The Frasnian-Famennian brachiopod extinction events: A preliminary review

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Racki, G. 1998. The Frasnian-Famennian brachiopod extinction events: A preliminary review. — *Acta Palaeontologica Polonica* **43**, 2, 395–411.

Preliminary review of taxonomy of the brachiopod order Atrypida and its stratigraphic distribution in the late Frasnian Kellwasser Crisis of several regions of Laurussia, western Siberia and South China point to their moderate diversity and stepdown but irregular extinction pattern. The distinctive character of the late Frasnian atrypid fauna is emphasised by several relict genera, marked by recurrent and possibly aberrant characters (mainly in ornamentation types), tendency to size reduction and homeomorphy in some taxa. The transgressive/hypoxic Lower Kellwasser Event and preceding eustatic changes during the *Palmatolepis rhenana* Zone had only a regional destructive effect, and were linked rather to an enhanced dispersal of the last generic set of atrypids. The Variatrypinae, Spinatrypinae and *Iowatrypa*-group seem to belong to the latest surviving atrypids. The final demise of the remaining atrypids (and some other articulate brachiopods, e.g., gypidulids) coincided with the transgressive/hypoxic Upper Kellwasser Event, followed by catastrophic eustatic fall during the late *Palmatolepis linguiformis* Zone (F-F Event). This was probably exacerbated by accelerated submarine volcano-hydrothermal activity, and consequent progressive regional eutrophication, and climatic destabilization. The level-bottom rhynchonellid-inarticulate biofacies crosses the fatal F-F boundary horizon without major changes. No reliable data exist for the presence of atrypids in the Famennian survival and recovery biota, even for the smooth lissatrypid *Peratos*. Sustained competition from radiating and diversifying productid-cyrtospirifrid-athyrid faunas may have provide an additional biotic factor in the collapse of the Frasnian shelly benthos at the time of stress, as well as in a post-extinction offshore repopulation from inner shelf habitats.

Key words: Brachiopoda, Atrypida, Pentamerida, biostratigraphy, palaeoecology, biogeography, mass extinction, Kellwasser Crisis, Frasnian, Famennian, Devonian.

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Introduction

Since the classic works of Copper (1966, 1973, 1986b), the brachiopod order Atrypida, a prominent benthic component of Middle Palaeozoic shelf ecosystems (Atrypid–Gypidulid Biofacies of Racki *et al.* 1993), is commonly cited as a prime victim of the mid-Late Devonian (Frasnian-Famennian; F-F) mass extinction. This was one of the severest global bio-crises in the Phanerozoic, termed by Schindler (1990) the Kellwasser (KW) Crisis (see Racki 1998). This biotic turnover corresponds to the late Frasnian to earliest Famennian series of extinction pulses, manifested primarily during the late Frasnian in the two eustatic/hypoxic Kellwasser events, culminating in the ecosystem collapse near the F-F transition (see summary in McGhee 1996 and Walliser 1996). A tangled combination of causal factors, especially profound oceanographic and climatic changes, probably brought about the bio-crisis (Joachimski & Buggisch 1996; Copper 1998; Racki in press).

Atrypid catastrophic collapse was examined at the family, subfamily and generic level by Copper (1986b). For other brachiopods, similar detailed data, but only on a regional scale, were gathered for gypidulid pentamerids (Godefroid & Racki 1991), another group that became totally extinct at the close of the Frasnian age.

The last (late Frasnian) phase in the atrypid history has been only in a preliminary manner studied until now, as emphasized by Copper (1986b). A major constraint has always been the limits of stratigraphic resolution, with precise reference to conodont zones available for few F-F brachiopod successions (see McGhee 1996), as exemplified by Baliński (1979, 1995a, 1996) and Cooper & Dutro (1982). Nonetheless, the resulting revised generic range chart in the substage framework exhibits the stepdown character of atrypid demise during the Frasnian time (Copper 1986b, 1998).

The results of the international collaboration research project, funded in part by the State Committee for Scientific Research (Project no. 6P201 019 05), and presented in the present issue, enable a more detailed discussion of this problem, including refined data from widely separated regions (Fig. 1).

Taxonomic and evolutionary framework

In a provisional generic and subgeneric range chart, Copper (1986b: fig. 2) showed the occurrence of five genera in the late Frasnian interval (starting from the Upper *Palmatolepis gigas* Zone = Late *Palmatolepis rhenana* Zone *sensu* Ziegler & Sandberg 1990). Copper (1998: fig. 1) recently showed the persistence of 15 genera/subgenera during this timespan. However, some of the data still require confirmation due to imprecise biostratigraphic dating (e.g., *Kyrtatrypa* in Western Australia) and/or ambiguous taxonomy. For example, the genus *Devonatrypa* (synonymised with *Neatrypa* by Copper 1967, and Rzhonsnitskaya 1975), and the representation of *Peratos* (= at least in part rhynchonellid juveniles in Late Devonian; Godefroid & Helsen 1998), need reexamination.

Undoubtedly, the Frasnian continued a phase of decline which commenced in the Givetian. As discussed by Copper (1998), strong extinction pulses, combined with low to zero origination rates, killed off the Frasnian atrypids. New taxonomic data, presented by Baliński (1997) and in this volume, partly refine the extinction pattern. The late Frasnian occurrence of five atrypid subfamilies, all assignable to two families, is documented herein. Of these, the Pseudogruenewaldtiinae (= the Frasnian member of Invertininae; Copper & Chen 1994) are particularly typical for the KW Crisis interval. The stratigraphic restriction to this timespan may be assumed for at least four genera and subgenera: *Pseudogruenewaldtia, Gibberosatrypa, Spinatrypa (Plicspinat-*

rypa) and *Waiotrypa*. Conversely, Copper (1998) has not found any distinctive species group originated in the late Frasnian, but the diversity analysis is still hampered by limited consistency in the taxonomy of the declining atrypids, in particular for the Russian faunas studied by Rzhonsnitskaya *et al.* (1998).

The atrypid dominance pattern varies from region to region, even within the same epicontinental sea, and was apparently controlled by facies. The available data enable only a tentative synthesis at the species level. An increasing number of species are recognized in the stratigraphically youngest Pseudogruenewaldtiinae, Spinatrypinae and Variatrypinae (e.g., Godefroid & Helsen 1998; Rzhonsnitskaya *et al.* 1998).

Morphologic tendencies. — Among the Frasnian atrypids, especially among species during the KW Crisis, several features (re)appeared or culminated:

(1) Copper (1973) established two mainly middle-late Frasnian species-groups, the origin of which appeared to be enigmatic due to a re-appearance of a rib structure typical of older, mostly Middle Devonian genera. *Iowatrypa* and *Pseudogruenewaldtia* exhibit a tightly imbricated, *Atrypa*-like shell surface, whilst *Costatrypa* closely resembles *Atryparia* in its undulose, shallow ribbing. On the other hand, some Variatrypinae, in particular *Radiatrypa*, lost growth lamellae and frills, exhibiting extremely simple, tubular rib structure; this tendency is known also in *Spinatrypina (Exatrypa)* (see Racki & Baliński 1998)

(2) Copper (1978: p. 299) noted a trend towards rib disappearance as typical of Frasnian *Spinatrypa* species. This character is most perfectly expressed by late Frasnian species from Iowa and New Mexico, such as *Spinatrypa obsolescens* Cooper & Dutro, 1982. Otherwise, a rapid transition from simple and coarse ribbing in the posterior part into bifurcated and thinner ribes in the anterior part is noticeable in some species of *Costatrypa*, e.g., *C. varicostata* (Stainbrook, 1945), *Waiotrypa, Iowatrypa* and *Spinatrypa* (see examples in Baliński 1997; Racki & Baliński 1998; Rzhonsnitskaya *et al.* 1998).

(3) Baliński (1997) has found that shell carination, manifested in an elevated rib pair forming a median keel on the pedicle valve and a corresponding narrow sinus on the brachial valve, is a diagnostic feature of the genus *Waiotrypa*, which is limited to the late Frasnian. A similar tendency is known among many other atrypids, but is mostly limited to the juvenile stages. Several more or less distinctive exceptions are known in the middle-late Frasnian taxa, as shown by *'Atrypa' svinordi*-group, *Spinatrypina (Exatrypa) relicta* Racki & Baliński, 1998, and *Spinatrypa bifidaeformis* (Chernyschev, 1887), as well as by *Gibberosatrypa* and the problematic carinanitid described by Yudina in Rzhonsnitskaya *et al.* (1998).

(4) The above features, combined with reduced shell size (typically less than 2.5 cm), strongly suggest the possible dwarfism and/or paedomorphosis in the late phase of atrypid evolution in several lineages.

At least some of these characters may be seen as aberrant or recurrent, even if others may be merely a random adaptation to peculiar niches. Likewise, homeomorphy with older taxa seems to have been widespread among the stressed Frasnian atrypids, as exemplified by *Spinatrypina, Iowatrypa* and *Waiotrypa* (e.g., Baliński 1997; Rzhonsnitskaya *et al.* 1998), as well as by *Gibberosatrypa, Carinatina(?)* and some *Spinatrypina (Exatrypa)*. Likewise, a similarity even to orthids is sometimes observable

(Baliński 1997), which is conspicuously expressed by *'Atrypa' svinordi* Venyukov, 1885, originally assigned to *Orthis* (see Nalivkin 1941; Lyashenko 1959).

Regional patterns of distribution

The distribution pattern of late Frasnian atrypids is summarized below for the four main Devonian continents (Fig. 1), with detailed documentation presented for three of them in papers in this volume: Laurussia (majority of analyses), southwestern Siberia and South China.

The eustatic cyclicity pattern of Johnson *et al.* (1985), improved by Sandberg *et al.* (1988, 1992), presents a convenient basis for 'natural' chronostratigraphy. The middle Frasnian coincides with the transgressive-regressive (T-R) Cycle IIc, while the late Frasnian is a gross equivalent of the complex T-R Cycle IId (but notably beginning from the *Palmatolepis semichatovae* transgression in the Early *Palmatolepis rhenana* Zone, following Ziegler & Sandberg 1997). The latest Frasnian corresponds to the key time interval following the second transgressive/hypoxic pulse within the Devonian eustatic highstand (= Upper Kellwasser Event), in the *Palmatolepis linguiformis* Zone.

Laurussia

South Polish-Moravian shelf. — The late Frasnian brachiopod fauna of the Holy Cross Mountains is still only partially known, but studies of the gypidulids (Godefroid & Racki 1990), biernatellids (Baliński 1995b) and other athyridids (Grunt & Racki 1998), rhynchonellids (Sartenaer *et al.* 1998), and atrypids (Baliński 1997; Racki & Baliński 1998) form a basis for evaluating extinctions in the shallow-water Atrypid–Gypidulid Biofacies (Racki *et al.* 1993). The occurrence of 15 taxa of Atrypinae (*Costatrypa*), Spinatrypinae [*Spinatrypa, Spinatrypina (Spinatrypina), Spinatrypina (Exatrypa)*], Pseudogruenewaldtiinae (*Iowatrypa, Waiotrypa*) and Variatrypinae (*Radiatrypa, Desquamatia*), is established, including two new species (Baliński 1997; Racki & Baliński 1998).

A diverse atrypid-gypidulid association, with *Spinatrypina (Exatrypa), Variatrypa, Desquamatia (Seratrypa)* and *Metabolipa* as the main component, is richly represented in the earliest middle Frasnian Kadzielnia-type, localized stromatoporoid-calcimicrobial bioherms developed on the gentle slope of the Dyminy Reef; similar faunas occur in variety of other reef margin to foreslope settings, especially in parautochtonous pockets near renalcid-dominated late Frasnian buildups (Racki *et al.* 1993). During the *Palmatolepis rhenana* Zone, atrypids were the dominant element of very diverse brachiopod assemblages (more than 40 belonging to at least 25 genera; mostly rhynchonellids, spiriferids and athyridids), thriving in declining perireefal habitats (see Racki *et al.* 1993; Grunt & Racki 1998). The taxonomic composition of the association remained generally similar, and in the 'reef-cap' phase (*sensu* Krebs 1974) thrived *Costatrypa varicostata* (Stainbrook, 1945), in particular the morphotype *extensa* of Cooper & Dutro (1982), and a larger-sized variety of *Iowatrypa*(?). A relatively large-sized *Desquamatia*(?) is also an end-member of the atrypid succession of fore-reef sequences, and persisted up to the F-F boundary. Biernat (1970) noted some atrypids in the early Famennian of Kadzielnia, but certainly they have been derived from the underlying Frasnian members in this locality.

Middle Frasnian deeper-water (level-bottom) faunas are marked by *Pseudoatrypa* or minute *Carinatrypa*(?) and *Spinatrypa*. The stratigraphically younger mid- to downslope faunas include abundant *Iowatrypa, Spinatrypina (Exatrypa), Costatrypa, Waiotrypa* and *Desquamatia*. Thus, rapid late Frasnian eustatic changes, especially during the *Palmatolepis semichatovae* transgression in the Early *P. rhenana* Zone (see Sandberg *et al.* 1992), were linked with a significant brachiopod immigration wave, and also with the evolutionary transition from *Metabolipa* to *Neometabolipa*

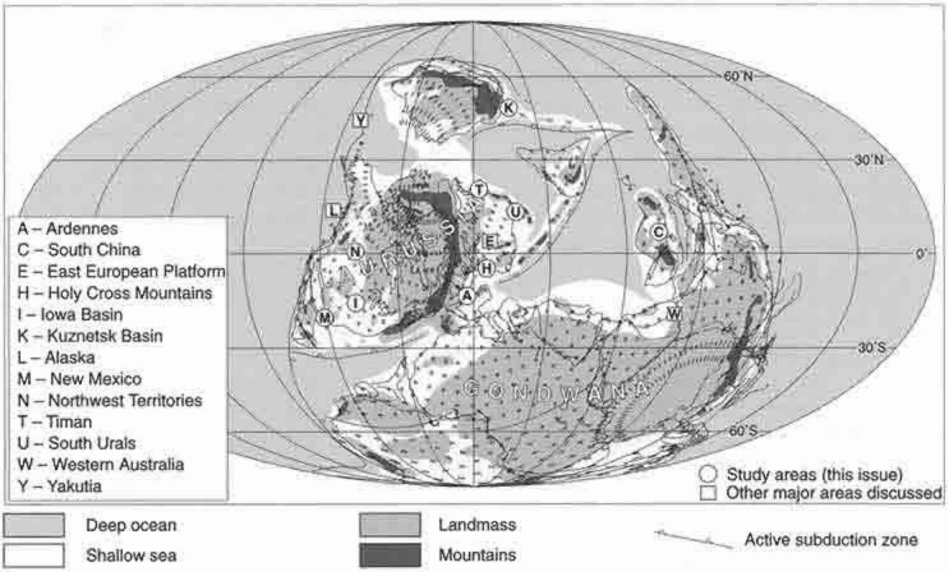

Fig. 1. Locations of studied and discussed brachiopod faunas against the Late Devonian palaeogeography (courtesy of J. Golonka, adapted).

among gypidulids (Godefroid & Racki 1990: fig. 9). The Lower KW Event was without catastrophic consequences for the brachiopod faunas here. In contrast, a regional extinction phase of at least downslope assemblages is linked with expanding anoxic conditions during the Upper KW deepening pulse in the late *Palmatolepis linguiformis* Zone. The ultimate extinction of deeper-water atrypids coincided with a severe eustatic fall (Event 6 in Sandberg *et al.* 1988: p. 296), recorded in episodic calcareous deposition of the F-F passage beds (Racki & Baliński 1998).

The dominant atrypids in the shallow-water, post-reef crest brachiopod-crinoid assemblages were progressively replaced during the later phase of the KW Crisis by impoverished (up to eight genera) faunas, comprising productids, cyrtospiriferids, athyridids (Grunt & Racki 1998), including the last biernatellids (Baliński 1995b), as well as orthids, mainly *Schizophoria* (see Racki & Baliński 1998). Establishment of far more diverse shelly faunas, with typical Famennian species, is indicated in the *Palmatolepis crepida* Zone (see review in Biernat 1988), as part of the sustained shelf ecosystem recovery. In general terms, continuity of the deeper-water rhynchonellid-inarticulate biofacies across the F-F boundary is well expressed in the marly successions (Racki *et al.* 1993). This is well exemplified by the transition within autochtonous monospecific assemblages from *Ryocarhynchus tumidus* (Kayser, 1871) to *Orbiculatisinurostrum laeve* (Gürich, 1903) in the eastern Holy Cross Mountains, in agreement with the rhynchonellid succession in the Cracow area (Baliński 1995a).

Coeval brachiopod faunas are well-known from the more southern (proximal) fragment of the Polish shelf (Dębnik near Cracow; Baliński 1979, 1995a). Persistence of the cyrtospiriferid-athyridid assemblage across the extinction level is noteworthy, terminating in a conspicuous brachiopod acme in the *P. crepida* Zone (Baliński 1996). Single middle Frasnian atrypid species of *Costatrypa* were succeeded by a species pair in the *Palmatolepis jamieae*–Early *P. rhenana* zonal interval. This includes species of *Iowatrypa*, probably *I. americana* (Stainbrook, 1945), and *Desquamatia* (*Desquamatia*) *alticoliformis* Rzhonsnitskaya, 1975, the latter possibly ranging even into the *Palmatolepis linguiformis* Zone. Due to poor outcrops, the brachiopod succession is not adequately documented across the F-F boundary.

Only disarticulated atrypid material has been found during the preliminar ycollectin gfrom the F-F sections of the Moravian shelf near Brno (Šumbera on Hady Hill and Lesni Lom), which represent shallow-water detrital successions ((Fig. 2; see Hladil & Kalvoda 1993). This includes representatives of two subfamilies typical of the fore-reef facies, Variatrypinae and Spinatrypinae. Only the former section has been available for detailed sampling, and the presence of two assemblages is established in the Late *P. rhenana–P. linguiformis* zones (Streitova 1994). The older assemblage is composed of small-sized *Radiatrypa*(?) and *Desquamatia*(?), whilst medium-sized spinatrypinids predominate in the succeeding assemblage. In addition, a productellid level occurs in an intervening position, whilst the basal Famennian beds are composed of intraclastic brachiopod-nautiloid-crinoid coquinas, with productellids (*Praewaagenoconcha*) predominant and schizophoriids, cyrtospiriferids and large costate rhynchonellids (*Ripidiorhynchus*) also present.

Ardenne-Rhenish shelf. — In the Dinant Synclinorium, pentamerids and atrypids become extinct well below (ca. 50 m) the F-F boundary, but above the highest reef level of the Neuville Formation (Godefroid & Racki 1990; Godefroid & Helsen 1998). In this region their extinction coincides more or less with the appearance of shale facies of the Matagne Formation, dated by conodonts as being in the Early *P. rhenana* Zone. Even if this facies turnover was correlated with the Upper Kellwasser Event as proposed by Johnson *et al.* (1985) and Sandberg *et al.* (1992), the current conodont datings document a more complex, diachronous regional facies change. hence, they also record earlier transgressive-hypoxic events during the KW Crisis. From the thirteen atrypid taxa described by Godefroid & Helsen (1998), only *Costatrypa variabilis* (Godefroid, 1970) and *Waiotrypa*(?) *pluvia* Godefroid & Helsen, 1998 occur above the basal boundary of the greenish argillaceous suite. These two species are rare from that point up to the appearance of the blackish shales. Notably, the frilled and abundant *C. variabilis* was adapted to the non-reef muddy and partly oxygen-depleted habitats, typical of the interval (F2i) between two last Frasnian reef levels (F2h and F2j). Several other species, belonging to *Spinatrypina*, *Iowatrypa*, and *Desquamatia* were apparently exterminated during the deepening-hypoxic pulse, even though these mostly small-sized forms preferred the shales and limestones deposited in the vicinity of the reef mounds. An alleged smooth species of Atrypida, *Glassia drevermanni* Maillieux, 1936 (see Copper 1986a), described from the latest Frasnian Matagne Formation, is now found (Godefroid & Helsen 1998) to represent immature specimens of the rhynchonellid *Ryocarhynchys tumidus* (Kayser, 1872). The lissatrypid genus *Peratos* is known from the Frasnian 'reef-cap' (Iberg) facies in Germany (Copper 1998). The Belgian late Frasnian bioherm (F-2j) atrypid association, which included *Spinatrypa tumuli* Godefroid & Helsen, 1998, and *Desquamatia (Seratrypa) derelicta* Godefroid & Helsen, 1998, still recalls in generic terms the early Frasnian reef (F2d; Arche Member) fauna, with *D. (S.) frasnensis* Godefroid, 1970 the dominant species. In summary, the Ardenne atrypid-gypidulid faunas, dominated by *Costatrypa, Desquamatia* (three species), *Iowatrypa* (two species), *Spinatrypa*, and *Neometabolipa*, are a good example of a regional extinction mostly in earlier phases of the KW Crisis, after the death of the last impoverished reefs.

In the Frasnian of the Boulonnais region (NW France), only early-middle Frasnian atrypids are described by Godefroid (1988), belonging to *Desquamatia* (three species), *Spinatrypina* (three species), *Spinatrypa* (two species) and *Costatrypa* (one species). The stratigraphically youngest atrypid-bearing argillaceous strata (Late *Palmatolepis hassi* Zone) has two species of *Spinatrypa*.

From the Rhenish Shelf, Copper (1966, 1967, 1973) mentioned a unique late Frasnian (F2h–F3) atrypid association in the Aachen area, ca. 50 km NW of the Eifel, generally grouped as the *'cuboides'* fauna. This is marked by an abundance of *Costatrypa, Spinatrypa* and *Iowatrypa* (of *I. timanica*-type), with the last taxon limited to the latest Frasnian (F3; Copper 1973; p. 495). However, this assemblage still awaits a more refined study as does another spinatrypid locality in Germany, in the Wildenfels Mountains of Saxony (Becker *et al.* 1991). Schüller (1949) placed his nodular '*Atrypa*-Kalk' (with presumed spinatrypinid *'Atrypa aspera'*) in the basal Famennian (*Cheiloceras* Stufe), but Schreiber (1985) referred this fossiliferous pyrite-rich limestone-shaly complex (39 m thick) to an intermediate level between the diabase series and the Upper KW Limestone, dated as the *P. gigas* Zone. Atrypids reported from the Famennian 'Langenaubucher Tuffbrekzie' by Drevermann (1901) are reworked late Frasnian faunas (Copper 1967).

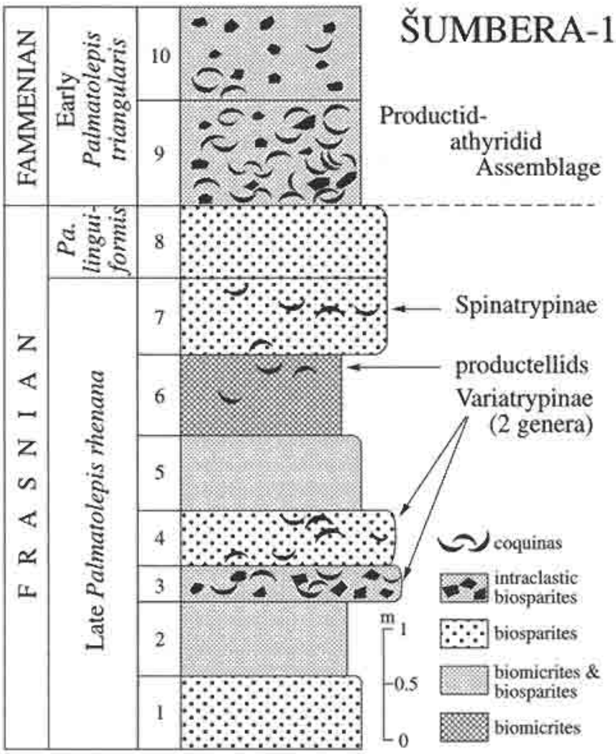

Fig. 2. Lithologic succession (after Streitová 1994) and brachiopod faunas of the F-F boundary beds at Šumbera, Moravia. Note the occurrence of atrypid- and productellid-rich levels.

Eastern European Platform. — Nalivkin (1941) documented the absence of atrypids in the late Frasnian shallowing basin of the Main Devonian Field (NW Eastern European Platform). The typical Frasnian genus *Anatrypa* was originally described from this area (for type species see Copper 1978), and remains essentially unknown from other regions. In a geographically broader study, Lyashenko (1959) recorded late Frasnian species. Decreasing diversity toward the end of the Frasnian is shown by the presence of 10 species (*Pseudoatrypa*?, *Desquamatia, Variatrypa, Spinatrypina, Iowatrypa*) in the early Frasnian Sargaevo suite (in the present sense; see Rzhonsnitskaya 1988), reduced to seven (*Pseudoatrypa*?, *Spinatrypa, Spinatrypina*) in the middle Frasnian Semiluki suite (*Palmatolepis punctata–P. jamieae* Zones; Menner & Ovnatanova 1996). However, the generic position of several species erected by Lyashenko remains doubtful (Copper 1967, 1973). No more than two species are reported from each of the later Frasnian carbonate-argillaceous units, mostly representing *Spinatrypina* and problematical *Pseudoatrypa* [*'Atrypa' symmetrica* Lyashenko, 1959] and *Desquamatia* [*'Atrypa' poljanica* Lyashenko, 1959]. The stratigraphically youngest *'Atrypa'* [= ?*Pseudoatrypa*; Copper 1973: p. 492] *tanaica* Nalivkin, 1950 (in Sarycheva & Sokolskaya 1950) is noted as a commonly occurring species in the central parts of the East European Platform from the Evlanovo suite, i.e., Late *P. rhenana* Zone. The impoverished brachiopod faunas are marked by the widespread, locally rock-forming spiriferid *Theodossia*, schuchertellids, productellids and cyrtospiriferids. The slightly more diverse Evlanovo benthic faunas were probably linked with more marine conditions, possibly during the transgressive Lower KW Event. The latest Frasnian fauna still contains rare undescribed atrypids and gypidulids (Lyashenko 1959: p. 200), and also the last *Theodossia*. The unconformably overlying Famennian strata are marked by an abundance of costate rhynchonellids, productids, cyrtospiriferids, and chonetids.

In the NE part of the East European Platform (Timan-Petchora Province), the current study by Yudina (1996; 1997; in Rzhonsnitskaya *et al.* 1998) revealed that *Desquamatia, Spinatrypa* and *Spinatrypina* persisted throughout the Frasnian, but never played a significant role. As a result of the Early *P. rhenana* Zone sea-level fall (Veimarn *et al.* 1997), a strong differentiation of facies and brachiopod assemblages was established. The entry of *Costatrypa vetlasjanica* (Yudina, 1997) in the shallow-shelf facies (Ukhta suite) and *Iowatrypa* in deeper-water marly facies (Lyaiol suite) coincides with this turnover. Surprisingly, an acme of atrypids is reported from the latest *P. rhenana–P. linguiformis* zonal interval in the same facies framework. The Ukhta carbonate shelf, grading upward into evaporite deposits, is typified by an impoverished *Theodossia ischmensis* assemblage, which commonly contains an endemic species, *Spinatrypina (S.) sosnovkensis* Yudina, 1998 (in Rzhonsnitskaya *et al.* 1998). In addition, the stromatoporoid-calcimicrobial reefs were dwelled by a rare *Hypothyridina–Gypidula* association, with subordinate small-sized atrypids: *Desquamatia (Desquamatia) alticoliformis* Rzhonsnitskaya, 1975, *Radiatrypa magnitica* (Nalivkin, 1947) and sporadic minute endemic *Carinatina*(?) *biohermica* Yudina, 1998. In contrast, coeval basin argillaceous sediments (Lyaiol suite) were populated by abundant brachiopod communities (*Biernatella timanica* assemblage), dominated by diverse but mostly endemic atrypid species: *Pseudogruenewaldtia tschernyschewi* Rzhonsnitskaya, 1964, *Iowatrypa*(?) *nebulosa* Yudina, 1998, and diminutive *Waiotrypa*(?) sp. A.

Urals. — Rich and diverse Frasnian brachiopod faunas from the Urals have been described in several studies (e.g., Nalivkin 1951; Lyashenko 1973; Markovskii 1989; Rzhonsnitskaya *et al.* 1998). The stratigraphic distribution of atrypids was recently summarized by Stepanova *et al.* (1985) for the east slope of the South Urals (Magnitogorsk Synclinorium), corresponding to an active margin zone, and by Rzhonsnitskaya & Markovskii (*in* Rzhonsnitskaya *et al.* 1998) for the west slope of the area.

As shown by Stepanova (*in* Stepanova *et al.* 1985: fig. 4), the atrypid association is invariably composed of four to five species in all the Frasnian substages, but generic assignment is mostly uncertain (*Desquamatia* sensu lato, probably *Spinatrypina, Iowatrypa* and *Costatrypa*). However, late Frasnian reefal (Koltuban suite; studied by Nalivkin 1951), volcanogenic and siliciclastic-carbonate deposits contain more diverse fauna (10 species listed in Stepanova *et al.* 1985: p. 126) of *Radiatrypa, Costatrypa, Spinatrypina* and *Iowatrypa*. Only *Atrypa* (= *Costatrypa*?) *posturalica* is restricted to this suite (its middle Iriklin horizon). Diminishing species diversity to the end of the Frasnian is shown in faunal lists of the succeeding horizons (nine, five and three species, respectively), and only long-ranging species have been quoted from the highest Ust'kolpak horizon: '*Desquamatia*' cf. *alticola* (Frech, 1901), *Spinatrypina tubaecostata* (Paeckelman, 1913) and *Spinatrypa* [= *Spinatrypina (Exatrypa)*] *bifurcata* (Markovskii, 1955 *in* Mikryukov 1955). Refinement of the late Frasnian (Early *P. rhenana* to *P. linguiformis*) interval by Rzhonsnitskaya & Markovskii (in Rzhonsnitskaya *et al.* 1998) reveals the presence of eight species, referred to *Pseudoatrypa, Gibberosatrypa, Desquamatia (Desquamatia), Radiatrypa, Iowatrypa* and *Spinatrypina*. This timespan is marked by the development of massive limestone facies with numerous brachiopod coquinas and nests. The appearance of six biogeographically new species was linked to the growth of 12 m thick reefs of the Askyn horizon, perhaps related to an immigration wave induced by the *P. semichatovae* transgression, even though an overall shallowing trend is noted for the late Frasnian of this domain (Veimarn *et al.* 1997). Some of the species might be endemic, e.g. *Gibberosatrypa gibberosa* (Markovskii, 1989), *Iowatrypa nalivkini* Rzhonsnitskaya & Sokiran, 1998 (in Rzhonsnitskaya *et al.* 1998), in the *Hypothyridina 'cuboides'–D. (D.) alticoliformis* association.

Stepanova *et al.* (1985) ascribed the two highest atrypid-bearing units to the Famennian *P. triangularis* Zone, but their correlation with the Askyn horizon (table 1 therein) clearly argues for a Frasnian age. In brachiopod limestones of the earliest *P. triangularis* Zone (bottom part of the Barma formation), the assemblage is dominated by rhynchonellids, athyridids, productellids (*Mesoplica*) and cyrtospiriferids.

Central and Western North America. — Later Frasnian atrypids from North America were studied by Fenton & Fenton (1924), Stainbrook (1945), Copper (1978), Cooper & Dutro (1982) and Day & Copper (1998), and their distribution was summarized by Day (1998). Eastern American and largely Canadian faunas await taxonomic revision or description, but it is known that the New York

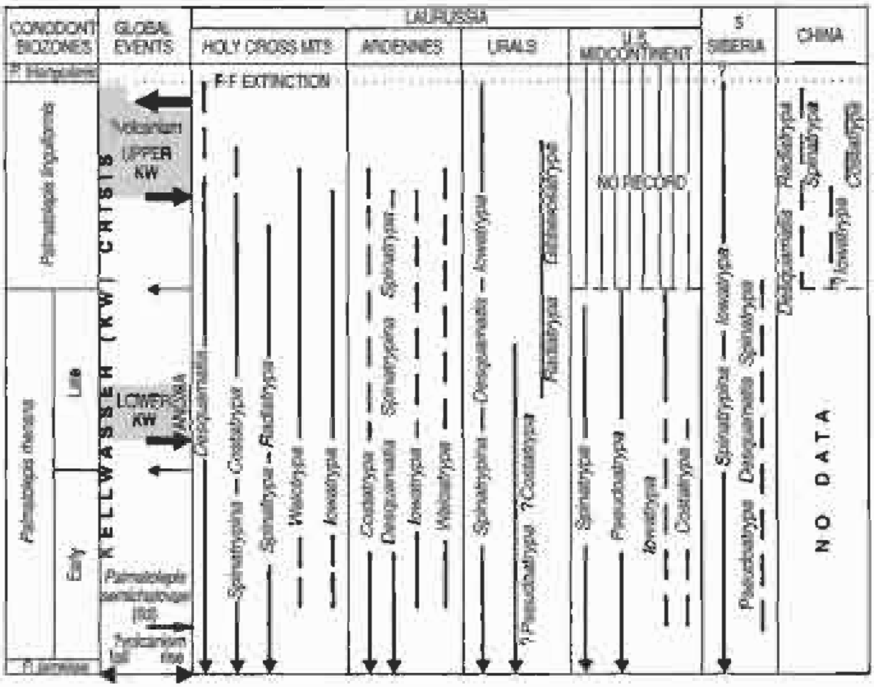

Fig. 3. Provisional range chart of the late Frasnian atrypid genera in particular regions under study (see Fig. 1) against the assumed event scenario in the Kellwasser Crisis (Racki in press). Data for Eastern European Platform and Urals compiled from Lyashenko (1959), Stepanova *et al.* (1985) and Rzhonsnitskaya *et al.* (1998); event stratigraphy for Ardennes mostly after Sandberg *et al.* (1992). Note a diachronous pattern of distribution.

(Catskill Delta) dysaerobic associations comprise conservative species of *Spinatrypa* and *Pseudoatrypa*. *Spinatrypa hystrix* (Hall, 1843) belongs to the most ecologically persistent dwellers in the nearshore domains (*Cyrtospirifer chemungensis* Assemblage; Dutro 1981: fig. 7). In addition, two species of *Spinatrypa* survived to the latest Frasnian in diverse level-bottom assemblages in New Mexico (Cooper & Dutro 1982; Dutro 1986).

In the case of well-known Central (Iowa Basin) and Western (New Mexico) faunas, the early Frasnian was a period of particularly high species diversity within six genera, mostly variatrypids, introduced during the IIb-2 transgression. Also diverse, but largely poorly documented, middle Frasnian assemblages coincide with the T-R cycle IIc, including *Spinatrypa*, *Pseudoatrypa*, *Radiatrypa*, '*Neatrypa*', and the newly introduced *Costatrypa* in the Mackenzie faunas.

The late Frasnian T-R cycle IId (*sensu* Day 1998) is again marked by an appearance of a distinctive atrypid generic set, with widespread *Pseudoatrypa*, *Spinatrypa*, *Iowatrypa* and *Costatrypa* in Central and Western American domains, supplemented by *D. (Seratrypa)* in the Canadian Arctic. The faunas experienced two waves of extinctions whose timing probably corresponds to the KW intervals. The only atrypids ranging into possible *P. linguiformis* Zone, and Upper KW timespan, were common *Pseudoatrypa devoniana* (Webster, 1921) and *Iowatrypa owenensis* (Webster, 1921) but a more diverse association probably existed in the tropical Canadian faunas. The rapid end-Frasnian regression after the Upper KW Event caused the platform successions to be eroded, prior to the early Famennian (IIe) transgression (Day 1998).

Dutro (1986) noted 14 genera that occurred both below and above the F-F boundary in New Mexico and New York, mostly orthids, strophomenids, spiriferids and rhynchonellids. However, only six species crossed the F-F extinction horizon in New Mexico (Cooper & Dutro 1982). Increasingly diverse rhynchonellids, spiriferids and productellids characterized the Famennian benthos (e.g., *Cyrtospirifer sulcifer* Assemblage Zone of Dutro 1981; see also Dutro 1986).

In addition, Savage & Baxter (1995) described late Frasnian (*P. rhenana* Zone) brachiopod fauna from SE Alaska (Alexander terrane). The deeper, offshore assemblage combines mostly endemic elements of ambocoeliid, gypidulid and rhynchonellid associations (and many corals; N.M. Savage 1998, letter communication), but only two atrypid taxa, *I. owenensis* and *Spinatrypa* cf. *S. trulla* (Stainbrook, 1945). Also the Famennian athyridid-rhynchonellid-spiriferid fauna is unusually provincial in view of the cosmopolitan nature of brachiopod faunas elsewhere at this age (Savage *et al.* 1978). Thus, Late Devonian Alaskan terrane faunas were not in good communication with coeval North American cratonic biota to the east, and the paleogeographic context remains equivocal (Savage & Baxter 1995).

Other continents

Siberia and adjacent microcontinents. — Frasnian atrypid faunas from the active southern margin of the Siberian continent were studied by Alekseeva (1962), Bublichenko (1974) and Rzhonsnitskaya (1975, in Rzhonsnitskaya *et al.* 1998). In generic terms, two stratigraphic assemblages are distinctive in the NW and W part of the Kuznetsk Basin (Kolyn'-Tomsk geosynclinal zone), and early Frasnian faunas contain *Spinatrypina (Exatrypa), Desquamatia, Atrypa* and *Sibiratrypa*. Later Frasnian time is marked by a more diverse atrypid assemblage, but the basal sandstone-mudstone series (Teryokhino suite) is without atrypids. The typical late Frasnian assemblage, from clayey and carbonate (Kurlyaki) and overlying limestone (Glubokaya) suites, consists of abundant *P. posturalica* and *D.(D.) alticoliformis*, accompanied by *Iowatrypa*(?) *kadzielnioides* (Rzhonsnitskaya, 1975) and *Spinatrypa* cf. *planosulcata* (Webster, 1887).

The late Frasnian mixed siliciclastic-carbonate succession (Solomino horizon), probably corresponding to the KW timespan (Yolkin *et al.* 1997), exhibits two different brachiopod assemblages. Only minute (stunted?) atrypids appear close to the F-F boundary within the more restricted marine *Anathyrella monstrum–Cyrtospirifer ussovi* Assemblage from the N and NE parts of the Kuznetsk Basin. In contrast, the more open marine *Anathyrella* fauna from the NW of Kuzbass contains a five poorly preserved atrypid species, including common taxa from the underlying members, as well as some limited to this interval, e.g. *Spinatrypa (Plicspinatrypa) plicata* (Rzhonsnitskaya, 1975) and *S. (Exatrypa)* cf. *bifurcata*. Of them, the latter species and *I.*(?) *kadzielnioides* persisted into the F-F transition. Atrypids, pentamerids and *Anathyrella* vanished at the critical level, although Yolkin *et al.* (1997) mentioned a single atrypid species crossing the F-F boundary. Succeeding faunas are marked by an abundance of productellids (with index *Mesoplica*), cyrtospiriferids and athyridids (see also Bublichenko 1974).

The recent study by Aleekseva & Komarov (in Aleekseva *et al.* 1996) supplied data on Frasnian atrypid faunas from East Yakutia and the Magadan district, corresponding to the Kolyma-Omolon microplate. The early Frasnian association includes *Pseudoatrypa, Spinatrypina, Desquamatia* and *Variatrypa. Variatrypa nalivkini* (Lyashenko, 1959) is an index species of the middle Frasnian brachiopod zone (ranging up to the *P. gigas* Zone), in which five taxa of the same generic set, supplemented by *Spinatrypa*, have been found. A late Frasnian fauna of the *Theodossia* Zone (Trogov suite) is marked by the presence of *D. (Seratrypa) mayselae tompoensis* Aleksseva, 1996, *Spinatrypina (S.)* sp., *Spinatrypina (Exatrypa) orientalis* Alekseeva & Komarov, 1996 and *Pseudogruenewaldtia elongata* Alekseeva, 1996. The endemic assemblage remains ambiguously dated by conodonts (Aleekseeva & Sidjachenko in Alekseeva *et al.* 1996: p. 28), but undoubted Famennian associations consist of numerous diverse cyrtospiriferids (with guide species), associated with productids (*Nigerinoplica*), athyridids and rhynchonellids.

China. — The South China shelf has been regarded as a potential refuge area for the atrypids (Jia *et al.* 1988; Ji 1990). Hou *et al.* (1992) cited the disappearance of the last atrypids (*Radiatrypa*?) in the Late *P. rhenana* Zone of Guangxi, below the Upper KW Event. However, they remarked that atrypid extinctions were not synchronous in the differentiated epeiric sea, and that two or three genera persisted even into the earliest Famennian (Early *Palmatolepis triangularis* Zone) in the nearby more shallow-water (upslope) habitats, while more diverse atrypids (like *Anatrypa*, = ?*Iowatrya*; P. Copper 1997, letter communication) have been found in the latest Frasnian in central Hunan.

The question of supposed Famennian atrypids in the Guangxi sections was clarified by Ma (1998). These brachiopod occurs in a light grey, massive, coarse grainstone bed of Famennian age (Middle *P. triangularis* Zone) yielding very abundant brachiopods which may represent a coquina bank deposit. However, the shelly material is inferred to be reworked. The reasons for this conclusion are the following: (1) the brachiopods are a transported assemblage, indicated by the lithology and the shell fragmentation and abrasion, and (2) there are associated Frasnian conodonts, and below this bed they are very abundant (Bai *et al.* 1994; fig. 7-7). In another locality, the Frasnian specimens from the Baqi section occur in similar grainstone which was slumped in the Famennian in the Early *Palmatolepis rhomboidea* Zone (Bai *et al.* 1994: figs 7–10), or alternatively the sediment and associated Frasnian conodonts were reworked.

In a preliminary account, Ma (1998) documented nine atrypid taxa from the *P. linguiformis* Zone of central Hunan and Guangxi. They were collected from marly and limestone facies, with abundant corals and brachiopods. Among representatives of *Spinatrypa* (three species), *Spinatrypina* (one species), *Costatrypa* (one species), *Iowatrypa*(?) (one new species), *Desquamatia* (two species) and *Radiatrypa* (one species), the highest records (ca. 1 m below the F-F boundary) reveal *Desquamatia shetienchiaoensis* (Tien, 1938) and *Radiatrypa maanshanensis* Yang & Chen, 1988, and perhaps *Spinat*rypa sp. B. The earliest Famennian faunas comprise numerous cyrtospiriferids, productellids (*Productella lachrymosa* var. *asiatica* Tien, 1938) and rhynchonellids (*Yunannelina*).

Gondwana and adjoining northern microcontinents. — Atrypids remain essentially unknown from most Gondwana sequences (e.g., from Morocco; R.T. Becker letter communication 1996), with only the conspicuous exception of the low-latitude reef-complexes of Western Australia. Grey (1978) presented a description of the distinctive low-diversity association (five species, mainly of *Spinatrypina*), marked by the relict appearance of *Atrypa (Kyrtatrypa)* and *Desquamatia (Synatrypa)*; the latter subgenus also occurs in the latest Frasnian of China (Mao 1998), and possibly in North Vietnam. Nevertheless, details of the stratigraphic ranges remain unclear. The atrypid-bearing reefal and perireefal (mostly Pillara and Sadler) formations from the Canning Basin comprise most of the Frasnian sequences (Becker *et al.* 1993). Only one species, *Spinatrypina prideri nurungunia* Grey, 1978, is cited by Becker *et al.* (1991) as still occurring in the *P. linguiformis* Zone. The latest Frasnian fauna also comprises other undescribed species, including larger-sized and frilled Variatrypinae (R.T. Becker 1996, letter communication). Recent observations confirm the conclusion of Grey (1978), that there is no Famennian record of atrypids in Western Australia.

Farsan (1986) showed that only the genera *Rhipidiorhynchus*, *Productella* and *Cyrtospirifer* cross the F-F boundary unchanged in South-Central Asia (Iran and Afghanistan). The only atrypid recorded this area is *Spinatrypa(?)*, but this is restricted to the middle Frasnian of Afghanistan.

From microplates located between Gondwana and Laurussia, Garcia-Alcalde (1990) cited atrypids in several late Frasnian faunas of the Cantabrian Mountains. Some details are given only for the more distal and deeper-water Palentine Domain, where black shales around the F-F boundary (Cardano Formation) have yielded many internal moulds of small biconvex, round-outlined and smooth-shelled specimens very close to the glassiid genus *Peratos*, possibly extending into the *P. crepida* Zone. Apart from this, Schindler (1990: pl. 5; fig. 13) also mentioned the glassiid genus *Peratos* from the *P. crepida* Zone of Morocco. The data need taxonomic and biostratigraphical confirmation (see below).

Rich atrypid faunas occur in the Armorican Massif but they are mostly limited to the Early and Middle Devonian (Copper & Racheboeuf 1985). Several cosmopolitan taxa, including *Pseudoatrypa*, *Costatrypa* and *Spinatrypina* appearred here during the early Frasnian. By mid-Frasnian time, however, atrypids disappeared from the area, with the exception of undetermined coarsely ribbed species of *Costatrypa*.

Conclusions

(1) Late Frasnian atrypids remain diverse and dominant among perireefal shelly faunas in the *Palmatolepis rhenana* Zone, and at least 15 genera/subgenera and at least 50 species persisted in the early interval of the KW Crisis. In general, this diversity is also similar to faunas from the older Frasnian levels, although distinctly less than in the Givetian; in fact, the main collapse in atrypid history is associated with the Early-Middle Devonian boundary, as summarized by Copper (1998: figs 1, 2). As for the three genera of gypidulids (Godefroid & Racki 1990), the decline phase of atrypids is characterized by a distinctive set of genera and species, possibly including four genera limited in range to the KW Crisis. Thus, the pre-extinction assemblages are more diverse, especially among Spinatrypinae and Pseudogruenewaldtiinae, than previously thought. The atrypid species attain a richness of at least 15 taxa in some regions (Holy Cross Mountains, Urals). However, middle Frasnian brachiopod faunas remain relatively poorly documented in some areas. Thus, there is still a gap in the knowledge of evolutionary lineages traced from the early Frasnian.

(2) The atrypid crisis fauna seems to be identified by distinctive trends in ornamentation types, an overall tendency to size reduction ("Liliput effect"; Baliński 1996) and homeomorphy, also to some orthids. This suggests possible paedomorphosis late in atrypid evolution, which is a common species response to large-scale perturbation (Harries *et al.* 1996). As discussed for the end-Permian brachiopod extinction by Carlson (1991), changes in the relative frequency of sets of characters (both homologous and non-homologous) must be evaluated. Morever, it seems that some environmental restriction and a tendency toward stenotopy characterized the last atrypids. For example, atrypids were common in Middle Devonian black shales and limestones (e.g., Copper 1965; Baliński & Racki 1981), but rather rare in widespread Frasnian oxygen-depleted (dark grey-black shale) facies and positioned upslope relative to low-diveristy'leiorhynchid' faunas (Rhynchonellid Biofacies of Racki *et al.* 1993; Racki 1989; J. Day 1998, letter communication). The regional atrypid demise, at least in Europe, was probably associated with pronounced ventilation changes and/or related factors during the late Frasnian deepening pulses (Godefroid & Helsen 1998; Racki & Baliński 1998), but the mechanism remains debatable (Copper 1998).

(3) A stepdown extinction pattern, proposed by Copper (1986b), has been confirmed in some detail. The hypoxic/transgressive pulse of the Lower Kellwasser Event and the preceding eustatic changes during the *Palmatolepis rhenana* Zone had only a regional destructive effect (see Day 1998, Godefroid & Helsen 1998). The events were linked rather to an enhanced dispersal of the last generic set of atrypids (e.g. *Iowatrypa* from the Timan-Uralian domain) as a result of interconnections established between hitherto semi-isolated epeiric seas (Copper 1973). The final demise and reduction to ca. 20 species (and 8–10 genera and subgenera) was related to the Upper KW Event and catastrophic eustatic fall during the late *Palmatolepis linguiformis* Zone (Sandberg *et al.* 1988, 1992). Joachimski & Buggisch (1996) emphasized repeated, possibly autocyclic co–occurrences of sea-level oscillations, anoxic conditions and climatic changes (probably toward a global cooling; Copper 1986b, 1998) during the KW Crisis. The stress may have been enhanced by at least regionally accelerated submarine volcano-hydrothermal activity (Veimarn *et al.* 1997), and consequent progressive eutrophication and thermal pulses

acmed in the F-F Event (Racki in press). The factors were certainly detrimental to the low-latitude and perhaps nutrient-limited stromatoporoid-coral reef ecosystems, as assumed by Wood (1993). Atrypid associations were closely linked with reefs since the Silurian (see Racki *et al.* 1993) and possibly include species that were either symbiotic with the major reef builders, or were highly specialised, occupying very narrow ecological niches (Copper 1973). However, Frasnian brachiopods not show any specific adaptation in response to the worldwide reef expansion (Copper 1998).

(4) An irregular spatial pattern of the extermination is evident from study of the vanished reef complexes, and different genera and species persisted within the intermittently drowned shelves (Fig. 3). Thus, it is difficult to envisage a global event scenario for the atrypid collapse. In general, the atrypid species that survived longest in the perireefal habitats belong to Variatrypinae, *Iowatrypa* and *Spinatrypina*, whereas in the stressed level-bottom (e.g. nearshore) environments it was species of *Spinatrypa* that were best able to cope with the conditions. Among Frasnian gypidulids, a three -step generic sequence, recognised in Belgian and Polish parts of the Laurussian shelf (Godefroid & Racki 1990), awaits confirmation in other areas.

(5) Literature data on Famennian atrypid occurrences are essentially not confirmed during this study (see review in Copper 1986b). Chinese occurrences are re-interpreted by Ma (1998) as reworked faunas, including those derived from slumped Frasnian blocks within the Famennian sequence. Also Uralian and Siberian atrypid-bearing strata, placed previously in the *P. triangularis* Zone, are now more or less firmly correlated with the late Frasnian units (Alekseeva *et al.* 1996; Rzhonsnitskaya *et al.* 1998), with a questionable exception in the Kuznetsk Basin (Yolkin *et al.* 1997). Smooth atrypid shells, reported as the lissatrypid genus *Peratos* from Famennian strata (Garcia-Alcalde 1990; Schindler 1990), may represent juvenile rhynchonellids (Godefroid & Helsen 1998). So, at least 'typical' ribbed species of Atrypida (atrypids *sensu stricto*; Copper 1973) vanished as a biomass during the catastrophic regression near the F-F boundary even in the potential refuges. This late Frasnian stepdown brachiopod crisis and a final extinction in the F-F Event is more or less evidenced not only among gypidulids (Godefroid & Racki 1990), but also e.g. in the common spiriferids *Theodossia* and the plicathyridines in the Russian successions (Lyashenko 1959; Rzhonsnitskaya & Modzalevskaya 1996; Rzhonsnitskaya *et al.* 1998).

(6) Despite generic losses (e.g., *Pammegetherhynchus*; Sartenaer *et al.* 1998), the apparent continuity of the deeper-water hypoxic rhynchonellid-inarticulate biofacies across the F-F boundary needs more strict evaluation in taxonomic and stratigraphic terms, including the relative advantage of inarticulates over articulates in stressful setting (Harries *et al.* 1996). It has been shown by Carlson (1991) for the end-Permian brachiopod record, that it is difficult to assess magnitude, pattern and ecologic-geographic selectivity, so long as detailed phylogenetic relationships remain uncertain or subject to arbitrary taxonomic convention.

(7) Regional extinction control may be more related to facies and biotic factors, i.e., accelerated competition of expansive productid-spiriferid-athyridid faunas (Ager 1968; Copper 1986b; Dutro 1986; Grunt & Racki 1998) (see Fig. 2), than with overall biogeographic circumstances, at least at the generic level (Copper 1973). This agrees well with the concept of ecodemity of atrypids (Copper 1966; Copper & Racheboeuf 1985). A tendency to endemism is observable, especially within particular reef com-

plexes and buildups (Grey 1978; Rzhonsnitskaya *et al.* 1998). The distinctive character of the Uralian-Timan, North American and Australian atrypid faunas does not agree with the consensus regarding late Frasnian faunal cosmopolitanism (see summary in Hallam 1996). A similar conclusion is presented for Frasnian conodont faunas (Klapper 1995), and certainly the Frasnian was not a time of cosmopolitanism in all groups even within tropical domains. Rapidly changing relative sea level during this Devonian tectono-eustatic highstand and increasing plate tectonic activity (Racki in press) established complex biogeographic and phylogenetic responses in epeiric settings (see McGhee *et al.* 1991). Such links have been shown by Sheehan (1975) for the end-Ordovican glaciation-induced brachiopod turnover, and await a more quantitative approach at species level for the KW Crisis.

(8) Copper (1986a, 1998) suggests repopulation of Famennian seas by deeper-cooler brachiopods, including surviving spiriferid-athyridid-productid assemblages from high-latitude domains. In addition, as assumed by Flessa (1973), an offshore recolonization by inner shelf shelly faunas, marked by eurytopic cyrtospiriferids, athyridids and productellids in the Frasnian, seems to be at least of similar significance during the recovery (Racki *et al.* 1993).

Acknowledgments

Collaborators of the research project supported by the State Committee of Scientific Research are gratefully acknowledged. I am also indebted to P. Copper and J. Day for thorough review of the manuscript and helpful comments. R.T. Becker and P. Copper kindly supplied many data useful for this synopsis. Special thanks go to J. Golonka and A. Feliga for supply palaeogeographic map for use in this issue.

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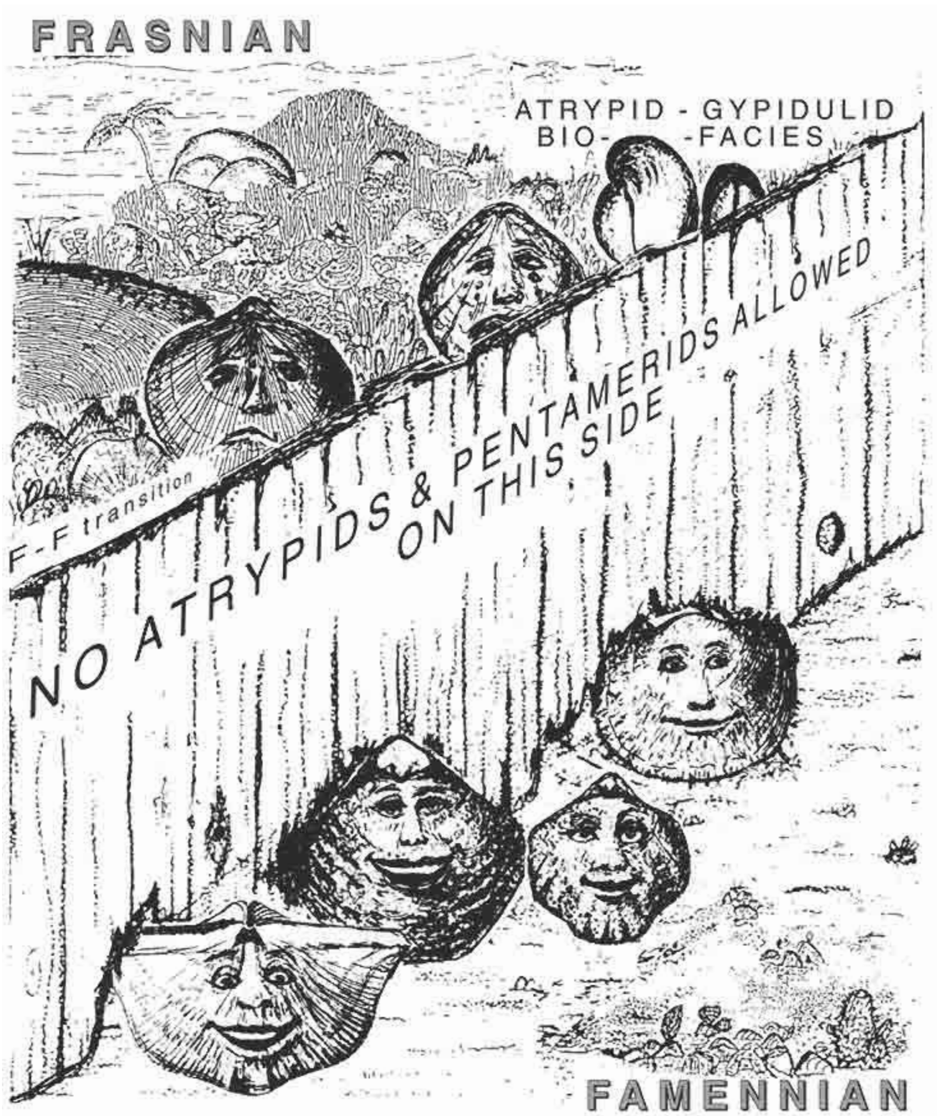
FRASNIAN
ATRYPID - GYPIDULID
BIO- -FACIES
F-F transition
NO ATRYPIDS & PENTAMERIDS ALLOWED
ON THIS SIDE
FAMENNIAN