

## TRILOBITES AT THE DEVONIAN-CARBONIFEROUS BOUNDARY

by

Carsten BRAUCKMANN<sup>1</sup>, Ivo CHLUPÁČ<sup>2</sup> & Raimund FEIST<sup>3</sup>

(30 figures)

**ABSTRACT.**- The drastic change within the trilobite succession close to the Devonian-Carboniferous boundary coincides with the Hangenberg Shale time equivalent which lies only a few hundred thousand years below the newly defined, conodont-based Devonian-Carboniferous boundary. The *Phacopida* became completely extinct, and of the Proetida only very few Brachymetopidae and Proetacea survived and gave rise to a new, final radiation of trilobites during the Permocarboniferous.

### INTRODUCTION

Trilobites declined in taxonomic diversity from the Middle Devonian and at the end-Frasnian mass extinction events, then diversified again in Famennian times and prior to the Devonian-Carboniferous boundary Hangenberg crisis (Feist, 1991). At this point, trilobite evolution is characterized by both substantial loss of higher rank taxa such as Phacopida, Cyrtosymbolinae and the major part of the Drevermanniinae and, concomitantly, adaptive radiations within numerous subfamilies such as Brachymetopinae, Archegoninae, Weaniinae and the *Pudoproetus* group all of which survived into the Carboniferous where they underwent major diversifications. Thus, the Devonian-Carboniferous transition is most significantly marked by the occurrence of short-ranged trilobite index taxa suitable for both, fine scale and global stratigraphical correlation of low latitude shelf areas.

The biostratigraphic significance of trilobites near the Devonian-Carboniferous boundary had been already clearly recognized by Richter & Richter (1951) and subsequent studies during the last four decades confirmed their ideas on a world-wide scale. In the meantime, trilobite faunas of this time-span are known from many European regions, i. e. from the Rhenish Massif (Sauerland, Bergisches Land), south England (Cornwall, Devon), Bohemian Massif (Frankenwald,

Thuringia, Moravia, N. Bohemia, Silesia), Holy Cross Mts. and recently particular from Montagne Noire and Carnic Alps. In addition, present knowledge has been significantly augmented by studies in North Africa (Morocco), South Ural, South China (Guizhou and Guangxi Provinces), and North America (Utah, Mid Continent).

Detailed investigation of sections, particularly those which were candidates for potential Devonian-Carboniferous boundary stratotypes in the N part of the Rhenish Massif (Becker *et al.*, 1984; Brauckmann & Hahn, 1984; Luppold *et al.*, 1984), Montagne Noire (Flajs & Feist 1988), South China (Zhu, 1988; Xiang, 1989) and the Carnic Alps (Feist, 1991) demonstrated the importance of trilobites in a most significant way.

Our contribution summarizes rather generally the present state of trilobite biostratigraphy near the Devonian-Carboniferous boundary, pointing also to some questions that remain open.

### LATE FAMENNIAN TRILOBITES

The stratigraphical distribution of Late Famennian trilobites has already been summarized, for example, by Brauckmann & Brauckmann, 1986 and Yuan, 1988. In the meantime, detailed investigations have been focussed on facies dependance (Feist, 1991

1 Fuhrrott-Museum, Auer Schulstrasse 20, D-W-5600 Wuppertal 1.

2 Katedra geologie na přírodovědecké fakultě, University Karlovy, Albertov 6; ČSFR-12843 Praha 2.

3 Laboratoire de Paléontologie, Université Montpellier II (U.S.T.L.), Place Eugène Bataillon, F-34095 Montpellier-cedex 05.

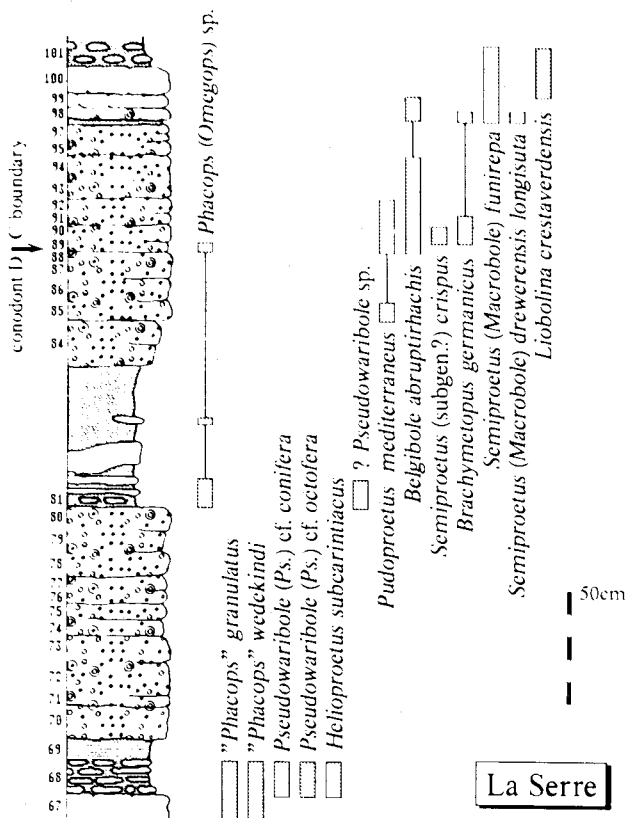


Fig. 1.- Stratigraphical distribution of trilobites at La Serre stratotype section (Montagne Noire, France).

and current researches). They show that there are striking differences between trilobites of the cephalopod limestone facies and those of the shallow neritic facies which are thus treated separately in the present paper.

**CEPHALOPOD LIMESTONE FACIES**

The late Famennian trilobites are best known from the pelagic "cephalopod" facies distinguished by grey or red micritic, frequently nodular limestones intercalated with a variable amount of clayey and silty material. Trilobites co-occur with variable frequency with cephalopods, entomozoan ostracodes, small bivalves and ubiquitous conodonts. Whereas trilobites with non-reduced vision occurred frequently within Famennian off-shore environments, there was a spectacular increase of blind and reduced-eyed forms at the end of the Famennian. Within the middle *costatus* Biozone, i.e. prior to the Hangenberg Shale, no demonstrably autochthonous trilobite with normal eyes has been observed from this facies (with the exception of the ubiquitous "*Phacops*" *granulatus*). In contrast, mixed faunas occur in transitional biofacies or are the result of current induced or gravitational transport; thus rare co-occurrence of trilobites

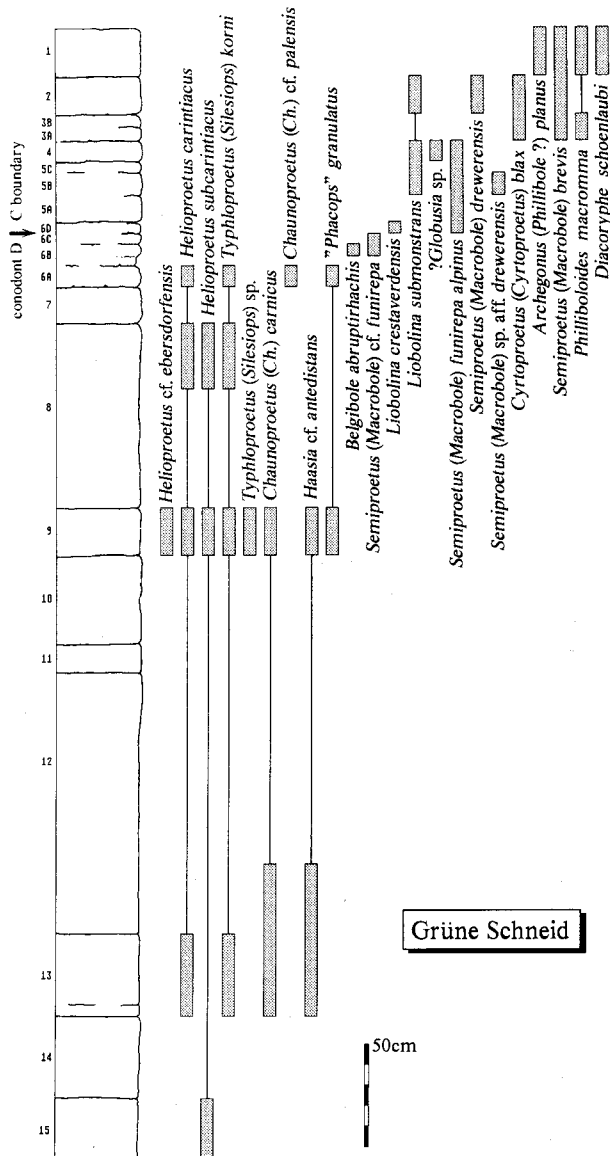


Fig. 2.- Stratigraphical distribution of trilobites at Grüne Schneid (Carnic Alps, Austria).

with non-reduced vision may point to allochthony. Trilobites with absent or reduced eyes are typical (*Chaunoproetus* Richter & Richter, 1919, *Typhloproetus* Rud. Richter, 1913, *Helioproetus* Richter & Richter, 1919, *Dianops* Richter & Richter, 1923 etc.) The lithology, biota and taphonomy suggest a low-energy, rather deep (below wave-base) and offshore environment of submarine ridges and platforms with low rates of sedimentation. Famennian trilobite faunas of this environment have many analogies in older Devonian trilobite assemblages (Chlupáč, 1983). Wide distribution of analogous facies along shelves of the Prototethys realm and with open possibilities of migration within the warm climatic zone may be responsible for the wide-ranging similarity of these faunas. Although the local abundance of trilobites is

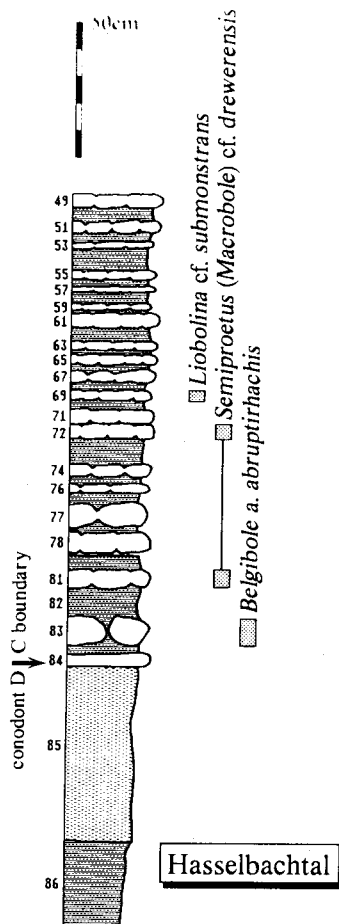
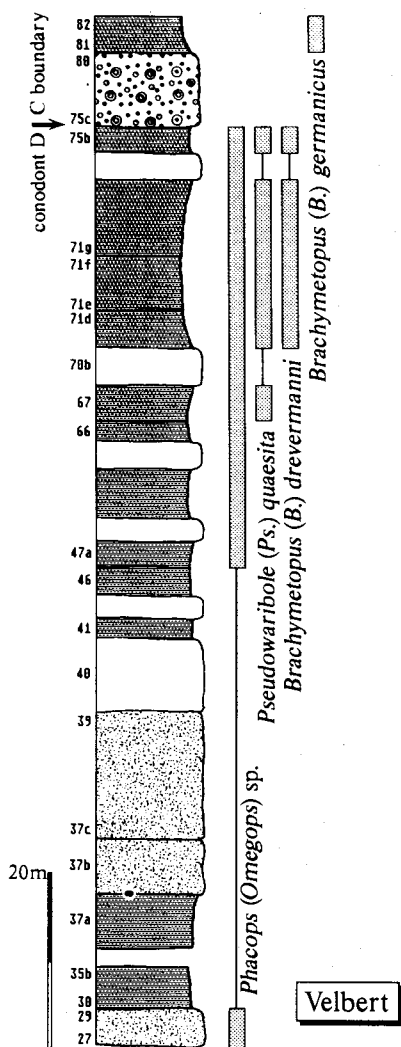


Fig. 3.- Stratigraphical distribution of trilobites in the Velbert section (Autobahnknoten Langenhorst; Rhenish Massif, West Germany). Modified from Brauckmann & Hahn, 1984 and Michels, 1986; comp. also Amler, 1992.

Fig. 4.- Stratigraphical distribution of trilobites in the Hasselbachtal section (Rhenish Massif, West Germany). Modified from Brauckmann & Hahn 1984 and Becker *et al.*, 1984.

strongly variable, the major portion of late Famennian trilobite localities belong to this facies.

Trilobites of the Late Famennian *Wocklumeria* Biozone, corresponding to the cephalopod biofacies, maintain the characteristic features of end-Devonian trilobite faunas : dominance of small-sized proetaceans (Drevermanniinae, Cyrtosymbolinae, early Archegoninae and Weaniinae), and still widely distributed phacopids.

Proetacean genera such as *Chaunoproetus* Richter & Richter, 1919, *Typhloproetus* Rud. Richter, 1913, *Helioproetus* Richter & Richter, 1919, *Mirabole* Osmólska, 1962, *Silesiops* Chlupáč, 1966, *Pseudowaribole* Hahn & Hahn, 1967, *Haasia* Yuan, 1988 (= *Pusillabole* H. Alberti, 1973, pt.), last representatives of *Cyrtosymbola* Rud. Richter, 1913, recently described *Bapingaspis* Yuan, 1988 and proposed *Devo-*

*nocoryphe* Yuan are definitely known from Europe to South China. Some other genera seem to have rather restricted geographic occurrence (*Parafriethjofia* Yuan, 1988, *Daihuaia* Yuan, 1988, etc.). In contrast, these genera have not been reported from the American Famennian.

Phacopids are fairly common and diversified in this biofacies : Most characteristic in the Late Famennian is *Dianops* Richter & Richter, 1923, marked by total absence of eyes and effaced exoskeletal relief. Small-eyed phacopids with *Cryphops*-like eyes (*Cryphops? ensae*/*Cr.? wocklumeriae* group) and the so far incompletely known *Rabienops* Struve, 1989 with a rather "normal" kidney-shaped outline of the visual surface indicate persisting lineages from older Devonian times up to the close proximity of the Devonian-Carboniferous boundary.

The widely distributed group of "*Phacops*" *granulatus* (Münster, 1840) with fairly large eyes and the somewhat smaller-eyed "*Phacops*" *wedekindi* (Richter & Richter, 1926) are in need of revision; should short

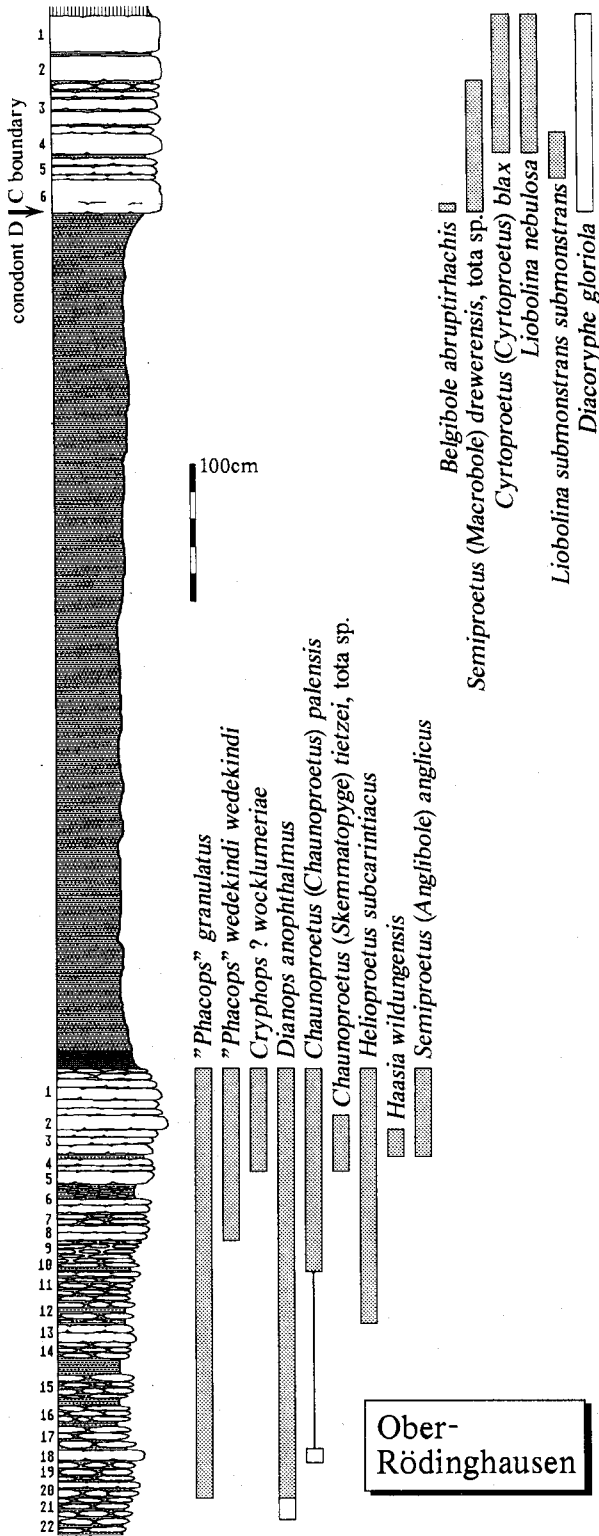


Fig. 5.- Stratigraphical distribution of trilobites in the Hönnetal section near Ober-Rödinghausen (Rhenish Massif, West Germany). Modified from Eickhoff, 1973 and Brauckmann & Hahn, 1984.

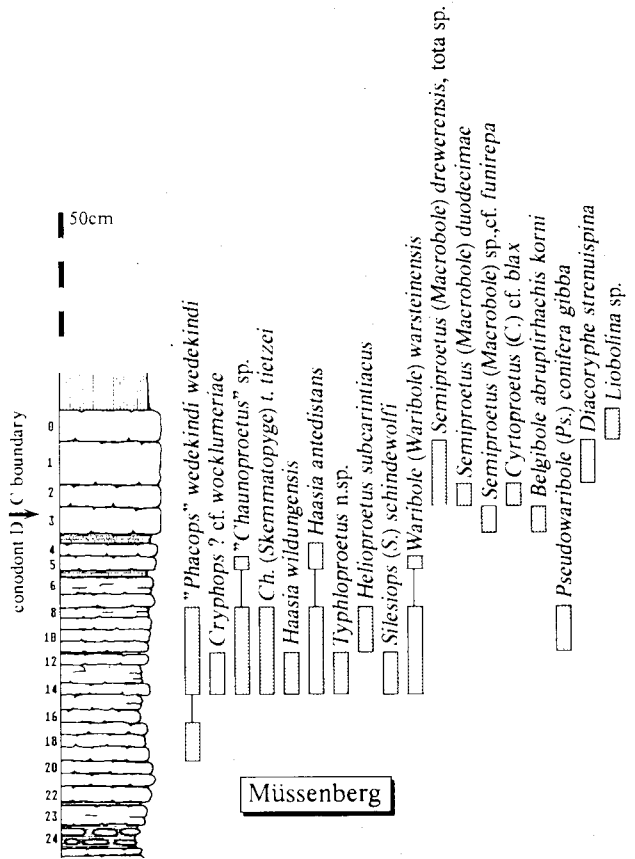
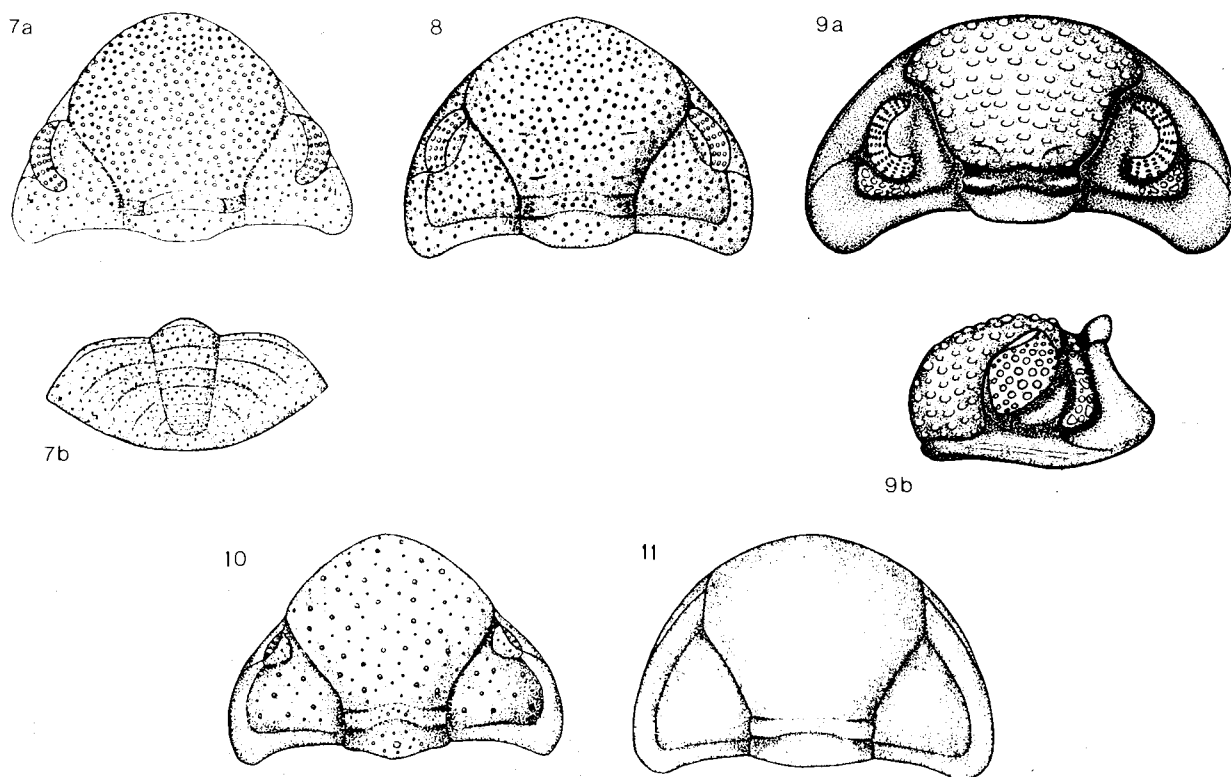


Fig. 6.- Stratigraphical distribution of trilobites in the Müszenberg section (Rhenish Massif, West Germany). Modified from Korn, 1981 and Brauckmann & Hahn, 1984. Additional and more complete collections have shown that *Perlioproetus* n. sp. as mentioned by Hahn in Luppold *et al.*, 1984 (repeated by Brauckmann & Hahn, 1984 and Brauckmann & Brauckmann, 1986) can now be determined as a species of *Semiproetus (Macrobole)*.

and less segmented pygidia (comp. Richter & Richter, 1926, pl. 8, fig. 39; Luppold *et al.*, 1984, pl. 2, fig. 8b) belong to cephalia included here, a new genus may be involved, whose relationships to *Rabienops* would be elucidated with the addition of new finds.

Trilobites of the *Wocklumeria* Biozone have been so far regarded as very closely related to those of the underlying *Clymenia* Biozone. This was generally supposed for faunas from European localities where conodonts and ostracodes occur together with trilobites (Hahn & Hahn, 1975; Brauckmann & Brauckmann, 1986; Osmólska, 1962; Chlupáč, 1966). A different view has been recently presented by Yuan (1988) who considered particularly the localities in South China and assigned to the *Wocklumeria* Biozone some European and N. African localities, which were formerly placed in the *Clymenia* Biozone. This resulted in a different picture of uppermost



Figs. 7-11.- Selection of late Upper Devonian phacopids, not to scale. 7. "*Phacops*" *granulatus* (Münster, 1840) (a = cephalon, b = pygidium). 8. "*Phacops*" *wedekindi wedekindi* Richter & Richter, 1926. 9. *Phacops* (*Omegops*) *accipitrinus bergicus* Drevermann, 1902 (a = dorsal view, b = lateral view of cephalon). 10. *Cryphops?* *wocklumeriae* (Richter & Richter, 1926). 11. *Dianops limbatus* (Reinh. Richter, 1848).

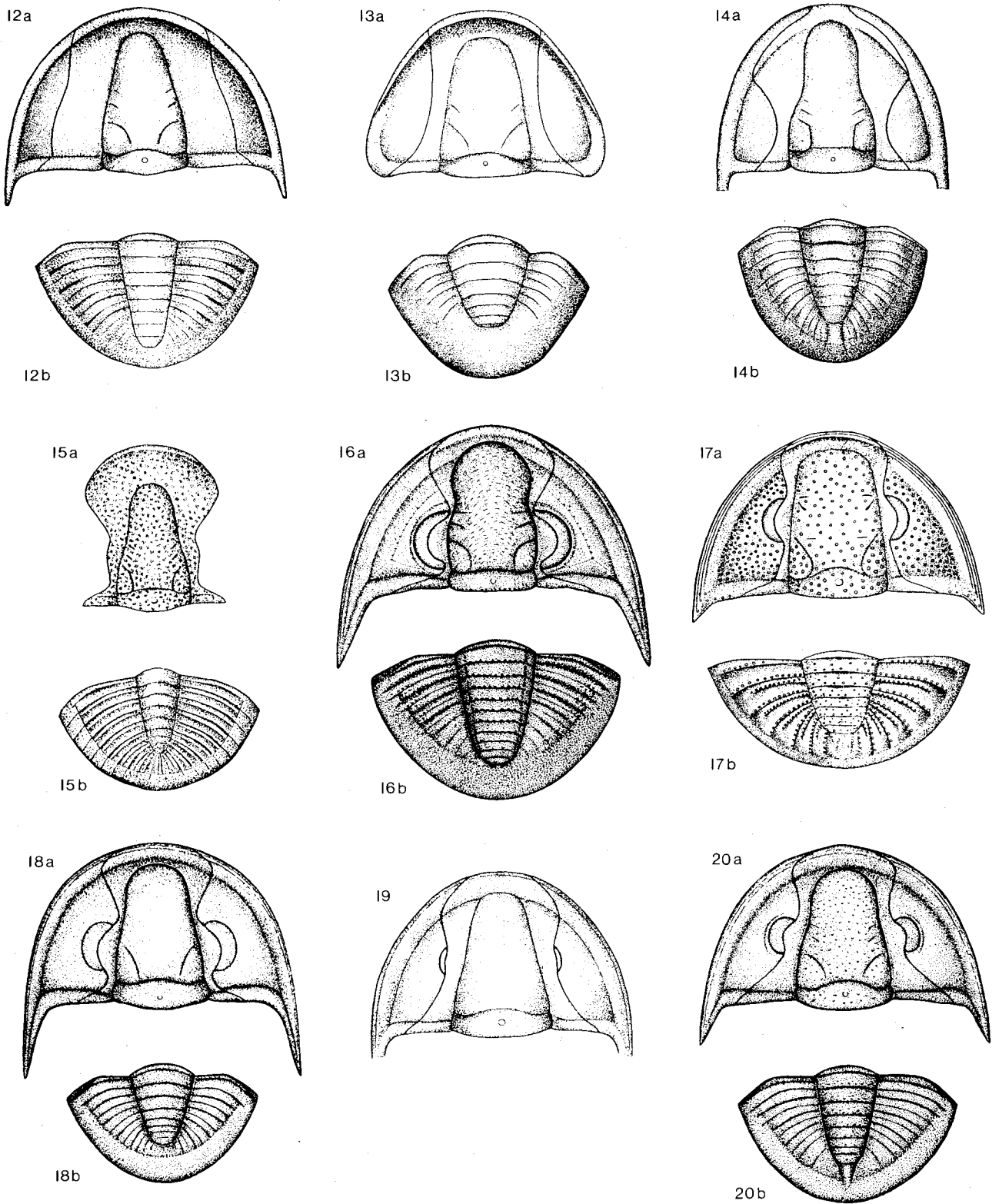
Famennian trilobite faunas, markedly distinct from those of the *Clymenia* Biozone. As Yuan's (1988) view is based mostly on indirect indications (similarities of trilobites) and as a new direct study of conodonts and other index fossils from the European localities be discussed has not been provided, his re-evaluation cannot as yet be regarded as conclusive.

### SHALLOW NERITIC FACIES

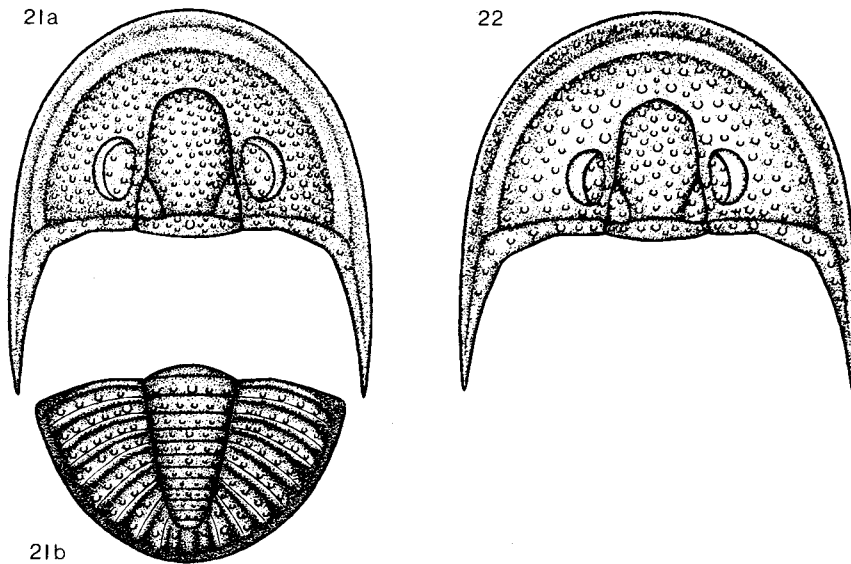
Late Famennian shallow-water, light, bioclastic carbonates with abundant benthos (brachiopods, corals etc.) of the Strunian biofacies are distributed in many areas but their trilobites are less common and poorly known. The wide occurrence of the *Phacops accipitrinus* group, i.e. *Phacops* (*Omegops*) Struve, 1976 is characteristic. Members of this group may also occur in turbidite, cephalopod or shale facies (H. Alberti, 1972). However, this may result from transport rather than indicating a lesser environmental dependence as comparable with some older Silurian and Devonian phacopids (e.g. some species of *Ananaspis*, *Eophacops* etc.; comp. Chlupáč, 1975,

1977). Generally, Famennian shallow-water benthic trilobite assemblages are as yet insufficiently known. Whereas on the North-American continent no trilobites are reported with the exception of the end-Famennian, the south Ural and Kirghiz Steppe (Weber, 1937) seem to show poor diversity, but these assemblages await further investigation. In addition to phacopids, shallow water Proetida (*Pseudowaribole* Hahn & Hahn, 1967, *Waribole* Richter & Richter, 1926, *Perliproetus* Richter & Richter, 1926, and *Brachymetopus* McCoy, 1847) occur in platform areas of the northern Rhenish Massif such as the Velbert anticline and near Warstein (Brauckmann & Hahn, 1984; Richter & Richter, 1926).

Somewhat different trilobite faunas are found in allodapic deposits originating from submarine rises or nearshore areas. These assemblages are characterized by the mixing of shallow water trilobites with normally developed eyes and blind deeper water forms. These facies are documented for example in the Hady Říčka Limestone in the Moravian Karst (Chlupáč, 1966, 1977), at La Serre (Flajs & Feist, 1988), and in the Nanbiancun section (Zhu, 1988).



Figs. 12-20.- Selection of late Upper Devonian proetaceans, not to scale (if not otherwise indicated : a = cephalon, b = pygidium). 12. *Drevermannia (Drevermannia) schmidti* Rud. Richter, 1913. 13. *Chaunoproetus palensis* (Rud. Richter, 1913). 14. *Helioproetus subcarintiacus* (Rud. Richter, 1913). 15. *Haasia antedistans* (Richter & Richter, 1926) (a = cranidium). 16. *Pseudowaribole (Pseudowaribole) quaesita* G. Hahn & C. Brauckmann, 1984. 17. *Perlioproetus marginatus* (Münster, 1842). 18. *Waribole (Waribole) warsteinensis* (Richter & Richter, 1926). 19. *Silesiops (Silesiops) schindewolfi* (Richter & Richter, 1919). 20. *Mirabole kielanae* (Osmólska, 1962).



Figs. 21-22.- Species of *Brachymetopus* near the Devonian-Carboniferous boundary, not to scale. 21. *Brachymetopus* (*Brachymetopus*) *drevermanni* G. Hahn, 1964, Strunian (a = cephalon, b = pygidium). 22. *Brachymetopus* (*Brachymetopus*) *germanicus* G. Hahn, 1964, early Tournaisian.

### TRILOBITES IN CLOSE PROXIMITY TO THE DEVONIAN-CARBONIFEROUS BOUNDARY

Summarizing the results of trilobite studies in sections of the Devonian-Carboniferous boundary beds investigated in detail particularly in the N part of Rhenish Massif (Brauckmann & Hahn, 1984; Luppold *et al.*, 1984; Hahn *et al.*, 1989), Montagne Noire (La Serre : Flajs & Feist, 1988), Carnic Alps (Grüne Schneid : Schönlaub *et al.*, 1988; Feist, 1992) and South China (esp. Nanbiancun : Zhu, 1988; Dapoushang : Xiang, 1989), the following may be stated :

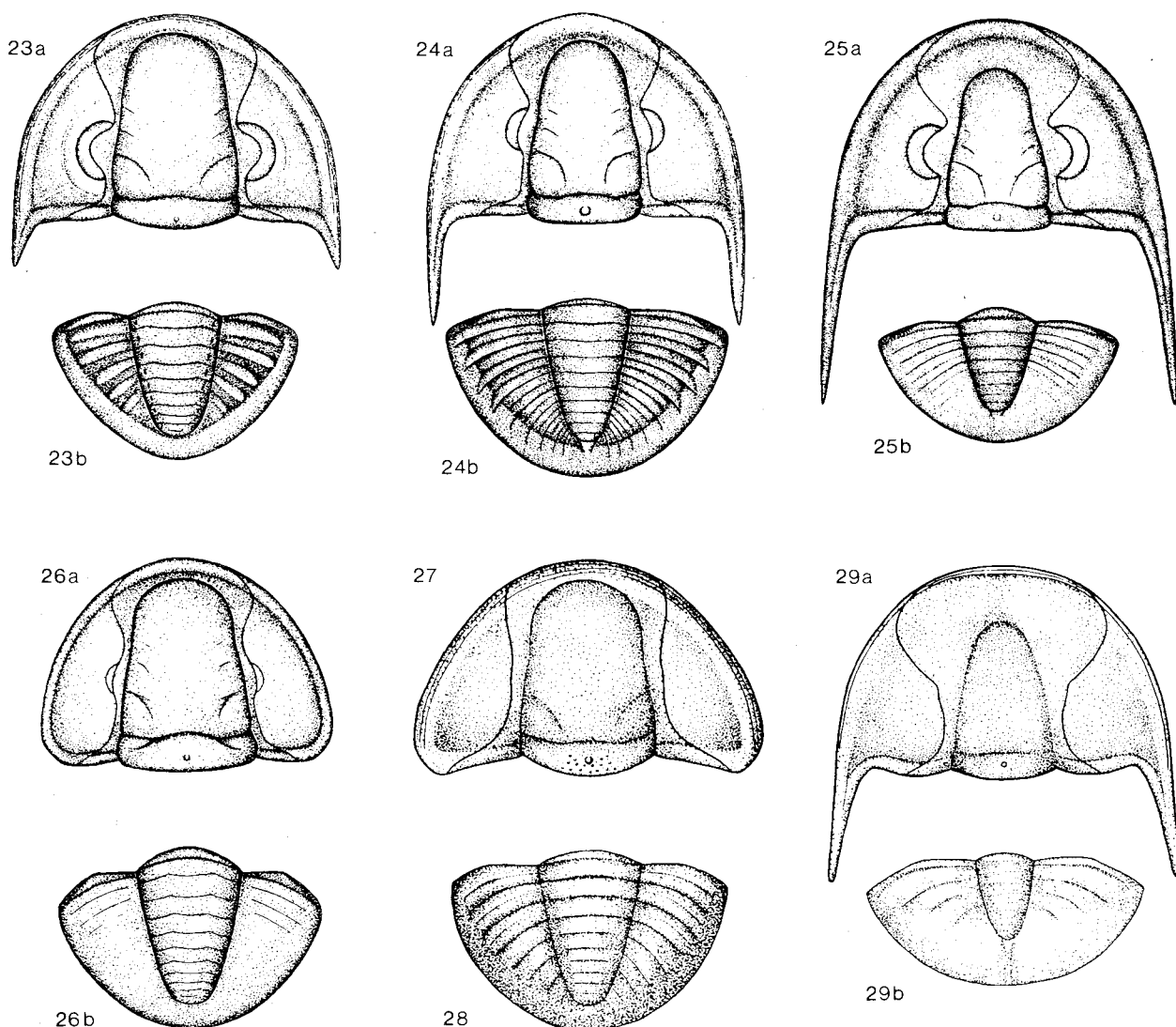
1.- Typical late Famennian proetacean represented by species of *Drevermannia*, *Chaunoproetus* (*Chaunoproetus*), *Ch.* (*Skemmatopyge*), *Typhloproetus*, *Helioproetus*, *Haasia* (= *Pusillabole*, pt.), *Silesiops* (*Silesiops*) and some *Pseudowaribole* species reach the Middle *praesulcata* Zone just below the Devonian-Carboniferous boundary, i.e. up to the base of the HS or its time-equivalent.

2.- All known Uppermost Devonian phacopids belonging to *Phacops* (*Omegops*), *Rabienops*, *Phacops?*, *Dianops* and *Cryphops?* reach approximately the same level below the HS time equivalent. The local overlap of *Ph.* (*Omegops*) in the lowest Carboniferous bed at La Serre (Flajs & Feist, 1988) is exceptional and possibly caused by transport and redeposition from the older beds.

3.- The HS or its equivalents have so far provided no determinable trilobite. However, anchimetamorphic shales at Ještědské pohoří, northern Bohemia, that may correspond to this level, constitute a potential for further investigation (Chlupáč, 1964).

4.- In the stratotype section at La Serre (Montagne Noire) the Devonian-Carboniferous boundary coincides with the appearance of *Belgibole abruptirhachis* (Richter & Richter, 1919). However, this index trilobite occurs earlier, below the onset of *Siphonodella sulcata*, at Müssenberg (Luppold *et al.*, 1984; Clausen *et al.*, 1989) and at Grüne Schneid (Feist, 1992) which may be due to facies controlled local absence of the latter. Whereas *B. abruptirhachis* seems to be characteristic for the basal Carboniferous (lower part of the *sulcata* Zone) (Hahn *et al.*, 1990), *Semiproetus* (*Macrobole*) *drewerensis* (Richter & Richter, 1951) appears somewhat higher in European sections (Brauckmann & Hahn, 1984; Feist, 1992), within the *duplicata* Zone, being represented by allied forms such as *S. (M.) nanbiancunensis* (Zhu, 1988) and *S. (M.) orientalis* (Xiang, 1989) [both probably subspecies of *S. (M.) drewerensis*] in South China (Nanbiancun, Dapoushang).

5.- Representatives of early *Pudoproetus* first appear below the HS time equivalent in North America, the Urals and in the Kirghiz steppe, and are still present in the lowermost Tournaisian *sulcata* Zone in Europe (La Serre) and South China (Nanbiancun) (Feist & Petersen, submitted).



Figs. 23-29.- Selection of Balvian trilobites (Phillipsiidae), not to scale (a = cephalon, b = pygidium). 23. *Belgibole abruptirhachis abruptirhachis* (Richter & Richter, 1919). 24. *Semiproetus (Macrobale) drewerensis drewerensis* (Richter & Richter, 1951). 25. *Waribole (Latibole) laticampa* (Osmólska, 1962). 26. *Cyrtoproetus (Cyrtoproetus) blax* (Richter & Richter, 1951). 27. *Liobolina nebulosa* Richter & Richter, 1951 (cephalon). 28. *Liobolina submonstrans submonstrans* Richter & Richter, 1951 (pygidium). 29. *Diacorphe Pfeifferi* Richter & Richter, 1951.

6.- The *Brachymetopus* lineage was likewise not interrupted near the Devonian-Carboniferous boundary: *B. drevermanni* G. Hahn, 1964 from the uppermost Famennian of the Velbert anticline seems to be the direct ancestor of the lower Tournaisian *B. germanicus* G. Hahn, 1964 known from the same area. The latter species occurs also at La Serre.

7.- The species of *Pseudowaribole*, although diverse in the uppermost Devonian and lowest Carboniferous, indicate possible ancestors of Tournaisian Weaniinae, Linguaphillipsiinae, Cummingellinae and other Late Paleozoic subfamilies. Particularly *Pseudowaribole (P.) quaesita* Hahn &

brauckmann, 1984 from the Velbert area points to this interpretation (Hahn & Brauckmann, 1984).

8.- Species of *Liobolina*, *Cyrtoproetus*, *Diacorphe*, *Globusia* etc. occur distinctly above the Devonian-carboniferous boundary and may be regarded as typical lower Carboniferous components in the sections studied.

#### EARLY DINANTIAN (BALVIAN) TRILOBITES

The pioneering work on Balvian trilobites was carried out by Richter & Richter, 1951 based upon collections from the NE part of the Rhenish Massif



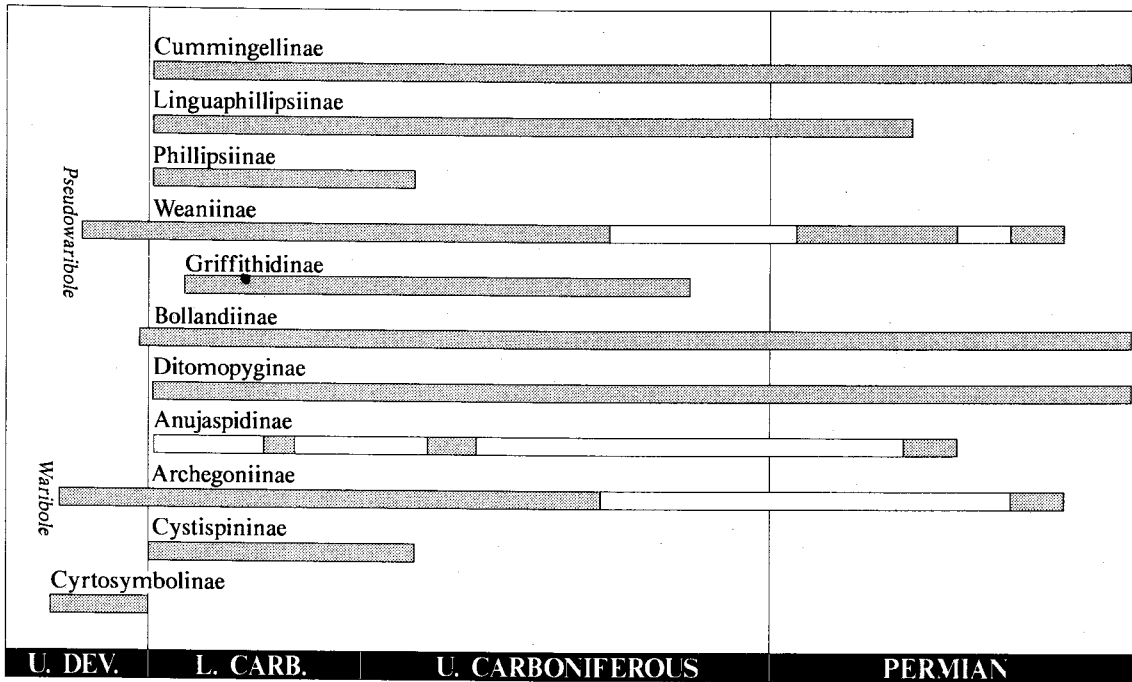


Fig. 30.- The subfamilies of the Phillipsiidae Oehlert, 1886 - the most prominent family of the final radiation of trilobites (systematics from Hahn & Hahn & Brauckmann, current researches; composition of Bollandiinae as used herein not generally accepted by all of the present authors).

(Sauerland) and from the East Thuringian Massif. Subsequently, large collections have been studied in detail, particularly from Poland (Holy Cross Mountains : Osmólska, 1962 and 1973) and from the Moravian Karst (Chlupáč, 1966). Hahn & Hahn, 1975 gave a compilation of the most important data. During the last few years several forms of nearly equivalent age have been mentioned from the W part of the Rhenish Massif (Belgium and adjacent areas : Hahn *et al.*, 1988, Hahn & Hahn, 1988; Wuppertal : Hahn *et al.*, 1989). Quite recently, as a part of a monograph on *Archegonus (Phillibole)* Richter & Richter, 1937, many Balvian species previously assigned to this taxon have been revised by Archinal, 1991, 1992. Similar researches are planned for other taxa in a project under the supervision of G. Hahn, and further current researches extend to the exact stratigraphic correlation of Early Dinantian trilobites with other fossil groups.

As far as is known, most species occur somewhat higher in the Balvian sequence. The most prominent taxon is *Semiproetus (Macrobole)* Richter & Richter, 1951 (as revised by Archinal, 1991) which was often previously regarded as belonging to the *drewerensis* group of *A. (Phillibole)*. It is widely distributed with several species and subspecies from W Europe to E Asia. The whole subgenus extends into younger Dinantian strata and is known from horizons as young as the Erdbachian of the Harz Mountains. Other important forms are *Cyrtoproetus* Reed, 1943, of

which, for example, *C. (C.) blax* (Richter & Richter, 1951) is very common in several European sections, and *Liobolina* Richter & Richter, 1951 as well as *Waribole (Latibole)* Hahn & Hahn, 1969 which seem to appear in higher parts of the Balvian. Less common, but more striking in morphological peculiarities, are representatives of the *Cystispininae (Diacoryphe)* Richter & Richter, 1951, *Globusia* Osmólska, 1973). Most of their species are characterized by distinctly inflated genal spines. In the latter, moreover, the glabella is extremely inflated, whereas in *Diacoryphe* the carapace is only slightly vaulted and the relief is very smooth. Also during the Balvian the first species of *Carbonocoryphe (Winterbergia)* G. Hahn & Brauckmann, 1975 occur.

The paleobiogeographic distribution of early Carboniferous trilobites has recently been compiled by G. Hahn, 1990. At least three trilobite provinces can be recognised : Europe, North America and Australia, with a possible fourth in Asia. At present the bathymetric zonation is documented best in Belgium and adjacent regions of Germany and the Netherlands where five different communities (depending on water depth) can be distinguished. A detailed trilobite-based stratigraphy for the Lower Carboniferous has been elaborated for parts of Europe (Hahn *et al.*, 1988; Hahn & Hahn, 1988; Thomas *et al.*, 1984) and eastern Australia (Engels & Morris, 1990). In North America the first steps in this direction

have been taken (Chamberlain, 1969), but less is known from other regions of the world.

After the serious decline in the very late Devonian, the few surviving forms, in particular *Waribole* and *Pseudowaribole*, but also *Brachymetopus*, *Namuropyge* and, in a minor degree, *Drevermannia* gave rise within the Balvian to another, final, radiation which extended to the late Permian. The time-span of this last radiation is nearly as long as that from the first appearance of the proetaceans in the early Ordovician till the Upper Devonian. In contrast to earlier radiations, in which several different groups of trilobites participated, the final radiation was restricted to the Proetida only. They alone were then able to invade all environments and ecological niches which were formerly shared with other groups. Thus it can be understood that the late Paleozoic radiation was very rich in taxa - much more than previously believed (and even still to be found in some text books) when Carboniferous and Permian trilobites were usually assigned to the few genera *Phillipsia*, *Griffithides* and *Brachymetopus*.

## CONCLUSION

The profound change of faunas close to the Devonian-Carboniferous boundary reflects an important turning point in the evolution and distribution of trilobites. This coincides with the Hangenberg Shale time equivalent which lies only a few hundred thousand years below the newly defined Devonian-Carboniferous boundary. It confirms the event-nature of this boundary (comp. also Walliser, 1984) which caused one of the most spectacular reductions in taxonomic diversity because 50 % of the then present orders and subfamilies disappeared. Only the Frasnian/Famennian boundary Kellwasser event is more drastically marked since such prominent trilobite taxa as Harpetina, Dalmanitacea, Odontopleurida and Scutelluida became extinct (mean diversity restriction = 60 %, Feist, 1991). The striking difference between these two extinction events however lies in the fact that lower rank taxonomic diversity at the Kellwasser event is extremely low whereas the Hangenberg event affects a rather diversified trilobite community.

The Silurian-Devonian boundary shows distinct analogies (Ormiston, 1977), although the general diversity (in families etc.) is much greater, composition of trilobite faunas different, and extinctions less expressive and rather gradual (Encrinuridae, Raphiophoridae). In spite of obvious environmental control of most proetaceans, some species or related groups of species show here unusually wide geographic

distribution and a lesser facies dependence : the importance of the *Warburgella rugulosa* (Alth, 1874) group above the Silurian-Devonian boundary may be compared with that of *Belgibole abruptirhachis* and *Semiproetus (Macrobole)* above the Devonian-Carboniferous boundary.

At the so far only internationally accepted major chronostratigraphic boundary within the Carboniferous - the "mid-Carboniferous boundary" - the trilobite faunas change slowly and are less well documented.

Similar to the situation at the Ordovician-Silurian boundary (comp. Fortey, 1989), faunal refugia should be presumed to have existed during the Famennian and near the Devonian-Carboniferous boundary. In these refugia particularly some brachymetopids and proetaceans survived the environmental changes up to their reappearance in the topmost Famennian and in the Tournaisian. These local refugia may be sought in shallow-water shelves where conditions favourable for these trilobites exceptionally persisted through the whole Famennian.

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## BIBLIOGRAPHY

- ALBERTI, H., 1972.- Ontogenie des Trilobiten *Phacops accipitrinus*. *N. Jb. Geol. Paläont. Abh.*, 141 (1) : 1-36, figs. 1-11, tabs. 1-6; Stuttgart.
- ALBERTI, H., GROOS-UFFENORDE, H., STREEL, M., UFFENORDE, H. & WALLISER, O.H., 1974.- The stratigraphical significance of the *Protognathodus* fauna from Stockum (Devonian-Carboniferous boundary, Rhenish Schiefergebirge). *Newsl. Stratigr.* 3 (4) : 263-276, figs. 1-2, Leiden.
- AMLER, M.R.W., 1992.- Shallow marine bivalves at the Devonian-Carboniferous boundary. *Ann. Soc. géol. Belg.*, 115 (2) : 405-423.
- ARCHINAL, A., 1991.- Neudefinition der Untergattung *Archegonus (Phillibole)* und die Gattungen *Semiproetus* und *Prolibole* (Trilobite, Ober-Devon und Unter-Karbon). *Senckenbergiana lethaea*, 71 (3/4) : 189-202, figs. 1-10; Frankfurt am Main.

- ARCHINAL, A., 1992.- Revision der Untergattung *Archegonus* (*Phillibole*) (Trilobita; Ober-Devon/Unter-Karbon). *Cour. Forsch.-Inst. Senckenberg* : 1-133, figs. 1-70, tabs. 1-13, pls. 1-2; Frankfurt am Main.
- BECKER, T. *et al.*, 1984.- Hasselbachtal, the section best displaying the Devonian-Carboniferous boundary beds in the Rhenish Massif (Rheinisches Schiefergebirge). In: E. Paproth & M. Streeb (eds.): The Devonian-Carboniferous boundary. *Cour. Forsch.-Inst. Senckenberg*, 67 : 181-191, figs. 1-6, pl. 1; Frankfurt am Main.
- BRAUCKMANN, C. & BRAUCKMANN, B., 1986.- Famennian trilobites : an outline on their stratigraphical importance. *Ann. Soc. géol. Belg.*, 109 (spec. Vol. "Aachen 1986") : 9-17, figs. 1-8; Bruxelles.
- BRAUCKMANN, C. & HAHN, G., 1984.- Trilobites as index fossils at the Devonian-Carboniferous boundary. In: E. Paproth & M. Streeb (eds.): The Devonian-Carboniferous boundary. *Cour. Forsch.-Inst. Senckenberg*, 67 : 11-14, figs. 1-5; Frankfurt am Main.
- CHAMBERLAIN, C.K., 1969.- Carboniferous trilobites : Utah species and evolution in North America. *J. Paleont.*, 43 : 41-68, figs. 1-4, pls. 11-13; Tulsa/Oklahoma.
- CHLUPÁČ, I., 1964.- Nový nález fauny ve slabě metamorfovaném paleozoiku Ještědského pohoří. *Čas. pro Mineral. Geol.*, 9 (1) : 27-35, fig. 1, pls. 1-4; Praha.
- CHLUPÁČ, I., 1966.- The Upper Devonian and Lower Carboniferous trilobites of the Moravian Karst. *Sborn. geol. Věd. Řada P (Paleont.)*, 7 : 1-143, figs. 1-35, tabs. 1-6, pls. 1-24; Praha.
- CHLUPÁČ, I., 1975.- The distribution of phacopid trilobites in space and time. *Fossils and Strata*, 4 : 399-408, figs. 1-7; Oslo.
- CHLUPÁČ, I., 1977.- The phacopid trilobites of the Silurian and Devonian of Czechoslovakia. *Rozpr. ústředn. Ústav. geol.*, 43 : 1-172, figs. 1-26, pls. 1-32; Praha.
- CHLUPÁČ, I., 1977.- The Late Devonian and Early Carboniferous trilobite faunas of Moravia. In: Holub, V.M. & Wagner, R.H. (eds.): Symposium on Carboniferous stratigraphy : 305-313; Praha.
- CHLUPÁČ, I., 1983.- Trilobite assemblages in the Devonian of the Barrandian area and their relations to palaeoenvironments. *Geologica et Palaeontologica*, 17 : 45-73, figs. 1-5, tabs. 1-5, pls. 1-3; Marburg.
- CLAUSEN, C.-D., KORN, D., LUPPOLD, F.W. & STOPPEL, D., 1989.- Untersuchungen zur Devon/Karbon-Grenze auf dem Müszenberg (nördliches Rheinisches Schiefergebirge). *Bull. Soc. belge Géol.*, 98 (3/4) : 353-366, figs. 1-3, tab. 1, pls. 1-5; Bruxelles.
- EICKHOFF, G., 1973.- Das hohe Oberdevon und das tiefe Unterkarbon im Bahneinschnitt Oberrödinghausen bei Menden (Rheinisches Schiefergebirge). *C.R. 7. Congr. internat. Stratigr. Géol. Carbonifère, Krefeld*, 2 : 417-440, fig. 1, tabs. 1-3, pls. 1-4; Krefeld.
- ENGEL, B.A. & MORRIS, L.N., 1990.- The biostratigraphic potential of Carboniferous trilobites from eastern Australia. *Cour. Forsch.-Inst. Senckenberg*, 130 : 189-198, tabs. 1-5; Frankfurt am Main.
- FEIST, R., 1991.- The late Devonian trilobite crisis. *Historical Biology*, 5 : 197-214, figs. 1-7; London.
- FEIST, R., 1991.- Trilobiten aus dem Devon/Karbon-Grenzprofil an der Grünen Schneid (Zentrale Karnische Alpen, Österreich). *Abh. geol. B.-Anst.*, 135 (1) : 21-47, figs. 1-2, pls. 1-4; Wien.
- FEIST, R. & PETERSEN, M.S. 1993.- Origin and spread of *Pudoproetus* (*Hessleraspis*), a survivor of the late-Devonian trilobite crisis. *J. Paleont.*, submitted.
- FLAJS, G. & FEIST, R., 1988.- Index conodonts, trilobites and environment of the Devonian-Carboniferous boundary beds at La Serre (Montagne Noire, France). *Cour. Forsch.-Inst. Senckenberg*, 100 : 53-107, figs. 1-15, pls. 1-11; Frankfurt am Main.
- FORTEY, R.A., 1989.- There are extinctions and extinctions : examples from the Lower Palaeozoic. *Phil. Trans. roy. Soc. London*, B325 : 327-355, figs. 1-9; London.
- HAHN, G., 1990.- Palaeobiogeographic distribution and biostratigraphic significance of Lower Carboniferous trilobites : a review. *Cour. Forsch.-Inst. Senckenberg*, 130 : 199-205, tab. 1; Frankfurt am Main.
- HAHN, G. & BRAUCKMANN, C., 1984.- Zur Kenntnis ober-devonischer Trilobiten aus dem Bergischen Land. *Jber. naturwiss. Ver. Wuppertal*, 37 : 116-124, figs. 1-3, tab. 1; Wuppertal.
- HAHN, G. & HAHN, R., 1975.- Die Trilobiten des Ober-Devon, Karbon und Perm. Leitfossilien (2nd edition, edit.: K. Krömmelbein), 1 : I-VIII : 1-127, figs. 1-4, tabs. 1-5, pls. 1-12; Berlin, Stuttgart (Borntraeger).
- HAHN, G. & HAHN, R., 1988.- The biostratigraphical distribution of Carboniferous Limestone trilobites in Belgium and adjacent areas. *Bull. Soc. belge Géol.*, 97 (1) : 77-93, figs. 1-22, tabs. 1-3; Bruxelles.
- HAHN, G., HAHN, R. & BRAUCKMANN, C., 1988.- Die Trilobiten des belgischen Kohlenkalkes (Unter-Karbon). 10. Biostratigraphie. *Geologica et Palaeontologica*, 22 : 55-72, fig. 1, tabs. 1-11; Marburg.
- HAHN, G., HAHN, R. & BRAUCKMANN, C., 1989.- Neue Kulm-Trilobiten aus Wuppertal (Bundesrepublik Deutschland). 2. Eine Fauna aus dem Devon/Karbon-Grenzbereich. *Jber. naturwiss. Ver. Wuppertal*, 42 : 183-200, figs. 1-6, tab. 1, pls. 1-2; Wuppertal.
- HAHN, G., HAHN, R. & WOLF, C., 1990.- *Belgibole abruptirhachis*, Leit-Trilobit an der Devon/Karbon-Grenze. *Senckenbergiana lethaea*, 70 (1/3) : 89-103, figs. 1-2, tab. 1, pl. 1; Frankfurt am Main.
- HESSLER, R.R., 1963.- Lower Mississippian trilobites of the family Proetidae in the United States, part I. *J. Paleont.*, 37 (3) : 543-563, tab. 1, pls. 59-62; Tulsa/Oklahoma.
- KORN, D., 1981.- Ein neues, Ammonoideen-führendes Profil an der Devon/Karbon-Grenze im Sauerland (Rhein. Schiefergebirge). *N. Jb. Paläont. Abh.*, 1981 (9) : 513-526, figs. 1-5, tab. 1; Stuttgart.
- LUPPOLD, F.W., HAHN, G. & KORN, D., 1984.- Trilobiten-, Ammonoideen- und Conodonten-Stratigraphie des Devon/Karbon-Grenzprofils auf dem Müszenberg (Rheinisches Schiefergebirge). *Cour. Forsch.-Inst. Senckenberg*, 67 : 91-121, figs. 1-7, tabs. 1-4, pls. 1-6; Frankfurt am Main.
- MICHELS, D., 1986.- Ökologie und Fazies des jüngsten Ober-Devon von Velbert (Rheinisches Schiefergebirge). *Göttinger Arb. Geol. Paläont.*, 29 : 1-86, figs. 1-22, tabs. 1-7, pls. 1-3; Göttingen.
- ORMISTON, A.R., 1977.- Trilobites. In: Martinsson, A. (ed.) : The Silurian-Devonian boundary. *IUGS Ser. A*, 5 : 320-326, figs. 1-2; Stuttgart.
- OSMÓLSKA, H., 1962.- Famennian and Lower Carboniferous *Cyrtosymbolinae* (Trilobita) from the Holy Cross Mountains, Poland. *Acta palaeont. polon.*, 7 (1/2) : 53-204, figs. 1-8, tabs. 1-7, text-pls. 1-9, pls. 1-17; Warszawa.

- OSMÓLSKA, H., 1973.- Tournaisian trilobites from Dalnia in the Holy Cross Mts. *Acta geologica Polonica*, 23 (1) : 61-81, figs. 1-2, tab. 1, pls. 1-2; Warszawa.
- PAPROTH, E., FEIST, R. & FLAJS, G., 1990.- Decision on the Devonian-Carboniferous boundary stratotype. *Episodes*, 13 (4) : 331-336, figs. 1-6.
- RICHTER, Rud. & RICHTER, E., 1926.- Die Trilobiten des Oberdevons. Beiträge zur Kenntnis devonischer Trilobiten. IV. *Abh. preuss. geol. L.-Anst.*, n. F., 99 : 1-314, figs. 1-18, tabs. A-C, pls. 1-12; Berlin.
- RICHTER, Rud. & RICHTER, E., 1951.- Der Beginn des Karbons im Wechsel der Trilobiten. *Senckenbergiana*, 32 (1/4) : 219-266, figs. 1-10, tabs. 1-2, pls. 1-5; Frankfurt am Main.
- SCHÖNLAUB, H.P., FEIST, R. & KORN, D., 1988.- The Devonian-Carboniferous boundary at the section "Grüne Schneid" (Carnic Alps, Austria) : A preliminary report. *Cour. Forsch.-Inst. Senckenberg*, 100 : 149-167, figs. 1-4, pls. 1-4; Frankfurt am Main.
- STRUVE, W., 1976.- Beiträge zur Kenntnis der Phacopina (Trilobita), 9 : *Phacops (Omegops)* n. sg. (Trilobita; Ober-Devon). *Senckenbergiana lethaea*, 56 (6) : 429-451, figs. 1-33, pls. 1-2; Frankfurt am Main.
- STRUVE, W., 1989.- *Rabienops evae* aus dem späten Ober-Devon des Rheinischen Gebirges. *Bull. Soc. belge Géol.*, 98 (3/4) : 335-342, figs. 1-3; Bruxelles.
- THOMAS, A.T., OWENS, R.M. & RUSHTON, A.W.A., 1984.- Trilobites in British stratigraphy. *Geol. Soc. London*, spec. Rep., 16 : 1-78, figs. 1-29; London.
- WALLISER, O.H., 1984.- Pleading for a natural Devonian-Carboniferous boundary. *Cour. Forsch.-Inst. Senckenberg*, 67 : 241-246, figs. 1-2; Frankfurt am Main.
- WEBER, V.N., 1937.- Trilobites of the Carboniferous and Permian system of the U.S.S.R., 1. Carboniferous trilobites. *Paleont. SSSR, Monogr.*, 71 : 1-160, figs. 1-78, tabs. 1-8, pls. 1-11; Leningrad and Moskow.
- XIANG, L.-W., 1989.- Trilobites. In: JI Q. *et al.*: The Dapoushang section, an excellent section for the Devonian-Carboniferous boundary stratotype in China : 41-43, 120-123, pls. 35-36; Beijing (Science Press).
- YUAN, J.-L., 1988.- Proetiden aus dem jüngeren Oberdevon von Süd-China. *Palaeontographica*, A201 (1/3) : 1-102, figs. 1-46, tabs. 1-4, pls. 1-15; Stuttgart.
- ZHU, ZH.-L., 1988.- Trilobites. In: YU CH.-M. (ed.) : Devonian-Carboniferous boundary in Nanbiancun, Guilin, China - aspects and records : 199-208, fig. 76, pls. 49-53; Beijing (Science Press).