Introduction

Acta Palaeontologica Polonica 47 (2): 186–188, 2002

Biotic responses to the Late Devonian global events: Introductory remarks

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Investigations of the Late Devonian successions have provided a great deal of evidence to support the hypothesis that the biospheric turning point near the Frasnian–Famennian (F–F) boundary was one of the most significant in Phanerozoic time. Considerable attention and debate have been focused on determining the cause(s) of these biocrises, and various mechanisms have been proposed for the extinction of a wide range of benthic, primarily low-latitude stromatoporoid-coral reefs, and pelagic organisms. The widely recognized stepwise pattern of extinction in major fossil groups in the late Frasnian argues against a single catastrophic ("bedding-plane") mass killings of biota at the end of the Frasnian (see concept of a prolonged Kellwasser [KW] Crisis; Schindler 1993). However, many aspects of this major biotic turning point remain conjectural, including timing and magnitude of ecosystem changes and mediated extinction dynamics. The overall biotic succession is far from reliably documented. Among the better known pelagic faunas, a conodont near-extinction and goniatite crisis are traditionally fixed precisely at the F–F boundary.

The main aim of this thematic issue is to present new high-resolution taxonomic data and ecologic interpretations that are currently available for the Kellwasser Crisis and other Late Devonian events from different parts of the Devonian world (see list of paper on the back cover of the issue). Nine contributions present results of studies of eastern Laurussian epeiric successions in the framework of the international project "Ecosystem Aspects of Late Devonian Biotic Crisis". This project was supported by the State Committee for Scientific Research (KBN grant no. 6 P04D 024 13 to G. Racki), and conducted jointly in 1998–2000 by scientists from the Silesian University and the Institute of Paleobiology of the Polish Academy of Sciences, in cooperation with specialists from Russia, Belgium, France, and USA. In this issue, there are six complementary articles, including those by invited authors from USA, China and France. A related paper to be soon published in this journal by Jerzy Dzik will provide a comprehensive synthesis of the emergence and collapse of Frasnian conodont and ammonoid communities in the Holy Cross Mountains. Noteworthy is that this project is a comprehensive continuation of the previous KBN grant for G. Racki, dealing exclusively with the F–F brachiopod faunas, presented recently in the Devonian thematic issue of *Acta Palaeontologica Polonica* (Racki and Baliński 1998). The remaining stratigraphic, litho- and palynofacies and geochemical results of this project are presented in three articles in the simultaneously appearing special issue of *Palaeogeography, Palaeoclimatology, Palaeoecology* (Racki and House 2002).

The regional case studies in this volume refine and emphasize various aspects of global-scale biotic changes in Late Devonian marine settings, arranged from west to east (see Fig. 1). From western Laurussia, Day and Over described a unique lowest Famennian brachiopod survivor fauna from an offshore setting in the Appalachian Basin. The cyrtospiriferid-productoid dominated benthos was typical of the remainder of the early Famennian in many Laurussian basins (see Baliński). Feist's investigation of the trilobite fauna from the F–F boundary beds of Morocco documents striking similarities in composition and evolutionary trends in contemporaneous faunas from North Africa and several European sections. This strongly argues against wide oceanic separations of Laurussia and Gondwana postulated by workers citing published paleomagnetic data.

The main group of eight articles document diversity of faunal records from different parts of the south Polish carbonate shelf of the south-eastern Laurussia, based mostly on data from exposures in the Holy Cross Mountains and the Cracow area (Baliński, Ginter). Vishnevskaya et al. present the first detailed documentation of a world-wide bloom of siliceous radiolarian-sponge biota during the KW Crisis (see also Yudina et al.). The latters also discuss paleooceanographic and evolutionary implications of the radiolarian-sponge bloom for both zooplankton and benthos. Papers by Casier et al. and Olempska focus on records of benthic and planktic ostracods. A combined, microfacies-palaeontologic study of a fore-reef succession by Casier and his colleagues points to a regressive episode that started close to the fatal F–F stage boundary interval, paired with very high rate of extinction in this well-oxygenated habitat. The paper by Olempska illustrates the role of entomozoacean ostracodes in tracing global climate and sea-level changes, and their effect on the ocean's water masses during the Upper KW Event. The entomozoaceans remained virtually absent during a long time interval after the stepped end-Frasnian collapse, and reappeared late in the early Famennian as new species of refugia lineages.

Krawczyński describes Frasnian gastropod reef- and lagoon-dwelling faunas, and their close link with shallowing-upward cycles and sedimentary evolution of the carbonate complex. In a high-resolution study of the brachiopod faunas, Baliński demonstrates that the post F–F survival interval was characterized by low diversity and low frequency cyrtospiriferid–rhynchonelloid or cyrtospiriferid–productoid assemblages that feature stunted phenotypes characteristic of disturbed and stressed habitats during the survivor phase following the extinction. Preliminary results from studies of Givetian to Frasnian bryozoan faunas are discussed in biogeographic and global event contexts by Morozova et al.

The paper of Głuchowski documents three successive Famennian repopulation faunas characterizing post-extinction recovery of crinoids (defined with the aid of stem-based taxa), and shows a close correspondence between successive repopulation radiations and eustatic transgressive-regressive cycles. Ginter outlines the impact of the F–F biotic crisis on the chondrichthyan fauna. He suggests that global cooling is responsible for the crash of the Frasnian subtropical extreme-stenothermal phoebodont sharks.

Two other articles focus on contrasting F–F environmental settings in different parts of the East European Platform. The evolutionary dynamics of successful rhynchonellid faunas affected by intermittent transgressions into the central region of the platform is analyzed by Sokiran, especially in the context of their early Famennian expansion. Newly refined stratigraphic evidence is available from a deep-shelf succession of the subpolar Urals in the study by Yudina et al. Many well known biotic and geochemical F–F phenomena (icriodontid and biosiliceous acmes, positive carbon isotopic shift) support the development of an unstable eutrophicated and oxygen-depleted crisis ecosystem in the tectonically disturbed Ural Ocean. The northernmost Laurussian sequence exhibits close similarities to the intra-shelf basin succession in southern Holy Cross Mountains.

The paper by Ma et al. presents interesting data concerning F–F extinction and recovery events among tetracorals, brachiopods and ostracods in central Hunan, South China. Finally, review of literature-based data on distribution of *Cyathaxonia* corals by Wrzołek indicates that the Devonian was a time of relatively high diversity of this deeper marine fauna, significant decrease in diversity of these corals this author sees rather at the Givetian–Frasnian boundary. The author proposes the new term "silent taxa" for those taxa, which are absent in significant intervals of their total range, exemplified by the Frasnian record of the *Cyathaxonia* coral group.

Two general conclusions emerge from the regional contributions, discussed above:

- The records of crinoids and radiolarians show minor changes across the F–F extinction interval. In those groups, their main taxonomic turnovers occurred either later (e.g., at the Devonian–Carboniferous boundary) or earlier (near the Middle–Upper Devonian boundary). This is also seen in records of some rugosan corals (*Cyathaxonia* faunas) and bryozoans. The records of sponges and gastropods remain sporadic.
- A biogeographic variability of extinction, survival and recovery patterns, previously recognized in other major mass extinctions (Erwin 1998), may be assumed at least for the F–F brachiopod and crinoid communities. Polish and North American survivor and recovery brachiopod faunas are quite similar in terms of genera involved, but quite distinct from those reported from Russia and China. Webster et al. (1998) implied that the crinoids were relatively unaffected by the F–F crisis, although significant extinctions of crinoids across the F–F interval are clearly recorded in Holy Cross faunas in Poland. In a taxonomic context, suggests that the post-extinction renewal of the brachiopod fauna was quite rapid (ca. 1.5–2.0 Ma), but a significantly delayed rebound and rediversification is known among other faunas, e.g. echinoderms (Lane et al. 1997; Erwin 1998).

As an integrative biostratigraphic synopsis, the data in this issue constrain some of the extinction interpretations and uncertainties. In particular, new taxonomic summaries from three Devonian continents (Fig. 1) yield more precise biostratigraphic control needed to determine timing of events occurring within Late Devonian global events. However, better understanding of complex biotic and environmental feedbacks leads to several new unresolved questions, and to following key broadly-defined paleobiologic matters for future interdisciplinary research:

- Major uncertainty is still evident because of common hiatuses in the critical F–F interval in many subtropical and near equatorial carbonate platform sequences. The quantitative approach to estimation of the true stratigraphic endpoints (see confidence intervals on fossil ranges, and review in Marshall 1998) should be applied to distinguishing between sudden and gradual biotic change. Records of many groups affected by the F–F extinctions are difficult to assess statistically because phylogenetic–taxonomic relationships in many fossil groups remain unclear. This ambiguity is evident in the study by (in press) in conodont apparatus-based taxonomic terms, as well as for rugosan faunas by Wrzołek.
- The UKW crisis did not particularly affect the phytoplankton (Streel et al. 2000), but a significant unbalanced excess of bacterially controlled productivity is a marked feature (Joachimski et al. 2001), resembling the disorganized biological pump after end-Cretaceous mass extinction. A major disturbance episode of the trophic web in the photic zone is clearly coupled with suppression of major pelagic consumers (conodonts, ammonoids), augmented by Ginter's data on top predator (shark) selective demise. Sudden lateral shifts in prolific pelagic faunas (from radiolarian to homoctenid-entomozoid to cephalopod communities) and contribution of potentially tremendous diatom productivity to the F–F biosiliceous event are also puzzling (see Schieber et al. 2000). Investigation of survival communities and environments should yield a look into post-extinction strategies and biogeochemical attributes.
- In a global ecosystem-geotectonic framework, reliable biotic and geochemical evidence is required to document and analyze the timing of climatic changes (see discussion in Streel et al. 2000), especially for suspected Kellwasser cooling pulses, and a resolution of the nutrient sources driving increased primary biological productivity that induced geographically variable anoxia (Yudina et al.) at different times in the Late Devonian.
- Greatly refined studies of taxon ranges are required from the widespread Middle Devonian carbonate platforms to the F–F carbonate crisis, particularly related to the many pulses of transgression, anoxia and reef losses known over this period. McGhee (2001) recently suggested that a climatic key to the KW Crisis enigma may be related to the Alamo impact in the overlooked early Frasnian timespan.

References

Dzik, J. (in press). Emergence and collapse of the Frasnian conodont and ammonoid communities in the Holy Cross Mountains. *Acta Palaeontologica Polonica.*

Erwin, D.H. 1998. The end and the beginning: recoveries from mass extinctions. *Trends in Ecology & Evolution* 13: 344–349.

Golonka, J., Ross, M.I., and Scotese, C.R. 1994. Phanerozoic paleogeographic and paleoclimatic modeling maps. *In:* A.F. Embry, B. Beauchamp, and D.J. Glass (eds.), Pangea; global environments and resources. *Canadian Society of Petroleum Geologists, Memoir* 17: 1–47.

Joachimski, M.M., Ostertag-Henning, C., Pancost, R.D., Strauss, H., Freeman, K.H., Littke, R., Damsté, J.S., and Racki, G. 2001. Water column anoxia, enhanced productivity and concomitant changes in ^{13}C and ^{34}S across the Frasnian–Famennian boundary (Kowala—Holy Cross Mountains/Poland). *Chemical Geology* 175: 109–131.

Lane, N.G., Waters, J.A., and Maples, C.G. 1997. Echinoderm faunas of the Hongguleleng Formation, Late Devonian (Famennian), Xinjiang-Uygur Autonomous Region, People's Republic of China. *Journal of Paleontology* 71 (Supplement to No. 2): 1–43.

Marshall, C.R. 1998. Determining stratigraphic ranges. *In:* S.K. Donovan and C.R.C. Paul (eds.), *The Adequacy of the Fossil Record*, 23–53. J. Wiley & Sons, Chichester.

McGhee, G.R. 2001. The "multiple impacts hypothesis" for mass extinction: a comparison of the Late Devonian and the late Eocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 176: 47–58.

Racki, G. and Baliński, A. (eds.) 1998. Brachiopods and the Frasnian–Famennian biotic crisis. *Acta Palaeontologica Polonica* 43: 135–411.

Racki, G. and House, M.R. (eds.) . 2002. Late Devonian biotic crisis: ecological, depositional and geochemical records. *Palaeogeography, Palaeoclimatology, Palaeoecology* 181: 1–374.

Schieber, J., Krinsley, D., and Riciputi, L. 2000. Diagenetic origin of quartz silt in mudstones and implications for silica cycling. *Nature* 406: 981–985.

Schindler, E. 1993. Event-stratigraphic markers within the Kellwasser Crisis near the Frasnian/Famennian boundary (Upper Devonian) in Germany. *Palaeogeography, Palaeoclimatology, Palaeoecolology* 104: 115–125.

Streel M., Caputo M.V., Loboziak S., and Melo J.H.G. 2000. Late Frasnian–Famennian climates based on palynomorph analyses and the question of the Late Devonian glaciations. *Earth-Science Reviews* 52: 121–173.

Webster, G.D., Lane, N.G., Maples, C.G., Waters, J.A., and Horowitz, A.B.S. 1998. Frasnian–Famennian extinction was a non-event for crinoids, blastoids and bryozoans. *Geological Society of America, Abstracts with Programs* 30 (7): 30–31.

Acknowledgements

We would like to express our thanks to the following scientists who have kindly assisted us by providing referee reports on manuscripts submitted for this Thematic Issue: Jonathan C. Aitchison, Francoise P. Bigey, Robert B. Blodgett, Denise Brice, Tomasz K. Baumiller, Jean-Georges Casier, Ivo Chlupač, Paul Copper, Jed Day, Jerzy Fedorowski, Richard A. Fortey, Jiri Frýda, Helga Groos-Uffenorde, Steve J. Hageman, Michael R. House, Gilbert Klapper, Krzysztof P. Krajewski, Norman M. Savage, James E. Sorauf, Jerzy Trammer, Gary D. Webster, and an anonymous reviewer.

Paleogeographic models on p. 185 after Copper (1986), modified.

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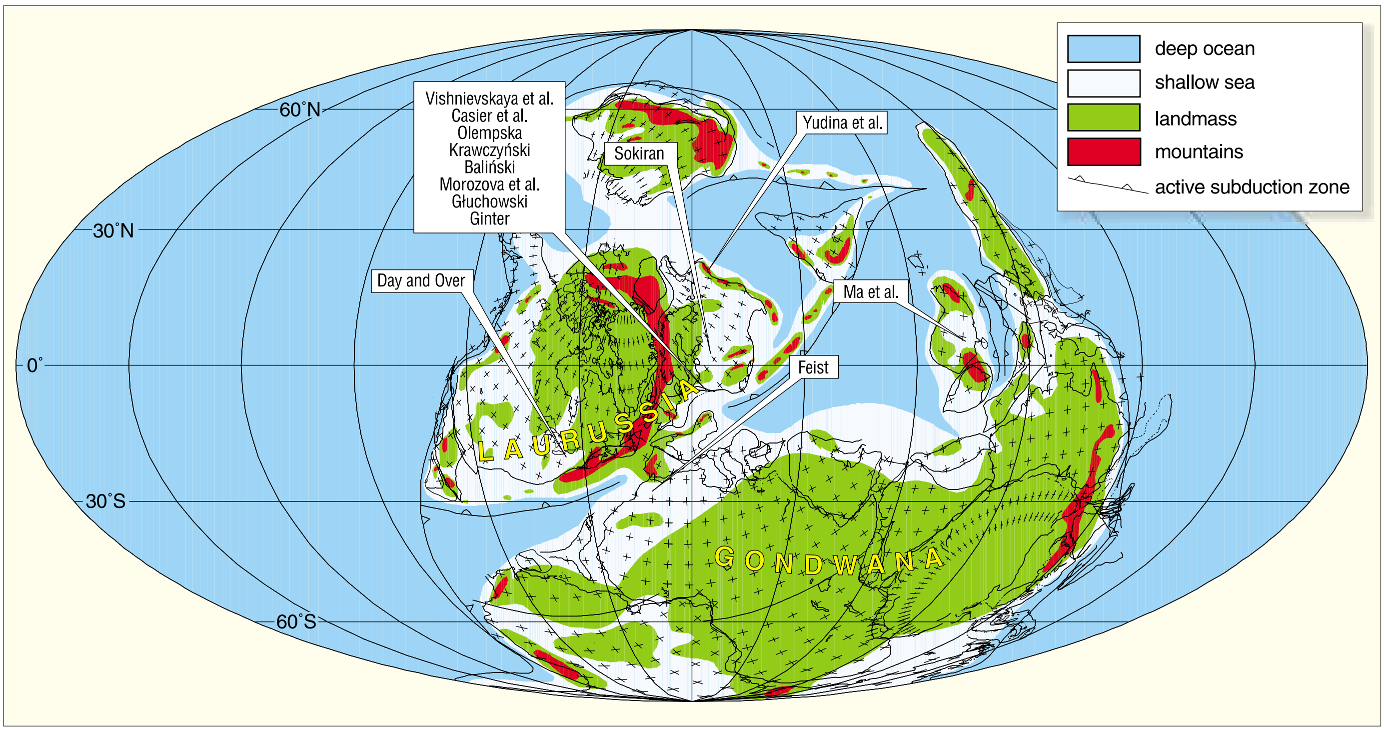

Fig. 1. Location of studied areas presented in this issue against the Late Devonian (363.0 Ma) palaeogeography (adapted from Golonka et al. 1994; courtesy of Jan Golonka).