Sáez, 1940, originaly described as a coelacanth, was reinterpreted as a primitive teleost by Cione and Pereira (1990) and, thus, represents the so far only valid teleost species in the Vaca Muerta Formation.

MAIN JURASSIC ICHTHYOFAUNAS

As shown in the paragraphs above, the record of Jurassic fishes is very poor in Gondwana, and many of these fishes are in need of revision. The incompleteness of the Gondwanan record of Jurassic fishes, together with the presence of several rich and excellently preserved Jurassic ichthyofaunas in the Northern Hemisphere, produce a very strong bias in our knowledge of the fish history during the early Mesozoic.

NORTHERN HEMISPHERE

The Early Jurassic of the Newark Supergroup in North America [Fig. 12(1)] and Lyme Regis in England [Fig. 12(2)], the Toarcian Posidonia Shale and equivalent beds in Germany, England and France [Fig. 12(3)], the Middle Jurassic Wanakah Formation [Fig. 13(1)] in the US and the Oxford Clay in England [Fig. 13(2)], the Middle to Late Jurassic Sundance Formation of western US [Fig. 14 (1)], the Kimmeridgian Lithographic limestone of Cerin, France [Fig. 14(2)], and the Kimmeridgian-Tithonian Lithographic limestone of Solnhofen, Germany [Fig. 14(3)], have yielded the best known Jurassic fishes, on which our current understanding of Jurassic fish evolution is based. It should be noted that the fishes of the British Purbeck (Woodward 1916-1919), which have been considered as typical Jurassic fish assemblages (*e.g.* Dineley and Metcalf 1999), are of Early Cretaceous age, according to the most recent stratigrahical studies (Ensome 2002, Cope 2008, see also Underwood and Rees 2002 for the precise stratigraphic record of the Purbeck selachian fishes).

Among the units mentioned above, only the faunas of the Sinemurian of Lyme Regis, the Toarcian of Europe, the Callovian of the Oxford Clay, and the Kimmeridgian-Tithonian of Solnhofen and Cerin have been studied thoroughly. According to our current knowledge (new taxa are still being discovered in these faunas), the taxonomic composition of each of these main icthyofaunas can be summarized as follows.

Lyme Regis [Fig. 12(2)]: More than 50 species of fishes have been described from Sinemurian marine sediments at the coast around Lyme Regis, Dorset, England (Dineley and Metcalf 1999). Lyme Regis is the most famous Early Jurassic fish site of the United Kingdom and one of the most important in the world, and has produced excellently preserved fossils since at least the end of the 18th Century. With the exception of the freshwater dipnoans, all other main groups of fishes are represented: holocephalians (4 genera, 5 species), hybodonts (3 genera, 6 species), neoselachians (3 genera, 4 species), coelacanths (1 genus, 1 species), non-neopterygian actinopterygians (7 genera, 10 species), including chondrosteans (2 genera, 4 species), basal neopterygians (4 genera and 18 species of holosteans), including basal halecostomes (1 genus, 6 species) and halecomorphs (3 genera, 12 species), and teleosteomorph teleosts (6 genera, 12 species). The environment of the fish fauna is interpreted to be shallow nearshore marine.

Posidonienschiefer [Fig. 12(3)]: The marine Lower Toarcian Posidonia Shale and equivalent beds of central and Western Europe have produced excellently preserved fossils. Permanent anoxic bottom water conditions have been proposed to explain the high quality of preservation, as well as the high accumulation of organic matter in these sediments. However, more recent studies have proposed variable oxygen availability, ranging from short oxygenated periods to longer-term anoxia (Röhl *et al.* 2001). Based on the best known localities (Whitby, England, La Caine, Elbes, and Sainte-Colombe, France, Holzmaden, Germany), the marine fish fauna was formed by holocephalians (2 genera, 2 species), hybodonts (1 genus, 1 species), neoselachians (2 genera, 2 species), coelacanths (1 genus, 1 species), non-neopterygian actinopterygians (3 genera, 3 species), including chondrosteans (2 genera, 2 species), basal neopterygians (5 genera and 12 species of holosteans), including basal halecostomes (3 genus, 8 species) and halecomorphs (2 genera, 4 species), and teleosteomorph teleosts (8 genera, 17 species), including several pachycormiforms (6 genera, 9 species).

Oxford Clay [Fig. 13(2)]: The lower Callovian Peterborough Member of the British Oxford Clay has produced a diverse fish marine fish fauna of holocephalians (4 genera, 5 species), hybodonts (2 genera, 3 species), several neoselachians (7 genera, 7 species), one chondrostean, basal neopterygians (5 genera and 7 species of holosteans), including basal halecostomes (3 genus, 5 species) and halecomorphs (2 genera, 2 species), and teleosteomorph teleosts (6 genera, 7 species), including one aspidorhynchiform and several pachycormiforms (4 genera, 5 species). The Peterborough Member represents an extensive shallow water shelf environment during the early phase of a large marine transgression (Martill and Hudson 1994).

Solnhofen and Cerin [Fig. 14(2) and (3)]: The Solnhofen platenkalk (Tithonian) is probably the most famous and best understood *lagerstätte* in the World. The exceptionally preserved fossils are contained in the sediments deposited in the deepest, hypersaline and anoxic bottons of the lagoons formed between the algal mounts. The local environment in these bottons was extreme and lethal, and the preserved fauna is thus allocthonous to the lagoons. Therefore, these fossils only represent a small sample of the probably very rich fauna that inhabited this Tithonian archipelago in the western Tethys. Probably not so diverse and certainly not so well studied, the lithographic limestones of Cerin (Kimmeridgian), France, represent a second *lagerstätte*. Different from the Solnhofen archipelago, the sediments in Cerin represent a costal lagoon environment. Although each of these *lagerstätte* shows numerous cases of endemism, the two fish faunas have many taxa in common. Here, despite the chronologic and environmental differences, we take the composition of the two faunas together as a gross example of the Late Jurassic fish faunas of the western Tethys, which is thus represented by holocephalians (2 genera, 2 species), hybodonts (2 genera, 2 species), many neoselachians (17 genera, 20 species), several coelacanths (4 genus, 9 species), a single chondrostean, many basal neopterygians (28 genera and 74 species of holosteans), including basal halecostomes (15 genus, 40 species) and halecomorphs (13 genera, 34 species), and many teleosteomorph teleosts (26 genera, 56 species), most of which are basal teleosts (14 genera, 33 species), but also including pachycormiforms (5 genera, 8 species), aspidorhynchiforms (2 ge-nera, 3 species), and teleocephalans (5 genera, 12 species).

GONDWANA

The Jurassic fish faunas of Gondwana look poor in comparison with the European faunas mentioned above, but this seems to be to a great extent due to the lack of thorough studies. There are several potentially very important Jurassic fish faunas in Gondwana. However, most of them are not only poorly studied, but also poorly explored, so that both research and fieldwork are utterly needed. The composition of the main Gondwanan Jurassic fish faunas can be summarized as follows.

Kota Formation [Fig. 12(4)]: Although only two hybodontoid sharks, one coelacanth, three basal halecostomes (two dapediids and one semionotid), and two possible halecomorphs are known from the Kota Formation of India (Tables 5-6, Jain 1973, Prasad *et al.* 2004), this is so far the best known fish fauna of probable Early Jurassic age in Gondwana. The age of the Kota Formation is controversial, it has been dated as Early Jurassic (Bandyopadhyay and Sengupta 2006) or Middle Jurasic to Early Cretaceous (Vijaya and Prasad 2001). We provisionally accept an Early Jurassic age because that is in agreement with the age indicated by the dinosaur fauna (Rauhut personal observation). As in the case of the dating, the depositional environment of the Kota Formation is also controversial. Studies of the sedimentology (Rudra and Maulik 1987) and the ostracod faunas (Tasch *et al.* 1973, Govindan 1975) in the Kota Formation indicate a freshwater environment. On the other hand, Bhattacharya (1980), based on petrographic, mineralogical, and geochemical analyses of carbonates and the presence of coccoliths, argued for an intertidal environment. This latter hypothesis, which is favoured by the stratigraphical and structural study of the Pranhita-Godavari graben of Raiverman *et al.* (1985), would fit better with our knowledge of the fish faunas, at least for the fish bearing sediments (Prasad *et al.* 2004). The presence of a coelacanth and dapediids in this fauna indicate a relationship with the contemporary European marine faunas. Therefore, the question arises whether this relationship is due to a palaebiogeographic relationship between northern Gondwana and Europe, or is a remnant of an earlier Pangeaic distribution of these taxa. With so little information about the Early Jurassic fish faunas of Gondwana, it is impossible to answer this question with certainty. However, the hybodontoid *Lissodus indicus* resembles closest some still undescribed *Lissodus* teeth from Hettangian sediments in Belgium (Prasad *et al.* 2004), supporting not only a Thethyan provincialism, but also an Early Jurassic age for the Kota Formation.

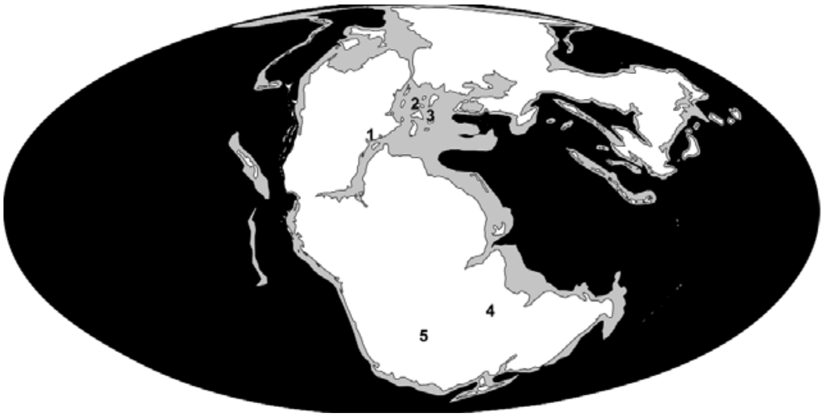

Figure 12: Palaeogeographic positions of Early Jurassic fish localities mentioned in the text. 1, Newark Supergroup. 2, Lyme Regis. 3, Posidonia Shale. 4, Kota Formation. 5, Clarens Formation. Map based on palaeogeographic maps by Ron Blakey (http://jan.ucc.nau.edu/~rcb7/RCB.html).

Stanleyville Beds [Fig. 13(3)]: Two important Jurassic fish faunas have been reported from the Stanleyville Group in DRC: a fresh water fauna from the bituminous mudstones and shales of the Stanleyville Beds (Saint-Seine 1950, 1955), and a marine fauna from the limestones of Songa (Saint-Seine and Casier 1962). The fresh water fauna includes coelacanths (1 genus, 2 species), basal halecostomes (3 genus, 3 species), and several basal teleosts (6 genera, 9 species), but no halecomorph (Tables 5-6). The marine fauna includes one hybodont shark (Table 3), basal halecostomes (3 genera, 3 species), one halecomorph, and basal teleosts (3 genera, 3 species) (Table 6). Based on the composition of these faunas, which was considered similar to that of the better known Late Jurassic fish faunas in Europe, the Stanleyville Beds were dated as Kimmeridgian (Saint-Seine 1955, Saint -Seine and Casier 1962). More recently, however, the Stanleyville Beds were dated as Aalenian-Bathonian on the bases of their palynoflora and ostracod fauna (Colin 1994). With the exception of the teleosts *Paraclupavus* (Fig. 9B) from the Songa limestones, which was recently revised by Taverne (2001), the two faunas are urgently in need of revision.

Quebrada del Profeta [Fig. 14(4)]: Several Jurassic localities in northern Chile have yielded fish remains (Arratia and Schultze 1999a). Among them, the Oxfordian Quebrada del Profeta in the Cordillera de Domeyco certainly produced the most diverse and best known Late Jurassic fish fauna of Gondwana. So far, semionotiforms (at least one taxon), pycnodontiforms (at least one taxon), pachycormiforms (at least one taxon), one halecostome of uncertain relationships, and several basal teleosts (at least nine taxa) have been reported. The presence of *Gyrodus* in the Oxfordian of Chile and the Caribbean part of the Tethys (Jagua Formation, Cuba) indicate that *Gyrodus* was the first pycnodont to spread into the developing Hispanic Corridor connecting the eastern Pacific and western Tethyan oceans (Kriwet and Schmitz 2005). The distribution of pycnodontiforms in general has recently been directly linked to the tectonic events associated with the breakage of Pangea (Kriwet and Schmitz 2005). The phylogenetic relationships of some of the teleosts from the Quebrada del Profeta further support faunal dispersal through the Hispanic Corridor (Arratia 1996). Three of the teleost genera described from the Quebrada del Profeta, together with *Luisichthys* from the Tithonian of Pinar del Río in Cuba, are recognized to form a monophyletic group, the family Varasichthyidae. The Varasichthyidae together with the European *Ascalabos* from the Solnhofen Limestone constitute one of only three monophyletic lineages that have been recognized among Late Jurassic teleosts. The other lineages are the *Siemensichthys*-Group (Arratia 2000), which is so far only known from the

Kimmeridgian-Tithonian of Europe (Solnhofen and Cerin), and the Ichthyodectiformes (Patterson and Rosen 1977), known from Middle Jurassic to Late Cretaceous localities worldwide.

Vaca Muerta Formation [Fig. 14(5)]: The Tithonian Vaca Muerta Formation of Argentina certainly includes one of the more diverse Jurassic fish faunas of Gondwana. Unfortunately, these fishes are still very poorly understood and even their alpha taxonomy needs to be revised. According to Cione (Cione *et al.* 1987, Cione and Pereira 1990, Cione 1999) this marine fauna includes neoselachians (one indeterminate batoid), semionotids, caturid-like halecomorphs, pachycormids, aspidorhynchiforms, and teleosts. Such an association is typical for the Late Jurassic marine faunas of Europe. Nevertheless, sharks, chimaeroids, coelacanths, pycnodontiforms, and macrosemiids, which are well represented in the European Kimmeridgian-Tithonian lithographic limestones, have not been recorded so far in the Vaca Muerta Formation. Cione *et al.* (1987) suggested different palaeoecological conditions as a possible explanation for the lack of those fish groups. The depositional environment of the main vertebrate localities in the Vaca Muerta Formation is interpreted as a shallow open sea about 100 km away from the nearest coast (Gasparini *et al.* 1995, Kietzmann and Palma 2007). Therefore, the palaeoecological conditions in the Vaca Muerta Formation were certainly different from those in the coastal lagoon environment of Cerin in France (Bernier *et al.* 1994), or the backreef archipelago represented in the Solnhofen limestones in Germany (Viohl 1996, 1998). However, when considering the absence of certain fossil groups in this formation, reasons such as biogeographic causes and insufficient sampling should not be excluded.

Tendaguru and Mugher Mudstone Formation [Fig. 14(6) and (7)]: The two main Late Jurassic coastal marine fish faunas of Africa are those from the Upper Saurian Bed (Tithonian) of the Tendaguru beds in Tanzania (Arratia *et al.* 2002), and the Mugher Mudstone Formation (Tithonian) of Ethiopia (Goodwin *et al.* 1999). The two faunas are characterized by the dominance of hybodont sharks (Table 3), the low representation of neoselachian sharks (Table 4). The site Dwa 5a of the Upper Saurian Bed of the Tendaguru beds, has yielded a very peculiar endemic hybodont-batoid selachian association, which might be related with a shallow coastal environment (Arratia *et al.* 2002). The faunas also include osteichthyan remains. Semionotids are represented by isolated teeth and the fragment of a dentary with teeth referred to *Lepidotes* in the Mugher Mudstone Formation, and *Lepidotes tendagurensis* in the Upper Saurian bed of Tendaguru. Pycnodontiforms and dipnoans are known from the Mugher Mudstone Formation only, being represented by vomerine dentition referred to *Pycnodus* and several tooth plates identified as *Asiatoceratodus tiguidensis.* Teleosts are unknown from the Mugher Mudstone Formation, but represented by indeterminate specimens in the Upper Saurian bed of Tendaguru. Generally, although all the identified species are endemic or only known from other localities in Africa or South America, the fishes from the Mugher Mudstone Formation and Tendaguru show affinities with European taxa (Goodwin *et al.* 1999, Arratia and Schultze 1999b, Arratia *et al.* 2002).

Figure 13: Palaeogeographic positions of Middle Jurassic fish localities mentioned in the text. 1, Wanakah Formation. 2, Oxford Clay. 3, Stanleyville Beds. 4, Kirkpatrick basalts. Map based on palaeogeographic maps by Ron Blakey (http://jan.ucc.nau.edu/~rcb7/RCB.html).

Almada Fauna [Fig. 14(8)]: The Middle to Late Jurassic continental sequences in central Chubut province, Argentina, previously collectively known as the Cañadón Asfalto Formation, have yielded a plethora of fossil vertebrates, which have largely contributed to our knowledge of vertebrate evolution in the Southern Hemisphere (Bonaparte 1979, 1986, Rich *et al.* 1999, Rauhut *et al.* 2001, 2002, 2005, Rauhut 2002, 2005, 2006a, b, Rougier *et al.* 2007a, b, Báez and Nicoli 2008). Two geological units are now recognized in this sequence, the Callovian Cañadón Asfalto and the (?)Tithonian Cañadón Calcáreo formations (Proserpio 1987, Rauhut 2006a, b). Although only a fragment of a large median fin of an indeterminate fish has been found so far in the Cañadón Asfalto Formation, the Cañadón Calcáreo Formation has yielded an important fresh-water fish fauna. The fishes come from the so-called "Estratos de Almada", which were defined on the western side of the Chubut river and the stratigraphic position of which has long been problematic. They have variously been regarded as Cretaceous (*e.g.* Volkheimer in Tasch and Volkheimer 1970), or included in the Cañadón Asfalto Formation (*e.g.* Turner 1983). However, the same beds are found on the other side of the Chubut river, in the Cañadón Santa Máxima and between this canyon and

Puesto Limonao, where they clearly form the basal layers of the Cañadón Calcáreo Formation (see Rauhut and López-Arbarello in press: fig. 5). Although several authors have dealt with the fishes in the Almada Fauna (Bordas 1943, Bocchino 1967, 1978, Cione and Pereira 1987), even their alpha taxonomy is still in need of revision and, thus, the fish fauna is very poorly understood. So far, one coccolepid and two monospecific genera of te-leosts have been recognized, but non-teleostean halecostomes might also be represented (ALA pers. obs.). These fresh water fishes closely resemble the fishes of the Talbragar Beds in Australia (see below).

Talbragar [Fig. 14(9)]: The Talbragar Beds in New South Wales, Australia, have yielded a second, very interesting, though also still not completely understood freshwater fish fauna. The age of the Talbragar Beds has been controversial, being referred to either as Middle or Late Jurassic, but, more recently, Bean (2006) reported a Late Jurassic age based on SHRIMP (Sensitive high mass Resolution Ion Micro Probe) dates on the zircons in the sediments immediately below the richest fish layer, which give the fish-bearing sediments a maximum age of 151.55 ± 4.25 Ma. The Talbragar Fauna includes a coccolepid, four monspecific genera of halecostomes of uncertain relationships that have been grouped in their own family Archaeomaenidae, and a basal teleost (Woodward 1895).

Besides these main fish faunas briefly described above, several independently recorded Jurassic taxa from Gondwana are noteworthy. So far, the only fish known from the Sinemurian-Pliensbachian Clarens Formation of South Africa [Fig. 12(5)], *Semionotus capensis*, is certainly the best-represented semionotiform from the Jurassic of Gondwana. Several articulated specimens of this species are known, and the fish shows close affinities with the Early Jurassic species of *Semionotus* from North America (ALA unpublished data). *Oreochima ellioti* from sedimentary intercalations in the Middle Jurassic Kirkpatric basalts (Aalenian, K-Ar about 179 Ma, Kyle *et al.* 1981) of the Transantarctic Mountains in Antarctica [Fig. 13(4)] is a very interesting, though poorly understood fish, which is probably related to the Late Jurassic Australian archaeomaenids of the Talbragar Beds (Schaeffer 1972, Grande and Eastman 1986). The fishes from the Late Jurassic of Longing Gap, Antarctica [Fig. 14(9)], are also very important finds. They include the southernmost record of the Aspidorhynchiformes during the Late Jurassic, and the oldest record of an ichthyodectiform in the Southern Hemisphere (Arratia *et al.* 2004). Another interesting unit of probable Late Jurassic age (see above) is the Pastos Bons Formation in Northeastern Brazil [Fig. 14(11)], which have yielded very interesting semionotiforms and basal teleosts.

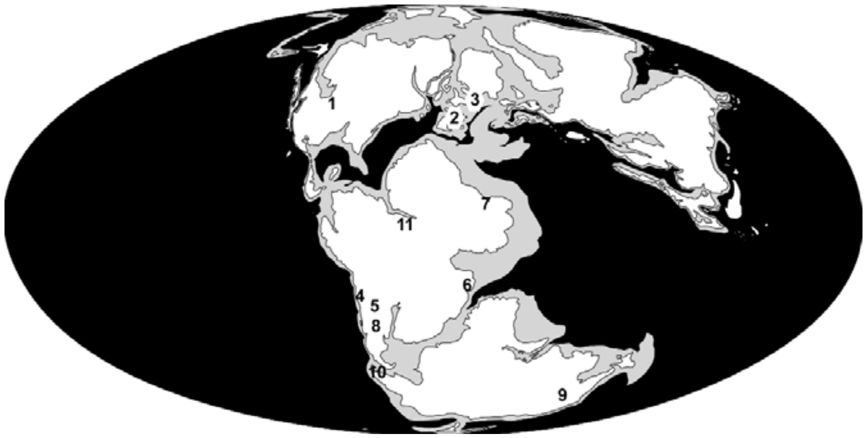

Figure 14: Palaeogeographic positions of Late Jurassic fish localities mentioned in the text. 1, Sundance Formation. 2, lithographic limestones of Cerin. 3, lithographic limestones of Solnhofen. 4, Quebrada la Profeta. 5, Vaca Muerta Formation. 6, Tendaguru Beds. 7, Mugher Mudstone Formation. 8, Cañadón Calcáreo Formation (Almada fauna). 9, Talbragar Beds. 10, Longing Gap. 11, Pastos Bons Formation. Map based on palaeogeographic maps by Ron Blakey (http://jan.ucc.nau.edu/~rcb7/RCB.html).

FISH EVOLUTION DURING THE JURASSIC

Two major radiations of fishes have been proposed to have occurred during Jurassic times: the first radiation of the Neoselachii (Maisey *et al.* 2004, Underwood 2006) and the first radiation of the Teleostei (Arratia 1996, 2004). Simultaneously, holocephalian and hybodontiform chondrichthyans on the one side, and non-neopterygian actinopterygians on the other side, gradually decreased in diversity during the Jurassic. Neopterygians are already one of the main components of the actinopterygian faunas in the Triassic, but are mostly represented by non-halecostomes neopterygians such as the perleidiforms. Halecostomes are also already present and well represented in the Triassic, mainly by the semionotiforms in Europe (López-Arbarello 2008) and the parasemionotiforms in Madagascar, South China, East Greenland, and Canada (Grande and Bemis 1998). However, most main lineages of the halecostomes first appeared and diversified during the Jurassic. Indeed, several halecostome groups are only represented in the Mesozoic: Semionotiformes (Early Triassic-Early Cretaceous), Ionoscopiformes (Middle Triassic to Early Cretaceous), Pachycormiformes (Early Jurassic to Late Cretaceous), Aspidorhynchiformes (Late Jurassic to Late Cretaceous). Pycnodontiforms are known from the Late Triassic to the Eocene. Besides these Mesozoic halecostomes, the Jurassic saw the appearance (amiiforms) and diversification (amiiforms and teleosts) of the modern halecostome lineages.

Sarcopterygian fishes are mainly Palaeozoic groups, being comparatively poorly represented by the actinistians and dipnoans during the Mesozoic and Cenozoic. Both groups are much better represented in the Triassic than later in the Mesozoic (Schultze 2004). Also, they are worldwide distributed in the Triassic, but gradually become restricted to their current distribution in the Southern Hemisphere during the Jurassic and Cretaceous (Schultze 2004). During the Jurassic, the fossil record of actinistians and dipnoans is especially poor. However, this might be due to biases in the fossil record, given that several ghost lineages and Lazarus taxa range through the Jurassic (Forey 1998, Schultze 2004).

From the information included in the previous sections, it is evident that the evolutionary patterns described above are almost exclusively based on the fossil record of the Northern Hemisphere. The patchy record, and the poor state of knowledge of most of the fish faunas, make it very difficult to derive hypotheses concerning the evolution of the Jurassic fish faunas of Gondwana, or, as it where, Pangea as a whole.

The Triassic fish record in Gondwana reflects the diversification of the non-halecostome neopterygians (Lehman 1952, Hutchinson 1973, Murray 2000, López-Arbarello 2004, López-Arbarello and Zavattieri 2008). During the Jurassic, however, the history of the Gondwanan actinopterygians is very poorly understood, with the exception of the marine teleosts from the Oxfordian of Chile. Several taxa have been named (Table 6), but their phylogenetic relationships are unknown and, thus, almost nothing can be said about the evolutionary and biogeographical history of the groups that they represent.

The Triassic record of semionotiforms in Gondwana is highly questionable. "*Semionotus*" *australis* and "*Semionotus*" *tenuis* from the Triassic of Gosford, Australia, have been synonymysed and removed from Semionotiformes into a new perleidiform genus, as *Zeuchthiscus australis* (Wade 1940). Similarly, "*Semionotus*" *vallejensis* and several isolated scales identified as *Semionotus* from the Triassic Cuyo Basin in western Argentina also probably represent more primitive actinopterygians than the Semionotiformes (ALA pers. obs.). Other semionotiform remains previously mentioned for supposedly Triassic sediments in Africa are now known to be of Jurassic age (*e.g. Semionotus capensis* from the Clarens Formation of South Africa, Woodward 1888). Therefore, there is no certain record of a semionotiform in the Triassic of Gondwana. The first Gondwanan records of the group are in the Early Jurassic and are limited to Africa and India. The group is unknown in Antarctica, and its Jurassic record in South America, Madagascar, and Australia is very poorly understood. Except for *Uarbrichthys lauts* from the Late Jurassic of Talbragar in Australia, South American, Madagassy and Australian semionotiforms are mainly represented by fragmentary and/or unstudied material (Arratia and Cione 1996, Arratia and Schultze 1999a, Thies and Turner 2002, Flynn *et al.* 2006). Other Jurassic records of South American semionotiforms are still uncertain, because the bearing sediments might be Early Cretaceous in Age (*i.e.* the Pastos Bons Formation in Brazil and the Tacuarembó Formation in Uruguay). Therefore, although the semionotiforms have a geographically broad Jurassic record in Gondwana and the group is furthermore very well represented in the Cretaceous of Africa and South America (Gallo and Brito 2004, Brito 2006, López-Arbarello and Codorniú 2007), most of these Jurassic records provide very limited information, apart from that the group is represented. Also, although the Early Jurassic *Semionotus capensis*, from the Clarens Formation of South Africa, and *Lepidotes deccanensis*, from the Kota Formation of India, are well represented by numerous, rather complete and articulated specimens, the phylogenetic and biogeographic relationships of these and other Gondwanan semionotiforms are still uncertain (with the exception of the lepisosteids, Brito 2006). Consequently the question arises, whether the Jurassic distribution of Gondwanan semionotiforms is a relict of an earlier Pangeaic distribution, or may it be the result of one or more dispersal events? As mentioned above, the group has not yet been confidently reported from the Triassic of Gondwana. In the Late Triassic and Early Jurassic, semionotiforms are especially well represented in marine environments in the western Tethys, which is probably related with the record of semionotids in the Early Jurassic Kota Formation in India and the semionotid scales reported from the Late Triassic-Early Jurassic Adigrat Sandstones and the Late Jurassic Mugher Mudstone in Ethiopia (Goodwin *et al.* 1999). On the other hand, the Early Jurassic *Semionotus capensis* from the continental Clarens Formation in South Africa is probably closely related to the also continental Early Jurassic semionotids from the Newark Supergroup in North America, suggesting a very different historical biogeography for the fresh water semionotids. Finding such apparently closely related continental fishes in such geographically disperse areas indicates a significant dispersal potential for these freshwater fishes, but whether this dispersal took place via interconnected freshwater systems in the supercontinent of Pangea, or if these fishes might have been able to tolerate some degree of salinity and thus spread through coastal waters cannot be answered at this time.

The marine actinopterygian fish faunas from the Jurassic of Gondwana generally agree in their composition with the equivalent faunas in the Northern Hemisphere. The Jurassic marine fish faunas of northern and eastern Africa show a Thethyan provincialism. In western Gondwana, although the teleosts of the Oxfordian of northern Chile have been shown to be endemic, they are closely related with the Late Jurassic teleosts of central Europe, indicating dispersal through the Hispanic Corridor (Arratia

1996). Such a faunal exchange is also supported by the presence of the pycnodontiform *Gyrodus* in the Oxfordian of Chile, the presence of pachycormiforms in the Late Jurassic of northern Chile and Patagonia (Martill *et al.* 1999, Kriwet 2000), and shared taxa of marine reptiles between the western Tethys and western Gondwana (Gasparini 1985, 1992, Gasparini *et al.* 2000).

On the other hand, at least three rich fresh water fish faunas are known from the Jurassic of Gondwana: the Talbragar fauna in eastern Gondwana, the Stanleyville fresh water fauna in central Gondwana, and the Almada Fauna in western Gondwana. The similarities between the probably Tithonian faunas of Almada and Talbragar do not only refer to the taxonomic composition of the faunas, but also to their possible mode of preservation: in both localities, fishes are found in mass-mortality layers that might be correlated with volcanic ashes (Bean 2006, ALA & OR, pers. obs.). However, both faunas are in need of revision and the taxa found should be studied in a phylogenetic framework. The same is true for the Middle Jurassic fauna of Stanleyville, which, in contrast, has been related to the Late Jurassic faunas of the western Thethys (Saint-Seine 1955).

Although the first radiation of teleosts took place during the Jurassic (Arratia 1996, 2004), the major radiation of the group only occurred in the Cretaceous, after the appearance of the modern lineages in the Late Jurassic (Elopomorpha, Ostariophysi, and Euteleostei) and Early Cretaceous (Osteoglossomorpha and Clupeomorpha). Among the earliest occurrences of modern teleosts are the oldest pachyrhizodontoids in the Tithonian of Chile (Arratia and Schultze 1999a), and one of the oldest ichthyodectiforms, *Antarctithrissops*, in the Late Jurassic of Antarctica (Arratia *et al.* 2004), indicating that early teleosts already had a wide distribution and that the center of origin of modern groups might not be the same for all groups.

Although the Jurassic record of chondrichthyans in Gondwana is relatively poor, a few interesting conclusions can be drawn. The most remarkable feature of the known selachian faunas of Gondwana is the dominance of hybodonts and the poor representation of neoselachian sharks in the Late Jurassic of the Mugher Mudstone Formation in Ethiopia and the Upper Saurian bed of Tendaguru (Goodwin *et al.* 1999, Arratia *et al.* 2002). According to their known Late Jurassic record, batoids apparently migrated southwards from their centre of origin in the Northern Hemisphere, probably in Europe (Arratia *et al.* 2002), probably during the latest Triassic or earliest Jurassic (Underwood 2006).

CONCLUSIONS

Our current knowledge of fish evolution during the Jurassic is almost exclusively based in the fossil record of the Northern Hemisphere. Among the Jurassic Gondwanan fishes, only the teleosts of the Oxfordian of Quebrada del Profeta in northern Chile and the teleost *Paraclupavus* from the Songa limestones in the DRC (Fig. 9B) have been incorporated in phylogenetic and biogeographical analyses. Otherwise, most Gondwanan Jurassic fishes are in need of revision. Although some of these taxa have been rather completely described, as is the case for the fishes of the Stanleyville Group (Saint-Seine 1955, Saint-Seine and Casier 1962), their systematic position needs to be reevaluated in the light of our current knowledge of fish systematics and phylogeny.

Despite of these problems, the importance of the Jurassic fish faunas of Gondwana can already be glimpsed at in many ways. Including approximately 26.840 living species (about 96 % of the Recent fishes), which are classified in 4.278 genera, 448 families y 40 orders (Nelson 2006), the teleosts constitute the most numerous and diverse group of Recent vertebrates. With their first records at the end of the Triassic, the group is already well established in the Late Jurassic and Early Cretaceous, with all major groups of Recent teleosts already almost worldwide represented. The Gondwanan Jurassic teleosts have been shown to play a very important role for our understanding of the early radiation of this group and are, thus, not only important to the knowledge of the history of fishes in this supercontinent, but also to the study of generalities of evolution and its processes, because the teleosts represent a model of rapid and successful evolution in an environment that was subjected to drastic climatic and environmental changes mostly due to the tectonic events related to the breakage of Pangea during the Jurassic and Cretaceous.

Moreover, Mesozoic freshwater fishes have been shown to reflect possible palaeogeographic relationships between ancient landmasses and they can be used for the reconstruction of possible former drainage systems (Patterson 1975). However, continental Jurassic sediments are rare when compared with contemporary sediments of marine origin and, accordingly, the record of Jurassic freshwater ichthyofaunas is very poor (Chang and Miao 2004, López-Arbarello 2004, Prasad *et al.* 2004, Wilson and Bruner 2004). Therefore, the several Jurassic freshwater fish taxa of Gondwana offer exceptional opportunities to explore palaeobiogeographic relationships, which might imply the existence of palaeohydrographical connections.

Apart from the work on the fish faunas themselves, more detailed studies on the geological and stratigraphical setting of many localities are also needed. Knowledge of the exact age of the fish faunas is essential for our understanding of the timing of major events in Gondwanan fish evolution.

And, last, but not least, it is of uttermost importance to collect more material from the known localities and, of course, to discover and explore new localities!

ACKNOWLEDGMENTS

We thank Ana María Zavattieri, Laura Giambiagi and Victor Ramos for the invitation to participate in the Jurassic Symposium in Mendoza and to contribute to this special volume. Many colleagues have contributed to this work, with access to specimens, discussions, and critical comments to ideas expressed in meetings or personal discussions over the years. It is not possible to mention all of them, but we are thankful to each and every one of them for this input. Special thanks are due to Gloria Arratia and Paulo Brito for fruitful discussions about the evolutionary history of South American fishes, to Louis Taverne and Matías Soto, who generously shared information on several South American and African faunas, and to Wolf Volkheimer for many insights into the Jurassic history of South America. Louis Taverne and Paulo Brito further contributed with very helpful reviews of the manuscript. We are very thankful to Zerina Johanson (NHM), Phil Hurst (NHM, Photography Unit), Louis Taverne, Daniel Baudet (RMAC), and M. Stéphane Hanot (RMCA) for rapidly providing the photographs included in the figures 6, 8, and 9. Parts of the research that led to this review paper were financially supported by fellowships from the CONICET (Argentina) and DAAD (Germany), and German Research Foundation (DFG) grants LO 1401/1-1 and 2-1 to ALA, and DFG grant RA 1012/ 9-1 to OR.

WORKS CITED IN THE TEXT

Arratia, G. 1996. The Jurassic and the early history of teleosts. In Arratia, G. and Viohl, G. (eds.) Mesozoic Fishes - Systematics and Paleoecology, Verlag Dr. Friedrich Pfeil, 243-259, München.

Arratia, G. 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements. In Arratia, G. and Schultze, H.-P. (eds.) Mesozoic Fishes 2 - Systematics and Fossil Record, Verlag Dr. Friedrich Pfeil, 265-334, München.

Arratia, G. 2000. New teleostean fishes from the Jurassic of southern Germany and the systematic problems concerning the 'pholidophoriforms'. Paläontologische Zeitschrift 74(1/2): 113-143.

Arratia, G. 2001. The sister-group of Teleostei: consensus and disagreements. Journal of Vertebrate Paleontology 21(4): 767-773.

Arratia, G. 2004. Mesozoic halecostomes and the early radiation of teleosts. In: Arratia, G. and Tintori, A. (eds.), Mesozoic Fishes 3 - Systematics, Paleoenvironments and Biodiversity, Verlag Dr. Friedrich Pfeil, 279-315, München.

Arratia, G. and Cione, A.L. 1996. The record of fossil fishes of southern South America. Münchener Geowissenschaftliche Abhandlungen 30(A): 9-72.

Arratia, G. and Schultze, H.-P. 1987. A new halecostome fish (Actinopterygii, Osteichthyes) from the Late Jurassic of Chile and its relationships. Dakoterra 3: 1-13.

Arratia, G. and Schultze, H.-P. 1999a. Mesozoic fishes from Chile. In Arratia, G. and Schultze, H.-P. (eds.) Mesozoic Fishes 2 - Systematics and Fossil Record, Verlag Dr. Friedrich Pfeil, 565-593, München.

Arratia, G. and Schultze, H.-P. 1999b. Semionotiform fish from the Upper Jurassic of Tendaguru (Tanzania). Mitteilungen aus dem Museum für Naturkunde zu Berlin, Geowissenschaftliche Reihe 2: 135-153.

Arratia, G. and Thies, D. 2001. A new teleost (Osteichthyes, Actinopterygii) from the Early Jurassic *Posidonia* shale of Northern Germany. Mitteilungen aus dem Museum für Naturkunde zu Berlin, Geowissenschaftliche Reihe 4: 167-187.

Arratia, G., Kriwet, J. and Heinrich, W.-D. 2002. Selachians and actinopterygians from the Upper Jurassic of Tendaguru, Tanzania. Mitteilungen aus dem Museum für Naturkunde zu Berlin, Geowissenschaftliche Reihe 5: 207-230.

Arratia, G., Scasso, R. and Kiessling, W. 2004. Late Jurassic fishes from Longing Gap, Antarctic Peninsula. Journal of Vertebrate Paleontology 24(1): 41-55.

Báez, A.M. and Nicoli, L. 2008. A new species of *Notobatrachus* (Amphibia, Salienta) from the Middle Jurassic of northwestern Patagonia. Journal of Paleontology 82(2): 372-376.

Bandyopadhyay, S. and Sengupta, D.P. 2006. Vertebrate faunal turnover during the Triassic-Jurassic transition: an Indian scenario. In Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C. and Kirkland, J.I. (eds.) The Triassic-Jurassic Terrestrial Transition. New Mexico Museum of Natural History and Science Bulletin 37: 77-85.

Bartholomai, A. 2004. The large aspidorhynchid fish, *Richmondichthys sweeti* (Etheridge Jnr and Smith Woodward, 1891) from Albian marine deposits of Queensland, Australia. Memoirs of the Queensland Museum 49(2): 521-536.

Bartram, A.W.H. 1977. The Macrosemiidae, a Mesozoic family of holostean fishes. Bulletin of the British Museum (Natural History), Geology 29(2): 137-234.

Bean, L.B. 2006. The leptolepid fish *Cavenderichthys talbragarensis* (Woodward, 1895) from the Talbragar Fish Bed (Late Jurassic) near Gulgong, New South Wales. Records of he Western Australian Museum 23: 43-76.

Bellwood, D.R. 1996. The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. Coral Reefs 15: 11-19.

Beltan, L. 1996. Overview of systematics, paleobiology, and paleoecology of Triassic fishes of northwestern Madagascar. In Arratia, G. and Viohl, G. (eds.) Mesozoic Fishes - Systematics and Paleoecology, Verlag Dr. Friedrich Pfeil, 479-500, München.

Benno, B., Verheij, E., Stapley, J., Rumisha, C., Ngatunga, B., Abdallah, A. and Kalombo, H. 2006. Coelacanth (*Latimeria chalumnae* Smith, 1939) discoveries and conservation in Tanzania. South African Journal of Science 102: 486-490.

Benton, M.J. 2005. Vertebrate Palaeontology. Third edition. Blackwell Publishing Ltd., 472 p., Oxford.

Bernier, P., Gaillard, C., Barale, G., Bourseau, J.-P., Buffetaut, E., Gall, J.-C. and Wenz, S. 1994: The underlying substrate of the Cerin lithographic limestone. Geobios, Mémoire Special 16: 13-24.

Bhattacharya, N. 1980. Depositional patterns in limestones of the Kota Formation (Upper Gondwana), Andhra Pradesh. In Cresswell, M.M. and Vella, P. (eds.) 5th Gondwana Symposium, A.A. Balkema Publishers, Proceedings: 135-139, Rotterdam.

Bocchino, A. 1967. *Luisiella inexcutata* gen. et sp. nov. (Pisces, Clupeiformes, Dussumieriidae) del Jurásico superior de la provincia de Chubut, Argentina. Ameghiniana 4(2): 91-100.

Bocchino, A. 1978. Revisión de los Osteichthyes fósiles de la República Argentina. I. Identidad de *Tharrias feruglioi* Bordas 1943 y *Oligopleurus groeberi* Bordas 1943. Ameghiniana 15(3-4): 301-320.

Bonaparte, J.F. 1979. Dinosaurs: a Jurassic assemblage from Patagonia. Science 205: 1377-1379.

Bonaparte, J.F. 1986. Les Dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique moyen de Cerro Cóndor (Chubut, Argentine). Annales de Paléontologie 72: 247-289, 325-386.

Bordas, A.F. 1943. Peces del Cretáceo del Río Chubut (Patagonia). Physis 19 (53): 313-318.

Brito, P.M. 1997. Révision des Aspidorhynchidae (Pisces, Actinopterygii) du Mésozoïque: ostéologie, relations phylogénétiques, données environnmentales et biogéographiques. Geodiversitas 19(4): 681-772.

Brito, P.M. 1999. The caudal skeleton of aspidorhynchids (Actinopterygii, Halecostomi): phylogenetic implications. In Arratia, G. and Schultze, H.-P. (eds.) Mesozoic Fishes 2 - Systematics and Fossil Record, Verlag Dr. Friedrich Pfeil, 249-264, München.

Brito, P.M. 2006. Considerações sobre os halecomorfos e os lepisosteídeos (Actinopterygii: Neopterygii) no Cretáceo da parte ocidental do continente Gondwana. In Gallo, V., Brito, P.M., Silva, H.M.A. and Figueiredo, F.J.d. (eds.) Paleontologia de Vertebrados, Interciência, Grandes Temas e Contribuições Científicas 53-70, Rio de Janeiro.

Brito, P.M. and Gallo, V. 2002. A new pleuroph([illegible])lid, *Gondwanapleuropholis longimaxillaris* n. g., n. sp. (Actinopterygii: Teleostei) from the Jurassic of north east Brazil. Comptes Rendus Palevol 1 (2002): 697-703.

Brito, P.M. and Suárez, M.E. 2003. Late Cretaceous *Belonostomus* (Pisces, Actinopterygii, Aspidorhynchidae) from Algarrobo, Chile, with comments on aspidorhynchid paleodistribution in South America. Revista Geológica de Chile 30(1): 117-127.

Cappetta, H. 1987. Mesozoic and Cenozoic Elasmobranchi. Handbook of Paleoichthyology 3B, G. Fischer Verlag, 193 p., Stuttgart.

Casamiquela, R. 1984. Los vertebrados mesozoicos. En Ramos, V.A. (ed.) 9° Congreso Geológico Argentino, Relatorio: 527-533.

Cavin, L. 2001. Osteology and phylogenetic relationships of the teleost *Goulmimichthys arambourgi* Cavin, 1995, rom the Upper Cretaceous of Goulmima, Morocco. Eclogae Geologicae Helvetiae 94: 509-535.

Cavin, L. and Suteethorn, V. 2006. A new semionotiform (Actinopterygii, Neopterygii) from Upper Jurassic - Lower Cretaceous deposits of North-East Thailand, with comments on the relationships of semionotiforms. Palaeontology 49(2): 339-353.

Cavin, L., Suteethorn, V., Buffetaut, E. and Tong, H. 2007. A new Thai Mesozoic lungfish (Sarcopterygii, Dipnoi) with an insight into post-Palaeozoic dipnoan evolution. Zoological Journal of the Linnean Society 149: 141-177.

Cerdeño, E. 2005. La colección de Paleontoloía del Museo de Ciencias Naturales y Antropológicas "J. C. Moyano" (Mendoza) y sus ejemplares tipo. Contribuciones del MACN 2: 1-61.

Chang, M.-M. and Miao, D. 2004. An overview of Mesozoic Fishes in Asia. In Arratia, G. and Tintori, A. (eds.) Mesozoic Fishes 3 - Systematics, Paleoenvironment and Biodiversity, Verlag Dr. Friedrich Pfeil, 535-563, München.

Chiappe, L., Rivariola, D., Cione, A., Fregenal-Martínez, M., Sozzi, H., Buatois, L., Gallego, O., Laza, J., Romero, E., López-Arbarello, A., Buscalioni, A., Marsicano, C., Adamonis, S., Ortega, F., McGehee, S. and Di Iorio, O. 1998. Biotic association and paleoenvironmental reconstruction of the "Loma del *Pterodaustro*" fossil site (Early Cretaceous, Argentina). Geobios 31(3): 349-369.

Chorn, J. and Whetstone, K.N. 1978. On the use of the term *nomen vanum* in taxonomy. Journal of Paleontology 52(2): 494.

Cione, A.L. 1999. First report of a Jurassic ray outside of Europe. In Arratia, G. and Schultze, H.-P. (eds.) Mesozoic Fishes 2 - Systematics and Fossil Record, Verlag Dr. Friedrich Pfeil, 21-28, München.

Cione, A.L. and Pereira, S.M. 1987. Los peces del Jurásico de Argentina. El Jurásico anterior a los movimientos intermálmicos. In Volkheimer, W. (ed.) Bioestratigrafia de los sistemas regionales del Jurásico y Cretácico de América del Sur, Editorial Inca, 1: 287-298, Mendoza.

Cione, A.L. and Pereira, S.M. 1990. Los peces del Jurásico posterior a los movimientos intermálmicos y del Cretácico inferior de Argentina. In Volkheimer, W. (ed.) Bioestratigrafía de los sistemas regionales del Jurásico y Cretácico de América del Sur, Editorial Inca, 2: 385-402, Mendoza.

Cione, A.L., Gasparini, Z., Leanza, H. and Zeiss, A. 1987. Marine oberjurassische Plattenkalke in Argentinien (Ein erster Forschungsbericht). Archaeopteryx 5: 13-22.

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

Cloutier, R. and Arratia, G. 2004. Early diversification of actinopterygians. In Arratia, G., Wilson, M.V.H. and Cloutier, R. (eds.) Recent advances in the origin and early radiation of vertebrates, Verlag Dr. Friedrich Pfeil, 217-270, Müchen.

Colin, J.-P. 1994. Mesozoic-Cenozoic lacustrine sediments in Zaire interior Basin. In Gierlowski-Kordeschand, E. and Keltz, K. (eds.) Global geological record of lake basins, I.G.C.P. Project 324, Cambridge University Press, 31-36, Cambridge.

Cope, J.C.W. 2008. Drawing the line: the history of the Jurassic-Cretaceous boundary. Proceedings of the Geologists' Association 119: 105-117.

Cuny, G. 1998. Primitive neoselachian sharks: a survey. Oryctos 1: 3-21.

Delsate, D., Duffin, C.J. and Weis, R. 2002. A new microvertebrate fauna from the Middle Hettangian (Early Jurassic) of Fontenoille (Province of Luxembourg, south Belgium). Memoirs of the geological Survey of Belgium 48: 1-83.

de Pinna, M.C.C. 1996. Teleostean monophyly. In: Stiassny, M.L.J., Parenti, L.R. and Johnson, G.D. (eds.): Interrelationships of Fishes 147-162. Academic Press, London.

Didier, D.A. 2002. Chimaeras. In Carpenter, K.E. (ed.) The living marine resources of the Western Central Atlantic. Volume 1: Introduction, mollusks, crustaceans, hagfishes, sharks, batoid fishes, and chimaeras. FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication 5: 592-599. FAO, Rome.

Dineley, D. and Metcalf, S.J. 1999. Fossil fishes of Great Britain. Joint Nature Conservation Committee, Review Series 16, 675 p., Peterborough.

Dolgopol de Sáez, M. 1940. Noticias sobre peces fósiles argentinos. Celacántidos titonienses de Plaza Huincul. Notas del Museo de La Plata, Paleontología 5(25): 295-298.

Dolgopol de Sáez, M. 1949. Noticias sobre peces fósiles argentinos. Revista del Museo de La Plata, Paleontología 14(96): 443-461.

Ensome, P.C. 2002. The Purbeck Limestone Group of Dorset, southern England: a guide to lithostratigraphic terms. Special Papers in Palaeontology 68: 7-11.

Flynn, J.J., Fox, S.R., Parrish, J.M., Ranivoharimanana, L. and Wyss, A.R. 2006. Assessing diversity and paleoecology of a Middle Jurassic microvertebrate assemblage from Madagascar. New Mexico Museum of Natural History and Science Bulletin 37: 476-489.

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

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

Friedman, M. and Blom, H. 2006. A new actinopterygian from the Famennian of East Greenland and the interrelationships of Devonian ray-finned fishes. Journal of Paleontology 80(6): 1186-1204.

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

Gallo, V. 2005. Redescription of *Lepidotes piauhyensis* Roxo and Löfgren, 1936 (Neopterygii, Semionotiformes, Semionotidae) from the ?Late Jurassic-Early Cretaceous of Brazil. Journal of Vertebrate Paleontology 25(4): 757-769.

Gallo, V. and Brito, P.M. 2004. An overview of Brazilian semionotids. In Arratia, G. and Tintori, A. (eds.) Mesozoic Fishes 3 - Systematics, Paleoenvironments and Biodiversity, Verlag Dr. Friedrich Pfeil, 253-264, München.

Gardiner, B.G. 1960. A revision of certain actinopterygians and coelacanth fishes. chiefly from the Lower Lias. Bulletin of the British Museum (Natural History), Geology 4: 239-384.

Gardiner, B.G. and Schaeffer, B. 1989. Interrelationships of lower actinopterygian fishes. Zoological Journal of the Linnean Society 97: 135-187.

Gardiner, B., Schaeffer, B. and Masserie, J.A. 2005. A review of the lower actinopterygian phylogeny. Zoological Journal of the Linnean Society 144: 511-525.

Gasparini, Z. 1985. Los reptiles marinos Jurásicos de America del Sur. Ameghiniana 22(1-2): 23-34.

Gasparini, Z. 1992. Marine reptiles of the circum-Pacific region. In Westerman, G.E.G. (ed.) The Jurassic of the Circum-Pacific, Cambridge University Press, 361-365, Cambridge.

Gasparini, Z.B. d., De La Fuente, M.S. and Fernández, M.S. 1995. Sea reptiles from the lithographic limestones of the Neuquen Basin, Argentina. In 2° International Symposium on Lithographic Limestones (Lleida-Cunca), Universidad Autónoma de Madrid, Extended Abstracts: 81-84, Madrid.

Gasparini, Z., Vignaud, P. and Chong, G. 2000. The Jurassic Thalattosuchia (Crocodyliformes) of Chile: a paleobiogeographic approach. Bulletin de la Societé géologique de la France 171(6): 657-664.

Góes, A.M. and Feijó F.J. 1994. Bacia do Parnaíba. Boletim de Geociências Petrobrás 8: 57-67.

González-Rodríguez, K. and Reynoso, V.-H. 2004. A new *Notagogus* (Macrosemiidae, Halecostomi) species from the Albian Tlayúa Quarry, Central Mexico. In: Arratia, G. and Tintori, A. (eds.): Mesozoic Fishes 3 - Systematics, Paleoenvironments and Biodiversity, Verlag Dr. Friedrich Pfeil, 265-278, München.

Goodwin, M.B., Clemens, W.A., Hutchinson, J.H., Wood, C.B., Zavada, M.S., Kemp, A., Duffin, C.J. and Schaff, C.R. 1999. Mesozoic continental vertebrates with associated palynostratigraphic dates from the northwestern Ethiopian Plateau. Journal of Vertebrate Paleontology 19: 728-741.

Govindan, A. 1975. Jurassic freshwater ostracods from the Kota Limestone of India. Palaeontology 19(1): 207-216.

Grande, L. and Bemis, W.E. 1996. Interrelationships of Acipenseriformes, with comments on "Chondrostei". In Stiassny, M., Parenti, L. and Johnson, G.D. (eds.) Interrelationships of Fishes, Academic Press, 85-115, San Diego.

Grande, L and Bemis, W.E. 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Society of Vertebrate Paleontology Memoir 4: 1-690.

Grande, L. and Eastman, J.T. 1986. A review of Antarctic ichthyofaunas in the light of new fossil discoveries. Palaeontology 29(1): 113-137.

Hilton, E.J., Grande, L. and Bemis, W.E. 2004. Morphology of *Coccolepis bucklandi* Agassiz, 1843 (Actinopterygii) from the Solnhofen Lithographic Limestone Deposits (Late Jurassic, Germany). In Arratia, G. and Tintori, A. (eds.) Mesozoic Fishes 3 - Systematics, Paleoenvironments and Biodiversity, Verlag Dr. Friedrich Pfeil, 209-238, München.

Hurley, I.A., Lockridge Mueller, R., Dunn, K.A., Schmidt, E.J., Friedman, M., Ho, R. K., Prince, V.E., Yang, Z., Thomas, M.G. and Coates, M.I. 2007. A new time-scale for ray-finned fish evolution. Proceedings of the Royal Society B 274: 489-498.

Hussakof, L. 1917. Fossil fishes collected by the American Museum Congo Expedition. Bulletin of the American Museum of Natural History 37: 761-767.

Hutchinson, P. 1973. A revision of the Redfieldiform and Perleidiform fishes from the Triassic of Bekker's Kraal (South Africa) and Brookvale (New South Wales). Bulletin of the British Museum (Natural History), Geology 22: 235-354.

International Comission of Zoological Nomenclature (ICZN) 1985. International Code of Zoological Nomenclature. Third Edition, The International Trust for Zoological Nomenclature, 338 p., London.

International Comission of Zoological Nomenclature (ICZN) 1999. International Code of Zoological Nomenclature. Fourth Edition, The International Trust for Zoological Nomenclature, London, United Kingdom (http: //www.iczn.org).

Jain, S.L. 1973. New specimens of Lower Jurassic holostean fishes from India. Palaeontology 16(1): 149-177.

Jain, S.L. 1974. *Indocoelacanthus robustus* n. gen., n. sp. (Coelacanthidae, Lower Jurassic), the first fossil coelacanth from India. Journal of Paleontology 48: 49-62.

Jain, S.L. 1983. A review of the genus *Lepidotes* (Actinopterygii: Semionotiformes) with special reference to the species from Kota Formation (Lower Jurassic), India. Journal of the Palaeontological Society of India 28: 7-42.

Janensch, W. 1925. Fische aus dem Dysodil des Wealden vom Libanon. Zeitschrift der Deutschen Geologischen Gesellschaft, A. Abhandlungen 76(1-2): 54-59.

Kear, B.P. 2007. First record of a pachycormid fish (Actinopterygii: Pachycormiformes) from the Lower Cretaceous of Australia. Journal of Vertebrate Paleontology 27(4): 1033-1038.

Kemp, A. 1998. Skull structure in post-Paleozoic lungfish. Journal of Vertebrate Paleontology 18(1): 43-63.

Kietzmann, D.A. and Palma, R.M. 2007: Facies, microfacies y ambiente deposicional de la Formación Vaca Muerta (Tithoniano-Berriasiano) en la sección del arroyo Loncoche, Malargüe, provincia de Mendoza. Ameghiniana 44 (4, Suplemento): 58R-59R.

Kriwet, J. 2000. Revision of *Mesturus cordillera* Martill *et al.*, 1998 (Actinopterygii, Pycnodontiformes) from the Oxfordian (Upper Jurassic) of Northern Chile. Journal of Vertebrate Paleontology 20(3): 450-455.

Kriwet, J. and Benton, M.J. 2004. Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the Cretaceous-Tertiary boundary. Palaeogeography, Palaeoclimatology, Plaeoecology 214: 181-194.

Kriwet, J. and Schmitz, L. 2005. New insight into the distribution and palaeobiology of the *pycnodont fish Gyrodus*. Acta Palaeontologica Polonica 50 (1): 49-56.

Kyle, P.R., Elliot, D.H. and Sutter, J.F. 1981. Jurassic Ferrar Supergroup tholeiites from the Transantarctic Mountains, Antarctica, and their relationship to the initial fragmentation of Gondwana. In Greswell, M.M. and Vella, P. (eds.) Gondwana Five, A. A. Balkema, 283-287, Rotterdam.

Lambers, P.H. 1995. The monophyly of the Caturidae (Pisces, Actinopterygii) and the phylogeny of the Halecomorphi. Geobios, M.S. 19: 201-203.

Lehman, J.P. 1952. Etude complémentaire des poissons de l'Eotrias de Madagascar. Kungl. Svenska Vetenskapsakademiens Handlingar, Band 2 (6): 1-201.

Lima M.R. and Campos D. de A. 1980. Palinologia dos folhelhos da fazenda Muzinho, Floriano, Piauí. Boletim do Instituto deGeociências da Universidade de São Paulo 11: 149-154.

Liston, J. 2004. An overview of the pachycormiform *Leedsichthys*. In Arratia, G. and Tintori, A. (eds.) Mesozoic Fishes 3 - Systematics, Paaleoenvironments and Biodiversity, Verlag Dr. Friedrich Pfeil, 379-390, München.

Longbottom, A.E. 1984. New Tertiary pycnodonts from the Tilemsi valley, Republic of Mali. Bulletin of the British Museum (Natural History), Geology 38(1): 1-26.

López-Arbarello, A. 2004. The record of Mesozoic fishes from Gondwana (excluding India and Madagascar). In Arratia, G. and Tintori, A. (eds.) Mesozoic Fishes 3 - Systematics, Paleoenvironments and Biodiversity, Verlag Dr. Friedrich Pfeil, 597-624, München.

López-Arbarello, A. 2008. Revision of *Semionotus bergeri* Agassiz, 1833 (Upper Triassic, Germany), with comments on the taxonomic status of *Semionotus* (Actinopterygii, Semionotiformes). Paläontologische Zeitschrift 82(1): 40-54.

López-Arbarello, A., Arratia, G. and Codorniú, L. 2002. The coccolepids from South America and the early history of Chondrostei. Journal of Vertebrate Paleontology 22: 80A.

López-Arbarello, A. and Codorniú, L. 2007. Semionotids (Neopterygii, Semionotiformes) from the Lower Cretaceous Lagarcito Formation, San Luis Province, Argentina. Journal of Vertebrate Paleontology 27(4): 811-826.

López-Arbarello, A. and Rauhut, O.W.M. 2006. Ein bemerkenswertes Exemplar von *Ptycholepis bollensis* Agassiz in ventraler Ansicht. Freunde der Bayerischen Staatssammlung für Paläontologie und Historische Geologie e.V., Jahresbericht und Mitteilungen 34: 37-41.

López-Arbarello, A. and Zavattieri, A.M. 2008. Systematic revision of *Pseudobeaconia* Bor-das, 1944, and *Mendocinichthys* Withely, 1953 (Actinopterygii: 'Perleidiformes', Triassic, Argentina)". Palaeontology 51(5): 1025-1052.

López-Arbarello, A., Rogers, R. and Puerta, P. 2006. Freshwater actinopterygians of the Los Rastros Formation (Triassic), Bermejo Basin, Argentina. Fossil Record 9 (2): 238-258.

Lu, L., Li, D. and Yang, L. 2005. Notes on the discovery of Permian Acipenseriformes in China. Chinese Science Bulletin 50(12): 1279-1280.

Maisey, J.G., Naylor, G.J.P. and Ward, D.J. 2004. Mesozoic elasmobranchs, neoselachian phylogeny and the rise of modern elasmobranch diversity. In Arratia, G. and Tintori, A. (eds.) Mesozoic Fishes 3 - Systematics, Paleoenvironments and Biodiversity, Verlag Dr. Friederich Pfeil, 17-56, München.

Marshall, C.R. 1986. A list of fossil and extant dipnoans. Journal of Morphology, Supplement 1: 15-23.

Martill, D.M. and Hudson, J.D. 1994. Fossilien aus Ornatenton und Oxford Clay: Ein Bestimmungsatlas. Goldschneck-Verlag, 224 p., Weinstadt.

Martill, D.M., Chong, G.D. and Pardo, R. 1998. A new pycnodont (Pisces, Actinopterygii) from the Jurassic of Chile. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 1988: 485-493.

Martill, D.M., Frey, E., Caceras, R.P. and Chong-Diaz, G. 1999. The giant pachycormid *Leedsichthys* (Actinopterygii) in the Southern Hemisphere: further evidence for a Jurassic Atlanto-Pacific marine faunal province. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1999(4): 243-256.

Martin, M. 1984. Révision des Arganodontidés et des Néocératodontidés (Dipnoi, Ceratodontiformes) du Crétacé africain. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 169(2): 225-260.

Murray, A.M. 2000. The Palaeozoic, Mesozoic and Early Cenozoic fishes of Africa. Fish and Fisheries 1: 111-145.

Nelson, J.S. 2006. Fishes of the World. John Wiley & Sons, Inc., Hoboken, 601 p., New Jersey.

Nybelin, O. 1974. A revision of the leptolepid fishes. Acta Regiae Societatis Scientiarum et Litterarum Gothoburgensis, Zoologica 9: 1-202.

Olsen, P.E. and McCune, A.R. 1991. Morphology of the *Semionotus elegans* species group from the Early Jurassic part of the Newark Supergroup of eastern North America with comments on the Family Semionotidae (Neopterygii). Journal of Vertebrate Paleontology 11(3): 269-292.

Patterson, C. 1973. Interrelationships of holosteans. In: Greenwood, P. H., Miles, R. S. and Patterson, C. (eds.): Interrelationships of fishes: 233-305. Academic Press, London.

Patterson, C. 1975. The distribution of Mesozoic freshwater fishes. Mémoires du Muséum

National d'Histoire Naturelle 88: 156-173.

Patterson, C. and Rosen, D.E. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. Bulletin of the American Museum of Natural History 158(2): 81-172.

Perea, D. and Martínez, S. 2003. La Formación Tacuarembó, su fauna y su edad Jurásico Tardío-Cretácico Temprano. In Veroslavsky, G., Ubilla, M. and Martínez, S. (eds.) Cuencas Sedimentarias de Uruguay, Ediciones DIRAC, Facultad de Ciencias, Mesozoico 5: 101-113. Montevideo.

Perea, D., Ubilla, M., Rojas, A. and Goso, C. A. 2001. The newest Gondwanan occurrence of the hybodontid shark *Priohybodus*, and the Late Jurassic-Early Cretaceous age of the Tacuarembó Formation, Uruguay. Palaeontology 44(6): 1227-1235.

Popov, E.V. and Beznosov, P.A. 2006. Remains of chimaeroid fishes (Holocephali, Chimaeroidei) from the Upper Jurassic deposits of Komi Republic, Russia. In: Modern paleontology: classical and latest methods - 2006: 55-64. PIN RAS. P., Moscow [in Russian with English abstract].

Popov, E.V. and Shapovalov, K.M. 2007. New finds of chimaeroid fishes (Holocephali, Chimaeroidei) from the Jurassic of European Russia. In: Modern paleontology: classical and latest methods -2007: 25-44. PIN RAS. P., Moscow [in Russian with English abstract].

Prasad, G.V.R., Manhas, B.K. and Arratia, G. 2004. Elasmobranch and actinopterygian remains from the Jurassic and Cretaceous of India. In Arratia, G. and Tintori, A. (eds.) Mesozoic Fishes 3 - Systematics, Paleoenvironments and Biodiversity, Verlag Dr. Friedrich Pfeil, 625-638, München.

Proserpio, C.A. 1987. Descripción geológica de la Hoja 44 e, Valle General Racedo, Provincia del Chubut. Dirección Nacional de Minería y Geología, Boletín 201, 102 p., Buenos Aires.

Raiverman, V., Rao, M.R. and Pal, D. 1985. Stratigraphy and structure of the Pranhita-Godavari graben. Petrology of Asia Journal 8(11): 174-190.

Rauhut, O.W.M. 2002. Los dinosaurios de la Formación Cañadón Asfalto: diversidad, filogenía y biogeografía. Ameghiniana 39 (4, Suplemento): 15R-16R.

Rauhut, O.W.M. 2005. Osteology and relationships of a new theropod dinosaur from the Middle Jurassic of Patagonia. Palaeontology 48(1): 87-110.

Rauhut, O.W.M. 2006a. A brachiosaurid sauropod from the Late Jurassic Cañadón Calcàreo Formation of Chubut, Argentina. Fossil Record 9(2): 226-237.

Rauhut, O.W.M. 2006b. Dinosaurier aus dem oberen Jura Südamerikas. Freunde der Bayerischen Staatssammlung für Paläontologie und Historische Geologie e.V., Jahresbericht und Mitteilungen 34: 56-70.

Rauhut, O.W.M. and López-Arbarello, A. 2008. Archosaur evolution during the Jurassic: a southern perspective. Revista de la Asociación Geológica Argentina 63 (4): 559-587.

Rauhut, O.W.M., López-Arbarello, A., Puerta, P. and Martin, T. 2001. Jurassic vertebrates from Patagonia. Journal of Vertebrate Paleontology 21 (suppl. to 3): 91A.

Rauhut, O.W.M., Martin, T., Ortiz-Jaureguizar, E. and Puerta, P. 2002. A Jurassic mammal from South America. Nature 416: 165-168.

Rauhut, O.W.M., Remes, K., Fechner, R., Cladera, G. and Puerta, P. 2005. Discovery of a short-necked sauropod dinosaur from the Late Jurassic period of Patagonia. Nature 435: 670-672.

Rich, T.H., Vickers-Rich, P., Gimenez, O., Cúneo, R., Puerta, P. and Vacca, R. 1999. A new sauropod dinosaur from Chubut Province, Argentina. National Science Museum Monographs 15: 61-84.

Richter, M. and Thomson, M.R.A. 1989. First Aspidorhynchidae (Pisces: Teleostei) from Antarctica. Antarctic Science 1(1): 57- 64

Röhl, H.-J., Schmid-Röhl, A., Oschmann, W., Frimmel, A. and Schwark, L. 2001. The Posidonia Shale (Lower Toarcian) of SW-Germany: An oxygen depleted ecosystem controlled by sea level and palaeoclimate. Palaeogeology, Palaeoclimatology, Palaeoecology 165: 27-52.

Rossetti, D.F. and Truckenbrodt, W. 1999. Nomenclatura estratigráfica de depósitos cretáceos expostos na bacia de São Luís (MA). In 5° Simpósio sobre o Cretáceo do Brasil, Rio Claro, UNESP, Boletim: 485-490, Rio Claro.

Rougier, G.W., Garrido, A., Gaetano, L., Puerta, P., Corbitt, C. and Novacek, M.J. 2007. First Jurassic triconodont from South America. American Museum Novitates 3580: 1-20.

Rougier, G.W., Martinelli, A.G., Forasiepi, A.M. and Novacek, M.J. 2007. New Jurassic mammals from Patagonia, Argentina: a reappraisal of australosphenidan morphology and interrelationships. American Museum Novitates 3566: 1-54.

Rudra, D.K. and Maulik, P.K. 1987. Stromatolites from Jurassic freshwater limestones, India. Mesozoic Research 1(3): 135-146.

Saint-Seine, P. (de) 1950. Contribution à l'étude des vertébrés fossiles du Congo Belge. Annales du Musée du Congo Belge, Tervuren (Belgique), série in 8°, Sciences Géologiques 5: 5-32.

Saint-Seine, P. (de) 1955. Poissons fossiles de l'étage de Stanleyville (Congo belge). Premiere Partie: La Faune des argilites et schistes bitumineux. Annales du Musée Royal du Congo Belge Tervuren (Belgique), Série in-8°, Sciences géologiques 14: 1-126.

Saint-Seine, M.P. (de) and Casier, E. 1962. Poissons fossiles des couches de Stanleyville (Congo). Deuxième partie. La faune marine des Calcaires de Songa. Annales du Musée Royal de l'Afrique centrale, Tervuren, Belgique, série in 8°, Sciences Géologiques 44: 1-52..

Santos, R.S. 1974. A idade gelógica da Formação Pastos Bons. Anais da Academia Brasileira de Ciências 46(3/4): 589-592.

Schaeffer, B. 1972. A Jurassic fish from Antarctica. American Museum Novitates 2495: 1-17.

Schaeffer, B. and Patterson, C. 1984. Jurassic fishes from the Western United States with comments on Jurassic fish distribution. American Museum Novitates 2796: 1-86.

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

Soto, M., Perea, D. and Da Silva, J. 2007. New findings of vertebrate remains in the Tacuarembó Formation (Late Jurassic-Early Cretaceous), Uruguay: *Ceratodus africanus* Haug (Osteichthyes: Dipnoi) and ?*Ceratosaurus* sp. (Dinosauria: Theropoda). Ameghiniana 44: 40R.

Stahl, B.J. 1999a. Mesozoic holocephalians. In Arratia, G. and Schultze, H.-P. (eds.) Mesozoic Fishes 2 - Systematics and Fossil Record, Verlag Dr. Friedrich Pfeil, 9-19, München.

Stahl, B.J. 1999b. Chondrichthyes III: Holocephali. Handbook of Paleoichthyology Verlag, Dr. Friedrich Pfeil, 4, 164 p., München.

Stahl, B.J. 2004. The structure of the early chimaeroid dentition. In Arratia, G. and Tintori, A. (ed.) Mesozoic Fishes 3 - Systematics, paleoenvironments and biodiversity, Verlag Dr. Friedrich Pfeil, 11-16, München.

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

Su, T. 1974. New Jurassic ptycholepid fishes from Szechuan, S. W. China. Vertebrata PalAsiatica 12 (1): 1-20 [In Chinese with English abstract].

Tasch, P. and Volkheimer, W. 1970. Jurassic conchostracans from Patagonia. The University of Kansas Paleontological Contributions 50: 1-23.

Tasch, P., Sastry, M.V.A., Shah, S.C., Rao, R.R.J., Raco, C.N. and Ghosh, S.C. 1973. Estheriids of the Indian Gondwanas: Significance for continental drift. In Campbell, K.S.W. (ed.) 3rd Gondwana Symposium, Australian National University Press, Proceedings 445-452, Canberra,.

Taverne, L. 1981. Les Actinoptérygiens de l'Aptien inférieur (Töck) d'Helgoland. Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg 51: 43-82.

Taverne, L. 2001. Position systématique et relations phylogénétiques de *Paraclupavus* ("*Leptolepis*") *caheni,* téléostéen marin du Jurassique moyen de Kisangani (Calcaires de Songa, étage de Stanleyville), République Démocratique du Congo. Museé royal de l'Afrique centrale, Tervuren (Belg.), Département du Géologie et Mineralogie, Rapportes Annual 1999-2000: 55-76.

Taverne, L. and Gayet, M. 2005. Phylogenetical relationships and paleozoogeography of the marine Cretaceous Tselfatiiformes (Teleostei, Clupeocephala). Cybium 29(1): 65-87.

Thies, D. and Turner, S. 2002. Jurassic actinopterygians from Monto, southeast Queensland. Alcheringa 25: 381-386.

Tintori, A. 1981. Two new pycnodonts (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy). Rivista Italiana di Paleontologia 86(4): 795-824.

Tintori, A. and Sassi, D. 1992. *Thoracopterus* Bronn (Osteichthyes: Actinopterygii): a gliding fish from the Upper Triassic of Europe. Journal of Vertebrate Paleontology 12(3): 265-283.

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

Traquair, R.H. 1911. Les poisons wealdiens de Bernissart. Mémoires du Musée royal d'Histoire naturelle de Belgique 5: 1-65

Turner, J.C. 1983. Descripción geológica de la Hoja 44d, Colan Conhué. Dirección Nacional de Minería y Geología, Boletín, 197: 1-78.

Underwood, C.J. 2006. Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. Paleobiology 32(2): 215-235.

Underwood, C.J. and Rees, J. 2002. Selachian faunas from the lowermost Cretaceous Purbeck Group of Dorset, southern England. Special Papers in Palaeontology 68: 83-101.

Vijaya and Prasad, G.V.R. 2001. Age of the Kota Formation, Pranhita-Godavari valley, India: A palynological approach. Journal of the Palaeontological Society of India 46: 77-93.

Viohl, G. 1996: The paleoenvironment of the Late Jurassic fishes from the southern Franconian Alb (Bavaria, Germany). In Arratia, G. and Viohl, G. (eds.) Mesozoic Fishes - Systematics and Paleoecology, Verlag Dr. Friedrich Pfeil, 513-528, München.

Viohl, G. 1998: Die Solnhofener Plattenkalke - Entstehung und Lebensräume. Archaeopteryx 16: 37-68.

Wade, R. T. 1940. The Triassic fishes of Gosford, New South Wales. Journal and Proceedings of the Royal Society of New South Wales 73(4): 206-217.

Wilson, M.V.H. and Bruner, J.C. 2004. Mesozoic fish assemblages of North America. In Arratia, G. and Tintori, A. (eds.) Mesozoic Fishes 3 - Systematics, Paleoenvironment and Biodiversity, Verlag Dr. Friedrich Pfeil, 575-595, München.

Woodward, A.S. 1888. On two new lepidotoid ganoids from the Early Mesozoic deposits of Orange Free State, South Africa. Quaterly Journal of the Geological Society 44: 138-143.

Woodward, A.S. 1895. The fossil fishes of the Talbragar Beds (Jurassic?). Memoirs of the Geological Survey of New South Wales, Palaeontology 9: 1-27.

Woodward, A.S. 1916-1919. The fossil fishes of the English Wealden and Purbeck formations. Palaeontographical Society 2: 49-104.

Recibido: 26 de mayo, 2008
Aceptado: 8 de agosto, 2008