

Introduction

## Middle Palaeozoic vertebrate biogeography: Palaeogeography and climate

The Middle Palaeozoic (Silurian and Devonian) was a time of major biotic change, with the initiation of complex terrestrial ecosystems, the first forests, and the expansion of diverse invertebrate and vertebrate faunas into fresh-water and terrestrial environments. For the first time in Earth history the land surface showed some resemblance to that experienced in modern times by the human species.

There were also dramatic changes in atmospheric composition, from high levels of CO<sub>2</sub> estimated at about 4000 ppmv during the Early-Middle Devonian, falling to about one tenth that concentration to approach modern levels by the Late Devonian. In addition, the Late Devonian Frasnian-Famennian boundary extinction was one of five major extinction events during the Phanerozoic, and there is considerable controversy about palaeogeographic change during the Devonian, in particular the timing of contact between the great southern supercontinent of Gondwana, and other continental areas now located in the Northern Hemisphere. The configuration of the continental blocks provides essential data concerning the extent and duration of a major equatorial ocean during the Middle Palaeozoic, a key consideration for reconstructing oceanic circulation patterns that would have profoundly influenced global climate change, as is the case today.

All these were motivating factors for proposing a new project under the UNESCO International Geoscience Program (IGCP Project 491), because we considered our information on Middle Palaeozoic vertebrates at various levels (morphological, systematic, biostratigraphic, biogeographic) to provide perhaps the most complex palaeontological dataset that can be applied to such questions.

IGCP Project 491 ran from 2003 to 2007, with five annual meetings held in conjunction with scientific symposia in various participating countries: Riga, Latvia (2003); Gramado, Brazil (2004); Yerevan, Armenia, and St. Petersburg, Russia (2005); Beijing, China (2006), and Uppsala, Sweden (2007). Published abstracts, papers or field guides from those meetings can be found in [Schultze et al. \(2003\)](#), [Stinkulis et al. \(2003\)](#), [Richter and Smith \(2004\)](#), [Rösler et al. \(2004\)](#), [Hairapetian and Ginter \(2005a,b\)](#), [Ivanov and Young \(2005\)](#), [Ivanov et al. \(2005\)](#), [Zhu](#)

[et al. \(2006a,b\)](#), [Blom and Brazeau \(2007\)](#), [Blom and Snitting \(2007\)](#), and [Ahlberg et al. \(2009\)](#).

In addition to enhancing our understanding of the anatomy and early evolution of the vertebrates (see [Janvier, 1996](#)), the study of Middle Palaeozoic fishes and tetrapods has long been applied to the solution of geological problems, mainly through investigation of biostratigraphy and biogeography. Documented diversity of early vertebrates has increased significantly in recent decades, revealing many remarkably endemic assemblages. Some widely distributed fishes evidently dispersed readily through the sea, but many highly endemic assemblages, lacking associated marine invertebrates, indicated constraint by marine barriers, and therefore provide one of the most reliable indicators of past connections or seaways between continental areas. The book edited by [Long \(1993\)](#) gave a global perspective on these aspects, but since then much new information has become available.

For biostratigraphy, the major publication by [Blieck and Turner \(2000\)](#), the final results volume of a previous IGCP Project (328: Palaeozoic vertebrate biochronology and global marine/non-marine correlation), updated the contributions in [Long \(1993\)](#) to provide improved age control on diverse early vertebrate assemblages integrated with global transgression-regression patterns for the middle Palaeozoic. This provided the global chronological framework within which to investigate the interplay of early vertebrates and their environments. For biogeography, a synthesis of knowledge from the Australasian area for most of the Phanerozoic was presented in [Wright et al. \(2000\)](#), with reference to a set of maps derived largely from palaeomagnetic data ([Li and Powell, 2001](#)). Related topics under IGCP Project 406 (Circum-Arctic Palaeozoic vertebrates) were published by [Ginter and Wilson \(1999\)](#).

Research associated with IGCP Project 491 has produced over 300 peer-reviewed papers. The contributions brought together in this special issue summarise recent research for some regions where many new vertebrate taxa have been documented in recent years, especially Asia ([Zhao and Zhu, 2010](#); [Wang et al., 2010](#)), and East Gondwana ([Burrow et al., 2010b](#); [Young et al., 2010](#)). Two other contributions provide updated synthe-

ses of the long-studied Devonian vertebrate communities of the Baltic Province (Lukševičs et al., 2010; Lebedev et al., 2010). We also have more general contributions on atmospheric O<sub>2</sub> levels in the Silurian (Qu et al., 2010), palaeomagnetic data and Gondwana–Laurasia interactions (Klootwijk, 2010), analytical methods in palaeobiogeography (Young, 2010), and global analysis of endemism–cosmopolitanism during the Middle-Late Devonian (Lebedev and Zakharenko, 2010). The remaining papers document new placoderm taxa from North Gondwana (Rücklin, 2010), South China (Zhang et al., 2010) and North China (Jia et al., 2010), and vertebrate microremains from Uzbekistan (Burrow et al., 2010a). There is no overall update of the ‘Old Red Sandstone continent’ of Laurussia (Euramerica), but Elliott et al. (2000) gave coverage of this well-studied region. For South America, included as part of West Gondwana in the overview by Lelièvre et al. (1993), Janvier (2007) has provided a recent update.

However we also note some significant regions that have been less accessible to scientific investigation, but contain diverse Devonian vertebrate assemblages that remain poorly documented. One such area includes Siberia, the Kara-Tajmyr block (Tajmyr and Severnaya Zemlya), and Kolyma, and a second includes the Palaeozoic Tianshan Belt of central Asia (Uzbekistan, Tadjikistan, Kyrgyzstan), Kazakhstan, and the Tuva-Mongolia belt. Blicek and Janvier (1993) provided an excellent overview of vertebrate localities across part of these areas; Ivanov (2002) commented briefly on unusual placoderms from southern Siberia and Kazakhstan, and Burrow et al. (2010a) have documented the Zinzilban section of Uzbekistan, but there is much more to be described. Future documentation of vertebrate assemblages across central Asia will provide crucial data for understanding the timing of connections between eastern Asia and Laurussia (Euramerica). Another less accessible region relevant to the question of Devonian east-west connections is the Middle East. Again, an excellent summary of localities was presented by Lelièvre et al. (1993; one additional locality is a dipnoan occurrence in the western Karkorum Hindu Kush region of northern Pakistan; see Talent et al., 1999, fig. 5). We regard documentation of the Devonian vertebrate assemblages in these regions as the most important focus for future research, to complete the global coverage of the vertebrate dataset for analysis of Middle Palaeozoic biogeography, palaeogeography, and climate.

As co-leaders of IGCP Project 491, we would like to thank all colleagues for their participation in the project, and especially those that put in the enormous effort of organising the annual meetings and associated symposia and field trips. We are indebted to Wenjin Zhao (IVPP), who worked tirelessly as the secretary of IGCP Project 491 to organize all aspects of the project, including all the documentation of annual reports, funding, minutes of meetings, etc.

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