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# Literaturbericht

## Palaeobiogeography and Stratigraphy of Advanced Gnathostomian Fishes (Chondrichthyes and Osteichthyes) in the Early Triassic and from Selected Anisian Localities (Report 1863-2009)

### Paläobiogeographie und Stratigraphie fortschrittlicher gnathostomer Fische (Chondrichthyes und Osteichthyes) in der Unter-Trias und ausgewählter anisischer Fundstellen (Bericht 1863-2009)

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With 2 figures in the text

**Abstract:** Present paper gives an updated summary of research history on the Chondrichthyes and Osteichthyes of the Early Triassic (Griesbachian, Dienerian, Smithian, Spathian) and primarily of the early Anisian. Early Triassic and Anisian marine and freshwater ichthyofaunas are found on all continents except South America, and much more fish assemblages are known from the Northern than from the Southern Hemisphere. The Early Triassic and the Anisian are times of major importance for the phylogeny of the Chondrichthyes and Osteichthyes. After the end-Permian mass extinction the surviving groups of the cartilaginous and bony fishes recovered, and many new forms appeared in the Early Triassic. The neoselachians as well as close relatives of the teleosteans evolved, clades to which nearly all extant fishes belong. Present publication also provides a revised data base for the distribution of Early Triassic and early Anisian chondrichthyan and osteichthyan fishes in time and space on which future research on their paleobiodiversity shall be guided.

Key words: Early Triassic, Anisian, Chondrichthyes, Selachii, Osteichthyes, Actinistia, Dipnoi, Actinopterygii

**Kurzfassung:** Die Verf. geben einen aktuellen Abriss zur Erforschungsgeschichte der Chondrichthyes und Osteichthyes der Unter-Trias (Griesbachium, Dienerium, Smithium, Spathium) und hauptsächlich des Unter-Anisium. Untertriadische und

anisische Ichthyofaunen des Süss- und Salzwassers finden sich auf allen Kontinenten mit Ausnahme von Südamerika. Dabei sind auf der Nordhemisphäre mehr Fischfundstellen bekannt als von der Südhalbkugel. Die Unter-Trias und das Anisium sind bedeutende Abschnitte in der Stammesgeschichte der Chondrichthyes und Osteichthyes. Nach dem Massenaussterben am Ende des Perm erholten sich die überlebenden Gruppen der Knorpel- und Knochenfische. Viele neue Formen erschienen in der Unter-Trias, so erste mögliche Neoselachier sowie nahe Verwandte der Teleostier. Zu den beiden zuletzt genannten Taxa gehören fast alle heute lebenden Fische. Die vorliegende Publikation liefert eine revidierte Datengrundlage der räumlichen und zeitlichen Verbreitung untertriadischer sowie unteranisischer Chondrichthyer und Osteichthyer, auf der weitere Untersuchungen zu deren Paläobiodiversität aufbauen können.

Schlüsselwörter: Unter-Trias, Anisium, Chondrichthyes, Selachii, Osteichthyes, Actinistia, Dipnoi, Actinopterygii

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## 1. Introduction

As early as 1926, Deecke for the first time summarized and discussed the Triassic fishes of the world, and in 1976 Schaeffer & Mangus gave a first brief report on the research history of Early Triassic fishes. Since then, only publications of a more general nature have appeared, and these deal either with the occurrence of Triassic fishes in certain macrogeographical regions (Goto 1994; Chang & Jin 1996; Poyato-Ariza et al. 1999; Schultze & Kriwet 1999; Murray 2000; Chang & Miao 2004; López-Arbarello 2004; Wilson & Bruner 2004) or with the distribution of specific lower or higher taxa of fishes during the Triassic or Mesozoic, respectively (Brough 1936; Beltan & Tintori 1981; Cappetta 1987; Beltan 1988; Kemp 1994, 1996; Neuman 1996; Arratia 2004; Maisey et al. 2004; Schultze 2004). Present publication should present an updated overview on the research history of the chondrichthyan and osteichthyan fish lineages of the Early Triassic and chiefly of the early Anisian, as well as their revised chronological and spatial distribution worldwide. This compilation provides an authentic data base for our future research concerning their paleobiogeography and paleobiodiversity.

Localities yielding Early Triassic and Anisian fossil fishes are known from all continents except South America. Most of them are situated in the Northern Hemisphere, namely Spitsbergen, Greenland, Germany, France, Poland, Lithuania, and Kaliningrad exclave of Russia, Spain, Bulgaria, Turkey, Israel, Canada (British Columbia, Alberta, Ellesmere Island), USA (Nevada, Idaho, Arizona, Alaska), Russia (North Siberia, Upper Volga River, South Primorye), Kazakhstan, Japan, China (Xinjiang, Shaanxi, Jiangsu, Anhui, Hubei, Zhejiang, Guizhou, Guangxi, South Tibet), India, and Pakistan as well as Nepal, Libya, Iran, and Oman. In contrast to the papers of Accordi (1953, 1955, 1956), fish fossils are unknown from

Early Triassic strata in Italy (see below). The same seems to be the case for Kirghizstan or Uzbekistan, respectively (compare below). In the southern hemisphere Early Triassic and Anisian fossil fish sites are located in South Africa and Zambia as well as Angola, Madagascar, Australia (New South Wales, Queensland, Tasmania), and Antarctica. During the Triassic period, all continents were merged together forming the Pangea continent. The paleogeographic positions as well as the environmental background (marine or freshwater) of the aforementioned fish lagerstätten are summarized in figure 1 (Early Triassic) and figure 2 (Anisian) (cf. Dercourt et al. 1993, 2003).

Among the primary water living vertebrates, aside from agnaths, only the advanced gnathostomian fishes, the Chondrichthyes and Osteichthyes, survived the Permian-Triassic mass extinction (Andrews et al. 1967; Benton 2007; Cappetta et al. 1993; Carroll 1993; Hurley et al. 2007; Schaeffer 1973; Schindewolf 1954; Schultze 1993; Thomson 1977). Acanthodians, placoderms and ostracoderm agnaths are not known from post-Palaeozoic strata. Other jawless fishes (early soft bodied forms: Janvier 1999; Shu et al. 1999, and Cyclostomata: Gess et al. 2006; Janvier 2006) are generally seldom found in the fossil record. So far, their occurrence in the Triassic is unconfirmed. The conodont-bearing animals, which are often interpreted as agnaths, also survived the Permian-Triassic boundary event, but are not subject of the present paper. Regarding the Chondrichthyes, so far only representatives of the selachian Elasmobranchii have been recovered from Early Triassic and Anisian deposits. Early Triassic and Anisian Subterbranchialia are yet to be found (Stahl 1999a, 1999b; Benton 2007). Batoids are also absent at the beginning of the Mesozoic, but then they first appear in the Early Jurassic. Concerning the Osteichthyes, both major lineages, the Sarcopterygii (Actinistia, Dipnoi) and the Actinopterygii, survived the Permian-Triassic biotic crises and are well represented in Early Triassic and Anisian strata (e.g. Bemis et al. 1987; Brough 1935; Cappetta 1987; Cloutier 1991a, 1991b; Cloutier & Forey 1991; Compagno 1991; Forey 1998; Gillis & Donoghue 2007; Gross 1966, 1973; Kemp 1998; Nolf 1985; Reif 1980; Schaeffer 1952; Zangerl 1981). The Early Triassic and early Middle Triassic (Anisian) are important stages in the phylogeny of modern chondrichthyans and osteichthyans. Both fish groups underwent rapid evolution, and therefore, numerous new taxa emerged in the aftermath of the end-Permian extinction event, amongst others the first possible neoselachians as well as close relatives of the teleosteans. The Neoselachii and above all, the Teleostei are the predominant fishes of the extant ichthyofauna. Already in the early Mesozoic, the most abundant of all primary water-living vertebrates are the actinopterygians, predominantely chondrosteans and (sub-)holosteans in the classical view, but chondrichthyans and sarcopterygians are also quite common. The bulk of cartilaginous fishes at that time are hybodontiform sharks. Apart from them, some typically Palaeozoic shark clades, such as the xenacanthiform (Poplin & Heyler 1989) and ctenacanthiform selachii (Cappetta 1987), also survived the Permian/Triassic boundary, but they are usually a minor component of Early Triassic and Anisian fish assemblages.



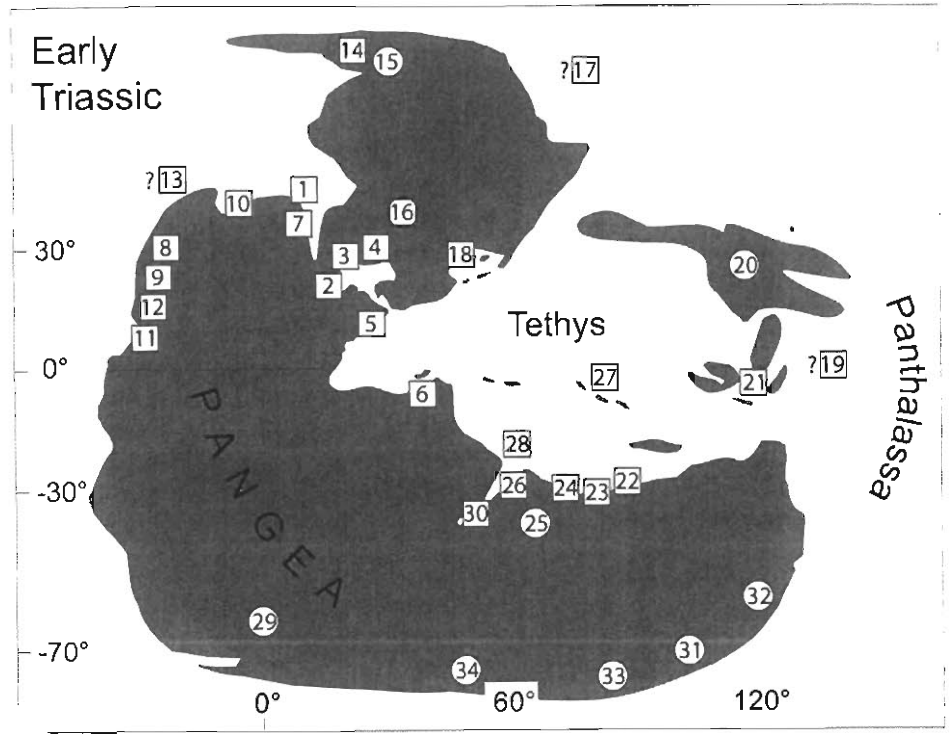


**Fig. 1.** Distribution of Early Triassic fish sites in respect to the Supercontinent Pangea: 1. Spitsbergen, 2. Germany, 3. Poland, 4. Lithuania and Kaliningrad exclave of Russia, 5. Bulgaria, 6. Israel (Early Triassic or Anisian), 7. Greenland, 8. Canada, British Columbia, 9. Canada, Alberta, 10. Canada, Ellesmere Island, 11. USA, Nevada, 12. USA, Idaho, 13. USA, Alaska, 14 and 15. Russia, Northern Siberia, 16. Russia, Upper Volga River, 17. Russia, Primorye, 18. Kazakhstan, 19. Japan, 20. China, North China Block, 21. China, South China Block, 22. China, South Tibet, 23. Nepal, 24 and 25. Indian margin (peninsular part: Early Triassic or Anisian), 26. Pakistan, 27. Iran, 28. Oman, 29. South Africa, Zambia and Angola, 30. Madagascar, 31. Australia, New South Wales, 32. Australia, Queensland, 33. Australia, Tasmania, 34. Antarctica. Marine depositional environments (sometimes with freshwater influence) denoted by squares. Freshwater depositional environments (lacustrine and/or fluviatile) denoted by circles. Palaeogeographic positions of the localities according to Dercourt et al. (1993; 2000). Question marks: Palaeogeographic position unknown.

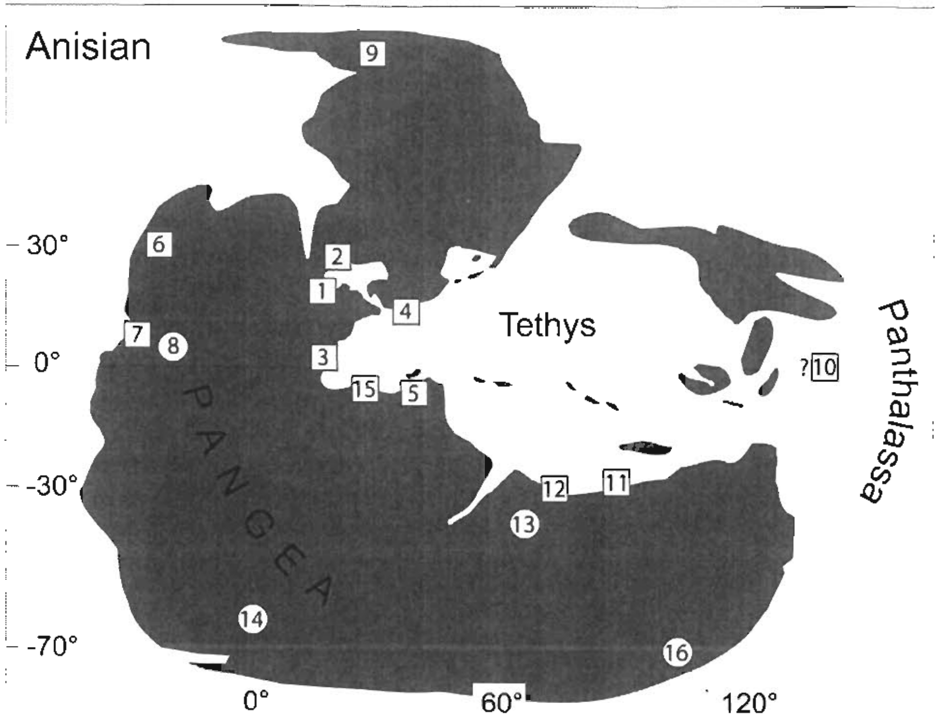


**Fig. 2.** Distribution of Anisian fish sites relative to the Supercontinent Pangea: 1. Germany and France, 2. Poland, 3. Spain, 4. Turkey, 5. Israel (Early Triassic or Anisian), 6. Canada, British Columbia, 7. USA, Nevada, 8. USA, Arizona, 9. Russia, Northern Siberia, 10. Japan, 11. China, South Tibet, 12 and 13. Indian margin (peninsular part: Early Triassic or Anisian), 14. South Africa and Zambia, 15. Libya, 16. Australia, New South Wales. Marine depositional environments (sometimes with freshwater influence) denoted by squares. Freshwater depositional environments (lacustrine and/or fluviatile) denoted by circles. Palaeogeographic positions of the localities according to Dercourt et al. (1993, 2000). Question mark: Palaeogeographic position unknown.



## 2. Global Distribution of Early Triassic and Anisian Fishes

### 2.1 Europe and Near East

#### 2.1.1 Spitsbergen

One of the major Early Triassic marine fish assemblages comprising quite large numbers of genera is known from western and southern Spitsbergen (Svalbard archipelago, Arctic Norway). Others are described from Greenland, Canada and Madagascar. Piveteau (1935) emphasized the resemblance between the Early Triassic fish biocoenosis of Spitsbergen, Greenland, and Madagascar.

The first expeditions to yield fish material from the Triassic of Spitsbergen were attempted in the years 1864 und 1868 (Hulke 1873). Additional Triassic fish remains were found in 1896 (Woodward 1912) und 1898 (Böhm 1913). In 1908, Wiman discovered the famous „fish level" (= *Posidonomya* shale), one of three fish-bearing Early Triassic horizons in the Ice Fiord area in western Spitsbergen (Wiman 1910, 1915; Diener 1915; Weitschat & Dagys 1989). In the summer months of the years 1908-1913, 1915-1918, and 1920 more excursions took place and abundant Triassic fish material was collected, which was comprehensively studied by Stensiö (1918, 1921, 1925). The fish fossils were found in the Olenekian Sticky Keep Formation (Smithian to Spathian) of the Sassendalen Group, but the main concentration with the most genera known is restricted to the so called „fish level" of the Smithian Iskletten Member (Buchan et al. 1965). Fishes, however, were also reported from the subsequent Kaosfjellet Member of the „*Grippia* Level" and from the „Lower Saurian Level" (Spathian) (Schaeffer & Mangus 1976). The bone beds above the „fish level" at Mount Viking and Mount Marmier (Sassendalen) that Stensiö (1921) described belong to the „*Grippia* level" (Frebold 1930: 27). According to Cox & Smith (1973), a total number of eighteen genera of fossil Chondrichthyes and Osteichthyes have been reported from these three horizons: *Acrodus* (Acrodontidae), *Hybodus* (Hybodontidae), *Palaeobates* (Polyacrodontidae), *Polyacrodus* (Polyacrodontidae, all previous genera are sharks), *Pteronisculus* (Palaeoniscidae, this form and the following taxa are actinopterygians), *Pygopterus* (Pygopteridae), *Acrorhabdus* (Acrolepidae), *Birgeria* (Birgeriidae), *Boreosomus* (Acrolepidae), *Bobasatrania* (Bobasatraniidae), *Perleidus* (Perleididae), *Saurichthys* (Saurichthyidae), *Axelia* (Coelacanthidae, the latter and the taxa till the end of this list are sarcopterygians), *Sassenia* (Coelacanthiformes), *Wimania* (Coelacanthidae), *Mylacanthus* (Coelacanthiformes), *Scleracanthus* (Coelacanthiformes) and *Ceratodus* (Ceratodontidae). Moreover, Stensiö (1921: 40-42) quoted three generically indeterminable fin spines representing two types of cestraciont sharks, which he later assigned to the genus *Nemacanthus* (Stensiö 1932: 15).

In 1960, the Polish Spitsbergen Expedition (Birkenmajer 1964: 14) recovered from the Hornsund area in southern Spitsbergen new fish material, which was described by Birkenmajer & Jerzmańska (1979). Later, numerous Polish expeditions were organized to the same area on Spitsbergen. In 1998, samples from the conglomerate of the Early Triassic Brevassfjellet *Myalina* bed were collected, which yielded many isolated shark teeth, mostly of the genera *Lissodus*, *Hybodus* and *Acrodus*. With the fossils from the Brevassfjellet *Myalina* bed, Blazejowski (2004) was able to contribute to a better understanding of the Early Triassic fish fauna from Spitsbergen. Moreover, Blazejowski's (2004) analysis of the microstructure of *Lissodus* teeth provided evidence for the coexistence of two types of histology within a single taxon, which closes the discussion considering ortho- and osteo-dentine as a taxonomic factor. The published material is from thin layers of the Dienerian fine-grained, iron rich conglomerate, belonging to the 5 to 6 m thick Brevassfjellet *Myalina* bed, exposed on the southeastern slope of the Hyrnefjellet (Mount Hyrne), Hornsund area. This bed represents the upper portion of the Urnetoppen Member of the marine Vardebukta Formation (Birkenmajer 1964; Harland 1997; Dallmann 1999).

Additional fish remains from the „fish level" were collected by the first two authors, the geologist Franz-Josef Lindemann, University of Oslo, and BSc Lui Unterrassner, Zurich, in August 2008 on Mount Stensiö, Sassendalen. The fish material, which is reposited within the *Paläontologisches Institut und Museum* of the University of Zurich, is currently under examination. Among the new fossils is a shark specimen bearing a branch of the lower jaw including tooth battery as well as a fin spine and numerous skin denticles. So far, it is the most complete shark fossil from the Early Triassic of Spitsbergen.

### 2.1.2 Germany and France

Since the middle of the 19th century, Triassic fish discoveries from the Buntsandstein Group (Early Triassic to early Anisian) were repeatedly announced, more precisely from the late Buntsandstein (Plattensandstein; early Anisian, Bachmann et al. 1999), which were found in the southern part of the Upper Rhine Trench (Baden-Württemberg, Germany). These fossils are often isolated finds, which are generally constrained to two areas, Dinkelberg north-east of Basel (Switzerland) and the area south of Kraichgau, east of Karlsruhe. Between 1841 and 1856, five ganoid fish specimens were collected from Dinkelberg. They were described by Deecke (1889) as ?*Semionotus* sp., *Semionotus alsaticus*, *Dictyopyge rhenana* and Palaeoniscidae gen. indet. Palaeoniscid fishes, amongst others the pygopterid *Pygopterus crecelii* (Wilser 1923), were described from southern Kraichgau while the lungfish *Ceratodus palaeoruncinatus* is known from Durlach near Karlsruhe (Frentzen 1924). The type material of *C. palaeoruncinatus* was, however, destroyed during World War II (Jörg 1969b). Jörg (1969a, 1969b) published a substantial fish fauna derived from a fossiliferous clay nodule of the early Anisian late Plattensandstein (Werkstein), which was collected in an abandoned quarry near Eisenhafengrund, south-east of Durlach. To summarize, the German Upper Bundsandstein fauna comprises actinopterygian taxa such as Palaeoniscoidei, Platysomoidei, Perleidiformes and Semionotiformes as well as dipnoan and chondrichthyan remains, with the following genera in alphabetical order: *Acrodus*, *Ceratodus*, *Dictyopyge*, *Dorsolepis*, *Pericentrophorus*, „*Praesemionotus*" (= *Dipteronotus*; Gall et al. 1974), *Pygopterus* and *Semionotus*.



Additional fish remains from Germany are known from the Early Triassic portion of the Buntsandstein. Krumbein & Wilczewski (1973), for example, reported a first tooth plate of the dipnoan *Ceratodus* from Heligoland (Schleswig-Holstein, Germany) in the North Sea. It was found in 1968 and is preserved on a slab which can be refered to the upper part of the Detfurth Formation (middle Buntsandstein, Scythian) (Bachmann et al. 1999).

A fish fauna coeval to that of the German Buntsandstein is known from Alsace-Lorraine, France (Buntsandstein supérieur des Vosges, early Anisian), at the western rim of the Germanic Basin, which includes, according to Firtion (1934), Grauvogel (1947), Gall (1971, 1972), Gall et al. (1974) and Gall & Grauvogel-Stamm (2005), the saurichthyid *Saurichthys*, the platysomid *Dorsolepis*, the semionotid *Pericentrophorus*, the perleidid *Dipteronotus* as well as indeterminable perleidiform and coelacanth material. In the famous Fossillagerstätte Grès à Voltzia of the northern Vosges Mountains, juvenile specimens of the aforementioned fishes often occur together with eggs of osteichthyans and selachians (*Palaeoxyris*) (Gall & Grauvogel-Stamm 1999). Paleoichthyological treasures from the French Buntsandstein are the actinopterygians *Dipteronotus aculeatus* and *Pericentrophorus minimus*, of which numerous juvenile and adult specimens of exceptionally good preservation are known. With this excellent material a detailed reconstruction of their anatomy and ontogeny was possible, which makes the actinopterygians of the Early Triassic Buntsandstein one of the best known fishes of the Mesozoic of Central Europe (Mader 1984). The sediments of Grès à Voltzia are interpreted as deposits of brackish water-bodies on a deltaic plain (Gall 1983, 1985; Gall & Grauvogel-Stamm 1984, 1999).

The Triassic fish associations of the southwestern part of the German Basin (Baden-Württemberg and Alsace-Lorraine) exhibit major relationships to associations from the Alpine Triassic (e.g. Monte San Giorgio, Switzerland, Bürgin 1992, 1998; Kuhn 1945, Kuhn-Schnyder 1974; Rieppel 1985, 1992), which points to the relatively early existence of a marine seaway between the Germanic Basin and the Tethyan Realm (probably middle Early Triassic; Beutler & Szulc 1999). However, the epicontinental southwestern German Basin is characterized by a less diverse fish fauna than those of the Alpine Triassic. The most abundant fishes in the aforementioned part of the German Basin are actinopterygians. Tooth plates of lungfishes are also quite common in sandy near-shore or limnic deposits. Coelacanthid fishes are rare. Hybodontiform sharks (*Acrodus*, *Hybodus*) probably invaded the Germanic Basin not earlier than the early Middle Triassic. A marine seaway between the Germanic Basin and the Boreal Realm was perhaps present during the earliest Triassic (Beutler & Szulc 1999). The fishes of the Germanic Basin represent two trophic levels: A benthic community (hybodont sharks, many actinopterygians, dipnoans), which fed on invertebrates with firm shells, and a nektonic group of carnivorous taxa such as *Saurichthys* and possibly actinistians (Schultze & Kriwet 1999).

### 2.1.3 Poland

Over the last 15 years several rich tetrapod faunas were found in the Triassic continental deposits of Poland (at the eastern rim of the Germanic Basin). They include the bone-bearing Mesozoic karst infillings of the Czatkowice area in southern Poland, which were discovered in 1978 by a team from the Institute of Geological Sciences, Jagiellonian University, Krakow (Paszkowski & Wieczorek 1982). Rock samples collected at that time were later generously forwarded to the Institute of Paleobiology and Museum of the Earth, Polish Academy of Sciences, Warsaw, for paleontological studies. The karst cavities yielding the bone-bearing breccias belong to the Early Carboniferous limestone (Tournaisian to Middle Visean, according to Paszkowski & Wieczorek 1982). The largest of these karst deposits, designated as Czatkowice 1, has yielded an Early Triassic microvertebrate assemblage (fissure filling) comprising about ten terrestrial taxa and fish remains. Recently, the site was newly dated as early Olenekian on the basis of the occurrence of the dipnoan *Gnathorhiza* and procolophonian remains. The early Mesozoic karst infillings of the Czatkowice area also contain, apart from *Gnathorhiza* and procolophonids, prolacertiforms, basal lepidosauromorphs, a basal archosaur, small amphibians (including a pre-frog) and additional fish material. However, the fish remains form a rather minor component of the Czatkowice 1 assemblage. Fishes are represented by occasional fin spines and cranial elements, which sometimes bear teeth (Borsuk-Bialynicka et al. 1999; Borsuk-Bialynicka & Evans 2003; Borsuk-Bialynicka et al. 2003).

Liszkowski (1993) gives a summary of the chondrichthyan fauna of the Polish Muschelkalk, in which he mentions amongst others the neoselachians *Reifia* and *Palaeospinax* from the early Anisian of Upper Silesia. Furthermore, the selachian relic forms *Acronemus*, *Phoebodus*, *Protacrodus* and *Orthacanthus* (and in the late Middle Triassic also the xenacanthiform *Pleuracanthus*; name preoccupied!) occur in the early Anisian Lower Muschelkalk of Poland. *Phoebodus* and *Orthacanthus* even survived until the Late Triassic (Schultze & Kriwet 1999). In contrast to the southwestern part of the Germanic Basin (Germany/Eastern France) where actinopterygians prevailed, in the fish fauna of the Polish part of the depression sharks dominated.

### 2.1.4 Lithuania and the Kaliningrad Exclave of Russia

Microremains of indeterminate actinopterygian fishes (scales, lepidotrichia and teeth) were found in the upper part of the Tauragė Formation (Kisnerius & Saidakovskij 1972; Karatajute-Talimaa & Katinas 2004). The Tauragė Formation, which outcrops in Lithuania and the Kaliningrad exclave of Russia (East Baltic region), represents shallow water deposits of the Dienerian subdivision of the Early Triassic. Romanov & Zotova (1962) made note of microremains of the actinopterygian *Gyrolepis* from the Early Triassic of the East Baltic region, but their material is most likely lost (Karatajute-Talimaa & Katinas 2004).



### 2.1.5 Spain

A few marine actinopterygians of the families Palaeoniscidae (*Gyrolepis*) and Perleididae/Colobodontidae (*Colobodus*, *Crenilepis*) (Mutter 2002, 2004a) are known from a shelf environment (Bauzá 1954; Poyato-Ariza et al. 1999) within the Anisian of Gorg Negre in Lérida, Catalonia.

### 2.1.6 Italy

Accordi (1953, 1955, 1956) quoted exceptional finds of fish fossils from the Early Triassic part of the Werfen Formation (Val Gardena and Valle del Cordevole, northern Italy), which he ascribed to *Archaeolepidotus leonardii* n. gen et n. sp. and *Paralepidotus*? *moroderi* n. sp. However, according to Renato Posenato (pers. comm. 2009), it is very unlikely that these specimens actually come from the Early Triassic part of the Werfen Formation. The remains are probably of Permian age.

### 2.1.7 Bulgaria

Stefanov (1977) studied sections of the Balkanide carbonate Triassic north of Sofia in detail and listed the stratigraphical occurrences of fish remains, for which he established three fish zones. The *Colobodus varius* Fish Zone with assemblages I, II, and III spans parts of the Early and Middle Triassic (late Scythian, early Anisian, Pelsonian), and consists of the hybodont shark genera *Acrodus* and *Hybodus*, the actinopterygian genera *Saurichthys*, *Colobodus* and *Gyrolepis* as well as the problematic conodont taxon *Nurrella* (Pomesano Cherchi 1967, 1969). In 1966, Stefanov described Triassic fishes of Bulgaria and quoted *Colobodus* teeth from the middle Anisian.

### 2.1.8 Turkey

Thies (1982) described a shark tooth with a modern, neoselachian type of enameloid from the middle Scythian of the Kocaeli (= Bithynian) Peninsula, east of the Bosporus in the Asian part of Turkey, Anatolia (Assereto 1972, Yurttas 1972). Thies (1982) ascribed the tooth to the genus *Palaeospinax*, though with doubt. It is the earliest occurrence of this supposed neoselachian.

### 2.1.9 Israel

The scene of ingressions and regressions of the Triassic Tethys over the Arabian craton took place along a relatively narrow belt, not wider than several tens of kilometers. This marginal belt has been traced over central Sinai (southern Israel), central Jordan, and northern Saudi Arabia. Within this belt three major ingression-regression cycles can be identified. The first sedimentary cycle (Scythian to early Anisian), which includes the Yamin Formation and Zafir Formation (both defined in boreholes in southern Israel), consists of shallow marine carbonates and sand bodies, near shore and lagoonal mudstones and sandstones as well as possible deltaic complexes (Werfen-type clastics of the Levant) (Druckman et al. 1982; Parnes et al. 1985). From this belt, a few chondrichthyan fish teeth, e.g. of the euselachian shark *Hybodus* or related genera, have been reported from Early Triassic or Anisian beds of Wadi Raman (later named Makhtesh Ramon), Negev Desert, in southern Israel (Brotzen 1955, 1956; Shaw 1947; Gans 1983; Werner 1982).

## 2.2 North America

### 2.2.1 Greenland

Early Triassic beds at Cape Stosch, Hold-With-Hope Peninsula, on the east coast of Greenland (Denmark), were discovered in 1926 in the course of the Cambridge expedition, and numerous invertebrates and a single fish fossil were reported. Additional Triassic fishes were collected at Cape Stosch between 1928 and 1930 by Norwegian trappers. Between 1929 and 1931, additional fish fossils were collected at Cape Stosch and Hird's fox farm (Hird Bay, Clavering Island, East Greenland) during the Danish expeditions (Stensiö 1932). Subsequent field trips between 1932 and 1938 to Cape Stosch and Hird Bay again yielded numerous specimens of Early Triassic fishes (Nielsen 1935, 1936, 1942, 1949). These fish fossils belong to the the Wordie Creek Formation (Griesbachian to Dienerian) of the Nordenskiöld Subgroup (Schaeffer & Mangus 1976; Stauber 1942), and they occur in six successive fish zones (I–VI) ranging from the early Griesbachian into perhaps the early Dienerian (Perch-Nielsen et al. 1974). The material from the fossiliferous bottom layers is fragmentary, but predominantly well-preserved. Articulated fish skeletons have been detected in the upper beds. Most of the fossil fishes were collected in the Cape Stosch area (Harper 2004). The number of genera and specimens in each zone vary considerably, but both have their maximum in fish zones II, III, and V (Schaeffer & Mangus 1976). No elasmobranchs have been found above zone II. Nielsen (1961) suggested that this variation in faunal composition were the result of environmental changes. The fish-bearing sediments were deposited in a shallow basin with a shifting connection to the open ocean. The conditions varied, therefore, from fully marine to brackish or freshwater with an overall transition from marine to non-marine. In 1935, Piveteau mentioned the resemblance of the Early Triassic fish biocoenosis from Greenland, Spitsbergen, and Madagascar.

Apart from the classical older studies of Stensiö and Nielsen on the Early Triassic ichthyofauna of East Greenland, there are also a few more recent contributions. Nybelin (1977), for instance, wrote a preliminary description of a small basal actinopterygian (*Helmolepis gracilis*) based on four specimens, one of which had already been briefly mentioned both by Stensiö (1932) and Nielsen (1936). The type series of *H. gracilis* from the early Griesbachian of East Greenland was apparently lost for some time, but was later rediscovered in the Geologisk Museum of the University of Copenhagen by Mutter (2005). The latter identified two additional specimens of this rare actinopterygian, one of which is presumably a juvenile. Mutter (2005) revealed new details and improved considerably the reconstruction of the skull skeleton of *H. gracilis*. Furthermore, Mutter et al. (2008) discovered undescribed fish remains from the Wordie Creek Formation of East Greenland in the Geologisk Museum of the University of Copenhagen, which they tentatively referred to as *Saurichthys* cf. *S. ornatus*. In total, at least nineteen genera of chondrichthyan, actinopterygian, and actinistian fishes are known from the Early Triassic of East Greenland: *Polyacrodus* (Polyacrodontidae), *Nemacanthus* (Galeomorphii incertae ordinis), *Parahelicampodus* (Edestidae, all previous genera are sharks), *Boreosomus* (Acrolepidae, this form and the following taxa are actinopterygians), *Pteronisculus* (= "*Glaucolepis*", preoccupied after White & Moy-Thomas 1940; Palaeoniscidae), *Birgeria* (Birgeriidae), *Acrorhabdus* (Acrolepidae), *Perleidus* (Perleididae), *Bobasatrania* (Bobasatraniidae), *Australosomus* (Pholidopleuridae), *Saurichthys* (Saurichthyidae), *Helmolepis* (Platysiagidae), *Ospia* (Parasemionotidae), *Broughia* (Parasemionotidae), *Parasemionotus* (Parasemionotidae), *Watsonulus* (Parasemionotidae), *Whiteia* (Whiteiidae, the latter fish and the taxa up to the end of this list are actinistians), *Sassenia* (Sasseniidae), *Laugia* (Laugiidae) and perhaps *Wimania* (Coelacanthidae) (Stensiö 1932; Nielsen 1935, 1936, 1942, 1949, 1952a, 1952b, 1961; Nybelin 1977; Forey 1998; Schultze 2004; Mutter 2005; Mutter et al. 2008).



### 2.2.2 Canada

Fossil fishes from the Early Triassic and the Anisian of Canada are known from two regions in British Columbia (vicinity of Wapiti Lake and Kakwa Recreation Area) as well as from Alberta and Ellesmere Island (Gardiner 1966; Gibson 1975; Pell et al. 1992; Mutter 2004b). The fishes from British Columbia and adjacent Alberta are predominantly derived from the Sulphur Mountain Formation. They can be found along an outcrop zone that stretches for hundreds of kilometers along the eastern edge of the Canadian Rocky Mountains. The fish fossils are mostly articulated.

#### 2.2.2.1 British Columbia

Whiteaves (1889) first turned his attention to fossils in the Triassic rocks of British Columbia, Western Canada. The marine fish fauna from the Early Triassic Vega-Phroso Member of the Sulphur Mountain Formation in the Ganoid Range of the Wapiti Lake area (Canadian Rockies, eastern British Columbia) was discovered by a group of researchers from the University of Wisconsin in 1947 (Laudon et al. 1949; Pell & Hammack 1992; Schaeffer & Mangus 1976; Wignall & Newton 2003). In 1961 and afterwards, joint Canadian/US-American field parties obtained a representative collection. However, others also gathered fossils from the Wapiti Lake area and thus contributed to the great quantity of fishes known from this region. More than one thousand mostly articulated specimens representing at least 16 genera were recovered (see revision by Mutter 2003; a shorter list of taxa can be found in Schaeffer & Mangus 1976). Three distinct fossil localities have been recognized. Today, the area is part of a protected Provincial Heritage Site (Brinkman & Neuman 1987; Pell & Hammack 1992). The fossil fishes from the Wapiti Lake area, which include chondrichthyans, actinopterygians, and actinistians, were first summarized by Gardiner (1966). Schaeffer & Mangus (1976) later studied them comprehensively and they emphasized that the site is very important for the field of paleoichthyology since the fossil assemblage serves as a reference fauna, which exhibits outstanding diversity. Neuman (1986) reviewed the Perleididae and Parasemionotidae from the Sulphur Mountain Formation in his diploma thesis, and later he also summarized the research history of the geology and faunal content of the Wapiti Lake area (Neuman 1992, 1996).

In 1991, a second Early Triassic fossil fish locality in eastern British Columbia, circa 50 kilometres (about 30 miles) south-southeast of Wapiti Lake, was encountered during the course of a mineral potential study in the protected Kakwa Recreation Area (Pell et al. 1992). Although the site was originally found in the early 1980's (A. Neuman and B. Richards, pers. comms. to Pell et al. 1992) it was not documented at that time. The fishes mentioned by Pell & Hammack (1992) are based on a number of scattered articulated specimens and numerous fossil fragments of actinopterygians, actinistians, and chondrichthyans, which were collected during brief visits to the site on a scree slope beneath outcrops of the Sulphur Mountain Formation.

Recently, research on the Early Triassic ichthyofauna of the Sulphur Mountain Formation was resumed by Mutter (2003). In 2004, he and colleagues carried out field work, which yielded a wealth of new fossil fish finds of chondrichthyans, actinopterygians, and coelacanths. They point out that there are several rock-units in the Vega-Phroso Siltstone Member, where concentrations of associated and well-preserved fossils can be found. These faunal assemblages are dated between early Smithian and Spathian and they appear rather primitive when compared with other Early Triassic faunas (Mutter 2004b; Mutter et al. 2007). In 2005, Neuman & Mutter reported of a new species of platysiagid actinopterygian, *Helmolepis cyphognatus* (Sulphur Mountain Formation; probably of early Smithian age after Mutter 2005). The chondrichthyans from the Sulphur Mountain Formation of Western Canada are rare but noteworthy. The newly established presence of *Listracanthus pectenatus* n. sp., which represents the only Mesozoic record of this genus, highlights the survival of an additional rare and enigmatic group of cartilaginous fish across the Paleozoic-Mesozoic boundary. Two kinds of frequently occurring dermal denticles numerous identified as *Listracanthus* are predominantly found in strata of probable early Smithian age (Mutter & Neuman 2006). Furthermore, Mutter et al. (2007) assigned the material previously referred to as cf. *Palaeobates* by Schaeffer & Mangus (1976), which at the time was the only reported hybodont genus from the Wapiti Lake area, to the new genus *Wapitiodus*. The heterodonty of its dentition, its fin spine morphology and the short, robust body shape imply that it represents a member of a new family, Wapitiodidae (?Hybodontoidea incertae sedis). The genus *Wapitiodus* so far comprises two species. In addition, several isolated teeth and other fragmentary material are referred by Mutter et al. (2007) either to the genus *Wapitiodus* or, though with doubt, to the genus *Polyacrodus*. Mutter & Neuman (2008a, 2008b) also made note of the caseodontid genera *Caseodus* and *Fadenia* as well as the new eugeneodontid genus *Paredestus* and further indeterminable eugeneodontid material from the Sulphur Mountain Formation of Western Canada. Apart from the aforementioned shark taxa, the shark fauna of Wapiti Lake also bears an elasmobranch of enigmatic affinities, represented only by peculiar denticles, which Mutter et al. (2007) described as „Genus A". Recently, two new species of *Saurichthys* were reported from the Vega-Phroso Siltstone member of the Sulphur Mountain Formation of Ganoid Ridge near Wapiti Lake (Mutter et al. 2008). The taphonomy of the ganoid fishes from the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation was studied by Anderson & Woods (2007). They point out that the taphonomy of marine fishes is still poorly known and they also underscore the importance of the British Columbia fish assemblage in this respect.



Fish remains of middle Anisian age from the Whistler-Llama Member of the Sulphur Mountain Formation are not yet well explored (Neuman 1992; Mutter 2003).

#### 2.2.2.2 Alberta

The Triassic fossils from the province of Alberta, Western Canada, have been studied later than those from British Columbia. In Alberta, fossil fishes from the Triassic Sulphur Mountain Formation were first found in the beginning of the foregoing century at a locality near Banff (Lambe 1914, 1916). In 1914, Lambe described a new species *Platysomus canadensis* (Platysomoidei) and two years later he mentions *Coelacanthus banffensis* (Actinistia), *Elonichthys cupidineus* (Palaeoniscoidea) and *Acrolepis laetus* (Acrolepidae) from the Upper Banff shale (Lambe 1914, 1916). However, *Elonichthys cupidineus* was later referred to the new genus *Albertonia*, i.e. *Albertonia cupidinia*, by Gardiner (1966), who also suggested that *Acrolepis laetus* might be attributable to the genus *Pteronisculus* (Schaeffer & Mangus 1976). Russell (1951) revised *Platysomus canadensis* and reascribed it to the genus *Bobasatrania*. *Platysomus brewsteri,* described by Warren (1936), was also synonymized with *Bobasatrania canadensis* (see Schaeffer & Mangus 1976).

Davies et al. (1997) presented a remarkable example of the ganoid fish *Albertonia* sp. (Parasemionotidae), which was discovered on a bedding plane in a core from the Early Triassic Montney Formation of Alberta, a time-equivalent of the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation. The presence of the subholostean *Albertonia* together with other fish species identified from Wapiti Lake might indicate that bottom water conditions were anoxic (Davies et al. 1997). Recently, Mutter et al. (2008) revised *Saurichthys dayi* (originally described as *Belonorhynchus dayi* by Raymond 1925) from the Early Triassic Spray River Formation of Alberta, a species, which they also discovered in the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation of British Columbia.

#### 2.2.2.3 Ellesmere Island

Two fish specimens from the marine Early Triassic (Smithian) Blind Fiord Formation (Blind Fiord, Ellesmere Island, Arctic Canada) were found by E. T. Tozer in 1962, and were identified by Schaeffer & Mangus (1976) as *Saurichthys* sp. (Saurichthyidae) and *Boreosomus* sp. (Acrolepidae), respectively.

### 2.2.3 United States of America

Early Triassic or Anisian fishes have been mentioned from Idaho, Arizona, Nevada and Alaska. While the ichthyofaunas of Idaho, Nevada, and Alaska are of marine origin, the fishes from Arizona are from freshwater deposits.

#### 2.2.3.1 Nevada

Sander et al. (1994) reported the genus *Saurichthys* and Actinopterygii indet. from the early middle Anisian of the Fossil Hill Member (Favret Formation) in Favret Canyon, Pershing County, Nevada. Later, more actinopterygians (*Saurichthys*, *Birgeria*, *Colobodus*, ?*Paralepidotus*, ?*Ptycholepis*), a lungfish (*Ceratodus*) and several elasmobranch genera (*Polyacrodus*, *Acrodus*, *Palaeobates*, ?*Palaeospinax*) were reported from the same locality (Rieppel et al. 1996). Cuny et al. (2001) described two new species of hybodontiform sharks, *Acrodus cuneocostatus* and *Polyacrodus bucheri*, and the new neoselachian taxon *Mucrovenator minimus* as well as elasmobranch dermal denticles and on genus level questionable actinopterygian remains. The shark fauna from the Middle Triassic of Nevada is dominated by durophagous hybodontiforms, but an important neoselachian component is also present.

Another locality, Candelaria in Esmeralda County (southwestern Nevada), was recently recognized as a potential collection area for Early Triassic fish. Two concretions containing articulated fossil fishes were inadvertently found while collecting ammonoids from the Candelaria Formation (Dienerian) in that region. These specimens are reposited with the New Mexico Museum of Natural History and Science, but they are on loan to the Paleontological Institute and Museum of the University of Zurich where they are currently under study.

#### 2.2.3.2 Idaho

Early Triassic marine fishes (chondrichthyans and osteichthyans) are known from the Bear Lake region, southeastern Idaho (Schaeffer & Mangus 1976). Evans (1904) quotes a new cestraciont spine attributable to *Cosmacanthus elegans* (*Nemacanthus* in Cuny et al. 1998: 665), which is probably of Induan age, and recently Mutter & Rieber (2005) described from the late early Spathian the new ctenacanthoid shark *Pyknotylacanthus spathianus*. The latter is based on a completely preserved fin spine recovered in association with dermal denticles. The osteichthyans are represented at Bear Lake by the laugiid actinistian *Laugia* and the actinopterygians *Birgeria*, *Bobasatrania*, *Haywardia* and a perleidid (Schaeffer & Mangus 1976: 552). According to Schaeffer & Mangus (1976), *Haywardia* is probably synonymous with *Bobasatrania*.

#### 2.2.3.3 Arizona

Welles (1947) described palaeoniscoid scales possibly attributable to *Boreosomus* and numerous fin spines of the hybodont selachian *Leiacanthus* from the continental early Anisian Holbrook Member of the Moenkopi Formation in northern Arizona (outcrops of this formation also occur in southern Utah). The large collection of vertebrates (fishes are rare), plants and coprolites obtained by Welles from the upper part of the Moenkopi Formation also included several isolated bones of an actinistian. These remains were not so identified by Welles (1947) but were later recognized as such by Westoll (letter to Welles) from the illustrations (Schaeffer & Gregory 1961: 3). Schaeffer & Gregory (1961) erected the new taxon *Moenkopia wellesi*, and they assigned *Moenkopia* to the family Coelacanthidae, whereas Schultze (2004) classified it as Mawsoniidae incertae sedis (Latimeroidei). Today, an interesting fish fauna composed of palaeoniscoids, coelacanths, and dipnoans is known from the Holbrook Member of the Moenkopi Formation (Lucas & Schoch 2002: 102).



#### 2.2.3.4 Alaska

Patton & Tailleur (1964) noted the presence of the actinopterygian *Boreosomus* and of an indeterminable coelacanthid from the Early Triassic part of the marine Shublick Formation near Killik-Itkillik, northern Alaska (Schaeffer & Mangus 1976; Platt 1975; Wilson & Bruner 2004).

### 2.3. Asia (excluding Near East)

#### 2.3.1 Russia and Kazakhstan

There are several scattered localities in Russia yielding Early Triassic and Anisian fish remains (Chang & Miao 2004). Berg (1941) and Obruchev (1967) described basal actinopterygians from the Lower Tunguska River area, Northern Siberia, a region which has attracted many researchers (v. Mojsisovics 1886; Berg et al. 1964; Yakovlev 1973; Selezneva 1983, 1985, 1988; Shiskin & Sytchevskaya 1998). The Triassic freshwater fish assemblages of the Lower Tunguska River basin belong to the lower member of the Burgarikta Formation, which is stratigraphically close to the Permo-Triassic boundary. Sytchevskaya (1999) restudied the specimens of Berg (1941) and Obruchev (1967) and revised their phylogenetic relationships. She confirmed the presence of the perleidid *Eoperleidus*, formerly cited as *nomen nudum*, and redescribed other genera such as the scanilepiform *Evenkia*, the semionotiform *Tungusichthys* and the pholidopleurid *Arctosomus*. Moreover, she demonstrated that "*Tungusichthys*" of Selezneva (1988) is based on the type material of *Eoperleidus*. Minikh (1981, 1982) made note of the occurrence of the predatory actinopterygian fish *Saurichthys* from several Early Triassic localities in Russia (Upper Volga River, Kolyma River Basin and perhaps Seredka River) and Kazakhstan (Mangyshlak peninsula) (Mutter et al. 2008). Selachian (*Acrodus*) and actinopterygian remains (*Birgeria*, *Perleidus*) were recovered from the Olenek River region and an area to the northeast (Schaeffer & Mangus 1976). Remnants of the large, marine actinopterygian *Birgeria* were also reported from an Early Triassic locality in the Lena River delta (Berg et al. 1964; Obruchev 1967; Schwarz 1970). Additional fish fossils were reported from the Verkhoyansk area (*Tompoichthys*) and the Magadan region (*Hybodus*) (Obruchev 1967; Schaeffer & Mangus 1976). Recently, Ivanov & Klets (2007) described new marine chondrichthyan and actinopterygian microremains from four regions in Northern and Eastern Siberia: Lena River Basin (Olenekian), Taimyr Peninsula (Olenekian and Anisian), Kotelniy Island (Olenekian), and the Magadan region (early Anisian). They reported from these sites isolated teeth and scale fragments of actinopterygians (e.g. colobodontids and redfieldiids) as well as various hybodontoid and neoselachian scales resembling those of *Fragilicorona*, *Duplisuggestus*, *Proprigalea*, *Synechodus*, and *Gracilisuggestus*. Yamagishi (2009) quoted new shark remains, *Acrodus*, *Hybodus* and *Polyacrodus*, from South Primorye (southeastern Russia).

### 2.3.2 Kirghizstan and Uzbekistan

In the third volume of „Mesozoic fishes“, SCHULTZE (2004) lists in Appendix 2 the lungfish *Asiatoceratodus sharovi* from the Early Triassic of Uzbekistan, and referred to VOROBYEVA (1967). In the same volume, CHANG & MIAO (2004), however, report *A. sharovi* of VOROBYEVA (1967) from Madygen, Fergena Depression, Kirghizstan, which they and SYCHEVSKAYA (1999) consider to be of Middle to Late Triassic age. Due to the apparent incertitude of the stratigraphic age of the appropriate sediments, this Early Triassic fish record is omitted in Fig. 1.

### 2.3.3 Japan

The Early Triassic and early Middle Triassic fish remains from Japan are all from marine deposits, and elasmobranchs dominate the ichthyofauna (CHANG & MIAO 2004). In 1994, GOTO summarized the Palaeozoic and Early Mesozoic fish faunas of the Japanese islands, and two years later, GOTO et al. (1996) published Mesozoic shark remains of Japan. According to GOTO (1994) and GOTO et al. (1996), the following fish remains are known from the Early Triassic and Anisian of Japan: A tooth of the hybodontoid shark *Polyacrodus minimus* and many dermal denticles identified as Hybodontidae indet. (Taho Formation, Shikoku Island, Scythian), a tooth of *Hybodus* (Waruishi Formation, central Honshu Island, early Anisian; GOTO et al. 1991) as well as a part of a fish body indentified as Osteichthyes indet. (uppermost part of the Middle Bed of the Rifu Formation, northeastern Honshu Island, Anisian; SHIKAMA & MURATA 1976). Recently, YAMAGISHI (2004) reported more than 350 isolated teeth, many placoid scales and some cephalic spines from the Taho Limestone of Shikoku Island (southern Japan). The teeth are attributed by YAMAGISHI (2004) to *Acrodus* (Acrodontidae), *Hybodus* (Hybodontidae), *Polyacrodus* (Polyacrodontidae), *Synechodus* (Palaeospinacidae, Neoselachii) and Euselachii indet., while the cephalic spines are assigned to the hybodontoid *Arctacanthus exiguus*. The shark remains from the Taho Limestone are of Smithian to early Middle Anisian age.

### 2.3.4 China (including Tibet)

There are numerous Early Triassic and Anisian fish localities within the People's Republic of China. The Triassic ichthyofaunas of North China are all from freshwater deposits, whereas those from South China, Tibet included, are all of marine origin (CHANG & JIN 1996, CHANG & MIAO 2004). Interestingly, the South Tibetan Early Triassic and Anisian fish assemblages are from the northern margin of the Indian Plate and therefore belong to the southern Tethys, whereas the other Scythian ichthyofaunas from China are from the East Pangaea and western Panthalassa Realm (Fig. 1 and 2).

According to SCHAEFFER & MANGUS (1976: 553), the actinopterygian *Saurichthys* (OBRUCHEV 1967) and the dipnoan *Ceratodus* (CHABAKOV 1932, OBRUCHEV 1967) were found in the Early Triassic of Mount Bogdo in Xinjiang (North China). Also from the Scythian of Xinjiang Province, LIU (1958) made note of the redfieldiiform *Sinkiangichthys longipectoralis* from Qitai, and LIU et al. (1990) described the palaeoniscid *Duwaichthys mirabilis* from Pishan. CHENG (1980) reported the dipnoan *Ceratodus heshanggouensis* from the Early Triassic of Xingxian (Shaanxi Province). In 1957, CHOW & LIU made note of the presence of five actinopterygian genera (*Gyrolepis*, *Palaeoniscus*, *Boreosomus*, *Perleidus*, *Saurichthys*) in the supposedly Early Triassic Yanan Formation in the northern Shaanxi basin (Qilingou, Hengshan). However, the Yanan Formation was later redated as Jurassic by MA (1998), and then as Late Triassic by LIU et al. (1999). Even though the Yanan Formation may be stratigraphically younger than Scythian, its fish fauna truly resembles that of typical Early Triassic localities (CHOW & LIU 1957; CHANG & JIN 1996; TONG et al. 2006).



From the Early Triassic of South China, PATTE (1935) mentioned the occurrence of the acrolepidid *Boreosomus* in Guizhou, and LIU (1964) reported a new marine actinistian (*Sinocoelacanthus*) from Guangxi. Remnants of *Saurichthys* were collected in the Early Triassic of Longtan (Nanjing, Jiangsu Province) (SU & LI 1983, LIU et al. 2002). Additional fossil bony fishes were described from the Early Triassic of Qingshan (Jurong, Jiangsu Province) by QIAN et al. (1997) and LIU et al. (2002), and at least four genera and eight species of perleidid and parasemionotid fishes were recognized. SU (1981) examined a fish specimen of Early Triassic age from Hexian, Anhui Province, and described it as a new species, *Perleidus yangtzensis*. SU also mentions that the Geological Survey of Anhui Province found some perleidid fishes in the Early Triassic of Majiashan (Chaohu, Anhui Province), but they were not studied at that time. A new fish taxon, *Plesioperleidus dayeensis* n. gen. et n. sp., was erected by SU & LI (1983) on the basis of a specimen from the Fourth Member of the Daye Formation in Tieshan (Huangshi, Hubei Province). Later, JIN et al. (2003) reexamined a few perleidids from the Early Triassic of the Lower Yangtze region (South China), which they identified as *Perleidus yangtzensis* and *P. jiangsuensis*. Since perleidids from the Early Triassic of the Lower Yangtze region lack a caudal fin with epaxial rays, which JIN et al. (2003) have shown is present in the type species of *Perleidus* from the Middle Triassic of Italy, and because JIN et al. considered *Perleidus jiangsuensis* to be synonymous with the type species of *Zhangina*, JIN et al. (2003) placed both *Perleidus jiangsuensis* and *P. yangtzensis* into the genus *Zhangina*. Nonetheless, because *Zhangina* and *Plesioperleidus* exhibit only minor differences, TONG et al. (2006) regarded *Zhangina* as a junior synonym of *Plesioperleidus*. Finally, an additional perleidid, *Paraperleidus changxingensis*, was reported by ZHAO & LU (2007) from the Early Triassic Yinkeng Formation in Changxing (Zhejiang, South China). WANG et al. (2001) described material consisting of several hybodontoid sharks and Osteichthyes indet. from the Olenekian of the Luolou Formation, Zuodeng area (Tiandong, Guangxi). They established a fish assemblage, which was the first zonation by Triassic fishes in China. Their paper also includes the first report on the occurrence of marine Early Triassic Hybodontoidea in China. A more recent study on Early Triassic fishes from South China was carried out by TONG et al. (2006). They introduced nine species belonging to five genera and some undetermined or unnamed fish specimens from the Early Triassic (Olenekian) of two Majiashan sections (Chaohu, Anhui Province). They also stressed that the fish assemblage from Majiashan includes most of the Early Triassic marine bony fish taxa known from China.

In 1973, Misra et al. reported fish scales, teeth and fragmentary skeletal remains from the Anisian of the classical Triassic sequence exposed close to the Niti Pass near Tulong (Dingri District; South Xizang = South Tibet). Later, Zhang (1976) described the edestid shark *Sinohelicoprion* from the same location. Also, members of the research group Hugo Bucher, Zurich, collected from the Dingri District of Tibet teeth and denticles of cartilaginous fishes as well as teeth of bony fishes and reptilian material. These remains were found in marine sediments of late Smithian age (see also Wignall & Newton 2003). In spite of the long list of localities, Chinese Early Triassic fishes are as yet still not well known, perhaps because of the scarcity or incompleteness of the fossils and stratigraphic uncertainties.

### 2.3.5 India, Pakistan and Nepal

The marine Triassic fish localities on the Indian subcontinent are located in the extrapeninsular part, whereas such ones situated on the peninsular part belong to freshwater deposits (Chang & Miao 2004).

In his comprehensive study of the Salt Range fossils of Pakistan (India at that time), Waagen (1895) reported teeth of the hybodontoid shark *Acrodus* as well as teeth and scales of the palaeoniscid *Gyrolepis* and the perleidid/colobodontid (Mutter 2002, 2004a) *Colobodus* from the middle Scythian Ceratite beds (Gee 1989; Guex 1978; Kummel & Teichert 1970; Schindewolf 1954; Wignall & Hallam 1993). De Koninck (1863) earlier reported isolated teeth from the Salt Range, which he ascribed to *Acrodus flemingianus*, *Acrodus* sp. and with doubt to *Saurichthys indicus*, but according to him these remains were derived from the *Productus* limestone (Permian). Waagen (1895: 8, 13), however, suggested that they more likely came from Triassic beds. R. J. Mutter (in Mutter et al. 2008: 120) considers the few teeth that De Koninck (1863) referred to *Saurichthys*? *indicus,* probably to be from a reptile. From the Salt Range, Surghar Range and Trans-Indus Ranges of Pakistan, Kummel & Teichert (1966, 1970) and the Pakistani-Japanese Research Group (1985) also mention the genera *Acrodus*, *Colobodus* and *Saurichthys*, which were found in the earliest Triassic Kathwai Member of the Mianwali Formation. *Saurichthys* is also known from Kashmir and Kumaun Himalayas in northern India (Early and Middle Triassic) and from the early Scythian of a locality near Jomsom in the Nepalese Himalaya (Sahni & Chhabra 1977; Beltan & Janvier 1978; Mutter et al. 2008). Finally, Mishra et al. (1990) made note of a teleostean fish from the Early Triassic of Chamba, Indian Himalaya. However, this taxonomic assignment seems doutbful to us.

From the peninsular part of the Indian subcontinent, remnants of *Saurichthys* as well as dental plates and vomerine teeth of the dipnoan *Ceratodus* were discovered by Jain (1984, 1986) in the freshwater Yerrapalli Formation in the Pranhita-Godavari Valley (Deccan, India). Associated with the Yerrappalli fishes that are late Early Triassic or possibly early Middle Triassic in age (Bandyopadhyay 1988) are a series of tetrapods, which are comparable to those of the *Cynognathus* Assemblage Zone of South Africa (Jain et al. 1964). Some fishes of the Yerrappalli fauna can be compared with those from Madagascar (Beltan & Tintori 1981; Beltan 1996) and British Columbia (Schaeffer & Mangus 1976).



### 2.3.6 Iran and Oman

A single specimen of the edestid shark *Helicampodus* was reported by Obruchev in 1959 (pers. comm. to Schaeffer & Mangus 1976) from supposedly Early Triassic marine beds in the vicinity of Djulfa (Jolfa) in northwestern Iran (Seyed-Emami 1971, 2003), adjacent to the border with the Nakhchivan Autonomous Republic of Azerbaijan. Later, Obruchev (1967) did not comment on the supposed occurrence of *Helicampodus* in Iran, but instead reported this form from the Early Triassic of Armenia, a province of the USSR at that time. However, it is possible that Obruchev referred to the same specimen in both cases.

A marine invertebrate and conodont fauna is known from the Griesbachian of the Central Oman Mountains (Krystyn et al. 2003, Twitchett et al. 2004). Recently, isolated fish teeth were detected in the Smithian of Oman by members of the research group Hugo Bucher, Zurich (Nicolas Goudemand, pers. comm. 2007).

## 2.4. Africa and Madagascar

### 2.4.1 South Africa, Zambia, and Angola

The vast majority of African Early and Middle Triassic fishes come from the Karoo Supergroup in the southern part of Africa (South Africa, Zambia, Angola, Madagascar). This Supergroup is the most complete sequence of Late Carboniferous to Early Jurassic strata on the African continent, and it contains one of the best exposed sedimentary series of non-marine Triassic strata in the world. For over a hundred million years the Karoo was an ample back-arc foreland basin covering an area of more than 400.000 square kilometers. During the Early Triassic and Anisian, the Karoo Basin of South Africa was a large freshwater system (fluviatile and lacustrine). Tetrapod and plant fossils are abundant and consequently, the strata are the standard for the global correlation of the continental Triassic. Fossil fishes, however, are relatively rare in the Karoo Basin, but a biostratigraphic and correlative potential exists for the areas in which they are present (Antunes & Schaeffer 1990; Bender et al. 1991; Bender 1998, 2000; Broom 1909; Brough 1931; Duffin 1985; Griffith 1978; Hancox 2000; Haughton 1934, 1936; Hutchinson 1973; Jubb 1973; Jubb & Gardiner 1975; Murray 2000; Oelofsen 1981; Teixeira 1978).

The *Cynognathus* Assemblage Zone (CAZ) of the upper Beaufort Series at Bekkerskraal, Rouxville (Orange Free State, South Africa) bears the most fossiliferous deposits of the Karoo's Triassic sequences. Hancox et al. (1995) subdivided the CAZ of the upper Beaufort Series into three subzones (A = lower, B = middle and C = upper CAZ) on the basis of temnospondyl index taxa. Given the present understanding of tetrapod faunas, the age of Subzone A is fairly well constrained as latest early Triassic because of correlation with better-dated Russian and European faunas (Damiani 1999, Hancox et al. 1995, Shishkin et al. 1995), and the overlying Subzone B as earliest Middle Triassic (early Anisian). Thus, the two faunas represent a transition from the Early to Middle Triassic non-marine realm, a period of time when a resurgence of biodiversity is known to have occurred in the marine realm (Twitchett 2001). The vast majority of the fossil fishes from the Triassic of the Karoo Basin come from Subzone B of the CAZ, but recent studies have revealed that fish remains are also numerous in Subzone A (Jubb & Gardiner 1975, Bender & Hancox 2004). The following osteichthyan fishes have been reported to date from the upper Beaufort series of Bekkerskraal (South Africa): the dipnoan *Ceratodus*, the actinistian *Coelacanthus* (*Whiteia* after Forey 1998: 345), the lower actinopterygians *Elonichthys* and *Dicellopyge*, the redfieldiiforms *Atopocephala*, *Daedalichthys* and *Helichthys* as well as the perleidiforms *Meidiichthys*, *Cleithrolepidina* and *Hydropessum* (Broom 1909; Brough 1931, 1935; Griffith 1978; Hutchinson 1973, 1978; Jubb & Gardiner 1975; Kemp 1996; López-Arbarello 2004; Murray 2000; Schultze 2004). Concerning the cartilaginous fishes, until now only the hybodont genus *Lissodus* has been reported (Duffin 1985, Murray 2000), of which an almost complete specimen exists (Jubb & Gardiner 1975: 410). Aside from the Bekkerskraal locality, outcrops of the upper Beaufort Series also occur near Burgersdorp (Farm Vaalbank and Farm Winnaarsbaken, South Africa), where remains of *Saurichthys* and *Ptychoceratodus* were found (Griffith 1978; Jubb & Gardiner 1975; Kemp 1996). The platysomid *Caruichthys ornatus* is known from the middle Beaufort Series (*Lystrosaurus* Assemblage Zone) of Doorn River (Cradock District, South Africa) (Jubb & Gardiner 1975; Murray 2000). Although most Early and Middle Triassic chondrichthyan and osteichthyan remains of southern Africa come from the Beaufort Series, other Early Triassic and Anisian beds of the Karoo Supergroup have also yielded fish fossils. From the Molteno beds (lower Stormberg Group) in South Africa, Jubb (1973) and Jubb & Gardiner (1975) reported material previously referred to *Semionotus* cf. *capensis* and *Ceratodus kannemeyeri*. The redfieldiiform *Ischnolepis* was described from sediments in Zambia that could be of the same age as those of the upper Beaufort Series of South Africa (Hutchinson 1973: 237). The Early Triassic Cassanga Series near Lutoe and Iongo and the Lui River (northern Angola) yielded an additional, apparently diverse but poorly understood ichthyofauna. Up to now, one hybodont (*Lissodus*), one dipnoan (*Microceratodus*), one perleidid (*Perleidus*), two actinopterygians of uncertain affinities (*Marquesia*, *Angolaichthys*) and indeterminable palaeoniscoids are known from the Cassanga Series of Angola (Antunes & Schaeffer 1990, López-Arbarello 2004, Murray 2000, Schultze 2004, Teixeira 1978).

### 2.4.2 Madagascar

Early Triassic fish faunas are known from northern and southern Madagascar (Malagasy Republic). However, localities in northern Madagascar are somewhat richer, both in variety and number of fishes, when compared with sites in the southern portion of the island. The Early Triassic ichthyofaunas of Madagascar were first comprehensively studied by Jean Piveteau and later by Jean-Pierre Lehman and Laurance Beltan (Piveteau 1929, 1930a, 1930b, 1930c, 1932, 1934a, 1934b, 1935, 1937, 1940, 1944-1945; Lehman 1948, 1952, 1953, 1956; Lehman et al. 1959; Beltan 1957, 1958, 1963, 1968, 1977, 1980a, 1980b, 1984, 1996). The fish faunas of Madagascar represent classical marine Early Triassic assemblages. Piveteau (1935) pointed out the resemblances between the Early Triassic fish biocoenoses of Madagascar, Spitsbergen, and Greenland.



There are several Early Triassic fossiliferous localities in the Diego Basin (Beltan 1996) or Ankitokazo Basin (Schaeffer & Mangus 1976) in northern Madagascar, and fossil fishes are found in the Dienerian portion of the Middle Sakamena Formation, which is part of the African Karoo (Beltan 1996). Expeditions to collect and study Scythian fishes from northern Madagascar began very early in the 20th century. Merle (1908), Woodward (1910), and Andersson (1916) first described Early Triassic fishes from northern Madagascar and quote the actinistian *Coelacanthus* and the ray-finned fish *Ecrinesomus*. Later, Priem (1924) investigated actinopterygian remains that he ascribed to *Boreosomus* and *Pristisomus*. *Pristisomus merlei* of Priem (1924) was later revised by Piveteau (1930b), who recognized it as a pholidopleurid and therefore erected the new genus *Australosomus*, with *Australosomus merlei* as the type species. Numerous later studies revealed a very diverse osteichthyan fauna (chondrichthyans are absent) composed of actinistians (*Whiteia*, *Piveteauia*), dipnoans (*Paraceratodus*, *Beltanodus*) and particularly actinopterygians (*Atherstonia*, *Birgeria*, *Saurichthys*, *Pteronisculus*, *Bobasatrania*, *Helmolepis*, *Perleidus*, *Ospia*, *Broughia*, *Watsonulus*, *Parasemionotus*, *Stensioenotus*, *Jacobulus*, *Thomasinotus*, *Lehmanotus*, *Devillersia*, *Piveteaunotus*, *Ambodipia*, *Icrealcyon*, *Errolichthys*), with the parasemionotids being the most diverse group (White 1932, 1933; Brough 1933; Piveteau 1929, 1930a, 1930b, 1930c, 1934b, 1944; Moy-Thomas 1935; Lehman 1948, 1952, 1953, 1956; Beltan 1957, 1958, 1963, 1968, 1977, 1980a, 1980b, 1984, 1996; Takai 1976, Rieppel 1980; Olsen 1984; Mutter 2005). The Triassic fish remains of northern Madagascar were studied from different points of view, e.g. regarding systematics, paleobiology, and paleoecology. The fishes of the Middle Sakamena Formation are preserved as negative imprints in siliceous-clayed, non-calcareous nodules, and they are often found together with other vertebrates (Stegocephalia, Proanura, Eosuchia), invertebrates, and plant remains. The fishes from northern Madagascar lived in marine water of a semi-arid environment.

The region in southern Madagascar that yields Early Triassic fish remains is located between Beroroha and Mandronarivo (Schaeffer & Mangus 1976). Priem (1924) reported from the vicinity of Mandronarivo a very fragmentary fish specimen that he ascribed with doubts to *Ptycholepis,* but it was mainly Tortochaux (1950) who called attention to the Early Triassic ichthyolites of southern Madagascar. For his thesis, Tortochaux (1950) worked on marine fish remains from the Middle Sakamena Formation (Dienerian) in the vicinity of Beroroha, and he mentions the actinopterygians *Watsonulus*, *Australosomus* and *Bobasatrania*, all of which are also known from the Early Triassic of northern Madagascar. From southern Madagascar, Guffroy (1956) described *Birgeria* sp. and *Boreosomus* sp., which are both typically Triassic taxa, but according to Lehman et al. (1959: 178, 216), Guffroy's specimens are actually derived from the Lower Sakamena Formation, which is Late Permian in age. Lehman et al. (1959) conducted a comprehensive study on the fossil fishes from the Middle Sakamena Group of southern Madagascar and state that the fauna comprises actinopterygians (e.g. *Sakamenichthys*, *Saurichthys*, *Thomasinotus*, *Parasemionotus*) and dipnoans (*Paraceratodus*); but actinistians are absent. Moreover, the existence of elasmobranchs is assumed on the basis of the occurrence of prismatic calcified cartilage. Chondrichthyans are as yet not known from the Middle Sakamena Formation of northern Madagascar. RIEPPEL (1980) reported additional specimens of *Saurichthys* collected in 1962 by Father O. APPERT near Sakeny, Beroroha District, and he also points out that all specimens are preserved in fine-grained calcareous nodules and that only the inner surface of the dermal bones or their impressions in the matrix is preserved.

#### 2.4.3 Libya

GARDINER (1988) described the new species *Cleithrolepis major* (Cleithrolepididae, Perleidiformes) from central Cyrenaica, Libya. They were found in borehole core material of Anisian age.

### 2.5 Australia and Antarctica

#### 2.5.1 Australia

Early Triassic and early Middle Triassic ichthyofaunas are known from New South Wales (Gosford, Brookvale), Queensland (The Crater, Duckworth Creek) and Tasmania. All represent freshwater deposits. LONG & TURNER (1984) published a list of fossil fishes from Australia, and KEMP (1991, 1993) restudied the Mesozoic lungfishes from that continent.

##### 2.5.1.1 New South Wales

Triassic fishes in the Sydney Basin of New South Wales are mainly restricted to three localities: Gosford, Brookvale and St. Peters (the latter is late Anisian in age and thus not within the scope of the present publication). The fish bearing levels at Gosford, which are approximately of middle Scythian age, are stratigraphically the lowest of the three. An Early Triassic vertebrate assemblage consisting of fishes and labyrinthodonts is known (COSGRIFF 1972) from the Gosford Formation (Narabeen Group) at Gosford, north of Sydney. The first comprehensive account of the fishes of the Gosford assemblage was given by WOODWARD (1890, 1891), which was later summarized, revised and augmented by WADE (1930, 1939, 1942a, 1942b). WADE (1939) lists from Gosford an indeterminable selachian, the dipnoan *Gosfordia truncata*, the palaeoniscids *Myriolepis* and *Apateolepis*, the saurichthyid *Belonorhynchus* (= *Saurichthys*, see STENSIÖ 1925) as well as perleidiforms and redfieldiiforms. The nature of the Gosford fish assemblage, which occurs in a clay deposit suggests a lacustrine paleoenvironment. The Gosford Formation is overlain by the Middle Triassic Hawkesbury Sandstone (Hawkesbury Group, dated as Anisian) and the principal locality in this level is a lenticular mass of shale exposed at Brookvale (Sydney Basin, New South Wales). It also represents a lacustrine community (COSGRIFF 1972). Between 1925 and 1929, WADE collected hundreds of fossil fishes from the Brookvale brick pits. Although he sent some specimens to WOODWARD in England, he himself worked on the others and might have described them occasionally (WADE 1932, 1933a, 1933b, 1935). HUTCHINSON (1973) revised the redfieldiiforms and perleidiforms from Brookvale. RITCHIE (1981) described the



first complete specimen of *Gosfordia truncate*, and KEMP (1994) investigated newly found skull bones of this lungfish. KEMP also published a three-dimensional reconstruction of the skull of *Ceratodus formosus* and established for this form the new genus *Ariguna* (= *Ariguna formosa*). The Brookvale fish fauna comprises dipnoans, palaeoniscids, redfieldiiforms, perleidiforms, pholidopleurids, saurichthyids and early neopterygians (WADE 1935; HUTCHINSON 1973; RITCHIE 1981; LONG & TURNER 1984; KEMP 1994). The fossil assemblage of Brookvale resembles that of Gosford in that both are largely composed of fishes with labyrinthodonts as subordinate faunal components. The Sydney Basin proved to be highly productive for fossil vertebrate material.

LÓPEZ-ARBARELLO (2004) lists fishes from Gosford and Brookvale and compares them with the approximately coeval ichthyofauna of Bekkerskraal in South Africa. However, LÓPEZ-ARBARELLO (2004) erroneously mentions the actinopterygians *Palaeoniscus* and *Pholidophorus* as well as the xenacanthiform shark *Pleuracanthus* from Gosford, all of which could not be ascertained based on the literature cited by her (see also LONG & TURNER 1984: 238, 242).

##### 2.5.1.2 Queensland

Outcrops of the Early Triassic Arcadia Formation in Queensland (northeastern Australia) are usually unfossiliferous. However, two sites in southeastern Queensland, The Crater and Duckworth Creek, yield fossil remains. From these localities, NORTHWOOD (2005) described coprolites, some of which contain actinopterygian and dipnoan skeletal remains including tooth plates and scales referable to the lungfish *Ptychoceratodus phillipsi*. Some of the coprolites can be refered to fishes. Apart from coprolites, isolated skeletal remains of *Ptychoceratodus*, *Aphelodus*, *Namatozodia*, *Saurichthys*, perleidids and acrolepidids are also known from the Arcadia Formation, but they are generally rare (TURNER 1982a, 1982b, KEMP 1991, 1993, NORTHWOOD 1997, 1999, 2005). Due to the fact that isolated fish fossils are uncommon in the Arcadia Formation, scientific work on coprolites can considerably enhance our knowledge of the Scythian fish diversity of Queensland. The Early Triassic sediments of The Crater and Duckworth Creek were derived from high sinuosity, meandering to anastomosing streams that were subject to frequent seasonal flooding (JENSEN 1975).

##### 2.5.1.3 Tasmania

The Early Triassic period is well represented with fluviolacustrine sequences at several sites in southeastern Tasmania. From outcrops of the Knocklofty Formation JOHNSTON & MORTON (1890, 1891) first quoted actinoptyerygian remains, e.g. two species of *Acrolepis*. BANKS et al. (1978, 1984) wrote on an Early Triassic stream community from a locality near Old Beach on the east bank of the Derwent River, north of Hobart. This site provided remains of fishes, amphibians and reptiles found in a conglomerate lens within the Knocklofty Formation, a sandstone unit of the Parmeener Supergroup of the Tasmania Basin. Compared to amphibians, however, fishes occur there rather rarely. DZIEWA (1977, 1980b) conducted a comprehensive study on the Early Triassic osteichthyans from the Knocklofty Formation and quoted the ceratodontid lungfish *Ceratodus gypsatus*, several actinopterygians (*Acrolepis*, *Cleithrolepis*, *Saurichthys*), and indeterminable coelacanthid material. *Ceratodus gypsatus* was recently synonymized with *Ptychoceratodus phillipsi* by Kemp (1996). Dziewa (1980b) emphasized that the Tasmanian Early Triassic ichthyofauna differs from other coeval assemblages by the absence of endemic genera.

### 2.5.2 Antarctica

To date, only a single lungfish tooth plate, provisionally referred to *Ceratodus*, as well as indeterminable fish fragments are known from the Early Triassic of Antarctica. These remains come from the lower part of the Fremouw Formation in the central Transantarctic Mountains, where numerous amphibians and reptiles were found as well (Cosgriff et al. 1978; Dziewa 1980a; Young 1991).

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