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The biostratigraphical and palaeogeographical framework of the earliest diversification of tetrapods (Late Devonian)

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Abstract: The earliest diversification of tetrapods is dated as Late Devonian based on 10 localities worldwide that have yielded bone remains. At least 18 different species are known from these localities. Their ages span the 'middle'–late Frasnian to latest Famennian time interval, with three localities in the Frasnian, one at the F/F transition (though this one is not securely dated) and six in the Famennian. These localities encompass a wide variety of environments, from true marine conditions of the nearshore neritic province, to fluvial or lacustrine conditions. However, it does not seem possible to characterize a freshwater assemblage in the Upper Old Red Sandstone based upon vertebrates. Most of the tetrapod-bearing localities (8 of 10) were situated in the eastern part of Laurussia (=Euramerica), one in North China and one in eastern Gondwana (Australia), on a pre-Pangean configuration of the Earth, when most oceanic domains, except Palaeotethys and Panthalassa, had closed.

The earliest record of tetrapods (four-legged vertebrates) in the Late Devonian is one of the key events in the evolution of vertebrates. It had a very important and lasting impact on the terrestrial ecosystem. These vertebrates are the oldest representatives of tetrapods, a major group of animals that today numbers some 24 000 living species.

Our understanding of the origin of tetrapods, better known popularly as the 'fish–tetrapod transition', has progressed greatly thanks to recent fossil discoveries. Today, eight Devonian tetrapod genera out of a total of 12 (and perhaps even 17 when counting the as-yet undescribed taxa; see below the taxonomic section) have been found in the last 15 years. These new finds have made it possible to reconstruct sequences of character change leading to tetrapod morphologies, eventually to improve phylogenetic analyses, and tentatively identify the genetic basis for some of these changes (e.g. Daeschler & Shubin 1998). However, these discoveries have raised new questions about the evolutionary context of the origin of tetrapods, questions which need to be answered if the event is to be properly understood (see, e.g. Schultze 1997; Clack 2002*b*; Long & Gordon 2004).

In this paper, we address the geological context of this event, that is, mainly the biostratigraphically based dating of the Late Devonian tetrapod-bearing localities, and their palaeogeographical context in the frame of a recently proposed global reconstruction (Averbuch *et al.* 2005). We also comment on

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the palaeoenvironmental interpretation of the various localities known to date, based upon the most recent discoveries of fossils (e.g. as in Belgium), and a cluster analysis of Famennian vertebrate localities worldwide (Lelièvre 2002).

Taxonomic overview

In this section, we briefly review the diversity of Late Devonian tetrapods, taking into account the most recent published data which are summarized in Table 1. We focus on the localities that have yielded tetrapod bone remains (either fragmentary remains or articulated skeletons), and we do not review the trace and trackway localities (for this topic, we refer the reader to Clack 1997 and 2002*b*, pp. 92–95).

Pennsylvania (late Famennian)

The limited Red Hill outcrop in Clinton County, Pennsylvania, USA, has provided more than one tetrapod genus. *Hynerpeton bassetti* is known from most of the left cleithrum with its scapulocoracoid (Daeschler *et al.* 1994), and a second left cleithrum. The posterior part of a right lower jaw has provisionally been assigned to the same genus (Daeschler 2000). *Densignathus rowei* (Daeschler 2000) is defined on very distinguishable lower jaws (a left lower jaw and the posterior portion of a right lower jaw, both supposed to be from a single individual). Another tetrapod remnant has been discovered recently from the same locality, i.e. an isolated left humerus (Shubin *et al.* 2004) and as yet undescribed cranial and post-cranial material (Blom & Clément pers. obs.).

East Greenland (late Famennian)

The tetrapods from East Greenland are the most complete and best known of all the Devonian taxa. To date, three genera and five species are known from more than 550 block specimens. The well-known *Ichthyostega* and *Acanthostega* are represented by a large number of well-preserved skulls and lower jaws, as well as almost complete post-cranial material (see, e.g. Clack 2002*b*). In a recent revision, Blom (2005) shows a morphological variation within the cranial material, which justifies the recognition of three species of *Ichthyostega: I. stensioei* Säve-Söderbergh 1932 *I. eigili* Säve-Söderbergh 1932 and *I. watsoni* Säve-Söderbergh 1932. Originally, Säve-Söderbergh (1932) defined the genus *Ichthyostegopsis* on the basis of a small skull with proportions and suture boundaries different from those of *Ichthyostega. Ichthyostegopsis* is no longer considered valid since the differences are regarded as an expression of juvenile characters (Blom 2005). However, a third tetrapod genus has recently been recognized based on jaw and tooth morphology from specimens collected on the south side of Celsius Bjerg (Blom pers. obs.; Blom *et al.* 2003; Clack *et al.* 2004).

Scotland (mid- to late Frasnian)

The tetrapod material from Scaat Craig near Elgin, Scotland, includes both cranial and post-cranial material (Ahlberg 1991, 1995, 1998; Ahlberg & Clack 1998; Ahlberg *et al.* 2005). Skull bones and lower jaw fragments, comprising the premaxilla plus median rostral and all of the lower jaw except the articular and medial wall of the adductor fossa, form the type material of the stem tetrapod *Elginerpeton pancheni* (Ahlberg 1995; Ahlberg & Clack 1998; Ahlberg *et al.* 2005). The postcranial material provisionally referred to *Elginerpeton* (Ahlberg 1998) comprises the dorsal part of a scapulocoracoid plus the ventral part of a cleithrum, an ilium and one specimen each of humerus, femur, tibia and neural arch (Ahlberg 1998). However, the identification of the humerus has recently been challenged (Shubin *et al.* 2004; see Ahlberg 2004 for a contrasting view).

Belgium (mid- or late Famennian)

Lohest (1888, pl. VIII: 2, 5) misinterpreted a Devonian tetrapod lower jaw as a large fish remain and assigned it to a new species of *Dendrodus*, *D. Traquairi* [*sic*]. This lower jaw was found in the Famennian of Strud, Namur Province, Belgium, from the Evieux Formation extending apparently from the Middle Famennian in this area. However, this taxon appears to be a representative of *Ichthyostega* ('*Ichthyostega*-like form' in Clément *et al.* 2004). The Devonian tetrapod occurrence in Belgium is today only based on this isolated right lower jaw, but current investigations at the rediscovered Strud locality lead us to expect the discovery of new tetrapod material.

Latvia and western Russia (Frasnian)

Obruchevichthys was originally described as a sarcopterygian fish (Vorobyeva 1977). Known only from lower jaw fragments, it may not have had true limbs and digits, although its phylogenetic relationships are likely to be close to tetrapods (Ahlberg 1991; Clack 2002*b*, p. 91; tetrapods in the sense used by Clack 2006: 'a vertebrate with limbs and digits, as this is the sense in which it is most readily understood by the non-specialist').

Table 1. *Devonian tetrapod localities of the world with their formation, age and environment*

Country	Locality	Tetrapod(s)	Formation	Age	Environment	References
Pennsylvania (USA)	Red Hill, Clinton County	*Hynerpeton bassetti* *Densignathus rowei* 3rd taxon (?)	uppermost Catskill Formation, Duncannon Member	upper Famennian, VH Miospore Zone	coastal alluvial plain	Daeschler *et al.* 1994 Daeschler 2000 Traverse 2003
East Greenland	Gauss Halvø and Ymer Ø	*Acanthostega gunnari*, *Ichthyostega watsoni*, *I. eigili*, *I. stensioei*, Tetrapoda gen. et sp. nov.	Aina Dal Formation and Britta Dal Formation	upper Famennian (higher part of GF Miospore Zone to upper or uppermost Famennian)	fluvial	Jarvik 1996 Marshall *et al.* 1999 Clack 2002*a*, 2002*b* Clack *et al.* 2003, 2004 Blom 2005
Scotland	Scat [Scaat] Craig, near Elgin	*Elginerpeton pancheni*	Scat [Scaat] Craig beds	'middle' or upper Frasnian	fluvial	Ahlberg 1991, 1995 Trewin 2002
Belgium	Strud, Namur Province	*Ichthyostega*-like tetrapod	Evieux Formation (?)	upper middle Famennian (lower part of the GF Miospore Zone)	coastal alluvial plain	Thorez *et al.* 1977 Bultynck & Dejonghe 2002 Clément *et al.* 2004 and this paper
Latvia & Russia	Velna-Ala, Abava riv., Latvia, and ?Novgorod district, Russia (exact location unknown)	*Obruchevichthys gracilis*	Ogre Formation, Latvia; unknown in Russia	upper Frasnian, equiv. *rhenana* Conodont Zone	shallow, near-shore marine	Vorobyeva 1977 Sorokin 1978 Ahlberg 1991, 1995
Latvia	Pavari and Ketleri	*Ventastega curonica* 'second tetrapod genus'?	Ketleri Formation	upper Famennian, equiv. lower *expansa* Conodont Zone (or younger)	low-tidal, near-shore, marine	Ahlberg *et al.* 1994 Esin *et al.* 2000 Luksevics & Zupins 2003, 2004
Russia	Andreyevka-2, Tula region	*Tulerpeton curtum* Tetrapoda indet.?	Khovanshchina Formation, Zavolzhsky Horizon	uppermost Famennian (Strunian) equiv. *praesulcata* Conodont Zone (or older)	marine (epi-continental sea)	Lebedev & Clack 1993 Alekseev *et al.*1994 Lebedev & Coates 1995
Russia	Gornostayevka, Oryol region	*Jakubsonia livnensis*	Zadonskian Regional Stage	lower Famennian, equiv. *crepida* Conodont Zone	deltaic near-shore, marine	Esin *et al.* 2000 Lebedev 2003, 2004
China	Ningxia Hui region	*Sinostega pani*	Zhongning Formation	Frasnian, better than 'upper' Famennian	non-marine	Pan *et al.* 1987 Ritchie *et al.* 1992 Zhu *et al.* 2002
Australia	Jemalong Gap, SW of Forbes, N.S.W.	*Metaxygnathus denticulus*	Nangar Subgroup, Cloghnan Shale	lower Famennian or upper Frasnian	fluvial	Campbell & Bell 1977 Young 1993, 1996, 1999 Young *et al.* 2000*a*

Latvia (Famennian: Pavari and Ketleri)

Ventastega is represented by virtually the whole skull and lower jaw, together with most of the shoulder girdle, part of the pelvis, and fragments of the axial skeleton (ribs and tail fin rays), that makes it the most complete Devonian tetrapod besides *Ichthyostega* and *Acanthostega*. Ahlberg *et al.* (1994, p. 322 and fig. 14) suggest the occurrence of a 'second tetrapod genus' in Ketleri, together with *Ventastega*, on the basis of a mandibular fragment. We propose that this conclusion must be considered with caution until more material is collected.

Russia (Famennian, Andreyevka-2)

The state of preservation of the material of *Tulerpeton* is 'perfect and three-dimensional' according to Alekseev *et al.* (1994, p. 44). In this locality, Lelièvre (2002, p. 151; also Lebedev 2004, table I) cites a Tetrapoda indeterminate, in addition to *Tulerpeton*, after Lebedev & Clack (1993) who have cautiously differentiated the holotype of *Tulerpeton* from all the other sarcopterygian remains in the locality. Lebedev & Clack (1993) believe that two different tetrapods occur at Andreyevka-2, on the basis of two types of tabular bones. These bones are variable among sarcopterygians, which could equally be the case among tetrapods. Moreover, one of the bones figured by Lebedev & Clack (1993, fig. 2 H–I) might not be a tabular. So, the supposed second tetrapod of Andreyevka-2 should be considered with caution, although Lebedev has been advocating two different taxa for 10 years. However, this hypothesis is not in disagreement with the fact that two tetrapods do occur together in the same locality of Pennsylvania, and that more than two tetrapods are known from East Greenland (Table 1).

Russia (Famennian, Gornostayevka)

The recently described material of *Jakubsonia livnensis* (Lebedev 2003, 2004) includes disarticulated cranial and postcranial (pectoral girdle) elements, and the posterior part of a skull roof questionably attributed to *Jakubsonia*.

China (Frasnian)

The record of a tetrapod from Asia, *Sinostega pani*, is restricted to an incomplete left mandible from the Zhongning Formation of the Ningxia Hui autonomous region, northwestern China (Zhu *et al.* 2002). Only the medial view is exposed, comprising most of the prearticular, together with the angular and postsplenial.

Australia (Frasnian/Famennian)

Metaxygnathus denticulus from the Cloghnan Shale, near Forbes, New South Wales, Australia was the first Devonian tetrapod to have been described outside Greenland (Campbell & Bell 1977). It is represented by a complete but poorly preserved right lower jaw.

Taxonomic conclusion

Twelve different genera of Late Devonian tetrapods are now known (Fig. 1) with one species each, except *Ichthyostega* with three species. This makes 14 different species. Nevertheless, other taxa have been mentioned or are still imperfectly known: a third taxon in Pennsylvania (?), a third genus in Greenland, a second genus in Ketleri, Latvia (?), and a second taxon in Andreyevka-2, Russia (?). This would give a total of 15 (sure) to 18 (sure and possible) different species, corresponding to 12 (sure) to 17 (sure and possible) different genera. Additionally, an undescribed tetrapod taxon has been recently announced by Clack *et al.* (2004) from the Upper Devonian of Timan, Russia (work in progress after Ervins Luksevics). This would settle the number of separate Late Devonian tetrapod species to 19.

Critical biostratigraphical review

Important associated flora and fauna are sometimes found with tetrapod remains. The vertebrate faunal composition (placoderms, chondrichthyans, acanthodians, actinopterygians, sarcopterygians) is now increasingly used to aid studies in biostratigraphical approach. Correlations between biostratigraphical subdivisions of the different tetrapod-bearing localities of the world (USA, Greenland, Europe, China, Australia) are currently being attempted by an international early tetrapod working group that assembled in Riga, Latvia, during the Gross Symposium 2 (Sept. 8–14, 2003; Schultze *et al.* 2003). Thus, comparisons with contemporaneous tetrapod-bearing localities will improve our understanding of palaeoenvironmental conditions in which the oldest tetrapods were living (see below) as well as their biogeographical distribution. Nevertheless, to be accurate, it is absolutely necessary for these studies to be based on a very consistent and internationally accepted biochronological framework.

Work in progress by the Subcommission on Devonian Stratigraphy has stabilized in favour of a three-fold subdivision of the Frasnian, and a four-fold subdivision of the Famennian (e.g. Bultynck 2004; Streel 2005). Four Famennian substages (lower, middle, upper, and uppermost Famennian or Strunian) could most probably be accepted by most Devonian vertebrate palaeontologists. The most important thing is that the different faunal levels are precisely defined and dated (see Clack 2006).

Pennsylvania (late Famennian)

All Devonian tetrapod remains come from a single limited locality known as Red Hill, Clinton County. These specimens were found in the Duncannon Member, the uppermost subdivision of the Catskill Formation. Palynomorph samples were collected from several levels at the Red Hill locality. According to Traverse (2003), the spore taxa assemblages would place these samples in the upper sixth of the Famennian Stage. Traverse noticed that Maziane *et al.* (1999), providing a revision based on sections in Belgium with faunal control, proposed that the VH Spore Zone (for *Apiculiretusispora verrucosa–Vallatisporites hystricosus*) becomes the upper part of the previous VCo Zone (with *Apiculiretusispora verrucosa* and *Vallatisporites hystricosus*, but without *Retispora lepidophyta*). However, the range of the VH Spore Zone is more extended in Pennsylvania (wet area) than in western Europe (dry area). The Red Hill outcrop is thus referable to the interval *trachytera* to middle *expansa* Conodont Zones of the upper Famennian Substage (Fig. 1; see Streel & Loboziak 1996).

East Greenland (late Famennian)

Palynological dating has recently unambiguously resolved the stratigraphical age of the tetrapod-yielding parts of the sequence (Marshall *et al.* 1999). Spore samples bracketing the upper and lower occurrences of tetrapods place them securely between the upper GF (upper Famennian) and LL to LN (upper to uppermost Famennian) Spore Zones. These data contradict the previously controversial study suggesting a Carboniferous age (Hartz *et al.* 1997, 1998). In fact, these authors did not suggest a Carboniferous age directly, only that the absolute age was much younger than previously expected, an absolute age that would normally put it in the Carboniferous—but all the other absolute dates could also have been wrong! They put an end to a long dispute on the age of the East Greenland tetrapods (Jarvik 1996; Stemmerik & Bendix-Almgreen 1998). More precisely, the lowest occurrence of *Ichthyostega* and *Acanthostega* is higher than, but close to the base of the latest *marginifera* Conodont Zone. Indeed, the GF Miospore Zone in East Greenland contains *Retispora macrotuberculata*, a marker for the base of the middle part of the GF Zone, i.e. the biostratigraphical level 15 of Streel & Loboziak (1996, fig. 4) (Fig. 1).

Scotland (mid- to late Frasnian)

In his original papers on *Elginerpeton*, Ahlberg (1991, 1995, 1998) gives the age of the Scaat Craig Beds, a possibly partial lateral equivalent of the Alves Beds in the South Moray Firth area, as 'upper Frasnian'. This late Frasnian age is indeed classically advocated for the Scaat Craig Beds (e.g. Friend & Williams 1978, fig. 13; Trewin 2002, fig. 8.28). However, it does not seem to be based upon firm data, independently of fishes. Miles (1968, table 2) correlates the Scaat Craig Beds with the lower part of the '*Phyllolepis* Series' of East Greenland (also Mykura 1991, table 9.3), which is now named the Kap Graah Group, and considered as lower Famennian (Jarvik 1996, fig. 9; Clack & Neininger 2000, fig. 2). The Kap Graah Group lies below the Agda Dal and Elsa Dal formations. The topmost part of the latter has been dated as GF Miospore Zone by Marshall *et al.* (1999), but corresponds (see East Greenland) to the middle part of that zone spanning the middle–upper Famennian boundary, i.e. the upper to uppermost *marginifera* Conodont Zone *sensu* Streel & Loboziak (2000). So, the Kap Graah Group might be at least pre-GF in age, that is lower to lower middle Famennian (*sensu* Streel & Loboziak 2000, in a four-fold subdivision of the Famennian), or older, i.e. upper Frasnian. This means that the Scaat Craig Beds may be or may not be late Frasnian in age. This late Frasnian age is based upon their fish assemblage (Miles 1968), and there is seemingly no independent biostratigraphical marker such as conodonts, miospores or other fossils. Nevertheless, two other arguments may be given for the Frasnian age of the Scaat Craig Beds:

1. The occurrence of the psammosteid ostracoderm genera *Psammosteus* and *Traquairosteus* in the Scaat Craig Beds (Miles 1968, p. 8) is an argument for a pre-Famennian age (see Ahlberg 1998, p. 102, and section China, here below).
2. Miles (1968, table 2) correlated the Scaat Craig Beds with the interval between the 'c-d Shelon-Ilmen' and the 'e-Stage' of the East Baltic area. The Ilmen and overlying beds of Latvia and the Main Devonian Field of NW Russia are correlated with the 'middle' Frasnian, Daugava Regional Stage (Paskevicius 1997, fig. 66), considered as equivalent to the 'middle' Frasnian *punctata* to *jamieae* Conodont Zones (Esin *et al.* 2000, fig. 1), and the 'e-Stage' is equivalent to the

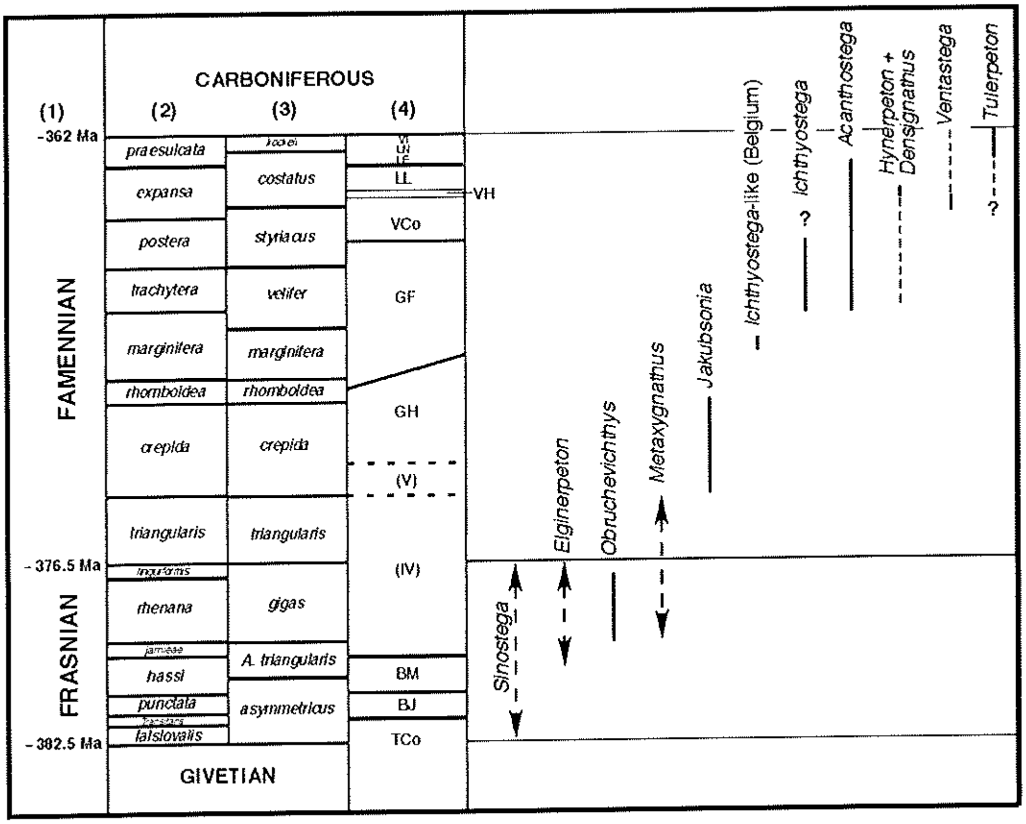

Fig. 1. Biostratigraphical distribution of Devonian tetrapods after data of Table 1. Note that, as stated by Marshall *et al.* (1999, fig. 4), this figure illustrates the age error bar of each taxon. These ages are not ranges, but age durations of conodont/miospore zones in which the taxa have been collected. Dashed lines with arrows indicate uncertainties in datations. *Notes*: (1) radiochronological scale of Williams *et al.* (2000, fig. 8); (2) standard conodont zones of Ziegler & Sandberg (1990, fig. 1); (3) older conodont zones after Ziegler & Sandberg (1990); (4) miospore zones *sensu* Streel in Bultynck & Dejonghe (2002, table 1).

Snezha and Pamusis regional stages, which correspond to the late Frasnian *rhenana* Conodont Zone. Ahlberg *et al.* (1999) correlated the Scaat Craig Beds with 'some part of the Pamusis–Snezha interval' judging from distribution of *Psammosteus*. We thus retain a 'middle' to late Frasnian age for the Scaat Craig Beds (Table 1 and Fig. 1).

The Scaat Craig fauna also comprises placoderms and acanthodians, and appears to be similar to that of two other localities of Scotland: Poolymore and Whitemire (Newman 2005). 'Poolymore was considered to be lower down in the Edenkillie Beds (Miles 1968)' (Newman 2005), that is, in a level equivalent to the 'middle Frasnian' Whitemire Beds (Mykura 1991; Trewin 2002). So, for Newman (2005), the three faunas (Scaat Craig, Poolymore and Whitemire) 'might be stratigraphically closer than considered hitherto' and *Elginerpeton* 'is even older than previously thought'.

Belgium (mid- or late Famennian)

The composition of the sandstone surrounding the tetrapod lower jaw is very unusual (fluviatile deposits generated by flood events). Such a lithofacies is usually known in the Evieux Formation in the northern part of the Dinant synclinorium, Ardenne Allochthon, and the Namur Synclinorium, Brabant Parauthochthon (Thorez *et al.* 1977; Bultynck & Dejonghe 2002) to which it was first attributed (Clément *et al.* 2004). The rediscovery of the one-century old abandoned quarry of Strud, and, more importantly, the finding in November 2005 of the stratum which most probably yielded the tetrapod material in this quarry, have allowed more accurate dating. The palynological study is still in progress, but already it conclusively shows that the Strud locality is older than previously thought (Clément *et al.* 2004). It is now considered to be upper middle Famennian in age (*sensu* Streel in Bultynck

& Dejonghe 2002; Streel 2005; but note that the subdivisions of the Famennian are still under discussion among the Subcommission on Devonian Stratigraphy), i.e. containing the lower part of the GF Miospore Zone and so close to but older than the East Greenland material (Fig. 1). This also means that the Strud quarry Evieux lithofacies might have the same age as the Souverain-Pré Formation elsewhere (Bultynck & Dejonghe 2002, fig. 7). However, a more precise correlation between the different Famennian sections of the Condroz area has still to be processed.

Latvia and western Russia (Frasnian)

The holotype of *Obruchevichthys* comes from the upper Frasnian Ogre Formation of Latvia, which correlates with the *rhenana* Conodont Zone (Esin *et al.* 2000). However, Vorobyeva (1977, pl. XIV: 4, and p. 204) inadequately attributed the sandstones of the type-locality of *Obruchevichthys* to the Nadsnezha Beds, a lithostratigraphical unit which is distributed in the Novgorod district of Russia, along the Lovat river. The type-locality of *Obruchevichthys* is Velna Ala, within the lower, Lielvarde Member of the Ogre Formation. This member consists mainly of fine-grained calcareous sandstones, with a gypsum cement in its lower part, and clay, silt and dolomitic marl in its upper part. Sorokin (1978) supposed that these deposits were formed in shallow waters of a narrow gulf of the Baltic palaeobasin, under conditions of variable salinity. In western Russia, the locality of *Obruchevichthys* is unfortunately not precisely known. Vorobyeva (1977, p. 204 and fig. 46) mentions that it originates perhaps from the Novgorod District. Judging by its state of preservation and the matrix, it is likely that it was collected somewhere along the Lovat river where a rich collection of *Bothriolepis maxima* and other fish remains was gathered. The *Bothriolepis maxima* placoderm 'zone' is biostratigraphically correlated to the *rhenana* Conodont Zone (Esin *et al.* 2000, fig. 1; Luksevics 2001, fig. 2).

Latvia (Famennian: Pavari and Ketleri)

The holotype and main portion of the *Ventastega* material comes from the Pavari locality where the fine-grained sandstone and sand of the Pavari Member of the Ketleri Formation crops out. Other material has been collected from the overlying Varkali Member of the Ketleri Formation represented also by weakly cemented sandstones. No spores or conodonts have been found in the Ketleri Formation, therefore the age of the formation (possibly corresponding to the *expansa* Conodont Zone; Esin *et al.* 2000) can be judged only from its position above the Zagare Formation; besides that, one needs to take into consideration the significant break corresponding to the erosional surface between the Pavari Member and lowermost Nigrande Member of the Ketleri Formation. Therefore, the possibility that the Ketleri Formation could be even younger, corresponding to the latest Famennian, cannot be excluded. Dolomite from the Zagare Formation in Lithuania yields conodonts allowing correlation of this formation with the interval from the *marginifera* to *postera* Zones (Esin *et al.* 2000). Furthermore, the underlying Svete Formation in Lithuania contains conodonts of the *postera* Zone (or Middle–Lower *styriacus* Zone of the previous conodont zonation, as it was reported by Zeiba & Valiukevicius 1972). So, an *expansa* Conodont Zone or younger age is retained for *Ventastega* (Fig. 1).

Russia (Famennian, Andreyevka-2)

The material of *Tulerpeton* comes from a section (ANE-1 or Andreyevka-2 in Alekseev *et al.* 1994) on the right bank of the Tresna river, south of the village of Andreyevka, in the Tula region, south of Moscow. It is located in the lower part of the Khovanshchina Formation, where a limestone-clay sequence contains stromatolites, ostracods, serpulids and charophytes. The skeleton of *Tulerpeton* was found in a layer with abundant sarcopterygian and other fish material. The Khovanshchina Formation is generally dated as equivalent to the *praesulcata* Conodont Zone, even though no conodonts have been found at Andreyevka-2 itself. However, ostracods do occur that are characteristic of the Khovanshchina Formation; they belong to the *Maternella hemisphaerica–Carboprimitia turgenevi* Zone, correlated to the 'Strunian' of the Franco-Belgian basin by Alekseev *et al.* (1994). Nevertheless, the *Maternella hemisphaerica–M. dichotoma* Zone has a much lower range in the Rhenish Massif, down to the upper *postera* Conodont Zone (Groos-Uffenorde *et al.* 2000, fig. 3). This gives the possibility of an older, late Famennian age for *Tulerpeton* (Fig. 1).

Russia (Famennian, Gornostayevka)

The material comes from the Gornostayevka quarry, SW of the town of Livny, Oryol Region of Central Russia, and is dated as equivalent to the *?triangularis–crepida* Conodont Zone (Lebedev 2004). In this locality, Lebedev (2003) cites *Bothriolepis* cf. *leptocheira*, an antiarchan placoderm. *B. leptocheira* is classically known from the Eleja Regional Stage (RS) of the Russian Platform (Main Devonian Field, including the East Baltic area; Luksevics 2001), a formation which is usually dated as basal Famennian (Esin *et al.* 2000, fig. 1). The Zadonskian RS of the Oryol region (Central Devonian Field), where the tetrapod comes from, is correlated by Esin *et al.* (2000, fig. 1) to the Joniskis RS of the Main Devonian Field, just above the Eleja RS (whose latest Frasnian or earliest Famennian age is, however, not solved by the most recent study of its conodont and fish content in Lithuania: Valiukevicius & Ovnatanova 2005). The Zadonskian would thus be equivalent to the upper *curonica* placoderm 'zone' of the Main Devonian Field, and to the *crepida* Conodont Zone (Esin *et al.* 2000), that is, lower Famennian.

China (Frasnian)

For this locality, Zhu *et al.* (2002) propose a 'late Famennian' age 'about 355 million years BP', a datum which may be understood as 'latest Famennian' or better 'Famennian/Tournaisian boundary' when using a classical radiochronological scale such as Odin's (1994). However, the most recent revisions of the Devonian scale give –362 to –359 Ma for the Devonian/Carboniferous boundary (Williams *et al.* 2000; Gradstein & Ogg 2004). So, an age of –355 Ma would fit the earliest Carboniferous better than the Famennian. In fact, Zhu *et al.* (2002) base their dating of this tetrapod locality upon Pan *et al.*'s (1987) book for the Famennian age of the Zhongning Formation (Pan *et al.* 1987, pp. 184–185). However, when considering the miospore assemblage of the Zhongning Formation as listed and figured by Gao in Pan *et al.* (1987, pp. 120–131, 184–185 and pl. 35–36), it is probably better considered older than the Famennian (G. Playford in litt. to Ritchie *et al.* 1992, p. 364; S. Loboziak pers. comm. to AB, 12.05.1989—now deceased). For Playford, it '... is certainly older than the latest Devonian *Retispora lepidophyta* Assemblage and could even be pre-Late Devonian ... (and) datable within the interval mid-Givetian to Frasnian' (Ritchie *et al.* 1992, p. 364). For Loboziak (unpublished), it is likely to be Frasnian. We will thus provisionally consider the *Sinostega* locality as Frasnian in age (Table 1 and Fig. 1).

Incidentally, if the Frasnian age of this locality is confirmed, it reinforces the generally accepted stratigraphical distribution of ostracoderms (*sensu* Janvier 1996). The Zhongning Formation has indeed yielded fragmentary remains of a Galeaspida gen. et sp. indet. (Pan *et al.* 1987, fig. 17, and pl. 1, 2, 3:1). As all other galeaspids are known only from the Lower to Lower Middle Devonian (Macrovertebrate Assemblages I to VI of China: Zhu 2000, pp. 375–376; Zhu *et al.* 2000, fig. 2), and as no other ostracoderm is known after the Frasnian (Blieck 1991), the galeaspid from the Zhongning Formation, if Famennian in age, would be the youngest record of galeaspids (Zhu 2000, p. 376), and the youngest record of ostracoderms. But if the Zhongning Formation is considered as Frasnian in age, it is consistent with no ostracoderm being younger than the Frasnian, and with the Frasnian/Famennian biological event being not a simple artefact for agnathans.

Australia (Frasnian/Famennian)

The first evidence of Devonian tetrapods from Gondwana was provided by trackways discovered in Upper Devonian strata of Victoria (Warren & Wakefield 1972). These evidently were made by several unknown tetrapod taxa (Clack 1997). Associated plant remains indicate a Late Devonian age, and Lewis *et al.* (1994) equated the relevant strata with the Merrimbula Group of southeastern New South Wales, where several fish faunas occur well beneath a Frasnian marine incursion (Young 1993, p. 215). An older trackway described from western Victoria by Warren *et al.* (1986) was probably not made by a tetrapod according to Clack (1997). The only tetrapod body fossil known from Gondwana is the lower jaw of *Metaxygnathus denticulus* Campbell & Bell (1977), found at Jemalong Quarry, SW of Forbes, New South Wales. The locality is in the Cloghnan Shale, with an associated fish fauna including lungfish (Campbell & Bell 1982; Ahlberg *et al.* 2001), and placoderms (Young 1993, 1999). Campbell & Bell (1977, p. 369) suggested a late Frasnian or early Famennian age, more likely at the younger end of this time interval, based on consideration of stratigraphical correlations with the Upper Devonian Hervey Group to the east. The tetrapod–fish assemblage was assigned to the 'Jemalong–Canowindra fauna' *sensu* Young (1993: Macrovertebrate Fauna 13), originally dated as early–middle Famennian (Young 1993, fig. 9.2; Young 1996, chart 14). However, a slightly older (late Frasnian) age for the Canowindra fish fauna was suggested by Young (1999, p. 145), indicating approximate alignment to the *rhenana/triangularis* Conodont Zone (MAV 13, Young & Turner 2000, fig. 2). The Canowindra fish fauna occurs near the base of the Hervey Group sequence, associated with evidence of a marine incursion. The tetrapod locality in the Cloghnan Shale is also near the base of the Upper Devonian sequence in the Jemalong Range. Detailed remapping and revision of Hervey Group stratigraphy in central NSW (Young *et al.* 2000*a*) supports the correlations initially proposed by Campbell & Bell (1977, pp. 374, 375; but note the nomenclatural change that the 'Pipe Formation' in the vicinity of the Canowindra fish fauna has been renamed the 'Mount Cole Formation').

In their discussion of correlations with the presumed marine/estuarine interval to the east, Campbell & Bell (1977, p. 375) recorded that 'marine rocks at Parkes are at the base of the Mandagery Formation', thus supporting a younger (Famennian) age for the Jemalong occurrence. However, Young (1999) noted that both the lingulid facies and the Canowindra fish fauna to the east of Parkes occur stratigraphically within transition beds between the Mandagery Formation (sandstone), and the overlying finer-grained Mount Cole Formation ('Pipe Formation'). Rather than 'at the base', this ?marine/estuarine interval occurs at the top of the Mandagery Formation, negating the earlier argument for a younger age. The basal marine/estuarine interval is succeeded by a stratigraphical thickness of the Hervey Group estimated in excess of 2.5 km. Both lycopod plants (*Leptophloeum*) and placoderm fishes near the top of the sequence indicate a Late Devonian rather than Carboniferous age (Young *et al.* 2000*a*). The only Late Devonian conodonts from this area (Jones & Turner 2000) come from the Catombal Group at Gap Creek near Orange, 100 km E of Jemalong, and 40 km NE of the Canowindra fish locality. Mawson & Talent (2003) have recently assessed these as indicating an early Famennian age (*crepida* Conodont Zone or younger). The horizon is at least 280 m above the lowest exposed Upper Devonian strata, where corals and bryozoans have been found (base of the sequence obscured by Tertiary basalt; R. K. Jones pers. comm. to GCY, 9.08.2004). A middle level in this sequence was reported to contain spores suggesting an age perhaps as old as Givetian (Webby 1972, p. 119). This is consistent with a SHRIMP zircon U/Pb isotopic age of 376 ± 4 Ma reported by Raymond (1998, p. 220) for the Dulladerry Volcanics, of which the Merriganowry Shale Member is a conformable sequence lying beneath the basal sandstones of the Hervey Group near Cowra (between Canowindra and Forbes; see Young 1999, fig. 1). Thus, the conodonts, bryozoans and brachiopods of the higher '*Lingula* limestone' horizon (Jones & Turner 2000, fig. 2) may represent a separate younger marine incursion (assigned to the Early *marginifera* Zone by Talent *et al.* 2000, p. 253), compared to the single incursion of Frasnian age previously assumed by Webby (1972) and Young (1993).

The similarity analysis of Lelièvre (2002, fig. 21, p. 172) groups the Jemalong–Canowindra fauna with various Northern Hemisphere Famennian tetrapod-bearing localities, including the Britta Dal and Aina Dal formations (East Greenland), the Catskill Formation (Pennsylvania), Andreyevka-2 (Russia), and Pavari (Latvia), but this is influenced by associated placoderms (phyllolepids, *Bothriolepis*, *Remigolepis*). This association is only recorded from Famennian strata in the Northern Hemisphere, but is clearly older (Givetian–Frasnian) in East Gondwana (based upon the whole palaeontological data: see reviews in Young 2003, 2005*a*–*b*). Thus, the problem of the age of the Jemalong fauna must also take account of such biogeographical considerations (Young *et al.* 2000*b*).

Biostratigraphical conclusion

After biostratigraphical information, it appears that most Devonian tetrapods are not exclusively late Famennian in age as thought previously (e.g. Jarvik 1996), but span at least the late Frasnian to late Famennian (Fig. 1; to be compared to Schultze 1997, fig. 1; Clack 2002*b*, fig. 3.2; Long & Gordon 2004, fig. 1). It is certainly difficult to say that tetrapods themselves can be used for correlation until a better fossil record is achieved. However, we need a good biostratigraphical framework which, together with a revised cladistic analysis of the various taxa now known, should lead to a renewed view of the early spreading of tetrapods in Devonian time (see earlier reviews by Schultze 1997; Clack 2002*b*; Long & Gordon 2004).

Palaeoenvironmental considerations

Devonian tetrapods are found in the Frasnian and the Famennian. They had a worldwide, nearly Pangaean palaeogeographical distribution (Laurussia, Gondwana, North China) and, although classically considered as being from terrestrial environments, are found in sedimentary rocks whose original environments are interpreted either as freshwater, brackish or marine (references on Table 1; also Schultze 1997; Lebedev 2004).

The question of the original environment of early tetrapods has been reviewed by Clack (2002*b*, pp. 99–104). She points out the influence of this question upon another one: 'why did tetrapods evolve?' Leaving the older scenarios aside, the question of the environment of Frasnian–Famennian tetrapods has been addressed through comparisons between faunal assemblages of fossiliferous localities by means of cluster analysis, and through analysis of co-occurring aquatic forms with tetrapods. Among others, the different trials by Schultze & Maples (1992), Schultze *et al.* (1994)

and Schultze & Cloutier (1996) (see a summary in Schultze 1997) proposed different analyses bearing on vertebrates, and vertebrates associated with invertebrates of different localities of Devonian and Carboniferous age, mainly from North America. All these analyses share the same phenetic method using general observed similarities of the fauna and flora to cluster the compared localities, where both absence and presence of taxa are considered, an assessment that is inherent to the methodology but that can be discussed depending on the use or not of hierarchical classifications.

More recently, one of us (Lelièvre 2002) has proposed a cluster analysis of 39 Famennian localities bearing early vertebrates. Different methods have been used, *viz.* classical hierarchical clustering and neighbour-joining (NJ). The latter method is advantageous in that it can use distances with metric and additive properties of the data in order to get a tree of minimal length. Fossil assemblages are treated at a taxonomic resolution to genus and family as most of the species described from those Famennian localities are monotypic. The result of running the NJ method on a localities/taxa matrix gives a single tree, an artefact due to the phenetic method. This tree shows that no assemblage defines a cluster of localities supposed to be freshwater (also Schultze & Cloutier 1996; Schultze 1997; Lelièvre 2002). Some of the localities, i.e. Greenland (where the Aina Dal and Britta Dal Formations are distinguished), Dura Den (Scotland), and Pavari (Latvia), cluster with marine localities such as Andreyevka-2 (Russia), or with coastal estuarine localities such as those from Belgium (Strud, Modave, Esneux, Evieux). This study concludes that vertebrate fossils cannot be used to define freshwater environment in the Upper Old Red Sandstone. The question of whether Late Devonian tetrapods were living in freshwater or nearshore marine environments relies upon other methods such as used in sedimentological and sequence-stratigraphical analyses (references in Friend & Williams 2000). Presently, biological and sedimentological data do not fully agree with each other concerning with this problem.

The recent discovery of a Famennian *Ichthyostega*-like tetrapod in Belgium emphasizes the problem (Clément *et al.* 2004). The bed that originally yielded the tetrapod fossil has been found and identified from its facies (see above). The microconglomerate-sandstone surrounding the lower jaw is composed of fine shale clasts and of palaeosoil clasts. These clasts were generated by flood erosion of the river banks, upstream from a deltaic flood plain. The tetrapod-bearing bed of Strud is thus considered as non-marine, according to one of us (Jacques Thorez): 'The sandstone surrounding the jaw is indicative of fluviatile conditions... This tetrapod therefore lived in rivers and estuaries, but the shoreline at the time of the Evieux Formation was oscillating south to north of Strud' (in Clément *et al.* 2004).

It means that the conclusion of Lelièvre (2002, pp. 175–179) has to be placed in the context of these new data. We can certainly no longer maintain that all Upper Devonian tetrapod-bearing localities were continental. Some were evidently marine such as Velna-Ala, Pavari, Ketleri, Andreyevka-2 and Gornostayevka in Latvia and Russia (references in Table 1; but Long & Gordon [2004, p. 704] propose that the carcass of *Tulerpeton* may have been floated to and deposited in the marine sediments of Andreyevka-2, and that *Tulerpeton* could be non-marine). On the contrary, we can probably not maintain that they all correspond to marine tidal zone deposits (Schultze 1997, 1999). The general idea is expressed by Clack (2002*b*, p. 99): 'The shallow, swampy waters of marine lagoons, newly populated by emergent plants, might have been the breeding ground for the earliest tetrapods...' [Note, however, that the author did not mean that emergent plants had arisen in Late Devonian time only, as they are known as early as the Silurian; J. Clack pers. comm.]. The Givetian–Frasnian was the time of appearance of substantial trees (Algeo & Scheckler 1998), but certainly not in swampy waters of marine lagoons.

If we add to this corpus of facts and hypotheses the newly developed idea that Late Devonian tetrapods were most probably all aquatic inhabitants, the only conclusion that can be put forward is that any theory of the origin of tetrapods (i.e. origin of limbs with digits, origin of walking, and origin of terrestriality; Clack 2002*b*, 2006) must be valid for the wide range of animals having occupied habitats ranging from proximal, nearshore marine localities to continental, freshwater lakes and/or rivers. This idea is consistent with the conclusions of Lebedev (2004) who ran a comparison of most Upper Devonian tetrapod sites. Lebedev recognizes that 'these animals dwelled within a wide range of aquatic environments' and that 'The presence of more than one tetrapod in the communities indicates many more diverse tetrapod trophic adaptations than previously considered'. This subject is the topic of a group of scientists from Latvia, Russia, Sweden, the United Kingdom, France, the United States and Australia who are hoping to co-ordinate their activities and produce a more complete theory at a global scale (Clack 2006).

Global palaeobiogeographical context

Because Late Devonian tetrapods are now known in a range of localities worldwide, it is important to consider the global palaeogeographical context of their origin and radiation. A recent palaeogeographical reconstruction is proposed in Figure 2 (Averbuch *et al.* 2005) with the location of tetrapod-bearing sites. Based primarily on Golonka *et al.*'s (1994) map, it shows Laurussia (=Euramerica) in a rather southern location, with in particular the palaeoequator running high across Greenland (see also Golonka 2000, time slices 10 and 11; Scotese 2002, maps Devonian). This is compatible with the miospore data, and converges with the position already published by Streel *et al.* (1990), and emphasized by Streel & Marshall (2006). A consequence is that most of Greenland, among other areas, was in the arid belt on the southern side of a very narrow equatorial belt.

One old question considering palaeogeographical considerations is 'where did tetrapods evolve first?' (if this question can be answered), and how did they disperse to gain a wide geographical distribution from Pennsylvania in the west to Australia in the east? However, we must take care not to fall into a circular reasoning. As Frasnian–Famennian tetrapods are all endemic, and restricted to the locality or region where they have been collected (with the possible exception of *Ichthyostega*, now known both in Greenland and Belgium), we cannot use the occurrence of shared taxa to establish biogeographical relationships among the continental masses with which we are concerned.

We cannot even use the phylogenetic relationships of those taxa compared with their palaeocontinental context because of the lack of consensus over their phylogeny (see discussions and references in Schultze 1997; Clack 2002*b*; Ruta & Coates 2003; Ruta *et al.* 2003). [The use that the latter authors make of the concepts of total-, crown- and stem-groups, may not be accepted by all of us, but a thorough discussion of this point is beyond the scope of the present paper.] The simplest thing that we can say is that, most probably, as based on current data, tetrapods may have originated in a generalized area including Euramerica, North China, and easternmost Gondwana. There is a higher probability that this occurred in the western, Euramerican part because the sister-group of tetrapods, the tetrapodomorph sarcopterygian taxa *Panderichthys*, *Elpistotege* and a new elpistostegid from Nunavut, Canada (Daeschler *et al.* 2004) occurred in Euramerica (Fig. 2).

The occurrence of tetrapods on those three landmasses suggests that the latter were closely related in the Late Devonian (e.g. see Scotese & McKerrow 1990; Streel *et al.* 1990; Golonka 2000; Scotese 2002; and the critical analyses of Young 1981–2003). Given the pre-Pangean disposition of the Late Devonian continents, it is not possible to distinguish between a hypothesis of a northern (through central and southern Asian continental blocks) or a southern (along the northern margin of Gondwana) migration route for tetrapods. Correspondingly, it is not possible to use the distribution of tetrapods to infer the position of the continents without a danger of circular reasoning, and the 'best fit' global palaeogeographical reconstruction should be drawn up on other grounds (for a critical review of this nomenclature, see Cecca 2002). On present knowledge, it is not clear whether major

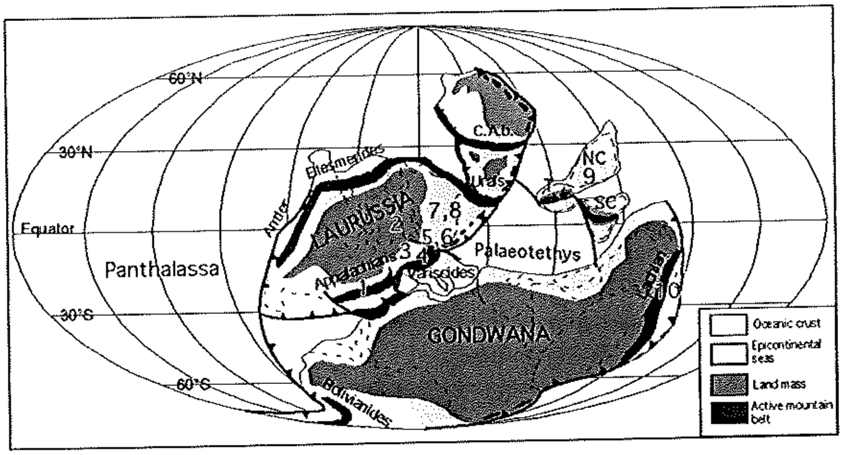

Fig. 2. Late Devonian tetrapod localities plotted on Averbuch's (in Averbuch *et al.* 2005) palaeocontinental reconstruction, showing geometry of active orogenic systems at the Frasnian/Famennian boundary. 1–Pennsylvania, 2–E. Greenland, 3–Scotland, 4–Belgium, 5–6–Latvia and nearby Russia, 7–Russia: Andreyevka-2, 8–Russia: Gornostayevka, 9–China, 10–Australia. Abbreviations: C.A.b., Central Asian belt; NC, North China; SC, South China; T, Tarim. [Palaeogeographical scheme kindly provided by O. Averbuch, University of Lille 1.]

marine barriers (e.g. between Gondwana and Northern Hemisphere blocks), which evidently separated the main continental areas in Early and Middle Devonian times, were significant in the early dispersal of tetrapods.

As emphasized both by the biotic dispersal of fishes (phyllolepid placoderms: Young *et al.* 2000*b*), land plants (*Callixylon* archaeopterids: Meyer-Berthaud *et al.* 1997), and their miospores (Streel *et al.* 2000) between Gondwana and Laurussia, palaeontological data point to a drastic continental re-organization around the Frasnian–Famennian boundary with, at best, a very narrow residual oceanic domain between these continents. Tectono-metamorphic data in the worldwide Upper Palaeozoic mountain belts corroborate this view, showing that the Late Devonian was characterized by intense tectonic activity with the incipient collision of major continental crustal blocks, *viz.* Laurussia, Gondwana, Kazakhstan and Siberia (Averbuch *et al.* 2005). This may not be evident in long-lasting carbonate platform sequences such as the Frasnian–Famennian of the Tafilalt-Maider and Anti-Atlas in Morocco, but is well known in regions such as the Ardenne Massif in France–Belgium, where the Frasnian is limy when the Famennian is siliciclastic (Bultynck & Dejonghe 2002). That collisional process of continental masses led to closure of oceanic domains and deformation and uplift of wide continental areas (Appalachian belt, European Variscides, Northern African Variscides, Arctic Ellesmerian–Svalbardian belt, Central Asian belt, South Uralian belt); contemporaneous Frasnian–Famennian oceanic subduction led to terrane accretion (western American Antler belt, South American Bolivianides, eastern Australian Lachlan fold belt). These events have certainly modified strongly several marine environments, and seem to have contributed to a significant global cooling event in earliest Famennian time (references in Averbuch *et al.* 2005). Such a cooling event is attested independently both by the miospore distribution on continental areas (Streel *et al.* 2000), and by the $\delta^{18}O$ signature of marine carbonates (Joachimski & Buggisch 2002). The origin and spreading of the first tetrapods is contemporaneous with this global changing context.

Conclusion

Do we know where, when, how and why tetrapod vertebrates appeared and radiated in Late Palaeozoic time? For the time being, we can schematically propose the following provisional answers:

- Where? Somewhere in the area delimited by Pennsylvania in the west and Australia in the east, with a higher probability for its western part because the closest sister taxa of tetrapods, *Elpistotege*, *Panderichthys* and a new elpistostegid from Nunavut were found in Euramerica. The original environments of those very first tetrapods are diverse, from true marine environments of the proximal neritic province to probably true continental environments (fluviatile and/or lacustrine), with apparently a predominance of shallow swampy marine lagoons.
- When? At least by the middle Frasnian, as both the oldest-known tetrapods and their sister-group (see above) are middle Frasnian in age (but see the more detailed argumentation of Ruta & Coates 2003; and the suggestion by Clack 2006, for a period between the mid-Givetian and the mid-Frasnian).
- How? This question is out of the scope of the present paper, and we refer the reader to the papers of Schultze (1997), Clack (2002*b*) and Long & Gordon (2004).
- Why? Various scenarios have been proposed, but none seems convincing enough to be uncritically accepted (see a review in Clack 2002*b*). We just note a coincidence between this biological event and a series of physical-chemical features of the Earth in Late Devonian time, linked to the building of a pre-Pangean configuration of continents.

We dedicate this paper to Michael R. House, and to two other SDS former officers: W. Ziegler and I. Chlupac. All three have been highly influential in the SDS past scientific activities, and in science in general.

This is a contribution to IGCP 491 'Middle Palaeozoic Vertebrate-Biogeography, Palaeogeography, and Climate', and SDS working groups 'Frasnian' and 'Famennian'.

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