The biostratigraphical distribution of earliest tetrapods (Late Devonian): a revised version with comments on biodiversification

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Abstract: The 13 presently known genera of Late Devonian tetrapods are situated in the recently completed miospore zonation of Western Gondwana and Euramerica, in relation to the standard conodont zonation. Some of them are still unprecisely dated. The stratigraphic sequences of East Greenland, North China and East Australia are briefly reviewed to discuss the age of the tetrapods collected there and to analyse consequences in relation to the Frasnian–Famennian and Devonian–Carboniferous boundaries. Two episodes of biodiversification seem to have occurred: the first in the Frasnian and the second in the late and latest Famennian. Due to the currently known fossil evidence, the consensus scenario advocates a late Middle Devonian to early Late Devonian origin of tetrapods on the Old Red Sandstone Continent (Euramerica) at a time of warm climate and recovering atmospheric oxygen level during the building of a pre-Pangaean configuration of landmasses.

The transition of life from water (either marine or fresh) to land, that is, terrestrialization, is certainly one of the most debated topics in evolutionary biology. Most recent results in palaeontology have shown that this event happened at various periods in Earth's history: Precambrian for bacteria, fungi and algae involved in the first palaeosoils (e.g. Altinok 2006), Ordovician for land plants (Early Ordovician for cryptospores and Late Ordovician for trilete spores; see Steemans *et al.* 1996; Strother *et al.* 1996), Silurian (or earlier in the Cambrian–Ordovician) for many invertebrates (annelids, arthropods, etc.; see MacNaughton *et al.* 2002) and Devonian–Carboniferous for vertebrates. Here, we focus on the Late Devonian, the earliest phase of vertebrate terrestrialization, when limbed vertebrates with digits (i.e. tetrapods) first appeared in the fossil record.

Several papers have recently reviewed various aspects of this earliest diversification of tetrapods either in terms of its palaeobiological context (e.g. Clack 1997, 2002, 2006, 2007; Schultze 1997, 2004; Ruta & Coates 2003; Ruta *et al.* 2003; Lebedev 2004; Long & Gordon 2004; Ahlberg *et al.* 2008) or its geological context (Young 2006; Blieck *et al.* 2007). A correct evaluation of the first diversification and adaptive radiation of tetrapods is in need of a well-controlled biostratigraphical framework of its successive steps (accurate dating of the fossiliferous localities) (Blieck *et al.* 2007). We return to this necessary precise biostratigraphy because new data have since been published. We will also explore some of the consequences that this biostratigraphical framework has upon the interpretation of the biodiversity and radiation of earliest tetrapods after the most recently published phylogenetic analysis (Ahlberg *et al.* 2008).

Biostratigraphical distribution

Blieck *et al.* (2007) have reviewed the Late Devonian tetrapod-bearing localities that have yielded bone remains (not the traces and trackways that are reviewed by Clack 1997, 2002). They commented upon the biostratigraphical dating of those localities to give the most precise ages possible to the various taxa of tetrapods. Among the oldest, three still have rather unprecise ages, namely: *Sinostega* (N. China) originally thought to be Famennian

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in age, but most probably Frasnian; *Elginerpeton* (Scotland) which is middle or late Frasnian in age; and *Metaxygnathus* (Australia) which is Frasnian or Famennian. All the taxa were plotted against the southeastern Euramerican miospore zonation (Blieck *et al.* 2007, fig. 1). However, new data have been published since that publication.

Among them, the southeastern Euramerican miospore zonation has been completed for the transitional late Frasnian to early Famennian time slice (Streel 2009). The interval of informal biozones IV, V and poorly defined biozone GH used by Blieck *et al.* (2007, fig. 1) is replaced by the two newly defined Oppel Zones BA and DV (Fig. 1). The Oppel Zone BA is subdivided into three new interval zones. Its uppermost subdivision, the *plicabilis* interval zone, extends across the Frasnian–Famennian boundary (Streel 2009).

Note that the vertical bars of Figure 1 (where the radiochronologic scale has been updated after Gradstein *et al.* 2004) do not correspond to the actual age distribution of tetrapods, but to the age duration of conodont or spore zones in which the taxa have been collected (Marshall *et al.* 1999). Because most early tetrapod finds are from only a single stratigraphical horizon, their fossil record is more sparse than what is indicated by Figure 1. The exception to this is in East Greenland (for *Ichthyostega, Acanthostega* and the new genus and species) where the sampling has been much more abundant (review in Blom *et al.* 2007).

Comments on the East Greenland localities

The recent paper of Blom *et al.* (2007) has reviewed the stratigraphical distribution of vertebrates in the Old Red Sandstone series of the east coast of Greenland and provides additional information on the age of the tetrapods. Fossiliferous localities are on Gauss Peninsula (Gauss Halvø) and Ymer Island (Ymer Ø). They have provided 50 different vertebrate taxa for the Middle and Upper Devonian (Blom *et al.* 2007, fig. 2), including the most diversified Late Devonian tetrapod fauna with *Acanthostega gunnari*, three species of *Ichthyostega* (*I. stensioei, I. watsoni, I. eigili* after the revision of Blom 2005) and a third, yet undescribed genus (Clack *et al.* 2004).

Contrary to our proposal (Blieck *et al.* 2007, fig. 1), both *Acanthostega* and *Ichthyostega* have the same stratigraphical distribution which spans the upper part of the Famennian from the Aina

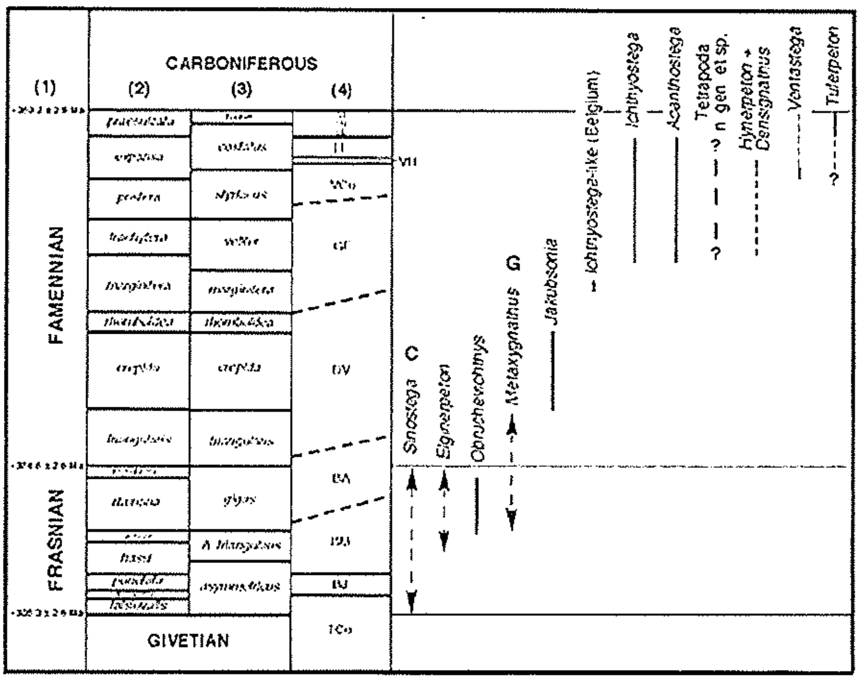

Fig. 1. Revised biostratigraphical distribution of Devonian tetrapods after Blieck *et al.* (2007). Each vertical bar illustrates the age duration of the conodont or miospore zones in which the corresponding taxon has been collected. Dashed lines with arrows indicate uncertainties in dates. (1) Radiochronologic scale of Gradstein *et al.* (2004, fig. 14.2); (2) standard conodont zones of Ziegler & Sandberg (1990, fig. 1); (3) older conodont zones after Ziegler & Sandberg (1990); and (4) miospore zones in the eastern part (now west Europe) of the south Euramerican area after Streel (2009). Palaeogeographic occurrences: C: North China; G: East Gondwana (Australia); all others are from the Old Red Sandstone Continent (Euramerica, Laurussia, Laureuropa).

Dal to the Britta Dal formations that have been correlated to the GF to LN spore zones (Marshall *et al.* 1999) (Fig. 1). The third tetrapod genus (Tetrapoda n. gen. et sp. on Fig. 1) is less securely dated; it comes from specimens collected on the south side of Celsius Bjerg, but it is not possible to assign these specimens to a precise stratigraphical level between the Aina Dal and the Britta Dal formations (see Blom *et al.* 2007, pp. 132 and 136; Clack *et al.* in press).

The East Greenland series highlights a problem: some of the vertebrate material, including *Holoptychius* sp. and *Groenlandaspis mirabilis*, has been collected in the uppermost part of the series (Bendix-Almgreen 1976; Schultze 1993). The sixth assemblage or *Grönlandaspis* Series (Blom *et al.* 2007, p. 136) is assumed to be earliest Carboniferous in age. This *Grönlandaspis* Series or *Grönlandaspis* Group is stratigraphically above the black shales (of the Obrutschew Bjerg Formation) containing actinopterygian material (*Cuneognathus gardineri*, Friedman & Blom 2006) which marks the Devonian–Carboniferous boundary on the south side of Celsius Bjerg (Marshall *et al.* 1999; Blom *et al.* 2007, pp. 128–129). This would therefore correspond not only to the only record of these taxa (*Holoptychius* and *Groenlandaspis*) in the Carboniferous (Blom *et al.* 2007, p. 128), but also to the only record of post-Devonian porolepiform sarcopterygians and placoderms.

This point concerns a more general problem of dating the last occurring placoderms which are usually assumed not to have survived the Devonian (see dating some of the Late Devonian Old Red Sandstone-like localities of Australia – references in Denison 1978; Long 1993; Young 1993, 2006, 2007). According to Blom *et al.* (2007), in East Greenland it is either a problem of taxonomic identification of the material or of dating the Devonian–Carboniferous boundary (DCB) in the stratigraphical sequence (or both). Indeed, the assertion that "the Devonian–Carboniferous boundary can be confidently placed within the Obrutschew Bjerg Formation" (Marshall *et al.* 2002) can be challenged. The miospore/conodont data in the Sauerland (Germany) demonstrate that the LN/VI miospore boundary level is clearly below but not at the DCB. The Obrutschew Bjerg Formation might well be entirely Devonian (Streel & Marshall 2006, table 2, level 15).

Comments on the North Chinese locality

Zhu *et al.* (2002) have published a locality of Late Devonian age from the Ningxia autonomous region of NW China, with a partially preserved mandible called *Sinostega*. It comes from the Zhongning Formation which is classically considered Late Famennian in age (Pan *et al.* 1987). This formation is well known for its fish assemblage together with plants and miospores. The fish assemblage is known as the *Sinolepis* assemblage (Macrovertebrate Assemblage XI of Zhu *et al.* 2000) and it includes Galeaspida indet., *Bothriolepis* sp., *Remigolepis major*, *R. microcephala*, *R.* sp., *R. xiangshanensis*, *R. xixiaensis*, *R. zhongningensis*, *R. zhongweiensis*, *Sinolepis szei* and Sarcopterygii indet (Pan *et al.* 1987; Zhu 2000). In this assemblage *Sinolepis* is a typically endemic placoderm genus for China and Australia (Ritchie *et al.* 1992). This assemblage with *Remigolepis* and *Bothriolepis* is comparable to that in east Greenland where it spans both the Frasnian and Famennian (Blom *et al.* 2007).

Miospores have also been prepared from the Zhongning Formation and published by Gao (Pan *et al.* 1987). They come from the topmost part of the Shixiagou section (bed 27) of the Zhongning Formation, and thus constrain the age of the top of this formation. Among them, on a total of 32 species, some have a more significant biostratigraphical value such as *Apiculatisporites microconus*, *Geminospora lemurata*, *Verruciretusispora magnifica* and *Archaeozonotriletes variabilis* (Pan *et al.* 1987). The age of this assemblage is within the interval Mid Givetian to Frasnian (Ritchie *et al.* 1992) or probably Frasnian (S. Loboziak pers. comm., 1989) and not Famennian (Blieck *et al.* 2007).

This dating of the Zhongning Formation has a consequence in the interpretation of the Frasnian–Famennian (FF) biotic event (crisis). If Famennian in age, the galeaspid of the Zhongning Formation would be the only post-Frasnian ostracoderm confirmed (e.g. Blieck 1991; Janvier & Blieck 1993; Janvier 1996). However, if the Zhongning Formation is Frasnian in age, as we believe, there is no post-Frasnian galeaspid in China, no post-Frasnian ostracoderm worldwide and the FF event is an actual crisis for armoured jawless vertebrates.

Comments on the SE Australian localities

Three tetrapod-bearing localities (two with trackways and one with *Metaxygnathus*; see Fig. 1) are known from the Devonian of Victoria and New South Wales, SE Australia (Young 2006, 2007). The Genoa River fish-tetrapod trackway assemblage (*Bothriolepis* sp., *Remigolepis* sp., *Groenlandaspis* sp., an osteolepiform and two tetrapod trackway types; Warren & Wakefield 1972; Clack 1997, 2002; Young 2007) comes from the Combyingbar Formation (formerly known as the Genoa River beds) of easternmost Victoria. This formation is aligned with the Twofold Bay Formation of southeastern-most New South Wales, and is therefore dated as Frasnian (Young 2007) as originally suggested by Warren & Wakefield (1972). The makers of the Genoa River trackways are unknown.

The *Metaxygnathus* lower jaw comes from the Cloghnan Shale at Jemalong quarry, central New South Wales, very often cited as Famennian (Ahlberg & Clack 1998; Clack 2006; Young 2006). Associated with *Metaxygnathus* is a fish assemblage which includes *Soederberghia groenlandica*, *Bothriolepis*, *Remigolepis*, *Groenlandaspis*, phyllolepids and possibly holoptychiid scales. This fits very well with the lower part of the fifth assemblage of Blom *et al.* (2007), that is, the *Remigolepis* series which also yielded *Acanthostega* and *Ichthyostega*. This is dated as Famennian because of palynological data from above and below the formations of this series (Marshall *et al.* 1999; Blom *et al.* 2007, fig. 2).

However, new geological mapping and lithostratigraphical correlations as well as comparison of the Jemalong fish-tetrapod fauna with the Canowindra fish assemblage (about 80 km east of Jemalong in New South Wales) led Young (2006) to suggest that the age of the Jemalong assemblage is not very different from that at Canowindra, and is also likely to be Frasnian. Both the Jemalong and Canowindra fish assemblages have been grouped by Young (1993) under the Macrovertebrate Fauna MAV13, originally dated as Famennian (Young 1993, fig. 9.2) and then considered as Frasnian (e.g. Young & Turner 2000, figs 2 & 3). We remain unconvinced by the Frasnian age of the Jemalong fauna which biostratigraphically correlates rather well with the fifth assemblage of Blom *et al.* (2007) and is more likely to be Famennian, and therefore consider the age of *Metaxygnathus* as unresolved (Fig. 1; Blieck *et al.* 2007).

One of the consequences of the supposed Frasnian age of the Canowindra-Jemalong fauna is that it constitutes one of the arguments used by Young (2003) to indicate that several groups of placoderms (including bothriolepids and phyllolepids) dispersed from eastern Gondwana to Euramerica (Laurussia); they would indeed be older (Frasnian) in Gondwana than in Euramerica (Famennian). However, if older ages for some of the Australian faunas are not confirmed, this contradicts Young's (2003) scenario.

The third SE Australian locality which is assumed to have yielded Devonian tetrapod remains (a trackway) is the courtyard of Glenisla Homestead in the Grampians Mountains, western Victoria (Warren *et al.* 1986). The source of the courtyard flagstones and their age have recently been resolved: they come from the Major Mitchell Sandtone of the Grampians Group, underlying the Silverband Formation (Gouramanis *et al.* 2003; Young 2006) which yielded turiniid thelodont scales and poracanthodid acanthodian scales and tooth whorls suggestive of a Late Silurian to Lochkovian (Early Devonian) age (Turner 1986; Young & Turner 2000, fig. 2 and p. 459: Microvertebrate Zone MV1; Burrow 2003). The Glenisla trackway is therefore either Late Silurian or earliest Devonian at the youngest (Young 2006, p. 418) and would be the oldest tetrapod remains known.

The only problem with the above theory is that it may not be a tetrapod. For Clack (1997), the tetrapod interpretation is very doubtful due to the lack of symmetry of the trackway and the absence of clear alternation in its assumed manus and pes tracks. For Gouramanis *et al.* (2003), it is attributable to a *Diplichnites* species made by an arthropod. Doubt therefore remains on what type of animal may have formed this trackway (Young 2006). The proper identification of the Glenisla Homestead track maker will have a huge impact on interpretations of the origin of tetrapods as discussed below.

Earliest diversification of tetrapods

The results of Figure 1 are used to plot the taxa included in the most recent phylogenetic (cladistic) analysis by Ahlberg *et al.* (2008). They are shown on Figure 2.

Comments on the origin of tetrapods

As already commented by various authors, a consensus arose on the age of origin of tetrapods which, based upon presently available evidence, would be late Givetian to early Frasnian. The earliest known fossil bony elements of tetrapods are Frasnian in age, and the elpistostegid (panderichthyid) sarcopterygians (now considered as paraphyletic, but including *Tiktaalik* + *Elpistostege*, the sister-group of tetrapods: (Daeschler *et al.* 2006, Ahlberg *et al.* 2008) are late Givetian at the oldest (Clack 2002, 2007; Schultze 2004; Blieck *et al.* 2007).

However, the recent paper of Young (2006) has highlighted the unresolved trackway from Glenisla, Victoria (Australia), originally described by Warren *et al.* (1986) and thought to be Early Devonian or even Silurian in age. After new geological and palaeontological information published, the age of this trackway is confirmed as being either Late Silurian, or earliest Devonian at the youngest (Young 2006, p. 418). If confirmed as a tetrapod trackway, this would immediately introduce a long ghost range of ca. 30 Ma for the elpistostegids, from the Silurian–Devonian boundary to the late Givetian. Discussing uncertainties regarding the phylogenetic relationships of sarcopterygian fishes (including the rhizodontids, the osteolepiforms, the actinistians and basal taxa from the Lower Devonian of China), Young (2006) suggests the possibility

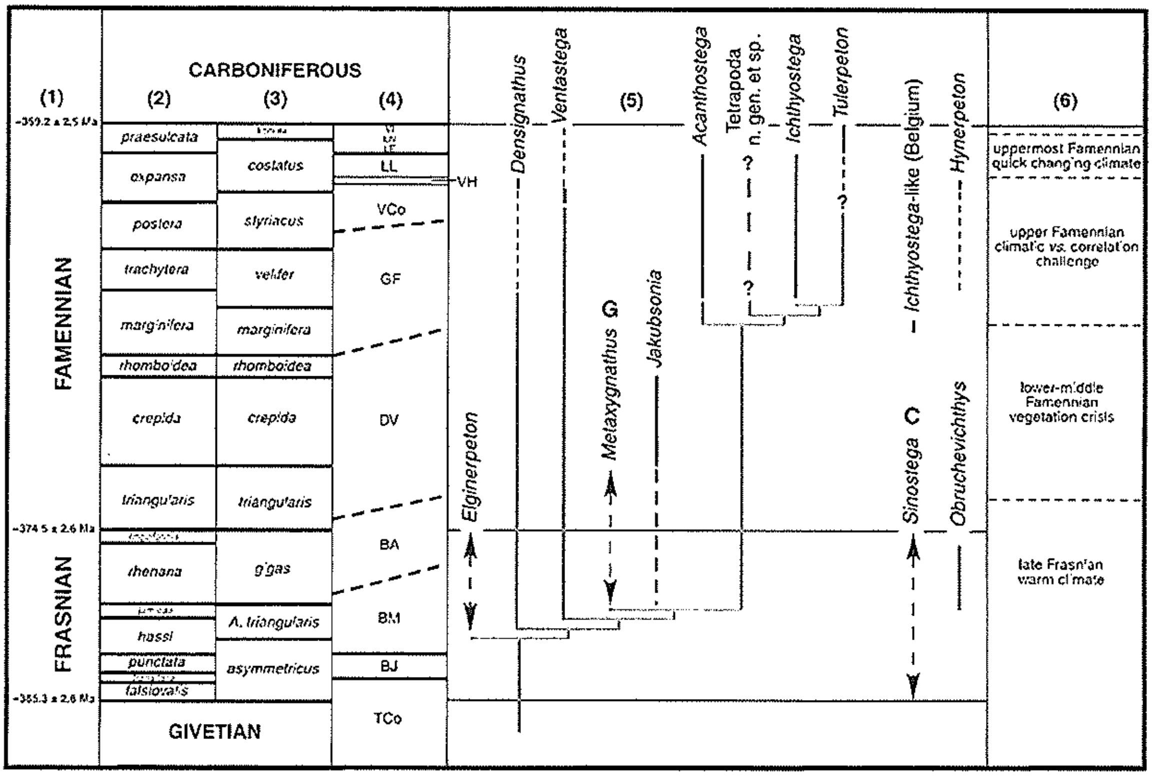

Fig. 2. Chronological, phylogenetic and global (climatic) context of earliest diversification of tetrapods. (1)–(4): as for Figure 1; (5) phylogenetic relationships (after Ahlberg *et al.* 2008; Tetrapoda n. gen. et sp. is MGUH VP 6088; taxa which are not included in this phylogenetic analysis are kept aside on the right; and (6) southeastern Euramerican climatic conditions after Streel (2007*a*, *b*). Note that the so-called 'upper Famennian climatic versus correlation challenge' is not yet solved due to contradiction in the relation conodont/miospore in the western part (now USA) of the south Euramerican area.

that tetrapod origins could date back to the earliest differentiation of these major clades sometime in the Silurian–Early Devonian. Young considers this hypothesis as a plausible alternative hypothesis to the present paradigm of the elpistostegids including the sister-group of tetrapods. This alternative is, of course, strongly supported by the age of the Glenisla trackway. However, the Glenisla trackway may instead be that of a large arthropod (a type of misinterpretation already encountered for other tetrapod tracks, Clack 1997), disproving Young's hypothesis.

As shown on the phylogenetic relationships in Figure 2, the most basal tetrapods are from the Old Red Sandstone Continent (Euramerica). *Sinostega*, from the Frasnian of China, is too incomplete to be included in a phylogenetic analysis and *Metaxygnathus*, from the Frasnian or Famennian of Australia, is assumed to be more derived than *Densignathus* and *Ventastega* (Ahlberg *et al.* 2008). Because the sister-group of tetrapods, namely *Panderichthys* (*Tiktaalik*, *Elpistostege*) or elpistostegids, is exclusive to the same palaeocontinent (e.g. Daeschler *et al.* 2006), a consensus arose on an out-of-Euramerica scenario for the origin of tetrapods (Clack 2002; Blieck *et al.* 2007).

In seeking an alternative to the consensus hypothesis, Young (2006) recalled that Late Devonian tetrapods are very frequently collected among fish assemblages that include placoderms (phyllolepids and antiarchs – *Remigolepis* and *Bothriolepis*; Leriche 1931; Clack 2006, table 1 where the locality of Strud, Belgium, has no placoderm mentioned but did yield placoderms: *Phyllolepis*, *Bothriolepis*, and *Groenlandaspis*), acanthodians (gyracanthids a.o.), dipnoans (*Soederberghia* being significantly known from Euramerica and Australia, Ahlberg *et al.* 2001), porolepiforms (*Holoptychius* being the most widespread), osteolepiforms and others. Considering various hypotheses for the palaeogeographical origins of those taxa, Young (2006) concludes that 'The various possibilities for faunal connection ("migration", "dispersal") between known tetrapod localities [his fig. 4] cannot be resolved on the available evidence' and that we should focus again 'on the possibility of a Gondwanan or Asian origin for the first land animals'.

Sinostega is from North China and appears to be older than originally published (Fig. 1). If it also appears to be a very basal taxon (unsolved on Fig. 2), this could of course be used to sustain the Asian origin. Nevertheless, we should not forget that *Elginerpeton*, a limbed tetrapod, is already in Scotland in the Frasnian. We consider here that the presently known fossil evidence is in favour of the out-of-Euramerica hypothesis for tetrapods in the globally distributed exchange of fish-tetrapod faunas (now known as the Great Devonian Interchange) between the major Late Devonian landmasses (Young 2006, p. 423).

Comments on the biodiversity of Late Devonian tetrapods

From data included in Figure 2, it seems that we are facing two episodes of diversification (one in the Frasnian and one in the late and latest Famennian) with a single record in between that is, *Jakubsonia*. All genera are monospecific except *Ichthyostega* (three species: Blom 2005), so that we would have four species for the Frasnian, one for the lower Famennian and ten for the upper-uppermost Famennian (Fig. 2). Even when removing the taxa which are not included in Ahlberg *et al.*'s (2008) phylogenetic analysis, two episodes of radiation appear: from the Frasnian and the late-latest Famennian. However, several critical remarks must be made:

- As long as the phylogenetic relationships of several taxa are unknown, this scheme is incomplete. For example, *Obruchevichthys* is out from Ahlberg *et al.*'s (2008) scheme, but was considered as the sister-group of *Elginerpeton* in some earlier analyses (e.g. Ahlberg 1995; Schultze 2004) where it was an element of the most basal group of tetrapods and hence characterized their very first diversification. It would also be interesting to know what groups *Sinostega* (Zhu *et al.* 2002) and the ichthyostegid of Strud (Belgium: Clément *et al.* 2004) are related to.
- We know that the fossil record of early tetrapods is incomplete. Undescribed Late Devonian taxa are awaiting description (e.g. Clack *et al.* 2004, in press, pers. comm., 2007) and the ca. 15 Ma long interval with almost no tetrapod remains in the Lower Carboniferous (Romer's Gap) may simply be due to a lack of fossil collection, related to the lack of suitable continental (stratigraphical) sequences for that period (Clack 2007, p. 11). This is perhaps also the case for the Lower Famennian. The apparent rarity of Early Famennian tetrapods might be a bias caused by lack of an extensive rock record from that interval, compared to more abundant Frasnian and late Famennian units (E. B. Daeschler, pers. comm., 2007).
- Most reviews of Late Devonian tetrapods usually include only those taxa named after preserved bony elements (e.g. Clack 2006, 2007; Ahlberg *et al.* 2008) because no phylogenetic analysis can be based upon tracks. Since the review of Clack (1997) it appears that a series of trackways are known from the Late Devonian and are still to be attributed to actual animals, making the fossil record (Figs 1 & 2) largely underestimated.

Comments on the global (climatic) context of earliest diversification of tetrapods

Several attempts at correlating the origin and early diversification of tetrapods to global events have been made (e.g. Clack 2002, 2006, 2007; Long & Gordon 2004; Carroll *et al.* 2005; Ward *et al.* 2006). One recent tendency is to try to link this to climatic changes in relation to plate tectonic/orogenic global events. Late Devonian tetrapods occurred during a period of intense tectonic activity (Acadian–Ligerian orogeny) due to the collision of major landmasses, reduction of most oceanic domains and building of a pre-Pangaean configuration of the Earth (Averbuch *et al.* 2005; Blieck *et al.* 2007).

At a global scale, the transition from fish to tetrapod occurred during the Givetian through Frasnian time slice which corresponds to a low level of atmospheric oxygen, rather high temperature (remember that the Givetian–Frasnian period corresponds to the maximum development of marine reefs in the fossil record) and a major time of plant diversification (increase in penetration depths of vascular plant roots in the soils and increase in the main axis diameter of land plants) (Ward *et al.* 2006; Algeo *et al.* 2007; Clack 2007). The earliest diversification of tetrapods is bracketed by the two first radiations of terrestrial arthropods: the first in the Early Devonian and the second in the Middle and Late Mississippian (Ward *et al.* 2006). However, putting such different events on a single diagram does not mean that there are causal relations between those events. For instance, when Ward *et al.* (2006, fig. 1) plot the earliest phases of diversification of terrestrial arthropods and of tetrapods together, they simply show that both phases apparently follow a period of low atmospheric oxygen rate which might be the trigger for the development of respiratory organs in air; it does not imply a trophic relation between terrestrial arthropods and earliest tetrapods which are now interpreted as aquatic animals (e.g. Clack 2002).

The earliest radiation of tetrapods is seen as a consequence of the increase in capacity of air breathing of their closely related fishes during a period of low oxygen rate (Clack 2007). After that episode, Frasnian–Famennian tetrapods radiated in a period of increasing oxygen level (Ward *et al.* 2006; Clack 2007) which might have some relation to the increasing rate of diversification of the vegetation (Streel 2007*a*, 2009).

The earliest tetrapods are contemporaneous with a late Frasnian warm climate phase on West Gondwana and Euramerica while their second phase of diversification in the late and latest Famennian occurs in a period of rapid climatic changes with fast (*c.* 100–200 ka long) sea-level changes (Fig. 2; Streel 2007*a*, *b*). The latter may have caused quick changes in the development of near-shore marine platforms and had impacts on the coastal plains and alluvial deposits with niches favourable to early tetrapods. However, such co-occurrences of events do not imply direct causal relationships between them. The global situation was certainly more complex and implied trophic relationships between the tetrapods and their locally associated fishes in very different environments from true freshwater to true coastal marine (e.g. Lebedev 2004). Between the two phases of biodiversification, the lower-middle Famennian vegetation crisis phase (Fig. 2) was controlled by a high climatic gradient between cool polar areas and a very warm, intertropical area (Streel 1992). This may have been unfavourable for the diversification of tetrapods, which are rare at that time.

Conclusions

The primary aim of this paper is to update the biostratigraphical scale in which most of the Late Devonian tetrapod-bearing localities worldwide can be placed (Fig. 1). Uncertainties still remain for several basal taxa such as *Elginerpeton*, *Metaxygnathus* and *Sinostega* (if the latter is basal). As several taxa are very incompletely known (either solely as lower jaws e.g. *Metaxygnathus*, *Sinostega* and the ichthyostegid from Strud, or as trackways) they cannot yet be integrated in a general phylogenetic analysis (Fig. 2). Despite such limitations, a consensus scenario arises where tetrapods seem to have originated on Euramerica in the Middle to Late Devonian transitional period. This was a time of warm climate and increasing atmospheric oxygen level, during the building of a pre-Pangaean configuration of landmasses (Young 2006; Blieck *et al.* 2007). As is now well known for the fossil record in general (e.g. Sheehan 1977), such scenarios are the result of the interpretation of sparse fossil data from discontinuous surfaces of preserved sediments that have been sampled in an incomplete geographical frame (N. America, Europe, Australia and China in the case of earliest tetrapods). As pointed out by Young (2006), alternative hypotheses to the consensus scenario may be envisaged. It might be that the out-of-Euramerica scenario (Clack 2002) is simply the scenario for western palaeontologists.

When reviewing the biostratigraphical ages of Late Devonian tetrapod-bearing localities, it appears that this has impacts on interpreting the Frasnian–Famennian (FF) biotic crisis and Devonian–Carboniferous (DC) event. Re-dating the *Sinostega* locality of N. China as Frasnian implies that there is no post-Frasnian ostracoderms (the galeaspid which comes from the same locality as *Sinostega* being also Frasnian, not Famennian) and that the FF crisis has been real for ostracoderms. Re-dating the East Greenland Middle to Late Devonian Old Red Sandstone sequence (Marshall *et al.* 1999; Blom *et al.* 2007) places the DCB in the Obrutschew Bjerg Formation. This implies that *Groenlandaspis* and *Holoptychius* still exist in the very Early Carboniferous, which is astonishing because placoderms and porolepiform sarcopterygians are usually thought to have disappeared before or at the DCB. This would mean that the DC event was not a total extinction for placoderms and porolepiforms, except if the DC boundary is higher in the East Greenland sequence.

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Note added in proof

While this paper was in the process of editing, Niedzwiedzki *et al.* (2010) have published a series of early Eifelian (Middle Devonian) tracks and trackways from the northern Lysogory region of the Holy Cross Maintains, Poland. This discovery confirms the recent paradigm that the earliest tetrapods have to be found before the Late Devonian, say at least in the Middle Devonian. This discovery as well as the re-appraisal of the supposed Early Devonian track from Australia (Warren *et al.* 1986) will be interpreted in another paper.

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