

## THE ANDRÉ DUMONT MEDALLIST LECTURE

### FROM ADAPTIVE RADIATIONS TO BIOTIC CRISES IN PALAEOZOIC VERTEBRATES: A GEOBIOLOGICAL APPROACH

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(13 figures)

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**ABSTRACT.** The oldest vertebrates are Early Cambrian, cephalized unossified species (craniates) from China. The oldest armoured species (euvertebrates) are Ordovician in age. After Talimaa's Gap, vertebrates have their first adaptive radiation during the Silurian when jawless species ('ostracoderms') are dominant; they have their second radiation during the Devonian when jawed species (gnathostomes), and particularly the placoderms (armoured fishes), are dominant. Tetrapods appear in the Middle Devonian among sarcopterygians (bony fishes with lobed fins); they were probably aquatic during all the Devonian period. Vertebrates did not appear in freshwater but in marine environments. Similarly, tetrapods most probably appeared in very shallow marine environments. Silurian vertebrates did occupy all the environments of the marine epicontinental platforms. Vertebrate assemblages of high energy environments ('ostracoderms' and placoderms in particular), took place with the development of late- and post-tectonic Old Red Sandstone facies (ORS). So, Devonian vertebrate assemblages are known from both marginal marine, intermediate and continental environments of the ORS, and from the marine platforms (carbonate and siliciclastic facies). Vertebrates did encounter the two end-Devonian biological crises: disappearance of 'ostracoderms' at the Frasnian-Famennian crisis, and disappearance of placoderms at the Devonian-Carboniferous boundary, with a major ecological turnover at the beginning of the Carboniferous when chondrichthyans (cartilaginous fishes) and osteichthyans (bony fishes, mainly actinopterygians) became dominant. Terrestrial tetrapods (both amphibians and reptiles) occurred only after the earliest Carboniferous Romer's Gap. Vertebrates suffered at the Mid-Permian Olson's Gap with a drastic decline of basal tetrapods (amphibians) followed by a radiation of reptiles. The end-Permian extinction does not seem to have been strong for vertebrates, except for tetrapods. On a geobiological point of view, at least two of the bioevents which are characteristic for the rise of Palaeozoic vertebrates may be related with an increase in the global marine oxygen rate, viz., appearance of euvertebrates during the Great Ordovician Biodiversification Event (GOBE), and the radiation of large gnathostomes (in particular placoderms) during the Devonian adaptive radiation and Predation Revolution of vertebrates. However, coincidence does not mean causal relationship. So, we must be cautious with scenarios that appeared in the scientific literature in the most recent years.

**KEYWORDS.** Agnathans, Amniotic Revolution, biodiversity, ecological turnover, ecosystems, gnathostomes, macroevolution, Nekton Revolution, mass extinctions, Old Red Sandstones, palaeoenvironments, Predation Revolution, tetrapods.

**RESUME. Des radiations adaptatives aux crises biologiques des vertébrés paléozoïques : une approche géobiologique.** Les plus anciens vertébrés sont des formes céphalisées non ossifiées (crâniates) du Cambrien inférieur de Chine. Les plus anciennes formes ossifiées (euvertébrés) datent de l'Ordovicien. C'est après la « lacune de Talimaa » que les vertébrés effectuent une première radiation adaptative au Silurien où dominent les formes agnathes (les 'ostracodermes'), puis une seconde au Dévonien où dominent les formes à mâchoires (les gnathostomes), en particulier les placodermes (poissons cuirassés). Les tétrapodes apparaissent au Dévonien moyen au sein des sarcoptérygiens (poissons osseux à nageoires charnues) ; ils sont aquatiques jusqu'au Carbonifère. Les vertébrés ne sont pas apparus en milieu dulcicole mais en milieu marin. De même, les tétrapodes sont probablement apparus dans des environnements marins très peu profonds. Les vertébrés siluriens ont occupé tous les milieux possibles des plates-formes épicontinentales marines. C'est avec le développement des lithofaciès tardi- ou post-tectoniques du type des Vieux Grès Rouges (VGR) que se mettent en place des assemblages de vertébrés caractéristiques de milieux agités ('ostracodermes' et placodermes en particulier). On connaît ainsi au Dévonien des assemblages très riches de vertébrés tant dans les milieux marginomarine, intermédiaires et continentaux des VGR que sur les plates-formes marines (faciès carbonatés et siliciclastiques). Les vertébrés subissent les deux crises biologiques de la fin du Dévonien : disparition des 'ostracodermes' à la crise Frasnien-Famennien, et disparition

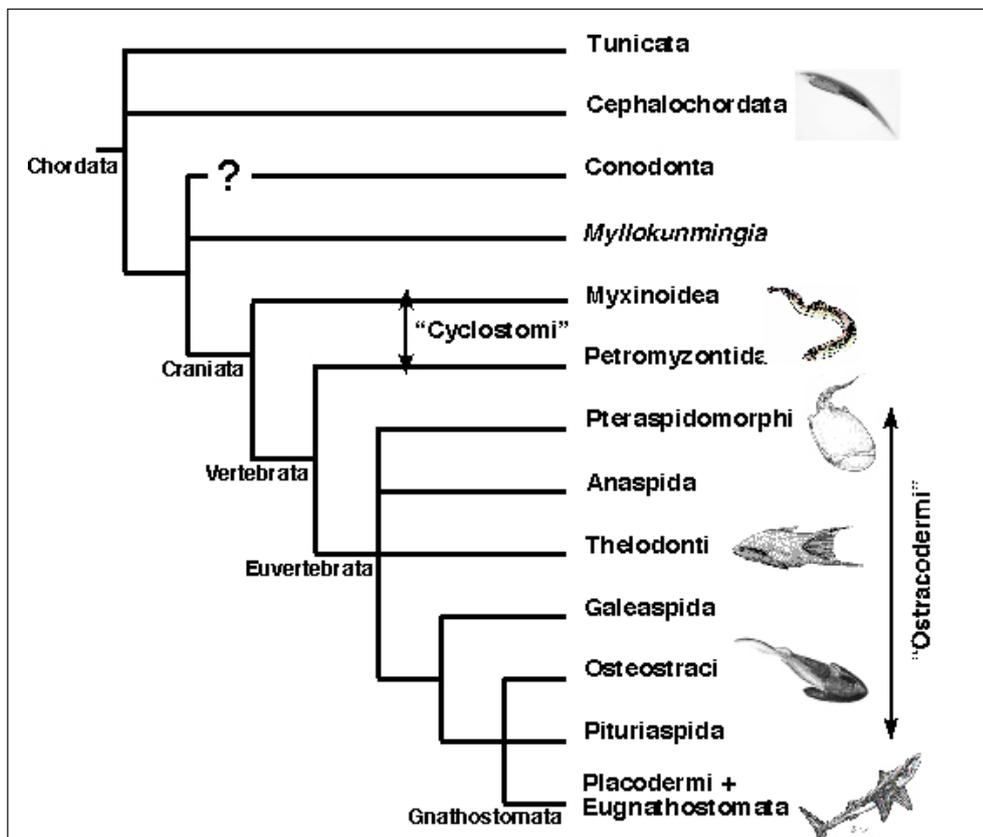
des placodermes à la limite Dévonien-Carbonifère, avec un relais écologique majeur au début du Carbonifère quand les chondrichthyens (poissons cartilagineux) et les ostéichthyens (poissons osseux, principalement les actinoptérygiens) deviennent dominants. C'est après la « lacune de Romer » du Carbonifère inférieur que se développeront les tétrapodes terrestres (amphibiens et reptiles). La « lacune d'Olson » du Permien moyen est caractérisée par un déclin drastique des tétrapodes basaux (amphibiens) suivi d'une radiation des reptiles. L'extinction de la fin du Permien ne semble pas avoir beaucoup affecté les vertébrés, à l'exception des tétrapodes. Au point de vue de la géobiologie, au moins deux des événements qui caractérisent le déploiement des vertébrés au cours du Paléozoïque peuvent être mis en relation avec un épisode d'augmentation du taux d'oxygène dans les mers du globe ; il s'agit de la mise en place des euvertébrés au cours de la Grande Biodiversification de l'Ordovicien (GOBE en anglais) et de la radiation des grands gnathostomes (en particulier les placodermes) au cours de la radiation adaptative du Dévonien et de la Révolution de Prédation des vertébrés. Cependant, coïncidence ne signifiant pas relation causale, il convient d'être prudent avec les scénarios invoqués dans la presse scientifique de ces dernières années.

**MOTS-CLES.** Agnathes, biodiversité, écosystèmes, extinctions en masse, gnathostomes, macroévolution, paléoenvironnements, relais écologique, Révolution Amiotique, Révolution de Prédation, Révolution du Necton, tétrapodes, Vieux Grès Rouges.

## 1. Introduction

At a global scale, the geological time slice which is considered here (Cambrian to Permian) does correspond to the Palaeozoic eustatic megacycle, with oceanic low levels at the beginning and at the end of the era, and a high level in the Ordovician-Silurian in relation with important volcanic activities of mid-oceanic ridges (Haq & Schutter, 2008). It is bracketed by two long-standing glaciation episodes, one at the end of the Neoproterozoic, and one at the Carboniferous-Permian transition (the Gondwanan glaciation). A third "Hirnantian" glacial event is known at the end of the Ordovician and during the early Silurian. Before and after this event, the development of carbonate

platforms and reef-builders in the Cambrian-Ordovician and the Silurian-Devonian is related to a green-house global environment. It is in this global frame that the development of marine trophic webs must be considered between the Neoproterozoic and the Devonian (Klug et al., 2010). Concerning vertebrates, we can distinguish a series of four steps : (1) first occurrence in the Cambrian; (2) appearance and development of the first ossified species (with a dermal bony carapace) in the Ordovician, these species are demersal; (3) a first adaptive radiation in the Silurian when fishes did occupy all possible niches of the marine platforms (this corresponds to the Nekton Revolution of vertebrates, which thus occurs before the Nekton Revolution of invertebrates in the Devonian: Klug



**Figure 1.** Schematic illustration of one of the topologies obtained in the phylogenetic (cladistic) analysis of chordates after Turner et al. (2010, modified). Some of the diagnostic features (synapomorphies) of the main taxa are as follows : Chordata- notochord; Craniata- skull; Vertebrata- arqualia (vertebrae); Euvertebrata- mineralized tissues of the skeleton (enamel or enameloid, dentine, bone); Gnathostomata- jaws; Eugnathostomata- teeth. Eugnathostomata include Acanthodii, Chondrichthyes and Osteichthyes (Actinopterygii + Sarcopterygii).

et al., 2010); and (4) a second adaptive radiation in the Devonian both in the marginal marine, intermediate and continental environments of the Old Red Sandstones, and the marine platform environments (both in carbonate and siliciclastic facies); Devonian species were demersal (nekto-benthic) or fully nektonic (the “pelagic” of Klug et al., 2010). Jawed fishes (gnathostomes) become dominant in relation to agnathans during the Devonian — this is what can be called the Predation Revolution of vertebrates (Blieck, 2009). At the Devonian–Carboniferous transition, after the Frasnian–Famennian and Devonian–Carboniferous biotic crises (Walliser, 1996), vertebrates do encounter a major ecological turnover when placoderms (the dominant group of Devonian armoured fishes) are replaced by chondrichthyans and osteichthyans (mainly actinopterygians; Long, 1990). Aquatic and terrestrial vertebrates make a third adaptive radiation during the Carboniferous, followed by a strong decline during the Mid-Permian Olson’s Gap. It is during this event that amphibians suffer of a strong decline, followed by an adaptive radiation of reptiles (Benton, 1993; Sahney & Benton, 2008) that might be called the “Amniotic Revolution of vertebrates”. However, except for tetrapods (Sahney & Benton, 2008), vertebrates do not seem to have strongly suffered at the end-Permian mass extinction.

The word ‘vertebrates’ is used by systematicists in two different ways: it refers either to Craniata (i.e., hagfishes + vertebrates *s.s.*) or to Vertebrata (lampreys and other vertebrae-bearing animals that Turner et al., 2010, proposed to name Euvvertebrata; Fig. 1). Craniata are characterized by their skull, Vertebrata by their arcualia (vertebrae), and Euvvertebrata by the occurrence of biomineralized hard tissues in their skeleton (enamel, enameloid, dentine, bone). Among euvvertebrates, basal taxa are represented by jawless (agnathan) ossified species, a.k.a. ‘ostracoderms’, from the Ordovician to the Devonian (ostracoderms are a paraphyletic group). More derived taxa are represented by jawed species (Gnathostomata), that is, Placodermi with jaws but no teeth, and Eugnathostomata with both jaws and teeth (chondrichthyans and osteichthyans, Fig. 1; Turner et al., 2010). Many uncertainties still exist about the phylogenetic relationships of basal chordates (tunicates, cephalochordates and craniates). One question is the relationships of conodonts to vertebrates. Donoghue et al. (2000) produced a phylogenetic analysis in which conodonts became part of the taxon Vertebrata, and were subsequently called ‘stem-gnathostomes’. This point has recently been critically re-analyzed by Turner et al. (2010) and Blieck et al. (2011) who consider conodonts to be basal chordates at the best. It must also be mentioned that the phylogenetic relationship of the only possible Cambrian vertebrate, viz. *Myllokunmingia* (synonym *Haikouichthys*) is still unsolved (Fig. 1; refs. in Turner et al., 2010).

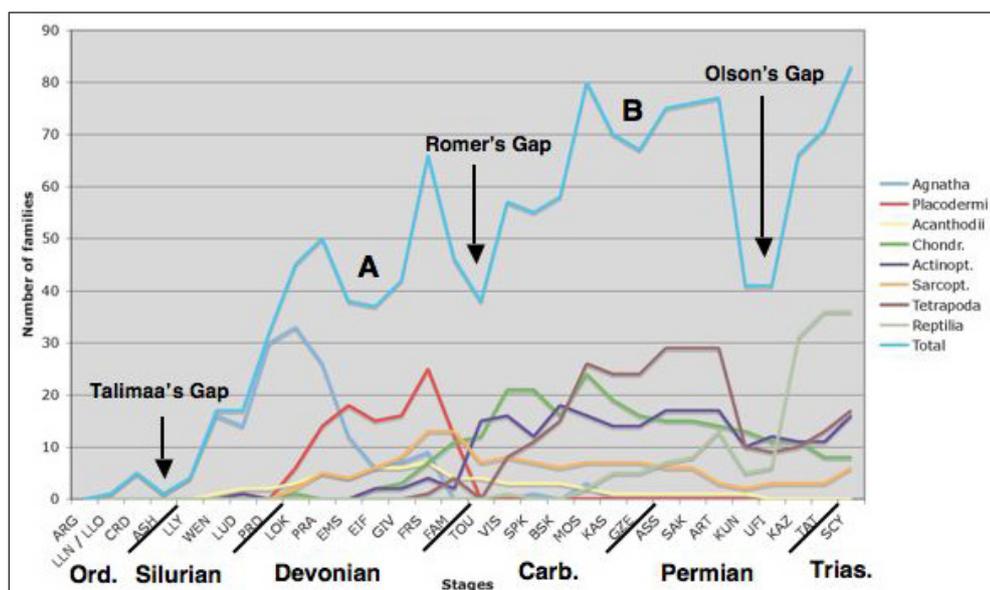
The original environment of early vertebrates and the question of interpretation of palaeoenvironments of the Old Red Sandstone in which they are often abundantly collected have been debated from the very

first discoveries (see refs. in Blieck, 1985; Janvier, 1996, 2009; Taquet et al., 2006). Satisfactory answers to this problem came recently after pluridisciplinary palaeoenvironmental analyses that will be discussed here. The same problems and questions (fresh water vs. marine environments) are met with for Late Palaeozoic fish-bearing sequences as well (e.g., Schultze, 2009).

## 2. General trends of Palaeozoic vertebrate biodiversity

### 2.1. Global pattern

It appears that no general diversity curve has ever been produced for all Palaeozoic vertebrates. Diversity curves have been published only for Silurian–Devonian fishes (Long, 1993) and for Late Palaeozoic tetrapods (e.g., Padian & Clemens, 1985; Benton, 1998; Sahney & Benton, 2008). The PaleoBiology Database (<http://www.paleodb.org/cgi-bin/bridge.pl>) is still very fragmentary for Palaeozoic vertebrates. In order to produce a Palaeozoic diversity curve of vertebrates, I thus used the database of *The Fossil Record 2* (Benton, 1993) (Fig. 2). However, no statistical analysis has been made on these data, and the curve should be corrected after more recently published data on the Ordovician vertebrates (Turner et al., 2004), the Late Devonian – Early Carboniferous vertebrates (Sallan & Coates, 2010), and the Permian tetrapods (e.g., Sahney & Benton, 2008). Vertebrates are understood here as defined by Turner et al. (2004, 2010; also Blieck et al., 2011), that is, excluding conodonts. No pre-Llanvirn/Llandeilo vertebrate is counted by Benton (1993), but *Myllokunmingia* (syn. *Haikouichthys*; Shu et al., 1999, 2003) from the Early Cambrian Chengjiang Fossil-Lagerstätte is a possible vertebrate; *Zhongjianichthys* from the same area of China, although attributed to a myllokunmingiid by Shu (2003), is even more problematic as a vertebrate; the first possible bony vertebrate (euvvertebrate) record might be from the latest Cambrian of Australia (Young et al., 1996); and other, Early Ordovician possible records are reported by Turner et al. (2004). Agnatha of Fig. 2 correspond to all basal jawless vertebrates (ostracoderms + cyclostomes), that is, Pteraspidomorphi (Arandaspida, Astraspida, Eriptychiida, Heterostraci), Thelodonti, Osteostraci, Anaspida, Galeaspida, Cyclostomata, plus Pituriaspida Young (1991), the latter being not reported by Benton (1993); the Ordovician agnathan and gnathostome record (Turner et al., 2004) is shown to be much more diverse than in Benton (1993). No Silurian placoderm is reported by Benton (1993), but Silurian placoderms are known (refs. in Zhu & Wang, 2000; Zhao & Zhu, 2007). No pre-Silurian acanthodian is reported by Benton (1993), but a possible Ordovician record has since been reported (see, e.g. in Turner et al., 2004). There is no pre-Eifelian chondrichthyan in Benton (1993), but Ordovician (Turner et al. 2004), Silurian (e.g., *Elegestolepis* Karatajute-Talimaa, 1973) and Early Devonian (e.g., *Leonodus* Mader, 1986) chondrichthyans are now known. Actinopterygii of Fig. 2 corresponds to basal actinopterygians of Benton (1993).



**Figure 2.** Family-level diversity curve of Palaeozoic vertebrates after Benton's (1993) database. Note that the occurrences are counted by Stage; no distinction is made for singletons, going-through taxa, or boundary-crossers. **Period and Stage name abbreviations:** Trias.-Triassic: SCY-Scythian; Permian: TAT-Tatarian, KAZ-Kazanian, UFI-Ufimian, KUN-Kungurian, ART-Artinskian, SAK-Sakmarian, ASS-Asselian; Carb.-Carboniferous: GZE-Gzhelian, KAS-Kasimovian, MOS-Moscovian, BSK-Bashkirian, SPK-

Serpukhovian, VIS-Viséan, TOU-Tournaisian; Devonian: FAM-Famennian, FRS-Frasnian, GIV-Givetian, EIF-Eifelian, EMS-Emsian, PRA-Pragian (Siegenian), LOK-Lochkovian (Gedinnian); Silurian: PRD-Pridoli, LUD-Ludlow, WEN-Wenlock, LLY-Llandovery; Ord.-Ordovician: ASH-Ashgill, CRD-Caradoc, LLO-Llandeilo, LLN-Llanvirn, ARG-Arenig. **Taxa name abbreviations:** Chondr.-Chondrichthyes, Actinopt.-Actinopterygii, Sarcopt.-Sarcopterygii. **Other captions:** A- Lower-Middle Devonian extinction and turnover from agnathans to gnathostomes (mostly due to radiation of placoderms: Long, 1993); and (B) an end-Carboniferous extinction of mostly chondrichthyans, followed by a slight radiation of actinopterygians and tetrapods. The Lower-Middle Devonian event might be interpreted as an ecological turnover from agnathans to placoderms, by comparison with the Devonian-Carboniferous ecological turnover from placoderms to eugnathostomes (Long, 1990).

Sarcopterygii relate to non-tetrapod sarcopterygians; no pre-Devonian sarcopterygian is counted by Benton (1993), but a Late Silurian record is now known from China (e.g., Zhao & Zhu, 2007). Tetrapoda of Fig. 2 are for basal tetrapods and amphibians; there is no pre-Frasnian tetrapod in Benton (1993), but Eifelian tracks and trackways have since been reported by Niedzwiedzki et al. (2010), as well as a supposed Lochkovian or older track by Warren et al. (1986) (see, e.g., Clack, 1997; Young, 2006; Blicek et al., 2010).

Even if we make corrections based upon the most recently published data, three main bioevents do appear (as shown on Fig. 2 which does not include those corrections). The first one corresponds to the Ordovician to Silurian transition with a possible (but not certain) end-Ashgill extinction, followed by the Rhuddanian (earliest Silurian) Talimaa's Gap (Turner et al., 2004) and a Silurian-Devonian radiation (see Long, 1993). The second one corresponds to the Devonian to Carboniferous transition which is composed of two bioevents: the Frasnian-Famennian extinction which resulted in a 19% loss in genus-level diversity and a slight re-organization in vertebrate assemblage composition (Sallan & Coates, 2010); and the Devonian-Carboniferous turnover (*sensu*, e.g., Long, 1990) which resulted in a 32% loss in genus-level diversity and a restructuring of vertebrate ecosystems worldwide (interpreted as a bottleneck event by Sallan & Coates, 2010). This is followed by the Romer's Gap in tetrapod diversity, which might well be due to an artefact of preservation and/or sampling (see, e.g., Clack, 2002). The third main bioevent is the Mid-Permian Olson's Gap which is related to a strong diversity loss in piscine osteichthyans (both actinopterygians and sarcopterygians),

reptiles and mostly amphibians; it is followed by the radiation of mostly reptiles (Fig. 2; Benton, 1993; Sahney & Benton, 2008). The end-Permian mass extinction is not visible on Fig. 2, but it does occur for tetrapods (Sahney & Benton, 2008). Two other bioevents are shown on Fig. 2: (A) a Lower-Middle Devonian extinction and turnover from agnathans to gnathostomes (mostly due to radiation of placoderms: Long, 1993); and (B) an end-Carboniferous extinction of mostly chondrichthyans, followed by a slight radiation of actinopterygians and tetrapods. The Lower-Middle Devonian event might be interpreted as an ecological turnover from agnathans to placoderms, by comparison with the Devonian-Carboniferous ecological turnover from placoderms to eugnathostomes (Long, 1990).

The first known vertebrates (or supposed vertebrates) from the Cambrian were unmineralized and naked. The first mineralized and armoured ones (euvertebrates) are Ordovician in age; they are agnathans (ostracoderms) such as the Pteraspodomorphi (Fig. 1), but jawed vertebrates (gnathostomes) did already exist. They are characteristic elements of the Great Ordovician Biodiversification Event (GOBE) which corresponds to the setting of the Palaeozoic Evolutionary Fauna (Sepkoski, 1981) that, in turn, may be correlated to the development of plankton (Servais et al., 2008, 2009). Owing to the presently known fossil record, it is difficult to say whether or not vertebrates did suffer of the Hirnantian crisis which is attributed to a glacial episode. Vertebrates seem to be involved in a small radiation event at that time, some of their taxa being still present in the Silurian. However, the number of vertebrate families does decrease at the end of the Ordovician, and there is a gap of record in the Rhuddanian (earliest Silurian) that we have

named Talimaa's Gap (Turner et al., 2004) (Fig. 2). The first actual radiation occurs in the Silurian and Early Devonian, it is mostly due to ostracoderms: this is the "Nekton Revolution of vertebrates". Klug et al. (2010) define this Nekton Revolution in the Devonian for invertebrates, but it is clear that it occurred earlier, i.e. in the Silurian, for vertebrates. The second diversity peak of vertebrates is Frasnian (Late Devonian) in age, and mostly due to placoderms and other predatory fishes (chondrichthyans and osteichthyans), this is what I proposed to name the "Predation Revolution of vertebrates" (Blieck, 2009). This second diversity peak may be partly due to a taphonomic artefact. We indeed know of several Frasnian Fossil-Lagerstätten, such as the localities of Miguasha in Québec, Gogo in Western Australia, or Wildungen (the Schmidt Quarry of fossil invertebrate experts) in Germany, that have provided several tens of fossil vertebrate species each (see, e.g., Carr, 1995). A recent reappraisal of the biodiversity of the Cleveland Member of the Ohio Shale by Carr & Jackson (2009) has also shown that the Famennian fish diversity is probably strongly under-evaluated. So, it may appear that the Late Devonian diversity peak of vertebrates does include both the Frasnian and Famennian, and not only the Frasnian. Alternately, the difference of biodiversity between the Frasnian and Famennian may be due to a high endemism in the Frasnian *vs.* a high faunal exchange rate in the Famennian (see below). Among the two end-Devonian extinction events, the Frasnian-Famennian one (at ca. -375 My) is related to the extinction of 'ostracoderms', but not of all agnathans because some problematic, naked agnathans which may be related to lampreys are known from the Silurian, and cyclostomes (hagfishes and lampreys) do exist from the Carboniferous to the Present (refs. in Janvier, 1996). The Devonian-Carboniferous boundary event (at ca. -360 My) is related to the extinction of placoderms.

The general trends of Early and Middle Palaeozoic vertebrate diversity, as said here above, have been based upon a family-level record (Benton, 1993; Long, 1993) which deserves to be corrected. However, these trends have been corroborated by checking, which has been carried out for placoderms (Carr, 1995 at genus level), for pteraspidomorphs (Novitskaya, 2007, 2008 at species and genus levels), and for all vertebrates (Klug et al., 2010 at genus level). The compiled record of Silurian-Devonian vertebrates of the Chinese palaeocontinents (North China, South China, Tarim: Zhao & Zhu, 2007, 2010) shows a different pattern from Long's (1993) one at a global scale (Fig. 2). Zhao & Zhu (2007, 2010) conclude that there was a main diversity peak in the Early Devonian, with two accessory peaks in the Early Silurian and Mid-Devonian. The main peak is mainly related to Galeaspida (Fig. 1), a group of 'ostracoderms' that is endemic to the Chinese palaeocontinents, and to Placodermi, the most widespread group of Devonian fishes. I have suggested (Blieck, 2009) that this unusual pattern of biodiversity is due to an artefact of prospecting and sampling. It is indeed

in the Silurian and mostly the Early Devonian sequences of South China (particularly of Yunnan) that several basal osteichthyan taxa have been collected in recent years (see, e.g., Zhu et al., 2009). This might well be the trigger for more active prospecting of the sediments of that age in order to find the oldest osteichthyan, the oldest sarcopterygian (which in turn includes the oldest tetrapod), and the centre of origin of those taxa (Blieck, 2009). But as every palaeontologist knows (or should remember), each centre of origin is a "cradle on castors" ...

The Devonian to Carboniferous transition has been a major step in evolution of vertebrates, with extinction of placoderms and radiation of chondrichthyans and osteichthyans (particularly actinopterygians) (Fig. 2). Long (1990) has proposed that chondrichthyans have been replacing placoderms in a great ecological turnover: Famennian durophagous, benthic placoderms such as ptyctodonts, mylostomatids and phyllolepidids would have been ecologically replaced by Early Carboniferous durophagous holocephalan chondrichthyans (a.k.a. as "bradyodonts"), the oldest representative of which has recently been discovered in the Givetian of Boulonnais, northern France (Darras et al., 2008) (see also Cressler et al., 2010). In the same time, Late Devonian marine dipnoans (a group of durophagous sarcopterygians) were replaced by Early Carboniferous freshwater dipnoans (Long, 1990). During the Carboniferous and Permian, the Palaeozoic Evolutionary Fauna (Sepkoski, 1981) which includes the earliest bony and cartilaginous fishes (basal osteichthyans and chondrichthyans) has survived, but without ostracoderms and placoderms which had disappeared during the Late Devonian. It suffered a strong decline at the Permian-Triassic (P-T) mass extinction. The Modern Evolutionary Fauna (Sepkoski, 1981) with its chondrichthyans and osteichthyans, was stable during the Carboniferous-Permian, suffered a strong decline at the P-T extinction, and then made a steady radiation. It is during the Carboniferous that tetrapods became fully terrestrial and made their first adaptive radiation, with faunas that were dominated by amphibians a.k.a. stegocephalians which were terrestrial or secondarily aquatic (Clack, 2002; Laurin, 2008; Steyer, 2009). Amniotic tetrapods (reptiles) became dominant over amphibians during the Permian (Fig. 2). When checking the Middle Permian tetrapod-bearing localities worldwide, a strong hiatus is evidenced between the younger pelycosaur-dominated assemblages of North America and the older therapsid-dominated tetrapod assemblages of Russia (Lucas, 2004). It has been named Olson's Gap (Lucas & Heckert, 2001). This hiatus is equivalent to most of Roadian time (earliest Guadalupian, nearly correlative of the Ufimian: Lucas, 2004), it is at least 2 million years long (Lucas, 2004) or longer (Fig. 2), and it is of global extent. Olson's Gap corresponds to a loss of two-thirds of terrestrial vertebrate life, and so, to a significant remodelling of the Permian tetrapod faunas (Lucas, 2004; Sahney & Benton, 2008). After a late Middle and Late Permian recovery, tetrapod faunas decreased strongly at the end-Permian mass extinction.

## 2.2. A geobiological approach

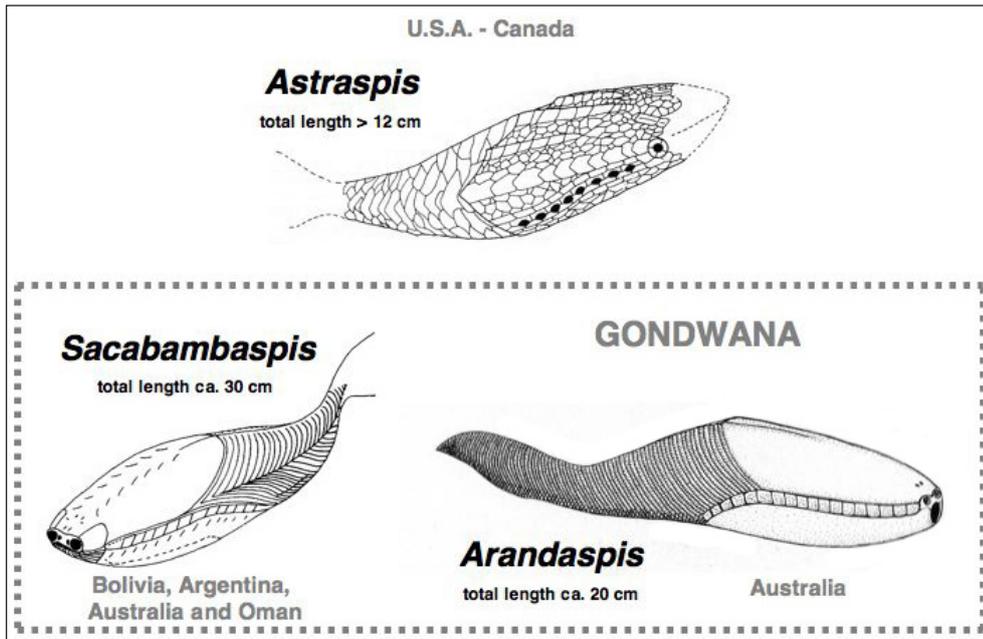
The three main extinction events of the Ordovician/Silurian (Talimaa's Gap), the Devonian/Carboniferous (Romer's Gap) and the Mid-Permian (Olson's Gap) (Fig. 2), are contemporaneous with low temperature episodes at the global scale, at ca. -450, -350 and -260 My respectively (Royer et al., 2004; Berner, 2009). However, they do not seem to be contemporaneous with particular sea-level changes (Haq & Schutter, 2008). The two other, Lower-Middle Devonian and end-Carboniferous extinction events (A and B on Fig. 2) also seem to be contemporaneous with low temperature episodes at ca. -390 / 400 My and -300 My (the latter corresponding to the Gondwanan Ice Age acme: Royer et al., 2004). We may hypothesize that these biotic events and global temperature drops are causally related, but strictly we cannot reject the fact that it might be a mere coincidence as well.

The two end-Devonian extinction events are linked to a global anoxic oceanic event (Walliser, 1996). The triggers of these extinctions are still being investigated. A sequence of tectonic events is confirmed: closing of the Iapetus Ocean, Svalbardian and then Acadian-Ligerian orogenies, deposition of Old Red Sandstones, climatic cooling episode, sea-level drop ... (Averbuch et al., 2005). This long series of global activities began at least in the Middle Devonian. The co-occurrence of an asteroid impact with at least one of both end-Devonian extinctions is still controversial (refs. in Lethiers, 1998).

Most recent hypotheses concerning the cause of at least two of the bioevents which are characteristic for the rise of Palaeozoic vertebrates put forward an increase in the global marine oxygen rate. The first one is the appearance of euvertebrates during the Great Ordovician Biodiversification Event (GOBE) (Saltzman et al., 2011). The second one is the radiation of large gnathostomes (in particular placoderms) during the Devonian adaptive radiation and Predation Revolution of vertebrates (Dahl et al., 2010). Both analyses are based upon the fact that the evolution of Earth's biota is intimately linked to the oxygenation of the oceans and atmosphere, a feature which may be studied with help of geochemical proxies. The Cambrian to Ordovician transition is characterized by a series of global geochemical events, viz., the Steptoean Positive Carbon Isotope Excursion (SPICE) related to a major increase in atmospheric O<sub>2</sub> in the Late Cambrian (Furongian), followed by an increase in plankton diversity in probable relation to increasingly oxic marine environments with a major re-organization of food webs that has triggered the Great Ordovician Biodiversification Event (GOBE) (Webby et al., 2004; Servais et al., 2008, 2009, 2010; Saltzman et al., 2011, fig. 6). In Dahl et al.'s (2010) model, this Cambrian to Ordovician transitional event is part of a first sequence of events that began in the Late Proterozoic (Ediacaran) and are in relation to the rise of animals (metazoans), and in particular an increase in vertebrate maximum length (Dahl et al., 2010, fig. 3). The Devonian rise in atmospheric and oceanic oxygen is larger than the Ediacaran to Ordovician one (Dahl et al., 2010,

figs 1 and 3). It occurred around - 400 Ma and would correlate with the diversification of vascular plants on land and "a pronounced radiation of large predatory fish, animals with high oxygen demand" in the marine realm (Dahl et al., 2010). This Devonian oxygen episode might even be the greatest oxygenation event in Earth history. Previous models of Phanerozoic atmospheric history already predicted a Devonian increase in pO<sub>2</sub> (refs in Dahl et al., 2010). The sequence of related events is presented by Dahl et al. (2010) as follows: radiation of vascular plants, which accelerated land erosion, enhanced global sedimentation rate and the hydrological cycle, and promoted the burial of refractory plant material, and this over long time scales. The enhanced burial of terrestrial organic matter acts as an O<sub>2</sub> source to the atmosphere, and thus to the oceans. The Devonian is also characterized by a strong ("dramatic" in Dahl et al.'s paper) increase in the maximum size of marine vertebrates (Payne et al., 2009) as well as the Nekton Revolution (*sensu* Klug et al., 2010) with "a marked increase in the proportional diversity of 'high energy' predators" (Dahl et al., 2010). Living fish are among the marine animals least tolerant toward hypoxia, and oxygen demand increases with living fish size increase (refs in Dahl et al., 2010). The geochemical results concerning the atmospheric and oceanic oxygen rate would thus "provide a complementary explanation consistent with available physiological data [Bambach, 1999] that the expansion of predators with high metabolic rates reflects increased oxygenation of the biosphere" (Dahl et al., 2010, p. 4).

Both scenarios for the Cambrian-Ordovician and Devonian organic evolution episodes are a pure practice of uniformitarianism in Earth sciences. They may be the best scenarios for explaining all contemporaneous global events of the Cambrian-Ordovician and Devonian bio- and geosphere, but mere coincidences cannot be dismissed. We do not know the detailed and complex interrelationships that existed between all organisms of Cambrian to Devonian ecosystems; we can just, in a few cases, establish rough schemes of trophic interrelationships in food webs. In such conditions, reconstructing all causally related factors of Cambrian-Ordovician and Devonian global geobiological functions is utopian. Additionally, "hypotheses linking evolutionary phenomena to atmospheric oxygen levels can be frustratingly difficult to disprove" (Butterfield, 2009), and "the fundamentally nonuniformitarian nature of Paleozoic and Proterozoic marine ecology must be taken into account" (Butterfield, 2011). In some cases, it has been shown that bioevents such as, for instance, arthropod gigantism and a possible relation to placoderm gigantism (Lamsdell & Braddy, 2010), are not directly related to pO<sub>2</sub>; in such cases it may be that the atmospheric-oceanic oxygen models are wrong as well (refs. in Butterfield, 2009). However, Dahl et al.'s (2010) and Saltzman et al.'s (2011) scenarios are attractive and represent possible solutions. This conclusion is applicable to most, if not all, geobiological scenarios through Earth history (see another example in Blieck, 2010 for the tetrapod origin and first radiation in the Devonian).



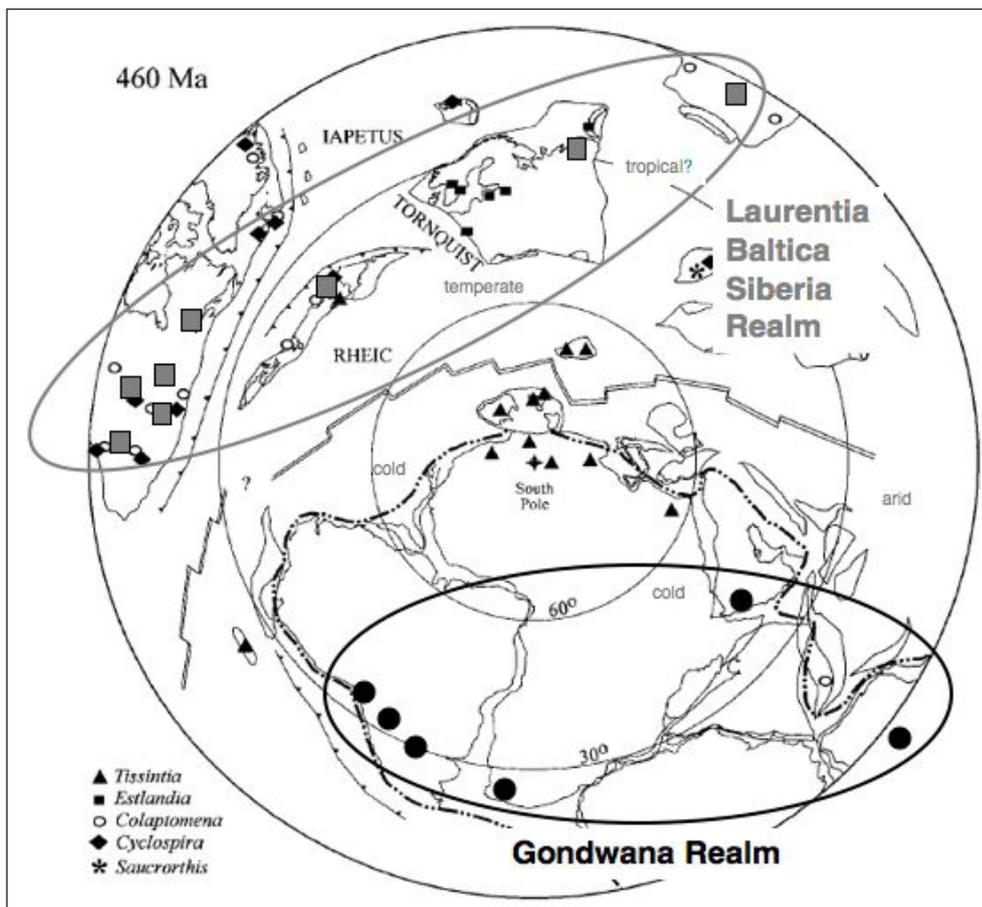
**Figure 3.** Reconstructions of some Ordovician pteraspidomorphs (agnathan euvertebrates) after Sansom et al. (2001, fig. 10.1-10.2).

### 3. A plethora of Early and Middle Palaeozoic armoured fishes

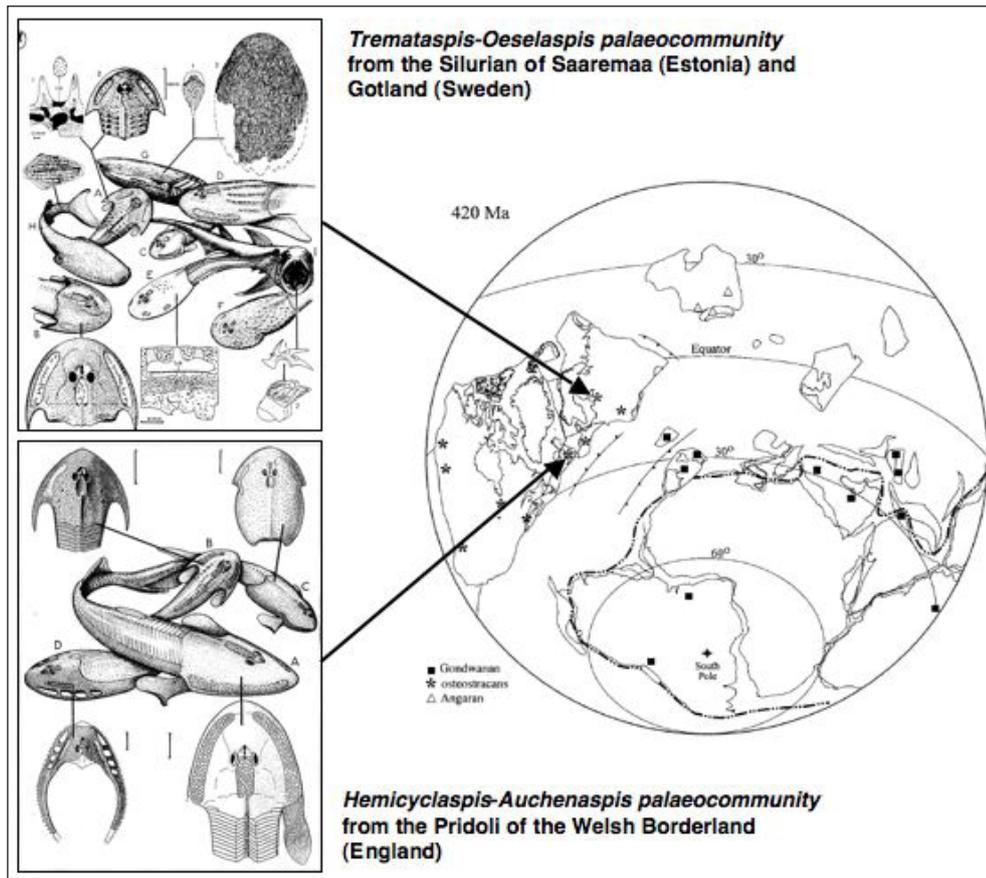
#### 3.1. Cambrian-Ordovician: the rise of fishes

The oldest organism to have been cited as the oldest vertebrate in the recent years is *Myllokunmingia fengjiaoa* (syn. *Haikouichthys ercaicunensis*) from the Early

Cambrian Maotianshan Shales of the Chengjiang Fossil-Lagerstätte of Yunnan, South China (Shu et al., 1999, 2003; Janvier, 2003). It is in fact a basal chordate whose phylogenetic relationships are not firmly established: it is resolved as either stemward to craniates (Fig. 1; Turner et al., 2010; Sansom et al., 2010, fig. 9C) or stemward to vertebrates (Sansom et al., 2010, fig. 9B). It seems to possess a head with two eyes, a series of lateral marks that



**Figure 4.** Palaeoclimatic context of Ordovician vertebrates. Distribution of euvertebrate assemblages: grey squares for the Laurentia-Baltica-Siberia Assemblage localities, and black circles for the Gondwana Endemic Assemblage localities of Blieck & Turner (2003). Nomenclature modified according to Zigaite & Blieck (in press). Palaeocontinental reconstruction for Mid-Ordovician time after Cocks & Torsvik (2002, fig. 5), with Middle and Late Ordovician climatic zones after Scotese (2002).

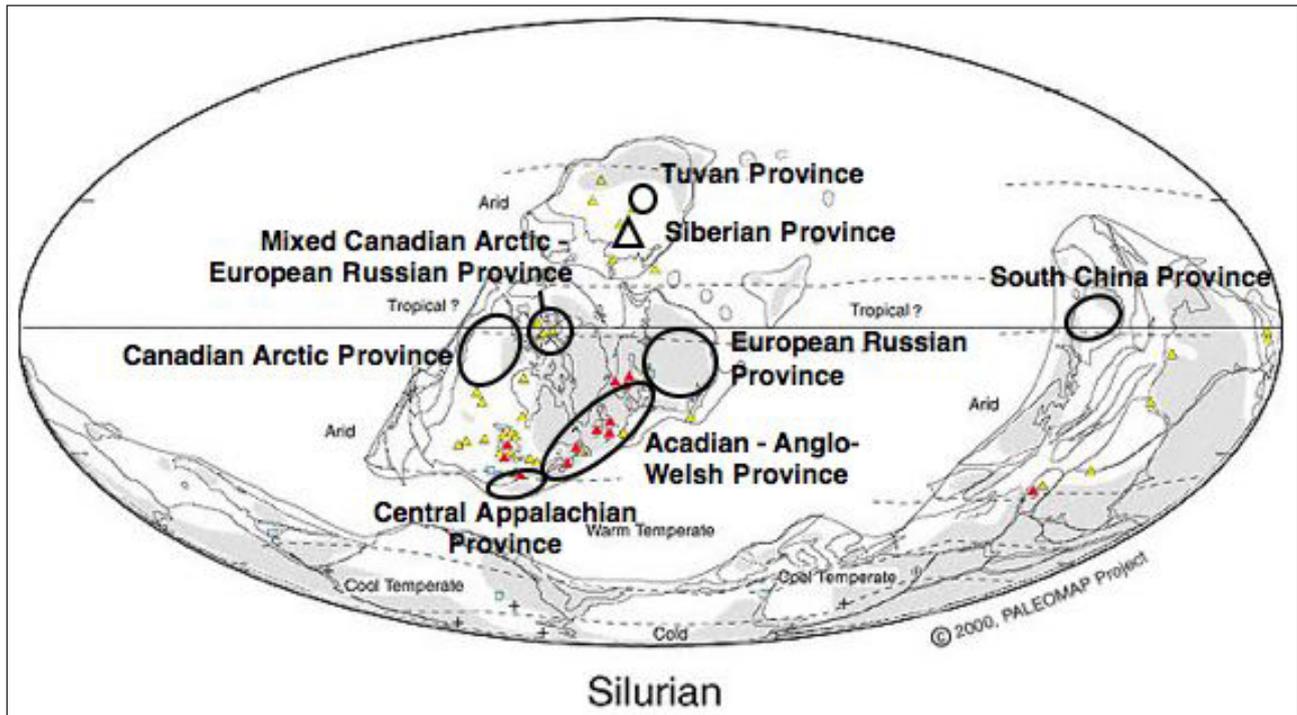


**Figure 5.** Reconstruction of two Silurian euvertebrate assemblages after Blicek & Janvier (1999, fig. 9.3 and 9.7) on the palaeogeographic reconstruction of Cocks & Torsvik (2002, fig. 8).

have been interpreted as paired branchial pouches, and a series of inner unpaired structures that have been interpreted as arcualia (vertebrae), a feature typical for vertebrates. However, it does not show any trace of biomineralized tissue, an argument for interpreting it as a basal taxon. *Zhongjianichthys* from the same area of China, although attributed to a myllokunmingiid by Shu (2003), is even more problematic as a vertebrate, and might just be a badly preserved *Myllokunmingia*. The appearance of vertebrates in the marine Maotianshan sequence is part of the Cambrian biodiversification event, a.k.a. the Cambrian Explosion, which is classically known for the first input of diverse biomineralizations (calcareous, siliceous, phosphatic) of complex animals at a global scale. So, it is astonishing that so few Cambrian vertebrates are presently known, and that they are unossified.

The oldest vertebrates with an outer ossified carapace (exoskeleton) or euvertebrates (Fig. 1) are Ordovician in age and mostly represented by Pteraspido-morphi, that is, agnathans without paired fins, several tens of cms long, and with a paired slanting row of external branchial openings (Fig. 3). Nevertheless, many other Ordovician taxa have been collected in the form of isolated microremains which have been attributed to either agnathans (pteraspido-morphs, thelodonts) or gnathostomes (chondrichthyans, acanthodians, placoderms and other problematic taxa). Except for some enigmatic latest Cambrian to Early Ordovician remains such as *Anatolepis*, the Ordovician taxa have been grouped under two

palaeobiogeographical and biostratigraphical entities: the Mid-Ordovician Gondwana Realm (formerly known as the Gondwana Endemic Assemblage), mostly characterized by the occurrence of arandaspid pteraspido-morphs, and the Late Ordovician Laurentia-Baltica-Siberia Realm (formerly known as the Laurentia-Baltica-Siberia Assemblage), mostly characterized by *Astraspis* and *Eriptychius* in North America (Fig. 3; Blicek & Turner, 2003; Turner et al., 2004; Zigaite & Blicek, in press). Few palaeoenvironmental analyses of North and South American localities have been made. The Harding Sandstone Formation localities of Colorado, USA (Sandbian, formerly Caradoc, with *Astraspis*, *Eriptychius* and others) have been re-interpreted as a shallow marine environment in a marine to coastal transitional zone (Allulee & Holland, 2005; Holland & Allen, 2008). The Anzaldo Formation localities of Bolivia (Darriwilian, formerly Llanvirn, with the arandaspid *Sacabambaspis*, lingulids and trace fossils) are interpreted as nearshore (obduction) deposits in a very shallow marine environment (Davies et al., 2007; Davies & Sansom, 2009). This leads to the conclusion that vertebrates did not originate in fresh water, but in marine environments as shown by the presently known Cambrian and Ordovician localities. The palaeobiogeographical analysis of Ordovician vertebrate assemblages shows that the Gondwana Realm was located in warm to temperate climatic zones, whereas the Laurentia-Baltica-Siberia Realm was in the warm tropical zones on both sides of the palaeo-equator (Fig. 4).



**Figure 6.** Palaeoclimatic context of Silurian euvertebrates. Distribution of agnathan assemblages after Blicek & Janvier (1999) and Lucas (2001). Nomenclature modified according to Zigaite & Blicek (in press). Silurian palaeocontinental reconstruction and climatic indicators after Scotese (2002): small yellow triangles are for evaporites, small red triangles for calcretes, and small blue squares for kaolinite.

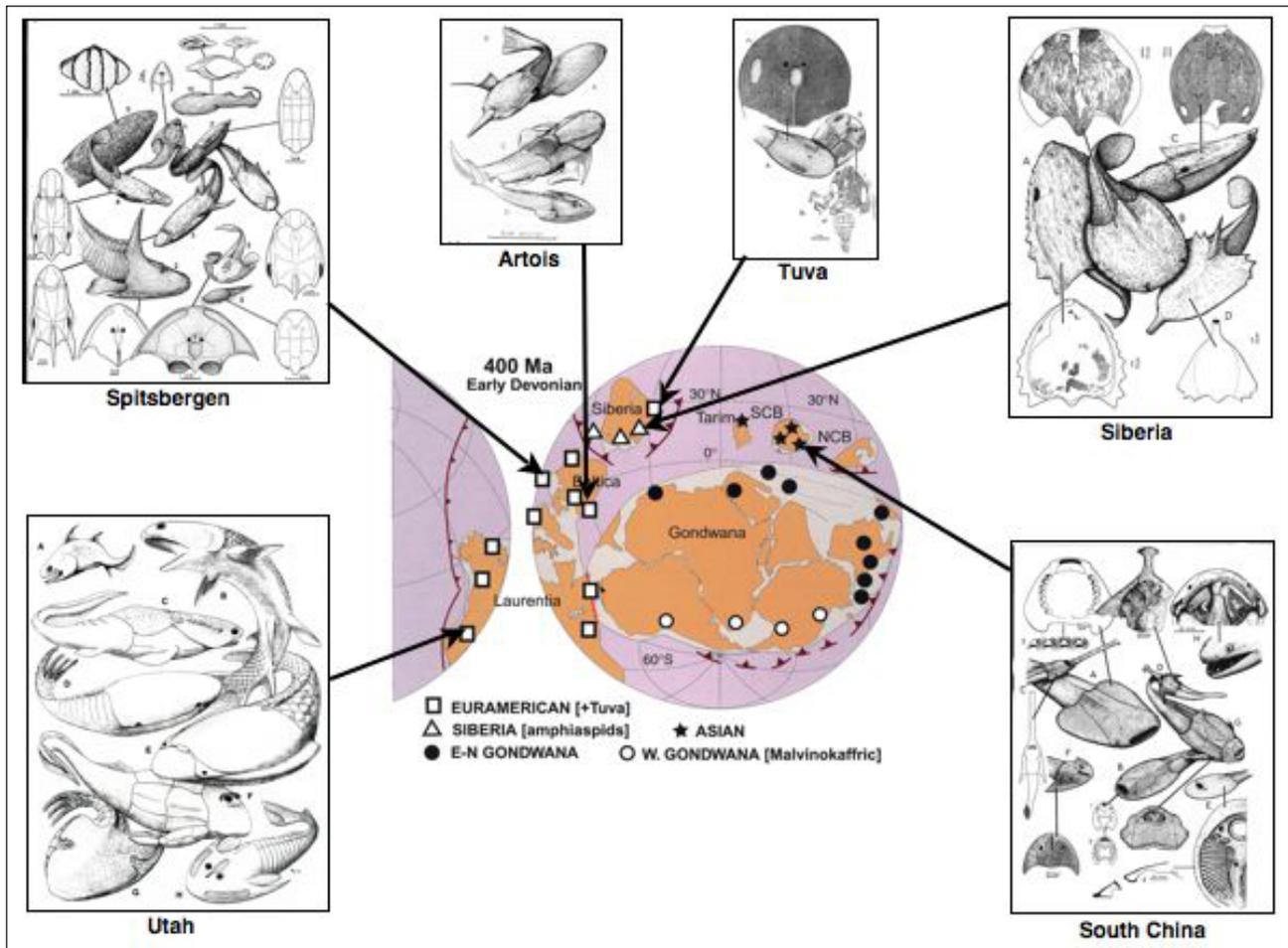
### 3.2. Silurian-Devonian: the age of fishes

It is in the Silurian that vertebrates do experience their first actual adaptive radiation into all possible ecological niches of the marine platforms. Agnathans are dominant in the assemblages (Pteraspidomorphi, Osteostraci, Anaspida, Thelodonti, Galeaspida), but gnathostomes are highly diversified as well (Placodermi, Chondrichthyes, Acanthodii, Osteichthyes) (Fig. 5). Most species are nektonic, either as demersal fishes (nekto-benthic) or as swimmers in the water column (“pelagic”). This pattern has been called the Nekton Revolution of vertebrates (Blicek, 2009), in comparison to the Devonian Nekton Revolution of invertebrates as defined by Klug et al. (2010). Various vertebrate assemblages have been collected on the Silurian marine platform of the Baltic area from very proximal, lagoonal or lagoonal-marine environments down to the outer platform (Märss & Ejnasto, 1978; Bassett et al., 1989; Schultze, 1999). Silurian vertebrates are sufficiently abundant and diverse to enable a biostratigraphic scale to be based upon their macro- and micro-remains. This scale has been mostly based upon thelodonts and acanthodians, and includes 13 biozones that have been correlated to the standard conodont scale (Märss et al., 1995, 1996; Märss, 2000). Several regional assemblages have been defined by Blicek & Janvier (1999), they characterize as many faunal provinces (renamed by Zigaite & Blicek, in press). They are mostly distributed over the warm climatic zones on both sides of the Silurian palaeo-equator (Fig. 6).

The diversification of aquatic vertebrates does increase during the Devonian. Gnathostomes, and in

particular placoderms and osteichthyans, become dominant over agnathans (Fig. 2). It is the “age of fishes”, in fact of armoured fishes (placoderms), which are known from about one thousand species (Carr, 1995, having already counted 720 placoderm species). Devonian fishes are so diverse and abundant that several biostratigraphical scales have been based upon them: heterostracans (and in particular pteraspids), thelodonts, acanthodians, placoderms and chondrichthyans (refs. in Blicek & Turner, 2000). The main difficulty resides in the correlation of those vertebrate-based scales with the standard scale of conodonts. The vertebrate scales have indeed been established after the rich vertebrate-bearing Old Red Sandstone facies and equivalents, which are usually devoid of marine bio-indicators such as conodonts, ostracodes, brachiopods, trilobites, cephalopods, corals.

Devonian vertebrates have occupied many different ecological niches from continental environments to the most distal environments of the marine platforms. Different morphological adaptations are known for species that were living near to the bottom of the sea (nekto-benthic / demersal), in the water column (nektonic), or near to the surface (epinektonic) (Janvier, 1996). Some demersal species, that may have been burrowing, were blind although others have developed bony spiny superstructures, most probably in relation to their high energy aquatic environment (Janvier, 1996, fig. 7.10G). All these species are endemic to either a region, or a marine platform, or even a palaeocontinental margin, and are thus good palaeocontinental markers (Young, 2003; continental *sensu* Rosen, 1974). Other species on the

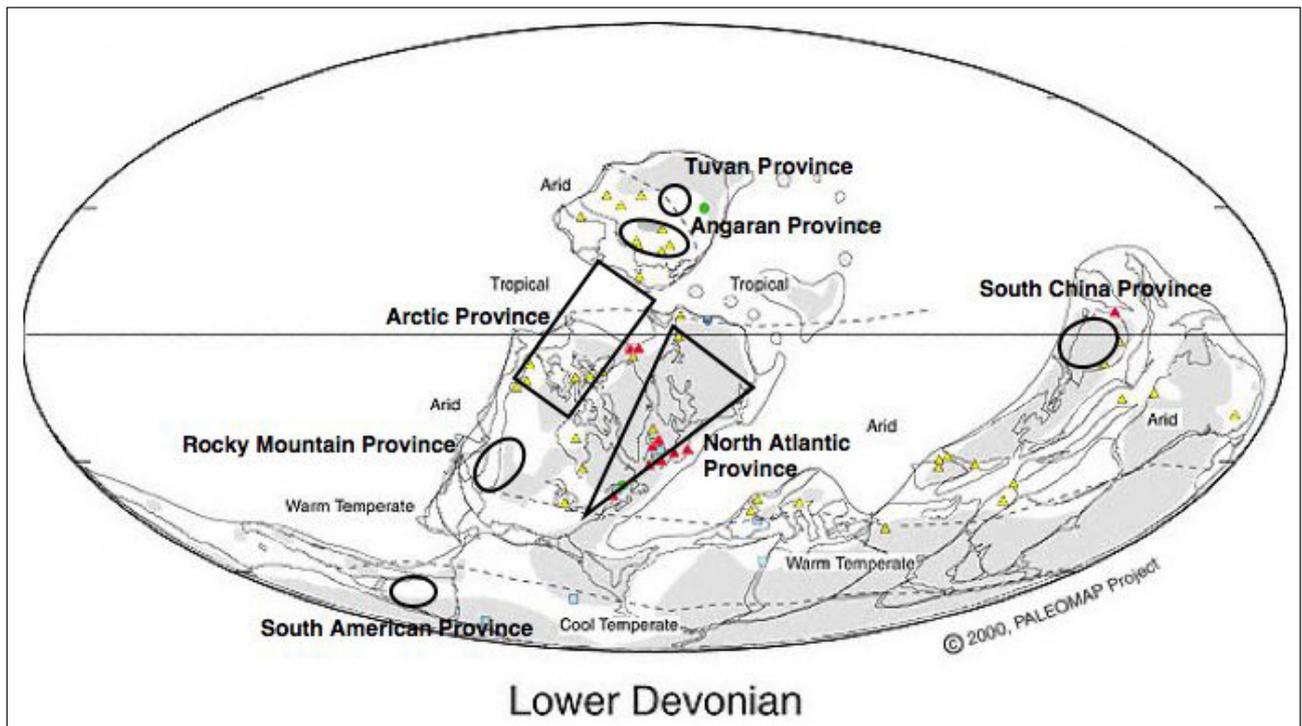


**Figure 7.** Reconstruction of some Early Devonian euvertebrate assemblages after Blicek & Janvier (1989, fig. 12; 1999, fig. 9.8, 9.11 and 9.13) and Elliott et al. (1999, fig. 1), on Li & Powell's (2001) palaeogeographic reconstruction (after Young, 2003, fig. 2), illustrating the Early Devonian vertebrate endemism (palaeobiogeographic provinces of Young, 2003).

contrary were “pelagic”, and eventually capable of transoceanic migrations; they are collected in sedimentary sequences of various palaeocontinents and constitute good biostratigraphical indicators. This is the case with some turiniid thelodonts and phoebodont chondrichthyans in Middle and Late Devonian carbonate facies (refs. in Blicek & Turner, 2000). Early Devonian assemblages show a rather high level of endemism (Fig. 7) in relation to dispersed palaeocontinental masses. This endemism is thought to have decreased in the Middle and Late Devonian in relation to a more compact pattern of land masses, in a pre-Pangaeian configuration of Earth (e.g. Golonka, 2000; Cocks & Torsvik, 2002; Scotese, 2002; Torsvik & Cocks, 2004; Young, 2003; Blakey, 2005; Averbuch et al., 2005). The Early Devonian vertebrate assemblages allow the definition of different faunal provinces, which are all distributed in the warm climatic belts, except a South American Province which does correspond to the Malvinokaffric Province (Malvinokaffric Realm of Boucot, 1975) of brachiopods in the cool temperate climatic belt (Fig. 8; Blicek & Janvier, 1999). This Early Devonian, South American Province of vertebrates has been analyzed in detail by Janvier & Maisey (2010) who define it as a « chondrichthyan- and acanthodian-

dominated fauna » with an endemic Emsian-Eifelian *Pucapampella-Zamponiopteron* community. The latter is also known in South Africa (refs. in Janvier & Maisey, 2010: 443-445).

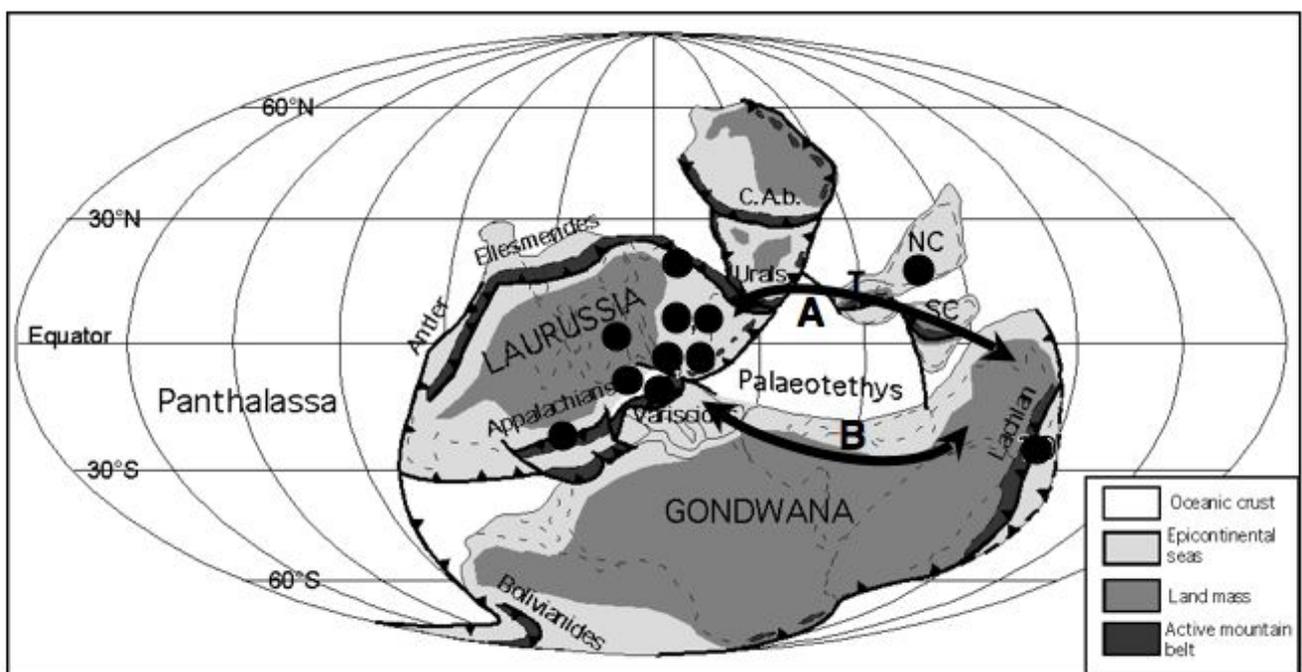
In the Middle Devonian, diversity of agnathans begins to decrease whereas gnathostome (placoderm and sarcopterygian) diversity correlatively increases (Fig. 2: A). As in the Early Devonian, vertebrate assemblages from the Old Red Sandstone are different from those of the marine carbonate platforms. However, similar assemblages at the genus level have been collected from the Middle Devonian of the Orcadian Basin of Scotland, the East Baltic Basin and the Boulonnais inlier of northern France, which has been used as an argument for marine influence within the Orcadian Basin (Lelièvre et al., 1988) (see sections 5.3 and 5.4). As said here above, during the Late Devonian, most palaeocontinental masses converged into a pre-Pangaeian configuration with closing of the Iapetus and then Rheic palaeoceans, a sequence of orogenic events which began earlier in the Middle Devonian. It is in this context that tetrapods appeared. They are derived from a special group of sarcopterygian fishes, that is the Panderichthyida (or Elpistastegalia) which are known from the Late Devonian of northern and



**Figure 8.** Palaeoclimatic context of Early Devonian euvertebrates. Distribution of agnathan vertebrate provinces after Blicek & Janvier (1999). Early Devonian palaeocontinental reconstruction and climatic indicators after Scotese (2002): same captions as on Figure 6, plus: small green circle for coal.

eastern Canada and of the Baltic States. Those first tetrapods are now mostly considered to have been aquatic animals (in particular *Acanthostega*; see Clack, 2002). They come from the Late Devonian of the Old Red Sandstone Continent (Laureuropa), North China and East Gondwana (some mentions from Brazil and Kazakhstan

are either incorrect or have not been confirmed). Their palaeoenvironments are interpreted as being either continental (fluvial, lacustrine), intermediate (alluvial plains, estuarine), or proximal marine (coastal) (Clack, 2002; Clément et al., 2004; Blicek et al., 2007). Their nearly worldwide distribution, even if the fossil record is

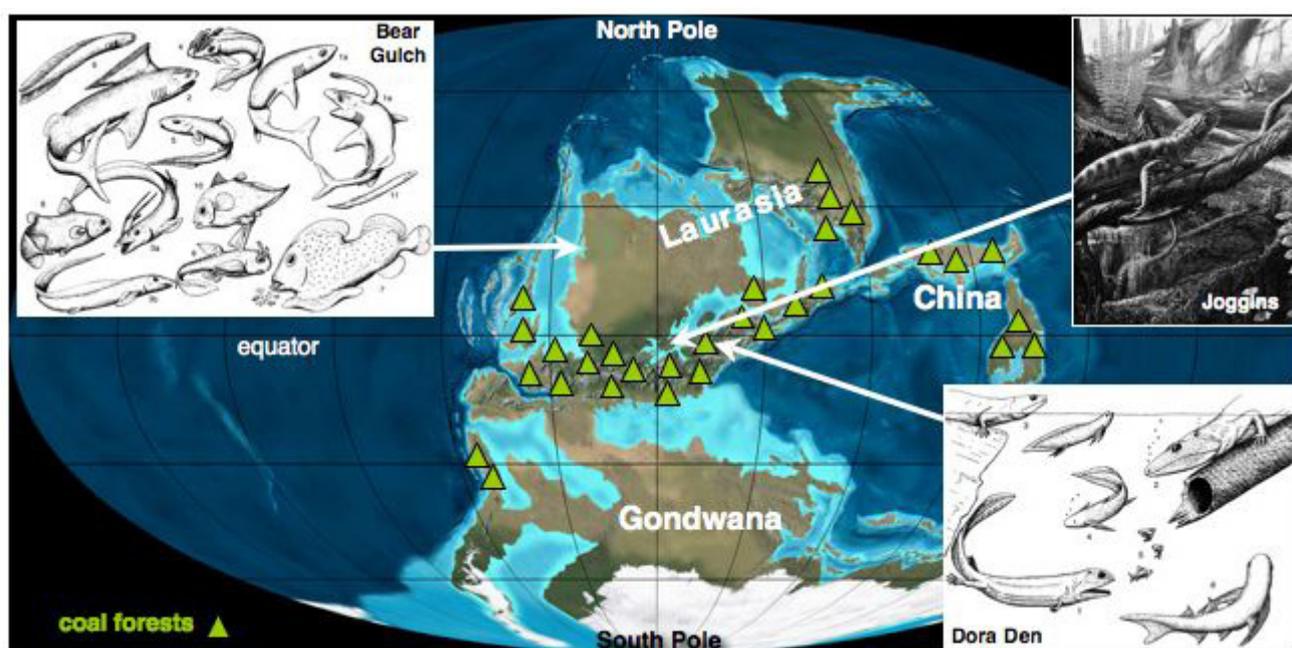


**Figure 9.** Distribution of the Late Devonian tetrapod-bearing localities on Averbuch et al.'s (2005) Frasnian-Famennian palaeocontinental reconstruction. Abbreviations: C.A.b.- Central Asian belt; NC- North China; SC- South China; T- Tarim (modified after Blicek et al., 2007, fig. 3). This distribution is based upon bony remains only, not trace fossils (tracks and trackways). Note the nearly worldwide distribution. Two dispersal routes, a northern one (A) or a southern one (B), may be hypothesized.

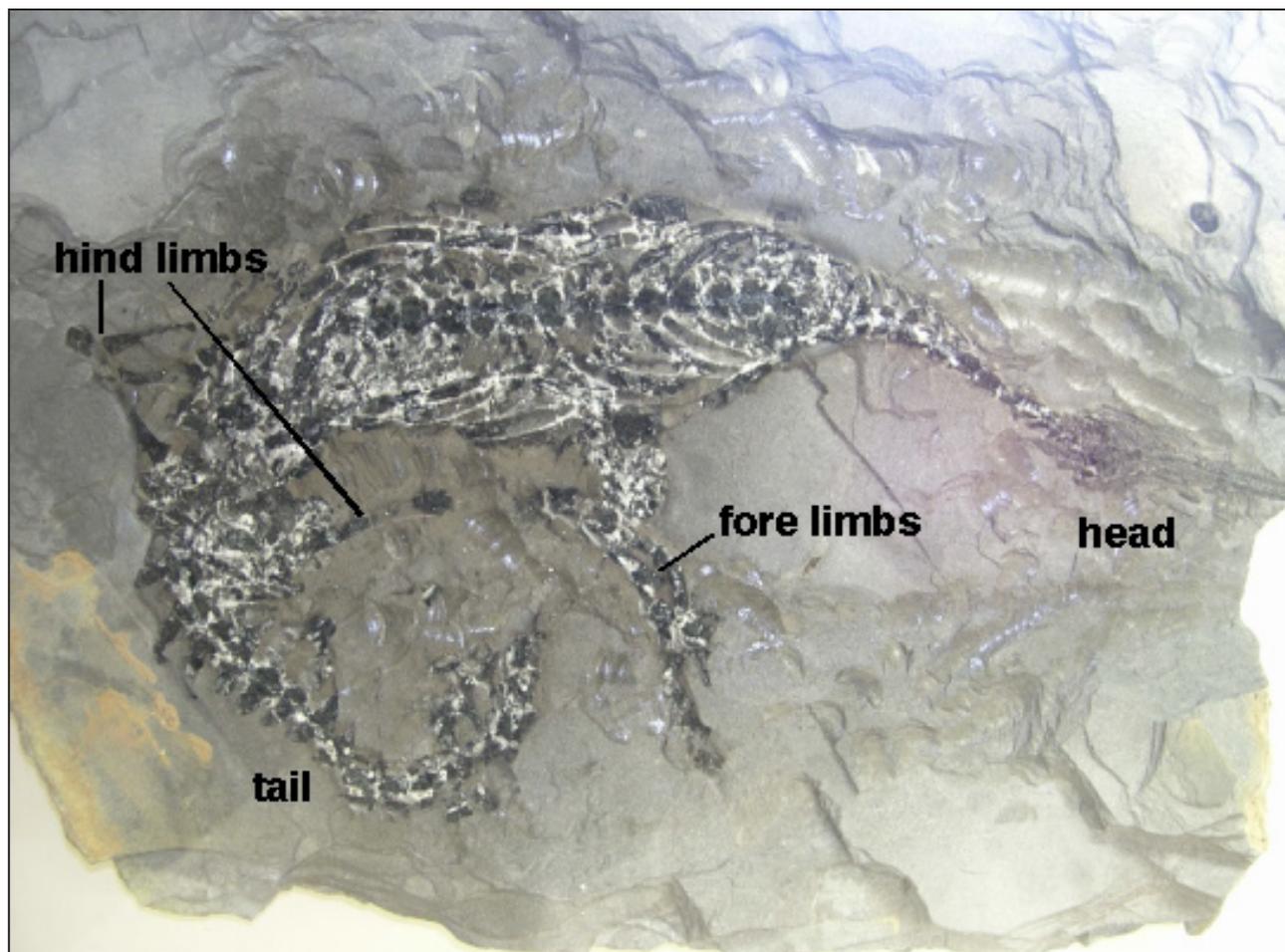
quite incomplete, may be used as an argument for a compact distribution of Late Devonian landmasses (Fig. 9). Many regions have not been prospected, and many museum and university collections have not been revised, so we can hope to find more Devonian tetrapods in the future as recently occurred in South Timan (Ahlberg et al., 2010; Luksevics et al., 2010). A recent and demonstrative case is the discovery of a Famennian "*Ichthyostega*-like" specimen in Belgium (Clément et al., 2004; *Ichthyostega?* sp. in Blicek, 2010): this specimen was originally attributed to a sarcopterygian fish by Lohest (1888b) whereas the first mention of a Devonian tetrapod in Belgium by Lohest (1888a) turned out to be of a dipnoan (Clément & Boisvert, 2006). Another recent discovery sheds new light on the earliest tetrapods. As was expected from the previously known fossil record, the origin of tetrapods might have occurred in the Middle Devonian (e.g. Clack, 2002, 2006b, 2007) or earlier in the basal Devonian (Young, 2006). The discovery of numerous tetrapod tracks and trackways from the Eifelian of Poland (Niedzwiedzki et al., 2010) has thus confirmed this prediction. The detailed stratigraphical and sedimentological analysis of Niedzwiedzki et al. (2010) clearly shows that these earliest known tetrapod remains were walking in nearshore shallow marine environments. Strictly it does not prove that tetrapods originated in marine environments. However, as we have no confirmed indication of older tetrapods in relation with freshwater environments, I will retain the marine hypothesis as the most parsimonious one. A possible Early Devonian tetrapod track from Australia has recently been re-analyzed by Young (2006) and Blicek (2010), but still deserves to be confirmed.

#### 4. The Late Palaeozoic rise of toothed fishes and terrestrialization of tetrapods

As already said, the Carboniferous-Permian fish assemblages are dominated by chondrichthyans and osteichthyans. One of the best examples is the Late Mississippian (Namurian) marine assemblage of Bear Gulch, in Montana, USA. The Bear Gulch locality is what is known as a Konservat-Fossil-Lagerstätte in which well-bedded limestone layers with rhythmic microturbidites contain extremely well-preserved fossils (The Bear Gulch Limestone is one of a series of limestone lenses within the Late Mississippian Heath Formation of Montana and North Dakota that have collectively been named the Bear Gulch Limestone Member). It has yielded one of the most diverse fossil fish assemblages in the world, with approximately 130 species of fish excavated over the last 35 years. The site also contains well preserved arthropods, sponges, starfish, conulariids, worms, and other soft-bodied organisms, as well as brachiopods, bryozoans and molluscs. The fishes of the Bear Gulch Limestone include a lamprey, an acanthodian, over 65 species of "sharks" (chondrichthyans), seven sarcopterygians including six coelacanths and a rhizodont, and several tens of species of ray-finned bony fishes (actinopterygians). Fossils are preserved along a taphonomic spectrum that ranges from scattered scales to completely preserved sharks with their arterial and venous systems and skin pigments intact (see refs. in Lund, 1990; Lund & Poplin, 1999; and on the Web site [http://www.sju.edu/research/bear\\_gulch/](http://www.sju.edu/research/bear_gulch/)). The Bear Gulch limestone is up to ca. 30 m thick and approximately 13 km in east-west extent, and was deposited in a shallow, muddy, tropical marine bay 318 million years ago (Grogan



**Figure 10.** Three "Middle" Carboniferous vertebrate-bearing localities (Bear Gulch, Montana, Namurian; Dora Den [East Kirkton], Scotland, Viséan; and Joggins, Nova Scotia, early Pennsylvanian) on a nearly Pangaeian configuration of landmasses with wide southern, Gondwanan glaciation. Reconstructions of vertebrate faunas of Bear Gulch and Dora Den after Janvier (1996, fig. 1.19 and 1.20), and of Joggins after the Joggins fossil cliffs Web site (15th UNESCO World Heritage Site; <http://jogginsfossilcliffs.net>, modified after an image of John Sibbick ©). Early Pennsylvanian palaeocontinental reconstruction of Blakey (2005) at -300 My.



**Figure 11.** Young individual of *Mesosaurus* (probably *M. tenuidens*, ca. 50 cm long), an anapsid reptile from the Irati Formation, late Early Permian of the Parana Basin in Brazil; specimen of the Centro de Paleontologia, Rio Negro, SE Parana, Brazil, photographed on May 29, 2004 during the post-congress field trip to the Palaeozoic of Parana Basin (10th International Symposium on Early/Lower Vertebrates & IGCP 471 + 491 meetings). Photograph kindly provided by Claire Derycke ©.

& Lund, 2002). The latitude of the bay was approximately  $12^\circ$  from the equator at the time of deposition. The climate of the surrounding area must have been seasonally quite arid, as there are gypsum beds in adjacent parts of the Heath Formation. Fish faunal diversity is high, while invertebrate diversity is only moderate. The high diversity of fish and the wide range of body forms (with several examples of convergent adaptations both in chondrichthyans and actinopterygians – such as eel-like or laterally flattened phenotypes) is evidence of a complex ecosystem most similar to modern bay or estuarine communities.

A little older than Bear Gulch is the Viséan (Brigantian) Fossil-Lagerstätte of East Kirkton, West Lothian, Scotland, composed of a ca. 15 m thick volcano-sedimentary sequence with laminated and spherulitic limestones. This sequence includes stromatolites and gypsum pseudomorphs (Rolfe et al., 1994), but also black shales, and is interpreted as having been deposited in a shallow lake, set within a richly vegetated landscape formed of volcanic cones a few hundred metres high (Clarkson et al., 1994). At times, water temperatures may have risen sharply through localised hot-spring activity which prevented normal aquatic life. The bulk of the

preserved biota consists of plants and dominantly land-living animals, including the oldest terrestrial tetrapods (amphibians and reptiliomorphs), large terrestrial-aquatic eurypterids, the first harvestman (opilionid arachnid) and rare millipedes. The occurrence of the black shales with a ‘standard’ Oil-Shale fish fauna (including chondrichthyans, dipnoans, actinopterygians and acanthodians) suggests that the lake had links with a larger fish-bearing water body (Clarkson et al., 1994).

Younger than those two latter fossiliferous sites are the Fossil-Lagerstätten of the Joggins Formation (early Pennsylvanian, Langsettian) of Nova Scotia, eastern Canada, which have yielded fossil parautochthonous assemblages with 96 genera (148 species). Three groups of ecosystems have been defined: retrograding coastal plains and brackish seas, wetland terrestrial ecosystems, and dryland terrestrial ecosystems with rich assemblages of fully terrestrial organisms (plants, arthropods, molluscs, annelids, tetrapods) (Falcon-Lang et al., 2006). Joggins records a completed terrestrialization of plants, invertebrates and vertebrates. Those three localities, Bear Gulch, East Kirkton and Joggins, give excellent examples of the marine and non-marine vertebrate life in the “Middle” Carboniferous (Fig. 10).

Vertebrate evolution in the Permian did occur both in the marine and non-marine realms, with a strong development of tetrapods. As shown on Figure 2, an important turnover took place from amphibians (stegocephalians) to reptiles (amniotic tetrapods). This occurred during Olson's Gap which is probably causally related to a cold climatic episode globally. Several representatives of the terrestrial clades of tetrapods did encounter a secondary adaptation to aquatic life, either freshwater or marine (Steyer, 2009). The only example that is considered here is the Early Permian (Artinskian) distribution of tetrapod faunas as defined by Milner (1993, fig. 13.3). It does include the Mesosaur Province based upon the genus *Mesosaurus*, the earliest-known amniote that was fully committed to an aquatic mode of life (Carroll, 1988, p. 205). *Mesosaurus* (Fig. 11) is famously known to have been used by Wegener (1915) as one of his palaeobiogeographic arguments for reconstructing part of the Gondwana palaeocontinent (Fig. 12) on his Pangaean model of Earth.

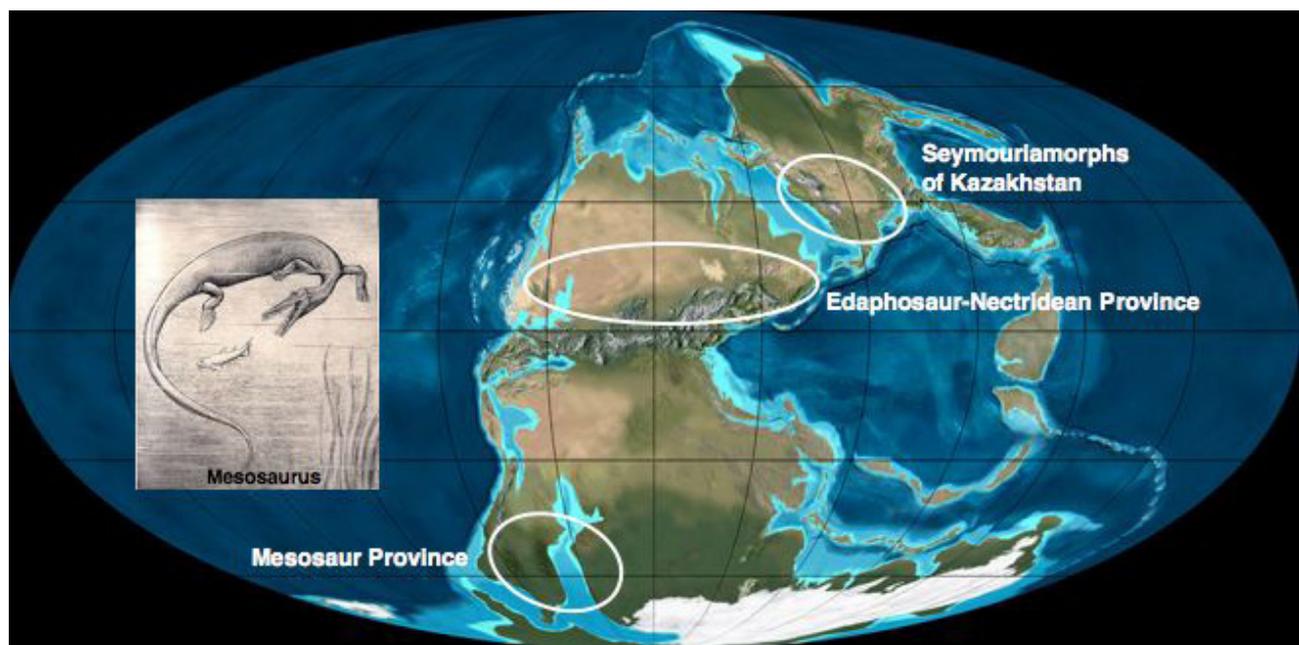
## 5. The special problem of environments of Palaeozoic fish-bearing siliciclastic facies

This problem does concern the Old Red Sandstone of mostly Devonian age as well as Late Palaeozoic (Carboniferous and Permian) siliciclastic vertebrate-bearing formations.

### 5.1. A short historical review

I will not give here a full review of the complex problem concerning the interpretation of palaeoenvironments of those deposits and their vertebrates. Many thematic volumes and books have been devoted to this topic (e.g.,

Friend & Williams, 2000; see also Blicek, 1985). I will simply give a short historical review of the problem for the Old Red Sandstones, followed by recent examples of studies proceeded in the Lower Devonian series of the Ardenne-Rhenish Slate Massif and other areas. The question of the original environment of Devonian vertebrates (fish) has been put forward as early as they were discovered in northern Europe (Scotland and the East Baltic area), when they were supposed to be freshwater (Sedgwick & Murchison, 1835; Kutorga, 1835). The first reviews of Old Red Sandstone (ORS) vertebrate localities have also considered these localities as representing freshwater deposits (Woodward, 1891; Romer & Grove, 1935). During the second half of the 20th Century, the situation has become more confusing. Some authors who based their arguments on geochemical analyses of fish-bearing ORS localities, have maintained the freshwater hypothesis for Devonian heterostracan-bearing localities of Podolia (Ukraine), Wales (UK), and Latvia (Schmitz et al., 1991). For others, geochemical, sedimentological and palaeontological data are in favour of at least partly marine environments (Dasch & Campbell, 1970; Bridge & Droser, 1985; Lelièvre et al., 1988; Marshall & Astin, 1996; Marshall et al., 1996; Knox & Gordon, 1999). For a third category of authors, the situation is more complex: if Ordovician and Silurian vertebrates were marine, their Devonian environments were more diversified, from marine to freshwater (Gross, 1950; Denison, 1956; White, 1958; Goujet, 1984; Blicek, 1985; Schultze & Cloutier, 1996; Lelièvre, 2002). Schultze (1999) has reviewed the fossil record of marine intertidal zones and his conclusions lead one to be cautious: "One should be careful in using fishes as indicators of a particular paleoenvironment ... In contrast to rocky



**Figure 12.** Early Permian (Artinskian) tetrapod provinces after Milner (1993, fig. 13.3) with reconstruction of *Mesosaurus* (Google Image; total length of fully grown adult specimens is ca. 1 m) on Blakey's (2005) Early Permian palaeocontinental reconstruction at –280 My.

shores, coastal areas with a soft bottom are well documented in the fossil record”, which introduces bias in interpreting the original environments of Palaeozoic fishes. So, what seems to come to a consensus to-day is the following:

- We are in a contrasting situation;
- Various techniques of analysis (micropalaeontology, sequence stratigraphy, palaeoecology, geochemistry, clustering methods for biodiversity analyses) give different conclusions;
- Most probably, in Devonian ORS and contemporaneous siliciclastic deposits, a wide array of environments did exist for early vertebrates.

### 5.2. Examples from the Lower Devonian of the Ardenne-Rhenish Slate Massif and other regions

The question can seriously be treated only after precise palaeoenvironmental and palaeoecological studies of selected localities. This has been made for some Ordovician and Silurian sites of North and South America and of the East Baltic region (see sections 3.1 and 3.2 here above; Allulee & Holland, 2005; Bassett et al., 1989; Davies et al., 2007; Davies & Sansom, 2009; Holland & Allen, 2008; Mårss & Ejnasto, 1978; Schultze, 1999). The general conclusion which follows is: (1) that the earliest known vertebrates come from coastal marine environments, and (2) that they colonized all possible environments of the marine Silurian platforms. The situation is more complicated for the Devonian (and sometimes for some Silurian localities as well) because of the deposition of the Old Red Sandstones (ORS) which are mostly composed of post- and late-orogenic siliciclastic sediments, laid down under warm and oxidizing climatic conditions (see, e.g., Friend & Williams, 2000). These sediments are generally devoid of classical marine indicators (such as trilobites, articulate brachiopods, corals, conodonts, most of the ostracodes, organic microfossils ...), which has been a reason to interpret them as continental deposits in a general sense (intermediate, freshwater, terrestrial; see a critical evaluation in Blicek, 1985).

However, recent studies of Lower Devonian localities from the Ardenne (Belgium and Luxembourg) and the Rhenish Slate Massif (Germany) do confirm that the ORS corresponds to various palaeoenvironments, from marine to terrestrial. The Tihange (Huy) section of Belgium has yielded very fragmentary remains of vertebrates (heterostracan pteraspidomorphs) and arthropods (Thirion & Blicek, in press) which probably result from an important *post mortem* transportation before deposition under high energy hydrodynamic conditions. These fossils are preserved in various fine to coarse siliciclastic lithofacies, including intraformational conglomerates. Goemaere et al. (2006) interpret the Marteau Formation of this section (MF, Lochkovian) as “indicative of a mature fluvial plain” and the Bois d’Ausse Formation (BAF, Lochkovian-Pragian) as “predominant shoreline environment of tidal type alternating with coastal plain deposits”, which indicates a progressive shift from a continental environment (MF) to

a more marine environment (BAF). In Luxembourg, Michel et al. (2010) have studied the mid-Emsian Clervaux Shale Formation of Himmelbaach Quarry in the Wiltz Synclinorium. The palaeoenvironmental analysis of this region is difficult because of structural deformation and lateral variations of facies, a feature which is encountered in nearly all Lower Devonian siliciclastic sections of the Ardenne-Rhenish Slate Massif. Michel et al. (2010) defined three different facies: (1) an argillaceous sandstone facies; (2) lenticular- to wavy-bedded sandy argillites, argillaceous sandstones and quartz arenites; and (3) a quartz arenite. These facies are interpreted as “a tide-dominated marginal-marine depositional model composed respectively of tidal channels (1), a tidal flat (2), and a tidal sand ridge (3)” (Michel et al., 2010). The section of the Alken a/Mosel quarry in Germany shows the late Early Emsian, Nellenköpfchen Formation. It is composed of well bedded sandstones with fine-grained intercalations (the Lower and the Upper Alken Fossiliferous Units), which have yielded both terrestrial and marine fossils, including vertebrates (heterostracan pteraspidomorphs, placoderms and sarcopterygians). This section has been interpreted as representing probably “a high energy marine-to-brackish coastal sedimentary depositional environment ... with intertidal conditions”, that is, a land/sea transitional environment at the margin of a possible Hunsrück Island or Archipelago (Wehrmann et al., 2005; also Stets & Schäfer, 2009).

Additionally, such analyses have been proceeded with in other Lower Devonian localities of the World. I give here only two examples, one from East Europe and one from North America. In East Europe, Uchman et al. (2004) have studied the Lochkovian red beds of the Dnestr Formation in Podolia, Ukraine. This ORS vertebrate-bearing series “record[s] an upward transition from marginal-marine to fluvial conditions”, with three facies associations: “offshore lagoon, inshore lagoon or bay, and a fluvial-estuarine plain” (Uchman et al., 2004), again at the land-sea transitional area. The long time “unique” placoderm and chondrichthyan faunal assemblage from this Early Devonian ORS series of Podolia (including the arthrodire *Kujdanowiaspis* whose species *K. buczacziensis* may be used to define the Lochkovian-Pragian boundary: Dupret & Blicek, 2009) has been found in a marine sequence of Spain, and thus challenges the non-marine status of the Podolian deposits and their vertebrates (Dupret et al., 2010). In North America, Zorn et al. (2005) have made a sedimentary and faunal analysis of the Lochkovian Man On The Hill (MOTH) vertebrate-bearing sequence, Mackenzie Mountains, Northern Territories, Canada. Their preferred interpretation is that “the vertebrate-bearing interval was deposited on the outer margin of a carbonate platform within an intra-shelf topographic low below storm-wave base”. What is interesting in this result is that the MOTH locality has many vertebrate taxa in common with the Lochkovian, typical ORS series of Spitsbergen (refs. in Blicek, 1984; Zorn et al., 2005). I use this result as an additional argument for the non-continental condition of most, if not

all, vertebrates of the Lower Devonian of Spitsbergen (see, e.g., Blicek, 1985).

### 5.3. Freshwater vs. marine habitats: a semantic problem

This problem has been put forward by several authors in the past, as e.g. by Goujet (1984), Blicek (1985), Lelièvre et al. (1988), Schultze & Cloutier (1996), Schultze (1999) and Lelièvre (2002). A series of words are concerned with, and needs to be (re)defined (see, e.g., <http://www.thefreedictionary.com/>):

- Continental: relating to, or characteristic of a continent;
- Continent: one of the principal land masses of the Earth (geography); part of the Earth's crust that rises above the oceans and is composed of sialic rocks, including the continental shelves (geology);
- Freshwater: relating to, living in, or consisting of water that is not salty; situated away from the sea, inland;
- Terrestrial: relating to, or composed of, or growing on land, not aquatic; or belonging to, or living or growing on the land as opposed to the sea or air.

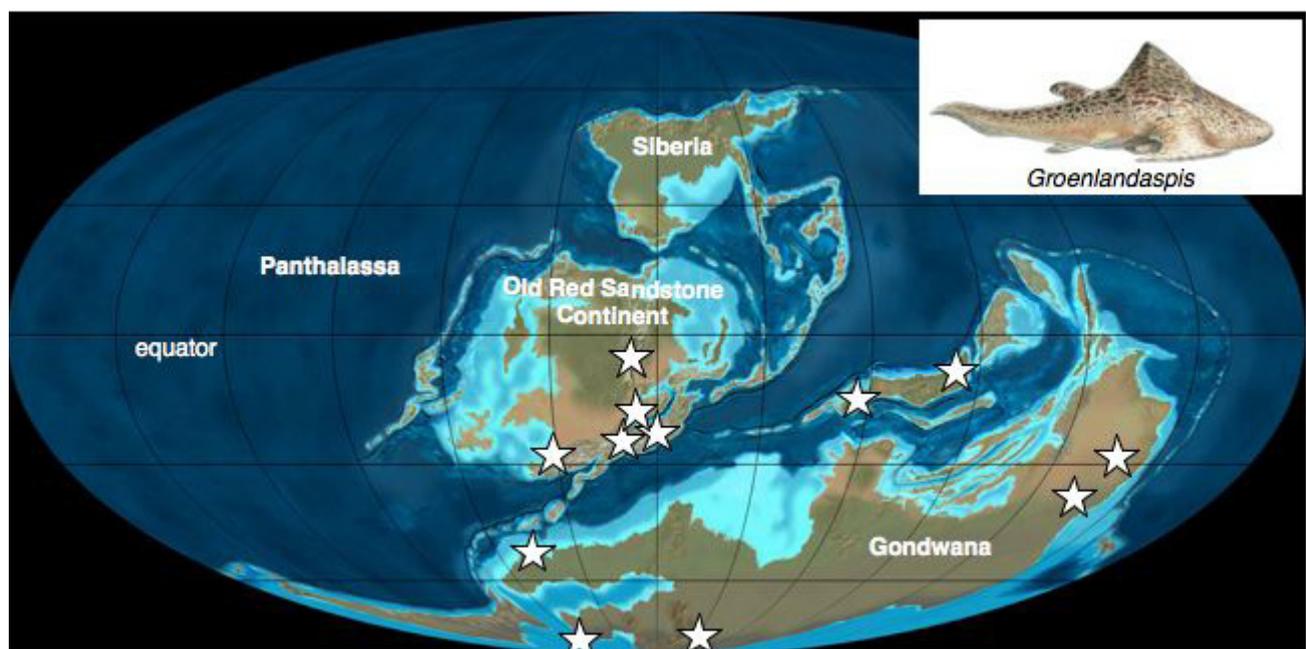
We are thus confronted with various problems: (1) in recognizing aquatic from non-aquatic conditions (sedimentology, palaeontology, palaeogeography, geochemistry, etc.); (2) in recognizing sediments deposited either on the geographical continent or on continental shelves (sedimentology, palaeontology, palaeogeography, etc.); and (3) in recognizing non-salty water (geochemistry) and/or connection or not with the sea (palaeogeography).

Gray (1988) defined eight criteria for recognizing the freshwater habitats: 1- depositional environment, 2- functional morphology, 3- taxonomic uniformitarianism, 4- behavior, 5- absence of marine fossils, 6- taphonomy,

7- community analysis, 8- palaeogeography. But for Schultze (2009) only criteria 6 and 7 are acceptable for identification of an environment, and for criterion 7 the freshwater taxa have to be identified, which is not so easy to do when based upon merely palaeobiological factors. Behrensmeier et al. (1992) defined “terrestrial” as “most known preservational circumstances for terrestrial organisms”; it includes the following environmental contexts: coastal marine (offshore, beach, lagoon, estuary), fluvial/deltaic, lacustrine, volcanigenic, eolian, others (their table 2.1). For instance: ‘lagoon’ and ‘small deep lake’ are both defined by occurrence of macroplant ++, microplant ++, invertebrate (+), vertebrate ++, and ichnofossil +/- remains; this does in fact introduce confusions between very different environments, particularly as concerned with the very proximal, coastal marine environments when they are treated as “continental” or “terrestrial”. An application of this is the problem of the Middle Devonian Orcadian Basin of Scotland which is considered as either totally disconnected from the NW European marine shelf environments or not (Lelièvre et al. 1988; Marshall et al. 1996, 2007; Newman & Trewin 2008), and can thus be interpreted as either a lacustrine environment or not (see also Marshall et al., 2010; Newman, 2010; Newman & Davidson, 2010). All this means that we are facing a real problem of semantics when working on such facies as the Old Red Sandstone and allied siliciclastic Palaeozoic facies with vertebrates and no classical marine indicators.

### 5.4. Devonian to Permian freshwater vs. marine habitats: more general considerations

Carr & Jackson (2009) clearly settle the problem of



**Figure 13.** Palaeogeographic distribution of the arthrodire genus *Groenlandaspis* (after Carr & Jackson, 2009, fig. 5.8 modified) on the Late Devonian palaeocontinental reconstruction of Blakey (2005) at -370 My. Reconstruction of *Groenlandaspis* from <http://www.fossilraptor.be/faunedudevonienvetebres.htm>, modified after <http://www.devoniantimes.org/who/pages/groenlandaspis.html> (image of Dennis C. Murphy ©).

freshwater vs. marine habitats for Devonian vertebrates:

- freshwater interpretations are often associated with arguments of negative evidence (lack of acritarchs, lack of detected marine invertebrates, ...);
- it is difficult to argue for the global dispersal of a freshwater taxon such as the arthrodire placoderm *Groenlandaspis* across all of Gondwana and Euramerica (the genus is known both in putative freshwater sediments and in marine deposits) (Fig. 13);
- the Famennian, Cleveland Member of the Ohio Shale (a.k.a. “Cleveland Shale”), with its 65+ fish species, clearly represents sediments deposited in a marine environment within the Appalachian Basin;
- in their vast majority, the late Devonian (Givetian to Famennian) vertebrate faunas are suggestive of marine or marginal marine interpretations for the sediments in which they are preserved (Schultze & Cloutier, 1996; Lelièvre, 2002);
- this implies that tetrapods originated in marine influenced habitats and that fully freshwater faunas are a product of the Carboniferous Period; this proposal is in contradiction with Retallack et al.’s (2009) conclusion of a terrestrial habitat for the tetrapods from the Famennian, Duncannon Member of the Catskill Formation, Pennsylvania, USA (see also Blicck, 2010).

Schultze (2009) reviewed the interpretation of freshwater vs. marine habitats for Permo-Carboniferous vertebrates:

- an aquatic environment can be characterized by organisms which lived in that environment only; terrestrial (tetrapods, plants) or flying (tetrapods, insects) taxa cannot be used as indicators;
- the distribution of aquatic taxa over different aquatic environments has to be investigated to identify the environments in which the taxa lived (faunal comparisons at same time intervals);
- only positive arguments can be used; so, only the occurrence of typical marine organisms (such as myxinids, articulate brachiopods, cephalopods, corals, ...) identify environments as marine;
- the lack of typical marine organisms does not indicate that the sediments were not marine, only that these indicators are absent (hostile environment, unfavorable depositional conditions, diagenesis, ...);
- a freshwater environment as well has to be identified by positive indicators (criteria 6 and 7 of Gray, 1988: taphonomy and community analysis);
- histological and geochemical data can also provide solid arguments to determine the palaeoenvironments (temperature, salinity, oxygenation, ...);
- sedimentological criteria may be useful (e.g. possible tidal sedimentation and relationship with taphonomy).

Under such conditions, it appears that many (but not all) Palaeozoic vertebrate experts are very critical about the following points:

- A freshwater origin of vertebrates is unlikely because, as said here above, Cambrian, Ordovician and Silurian vertebrates are certainly marine; another positive argument

comes from the phylogenetic relationships of vertebrates: the sister-group of the taxon “craniates (vertebrates (euvertebrates))” is a group of marine organisms, viz., the “protochordates” or tunicates + cephalochordates (Fig. 1 without taking into account the controversial relationships of conodonts) ; so, the most parsimonious hypothesis is that vertebrates did originate in the marine realm.

- A freshwater environment for most (if not all) Devonian vertebrates of the Old Red Sandstone facies is unlikely when critically considering the set of criteria used for establishing their palaeoenvironments; Devonian vertebrates are also known in typical marine environments where they are associated with classical marine invertebrate indicators (articulate brachiopods, trilobites, corals, echinoderms, bryozoans, cephalopods, conodonts ...) (see here above, in section 5.2, the examples from the Ardenne-Rhenish Slate Massif, Podolia and the Northern Territories of Canada).

- The latter general proposal does also apply to Carboniferous and Permian fish-bearing localities; the situation is of course different concerning localities with true terrestrial inhabitants as many tetrapods are (see, e.g., Carroll, 1988; Steyer, 2009); fully terrestrial tetrapods are indeed known as fossils only after the Tournaisian Romer’s Gap (Clack, 2002) and cannot be used as terrestrial palaeoenvironmental markers in the Devonian.

## 6. Conclusions

I propose to summarize the macroecological steps of the evolution of Palaeozoic vertebrates as follows :

- origin in the Early Cambrian or earlier;
- first mineralized species at least in the Ordovician when vertebrates are demersal (nekto-benthic); this would be correlated with an increase in atmospheric and oceanic oxygen rate;
- a ca. 3 My long Talimaa’s Gap in the earliest Silurian (Rhuddanian);
- Silurian species are both demersal and fully nektonic, but dominated by agnathans; it is the Nekton Revolution of vertebrates;
- progressive increase of gnathostome diversity upon agnathans during the Devonian, when all environments from marine to “continental” are colonized; it is the Predation Revolution of vertebrates; this would be correlated with a second and greater increase in atmospheric and oceanic oxygen rate;
- extinction of both jawless and jawed “armoured fishes” (‘ostracoderms’ and placoderms) at the Frasnian-Famennian (F/F) and the Devonian-Carboniferous (D/C) boundaries respectively, with a more important turnover at the D/C boundary;
- a ca. 15 My long Romer’s Gap in the earliest Carboniferous (Tournaisian);
- after the D/C ecological replacement of placoderms by both chondrichthyans and osteichthyans, radiation of these toothed fishes, with terrestrialization of tetrapods in the Early Carboniferous;
- a ca. 2 My long Olson’s Gap in the “Middle” Permian (Kungurian + Ufimian, so perhaps as long as 10 My)

mostly due to a strong decline of basal tetrapods (amphibians);

- a recovery in the Late Permian, mostly due to the radiation of reptiles; it is the Amniotic Revolution of vertebrates;

- no real end-Permian extinction except for part of the tetrapods.

A macroevolutionary rule may be hypothesized: biotic events and macroecological novelties in vertebrates follow those in plants and invertebrates; this would be due to the structure of food webs in the biosphere at a global scale, and in ecosystems locally. It indeed seems that biotic events in vertebrates follow those in plants and invertebrates as, e.g.: (i) the Early Devonian decrease in family diversity of vertebrates (Fig. 2: A) which follows the end-Silurian decrease of invertebrates; (ii) the Late Devonian increase in genus diversity and in size (gigantism) of arthrodire placoderms and sarcopterygian fishes which follows the Late Silurian-Early Devonian increase of eurypterids (Cope's Rule + Romer's theory: Lamsdell & Braddy, 2010); (iii) the D/C - Tournaisian turnover of vertebrate faunas which follows the F/F + D/C crises of invertebrate faunas. Macroecological novelties (innovations) in vertebrates follow those in plants and invertebrates as, e.g. the terrestrialization of vertebrates in the Early Carboniferous (with aquatic forerunners in the Devonian) which follows terrestrialization of invertebrates in the Silurian (or earlier), of plants in the Ordovician (or earlier), and of lower organisms (bacteria, 'algae', fungi) in the Precambrian (see a summary in Blicek, 2008). This macroevolutionary hypothesis would certainly deserve being studied in detail.

The phylogenetic relationships of basal vertebrate taxa, and in particular of ostracoderms, are not yet fixed, but several major steps of evolution can be defined: skull > mineralized tissues > jaws > teeth > lungs > limbs and digits > amnios ... (Fig. 1). Vertebrates, and in particular fish macro- and micro-remains, are useful biostratigraphic indicators mostly in Silurian-Devonian marine series. They are good markers of palaeocontinental margins ("continental" *sensu* Rosen, 1974). They occupied a wide range of environments: proximal marine to restricted marine in the Ordovician; all along the marine epicontinental shelves in the Silurian; from freshwater to deep marine in the Devonian, with a special mention for the Old Red Sandstones; same in the Carboniferous and Permian, but with occurrence of true terrestrial taxa. Identifying aquatic from non-aquatic, continental from non-continental, terrestrial from non-terrestrial, freshwater from non-freshwater, marine from non-marine vertebrates and environments in the Palaeozoic remains very difficult: wide, multi-authored, pluridisciplinary studies are in need: paradigms or so-called well-known theories and authors have to be considered with caution. At the considered time-scale (Palaeozoic), evolution of vertebrates would follow the Court Jester model (Barnosky, 2001) better than the Red Queen model, i.e., their biodiversity depends on fluctuations in climate, landscape,

food supply ... (Benton, 2009). This is another point to be tested.

## 7. Acknowledgements

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