



*INTERNATIONAL UNION OF
GEOLOGICAL SCIENCES
COMMISSION ON STRATIGRAPHY*

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**SUBCOMMISSION ON
DEVONIAN STRATIGRAPHY**

NEWSLETTER NO. 9

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I.U.G.S. Subcommittee on Devonian Stratigraphy

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The *Newsletter* appears biannually at approximately 6 month intervals in the spring and fall. This schedule will generally coincide with SDS meetings and should better serve the membership. Contributions may be sent to the Editor any time during the year for inclusion in the next issue. The initial printing of this issue is 125 copies with 78 mailed to titular and corresponding members, 13 to honorary members and friends and 3 to libraries.

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EDITORIAL NOTES

- The next issue will be mailed in fall 1993 in order that the membership may receive news of the Göttingen meeting in a more timely manner. Thereafter the *Newsletter* will appear biannually at approximately 6 month intervals in the spring and fall. This schedule will generally coincide with SDS meetings and should better serve the membership. Please send information you wish included in the *Newsletter* at any time during the year and every effort will be made to include this material in the next issue.
- The SDS reference data base is being updated periodically as articles are gleaned from published records and from member contributions. I have recently converted systems from IBM-PCs to Macintoshes and am in the process of converting the data base to FoxBase Pro on the Macintosh. The PC data base will be discontinued by the end of summer 1993, however, the data base will continue to be available on DOS disks in several formats readable by DOS based data bases, spreadsheets and text editors. All Macintosh formats are supported. Text files are arranged in reference format and can be searched with any basic word processor. Copies are free to members and friends. Indicate the computer system and choice of format or formats. The modified data base listing will be mailed to all SDS members in August 1993. If you wish a copy on disk, drop the Editor a note before 1 August.
- All members should have received notification and details of the combined SDS meeting / Gross Symposium to be held in Göttingen 4-7 August 1993. If not please contact the organizing committee of Prof. Michael House (SDS), Dr. Susan Turner (Australia), Dr. Alain Blicq (France), Dr. Tiiu Märss (Estonia), Dr. Peter Schultze (USA) or Dr. Otto Walliser (Germany).

GENERAL NEWS FROM MEMBERS AND FRIENDS BY REGION OF INTEREST

AUSTRALIA

- Michael HOUSE (The University, Southampton, UK), Thomas BECKER (Freie Universität Berlin) and Rex CRICK (Univ. Texas at Arlington) will join with Phillip PLAYFORD (Western Australian Geological Survey) in late June for work in the Upper Devonian of the Canning Basin. Gilbert Klapper (Univ. Iowa) will join the group in July before going on to additional work in the Cook Islands.
- Dr. Susan TURNER (Queensland Museum), co-leader (with Gavin Young, BMR, Canberra) of IGCP Project 328 Paleozoic Microvertebrate Biochronology and Global Marine/non-Marine Correlations, has supplied information about the second International Paleozoic Microvertebrate Symposium which will be held in Germany 4-7 August 1993. This meeting will incorporate the aims of IGCP project 328 and the marine/non-marine committee of the Subcommission for the Devonian System as well as providing an opportunity to celebrate the anniversary of the 90th birthday of Professor Walter Gross, a pioneer worker in Devonian fish and Paleozoic microvertebrates studies. Scientific sessions and workshops will be conducted from August 4th to 6th with an SDS field trip to Thuringia preceding the meeting 31 July - 2 August. The venue is now definitely in the Institut und Museum für Geologie und Paläontologie, University of Göttingen. Resulting from the meeting IGCP 328 hopes to publish a symposium volume and to prepare a first correlation table for Devonian microvertebrate assemblages. Please contact Dr. Susan Turner [617-846-1918 (fax)] for further details.

Dr. Turner also contributed the following news and information:

International Geological Correlation Programme 328: Palaeozoic Microvertebrate Biochronology and Global Marine/non-marine Correlations was awarded as an on-going project in 1991 for five years. Project leaders, elected at the first formal IGCP 328 meeting held at the 7th International Studies of Early Vertebrates meeting in Miguasha, Québec in June 1991, are Dr. Susan Turner FGS, formerly of Reading and Newcastle-upon-Tyne Universities, now Research Fellow at the Queensland Museum in Brisbane, funded by the Australian Research Council, and Dr. Gavin C. Young of the BMR, Canberra. An active group of around 200 participants from over 40 countries includes several UK participants in England, Wales and Scotland. Both professional and amateur paleontologists can contribute to this project by investigating Palaeozoic microvertebrates and their uses in correlating rocks and especially assisting in the correlation of marine and non-marine sequences.

Fish have always been uppermost as age indicators in the classic Old Red sequences where there is a dearth of most other fossils. The vertebrates through their microremains have the advantage of all microfossils in being redeemable from small hand specimens, including core and shot point samples. By their lifestyle fish were able to disperse into environments which other useful zone fossils, such as conodonts, couldn't reach, thus enhancing their use for marine/non-marine correlation. The microremains comprise scales, tesseræ, spines, teeth and tooth plates, otoliths, claspers and other modified denticles, and ornamental bones of the seven major groups of fishes:

Agnatha (jawless fishes), Chondrichthyans ("sharks"), Placoderms, Acanthodii, Actinopterygins (bony fishes), Crossopterygians (lobe fins) and Dipnoi (lungfish).

IGCP 328 plans to hold a meeting in conjunction with SDS on marine-non-marine correlation in Southampton in 1994. The 1992 annual meeting will be held at the Economic Significance of the Devonian Symposium (ISDSEOMR-92) being held in Guilin in September 9-12, 1992. A first international symposium on Palaeozoic Microvertebrates is to be held in Germany in mid 1993 in honour of Professor Walter Gross, one of the pioneers in this work. One of the key aims of the project is to produce a data base for all Palaeozoic fish which can aid sequence stratigraphy and biostratigraphical, palaeogeographical, palaeoenvironmental and basin analysis. More information can be obtained from Dr. Susan Turner, Fax number 617 846 1918, who edits "Ichthyolith Issues" the IGCP 328 Newsletter (Issues 1-9 available).

A list of recent articles supplied by Dr. Turner has been added to the SDS reference data base.

EUROPE & IBERIA

- Dr. Alain BLIECK (GRECO 7 du C.N.R.S.) kindly provided copies of the title page and contents of the book *Palaeozoic Vertebrate Biostratigraphy and Biogeography* which appear on page 22. The book is edited by John A. Long and published by Belhaven Press (1993). Dr. Blicck also provided a list of recently published papers having bearing on some aspect of the Devonian and a list of members and publications of the *Groupe Français du Paleozoique*. These papers have been added to the SDS reference data base.
- Drs. Ph. STEEMANS and M. STREEL (Services Associes de Paleontologie, Universite de Liege, Liege) have contributed a number of articles authored by members of their laboratories and which touch on some aspect of Devonian plants, miospores or acritarches in France and north Africa. These have been added to the data base.
- Dr. J. HLADIL provided the following address correction and additions

Dr. J. Hladil, Cesky geologicky ustav, (Czech Geological Survey), Malostranské n. 19, 118 21 Praha 1, Czechoslovakia. Telephone numbers for Dr. Hladil are: 42-2-523-351 (office), 42-2-352-523 (home), 42-2-521-280 (fax), 42-2-521-564 (fax).

Dr. Hladil was kind enough to point out that many articles listed in Newsletter #8 and attributed to him were supplied without his knowledge and that many of these articles either did not contain information about the Devonian or were unpublished reports owned by Czech oil or survey companies. The Editor's apologies to all. The list was contained in a package of information passed along with no documentation regarding its origin. Dr. Hladil also passed along additional references which will be added to the growing reference data base.

NORTH AFRICA

- Work to be published shortly by Drs. A. El HASSANI and A. TAHIRI (Institut Scientifique, Rabat, Maroc) contains much new information about the Paleozoic of the Moroccan Meseta and strengthens the view that all north of the Atlas fault zone is not Gondwanan.
- In October 1992 Rex CRICK (Univ. Texas at Arlington) returned to the Tafilalt Basin (Anti Atlas, Morocco) and sampled nautiloid faunas over the length and breadth of the basin. Some 400 Kg of Ludlow and Pragian through Famennian nautiloids were collected. The work was a success in large part because of the unselfish sharing of unpublished sections by Michael House, Thomas Becker and Otto Walliser and the superb and absolutely invaluable assistance of Drs. El Hassani and A. Tahiri (Institut Scientifique, Rabat, Maroc) both in and out of the field.

NORTH AMERICA

- Allen PEDDER (Institute Sedimentary & Petroleum Geology, Calgary) and Bill OLIVER (Smithsonian Institution) were invited by Christ SCOTESE (PaleoMap Project, Univ. Texas at Arlington) to share knowledge about Devonian coral distributions and details of paleogeography with the goal of realizing a better "fit" between observed coral distributions and Devonian reconstructions.
- Rex CRICK (Univ. Texas at Arlington) is organizing a revision of *The Treatise on Invertebrate Paleontology Part K - Mollusca 3* (Cephalopoda General Features, Endoceratoidea, Actinoceratoidea, Nautiloidea) scheduled for publication in 2000. The collected authorship of sections of the volume will be decidedly more international than the original volume.
- The fifth meeting of the North American Paleontological Convention was held in Chicago, Illinois (July 1992). The

Devonian was reasonably well represented as some 6% of the abstracts dealt with all or some part of the period. These abstracts and program summary are reproduced here beginning on page 23.

SOUTH AFRICA

- Dr. J.N. THERON provided the following information pertaining to various research projects on the paleontology of the Early- to Mid-Paleozoic marine sediments of the Cape Supergroup now in progress. References supplied by Dr. Theron have been added to the data base.

Initial work by J.N. Theron and J.E. Almond (Geological Survey) is focusing on new and previously collected marine trace fossil material of the ichnogenera *Cruziana*, *Asteriacites* and *Scolicia*. Various species illustrating an interesting variety of behaviour, have now been recorded from several levels in the Table Mountain and Bokkeveld Groups. 7 *Cruziana* from the lower (Emsian) part of the Bokkeveld Group represents an exceptionally rich Devonian trilobite ichnoconosis.

Current work on the marine invertebrate faunas from the Bokkeveld and Witteberg Groups includes revision of the trilobites (J.E. Almond), brachiopods (N. Hiller, Rhodes University), the systematics of the diverse, poorly-known bivalve fauna as well as a variety of minor groups, and the taphonomic analysis of the shelly assemblages. A comprehensive, well-illustrated atlas of the whole fauna is in preparation (J.E. Almond, N. Hiller and J.N. Theron).

Recent road excavations through the upper units of the Witteberg Group in the Eastern Cape have yielded numerous plant remains as well as a number of fish fossils. Detailed investigation by M.E. Anderson (JLB Smith Institute of Ichthyology), N. Hiller and F.F. Taylor (Rhodes University) have indicated a much greater diversity of plant remains than previously described from the Cape Supergroup, including specimens of the Late Devonian genus *Archaeopteris* and several enigmatic forms that bear no resemblance to anything as yet known from the south African Devonian. The fish remains include an acanthodian spine, a chondrichthyan, a lungfish and dermal plates of the antiarch (*Bothriolepis* and two arthrodires (a phyllolepid and groenlandaspid). The association is regarded as typical of the latest Devonian (Famennian) and the first record of this age in western Gondwana. The fauna invites comparison with Devonian occurrences of Australia and Antarctica.

Analysis in progress of the sedimentological evidence associated with the varied fossil assemblages indicates a shallow, near-shore marine environment, often prone to storm activity (J.N. Theron).

Petrographical and Diagenetic aspects of the thick Early- to Mid-Palaeozoic arenitic successions in South Africa (Cape Supergroup) and Israel (Nubian) are being compared by T. Weissbrod (Israel) and J.N. Theron.

A survey of microfossil assemblages from the Cape Supergroup is also being attempted by local and overseas workers. (J.N. Theron et al.)

SUBCOMMISSION ON DEVONIAN STRATIGRAPHY - 1993 MEETINGS

Your attendance is requested at the next Business Meeting of the Devonian Subcommittee to be held at 2.00 pm on Thursday 5th August 1993 at the Geologisch-Palaeontologisches Institute, Universität Göttingen, Goldschmidt Strasse, Göttingen, Germany, through the kind arrangements Professor O.H. Walliser and the Project Leaders of IGCP 238. The Business Meeting will be preceded at 9.00 the same day by a review of Devonian correlation problems related to decisions of SDS. Details of which are given on the next page. Details of the preceding field trip sent earlier.

AGENDA

1. Introduction and apologies for absence
2. Minutes of the previous meeting held at Guilin, 8 September 1992
3. Chairman's business
4. Review of work since Guilin meeting.
 - A. Base of Givetian and ICS Ballot for GSSP
 - B. Base of Famennian and ICS Ballot for GSSP
 - C. Base of Emsian and ICS ballot for GSSP

5. International Devonian correlation review
6. Devonian Marine-Nonmarine Correlation
7. Documentation of Devonian Bioevents
8. Devonian Global Sea Level changes
9. Devonian substages
10. Future tasks. Consideration of other Priorities
11. Membership
 - A. Responses from invited new members
 - B. Withdrawals from Membership
 - C. Election of new CMs
 - D. Election of new TMs

NOTE: at the Frankfurt meeting it was decided that all nominations for CMs and TMs should be received in writing by the Secretary before the meeting at which elections are proposed and that nominations should be accompanied by full relevant details of the interests and address of the candidate.

12. Reports
 - A. Marine/Non-Marine correlation
 - B. SDS Newsletter
 - C. South American Activities
 - D. Financial report
13. Future meetings

Arrangements are under discussion for the 1994 Business Meeting to be held in Moscow with a symposium on Devonian Sea Level Changes followed by a field trip to the Timan. Dates to be agreed. The Geological Society of London proposed meeting on Marine-Nonmarine correlation seems now deferred.

14. Any Other Business

1. Discussion Meeting on Devonian Correlation. This meeting will be held at 8.30 in the Geol. Pal. Institut, Göttingen. The following have indicated they will speak on their areas: HOUSE and others, Great Britain, BULTYNCK & STREEL, Ardennes, WEDDIGE, Germany, RACKI and others, Poland FEIST, Montagne Noire, GARCIA-ALCALDE, Cantabria, TURNER, Australia, WANG, China, KIRCHGASSER & OLIVER, Eastern North America. **WOULD SPEAKERS PLEASE SEND A SHORT ABSTRACT TO SUSAN TURNER, Queensland Museum, PO Box 3300, South Brisbane, Australia, SOON AS POSSIBLE.** Would members unable to attend who are responsible for other areas please send to the Secretary, Pierre Bultynck, a one or two page statement with references well before the meeting for circulation at the meeting. Please note that there may be additional speakers and about a quarter of an hour will be available for presentation. It would be most helpful if speakers could bring one or two page summaries with references for distribution at the meeting.

2. Proposed meeting in the Timan 1994. Summary of responses from SDS members regarding possible field trip to the Timan 1994:

Planning to attend: BRICE, BULTYNICK, GARCIA-ALCALDE, FEIST, HOUSE, KIRCHGASSER, OLIVER, SANDBERG, TURNER, TURNAU, YU CHANG MIN. Possibles: BECKER, BLIECK, LADIL, MAWSON, STREEL, TALENT, WEDDIGE. Discussions are in progress with TM Menner and others and it is hoped that details will be available at the meeting.

3. Newsletter. Items for the Newsletter should be sent without delay to the Editor, Prof. Rex Crick, Department of Geology, UTA Box 19049, The University of Texas at Arlington, Arlington, TX 76019-0049.

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PROPOSAL FOR THE GLOBAL STRATOTYPE SECTION AND POINT (GSSP) FOR THE FRASNIAN—FAMENNIAN BOUNDARY.

CONCERNING: Proposal for the Global Stratotype Section and Point (GSSP) for the Frasnian - Famennian boundary.

FROM: Subcommittee on Devonian Stratigraphy

TO: ICS and IUGS for acceptance and ratification

30 October 1992

(1) The Subcommittee on Devonian Stratigraphy (SDS) wishes to recommend an horizon and locality for a basal Famennian GSSP at the base of Bed 32 of the Upper Quarry at Coumiac, Montagne Noire, France. Two candidate sections were on a preliminary Ballot held on 31 March 1991, Coumiac and Steinbruch Schmidt (Germany). This gave a 59% majority vote in favour of Coumiac, but not the 60% required under the rules. A Final Postal Vote naming only Coumiac was held on 1st July 1991 with the following result. In favour; Chlupac, Dineley, Feist, Garcia-Alcalde, Hou, House, Oliver, Pedder, Richardson, Talent. Against, Bultynck, Sandberg, Street, Walliser, Yolkin, Ziegler. No replies counted under the Rules as Yes votes; Hünicken, Klapper, Yu. This gave 13 votes in favour of Coumiac and 5 against, or 70% of Titular Members in favour of Coumiac.

(2) In earlier phases of the deliberations of the SDS potential GSSP's had been considered in Belgium, Germany, France, Morocco, P.R. China, and the USA. It had been agreed that a boundary at the base of the Lower *triangularis* conodont Zone would be preferred.

(3) In accordance with the requirements for submission to the ICS of a candidate for a GSSP, statements required under the *Guidelines and Statutes* are given in the attached Appendix together with full details of the section and its locality with full illustration (Appendix Figures 1-11).

Michael House

M.R.House, Chairman

CONCERNING: Proposal for the Global Stratotype Section and Point (GSSP) for the Frasnian - Famennian boundary.

FROM: Subcommittee on Devonian Stratigraphy

TO: ICS and IUGS for acceptance and ratification

APPENDIX

1. Motivation for choice of boundary level

Historically several different levels have been used to define the base of the Famennian. In the type area for the naming of the stages in southern Belgium, precise documentation in recent years has been given to a new reference section replacing the now-infilled classic section in the Senzeilles railway cutting (Bultynck *et al.* 1988). Largely resulting from work in the first quarter of this century in Germany another boundary has been that based on the entry of the goniatite *Cheiloceras* in the pelagic realm. In the latter half of this century the considerable growth of conodont studies has led to much refinement of the biostratigraphy. But the level taken as the base of the Famennian has varied between a level at the base of the *crepida* Zone down to the base of the Lower *triangularis* Zone. The need for an international definition has become urgent. The Subcommittee has given careful consideration to which level is most appropriate for international correlation and it decided, at a meeting in Washington in 1989, that a GSSP should be sought in relation to the base of the Lower *triangularis* conodont Zone. The Final Postal Ballot was on that basis.

2. Correlation of the proposed boundary level

The boundary proposed represents perhaps the best correlated horizon in the Devonian. A review of more than 30 international sections has been presented by Sandberg, Ziegler, Dreesen & Butler (1988) including localities in North America and Europe. Documented correlation is established in North Africa (Becker, House & Ashouri 1988), China (Jae *et al.* 1989) and Australia (Becker *et al.* 1992). The boundary corresponds to the extinction of the conodonts *Ancyrodella* and *Ozarkodina* and the loss of all but a few species of *Icriodus*, *Ancyrognathus*, *Palmatolepis* and *Polygnathus* (Sandberg *et al.* 1988). There is a well-known extinction among goniatites of the Gephuroceratidae and Beloceratidae and the record for both conodonts and goniatites at Coumiac demonstrated this well. The last of the brachiopod Atrypidae occurs just below the boundary level (Becker *et al.* 1992). At the GSSP 78% of all known Upper Frasnian trilobite species are represented. Of special importance is the youngest documented occurrence of Dalmanitidae, Odontopleuridae, Harpidae and Aulacopleurinae which all disappear at the base of the end-Frasnian Upper Kellwasser Bed level of Bed 31g. There is a major spore change in the Belgian sequence (Vanguestaine *et al.* 1983) and an extinction of corals (Sorauf & Pedder 1986, Scrutton 1988) and stromatoporoids (Stearn

1987) has also been well documented. A changeover of benthonic ostracod faunas across the boundary at Coumiac has been published (Lethiers & Feist 1991).

3. Motivation for the choice of the stratotype

It has been recognised by the Subcommittee that, in general, Devonian sections in pelagic realm facies are more likely to be complete than those in the neritic facies. The pelagic facies forms a better basis for biostratigraphic precision needed for international correlation. In particular the conodont and goniatite records are better in those facies. That is not to imply that there are not facies rich in other groups, spores and brachiopods, for example, which are very important for correlation, but it is normally easier to correlate into such sections secondarily from primary sections in the pelagic facies. In the last resort the Subcommittee concentrated on two such sections, one at Steinbruch Schmidt (Sandberg *et al.* 1990, Schindler 1990) and the other at Coumiac (Feist (Ed.) 1990).

The sequence chosen shows a complete succession through the early Frasnian to late Famennian. It is unfaulted and has no tectonic problems. The beds are approximately vertical. Equivalent sections can be found elsewhere in the area. The rocks are of low grade metamorphism and thermal maturity (CAI 2-3) and comprise an homogeneous pelagic calcilitite sequence without marly or shaly interbeds. There is a complete zonal succession with a rich fossil content, especially of the index groups of conodonts, ammonoids, trilobites, tentaculites and ostracods. Detailed documentation is provided later of this (Figures 5-11). Geochemical work has been published across the boundary at Coumiac (Goodfellow *et al.* 1989, Grandjean *et al.* 1989, Grandjean *et al.* 1992, Jnachimski & Buggisch 1992) and currently other investigations are being undertaken. Magnetostratigraphic work indicates the area was remagnetized during the Permian.

4. Location of type section

The recommended GSSP is above the Upper Quarry at Coumiac, near Cessenon, Montagne Noire, France (Figure 1). The section is situated in the southeastern Montagne Noire, Département Hérault, District of Cessenon (topographic sheet 1:25000, No. 2544 E Murviel-les-Beziers; Lambert's coordinates: $x = 130,375$, $y = -658,55$). It is adjacent to the southeastern border of the disused upper marble quarry (UQ) of Coumiac at 175 m WSW of Les Grange farmhouse, at about 1.5 km NE of Cessenon village. It can be reached easily by a path running up the hill from Les Grange farm house near to the road D 136 from Cessenon to St Nazaire-de-Ladarez.

Protection: The ground is owned by the commune of Cessenon and is already protected being part of a water supply area. Conservation and protection of the section has been assured by communal and departmental officials. Free access for scientists is confirmed.

5. Description of type section

The Upper quarry at Coumiac comprises most of the Frasnian and the succession continues above the quarry to the proposed GSSP. Higher is a succession to the late

Famennian and above (Figure 3). The sequence (Figures 4,5) is one of pelagic micrites and calcilitites, mostly red tinted and represents a well-bedded sequence the bedding probably related to Milankovitch-Band climatic control during sedimentation. The sequence has been described in published accounts (Becker *et al.* 1989, Klapper 1989, House *et al.* 1985). The section is shown in Figure 4. Distinctive is Bed 31g, which is

correlated with the Upper Kellwasser Kalk, and shows a hypoxic grey calcilitite to calcarenite above which is the most marked faunal boundary. But both Bed 31g and 32a are pelagic in their character.

The faunal description is given in a series of diagrams submitted to the SDS and included in Feist (Ed.) 1990 by group specialists. Figure 6, submitted by R.T. Becker and M.R. House gives the goniatite ranges. Figure 7 gives the conodont data of G. Klapper giving critical zonal definition and showing the remarkable extinctions at the boundary. Figure 8 by R. Feist shows the range of trilobite taxa; high correlative value of the latest Frasnian prior to the Upper Kellwasser level is best documented by phylogenetic lineages of *Palpebralia* and *Cryphops* which are both characterized by unidirectional trends of eye reduction and whose representatives are known from distant areas such as the Rhenish Slate Mountains, the Harz Mountains, as well as the Canning Basin of Western Australia (Feist 1991). The brachiopoda and bivalve preliminary records of C. Babin and P.R. Rachebeuf are given in Figure 9. Rich homocetid faunas are recorded on Figure 10 determined by M. Tryols-Massoni. Ostracod data of F. Lethiers is given on Figure 11 where more than 30 different species are recognised in the topmost beds; among the benthonic forms, the Frasnian/Famennian boundary is characterized by a major extinction since 65% of all recorded taxa disappear there (Lethiers & Feist 1991). It bears evidence of an extraordinary breadth of faunal representation which enables correlation into regimes with better spore and acritarch records. The SDS views this documentation as the best it has achieved for any of the levels it has recommended.

6. Relationship to marker horizons

The main sedimentary marker of the horizon is the top of the distinctive level known in Germany as the Upper Kellwasser Kalk. Black hypoxic limestones occur at several levels around the Frasnian/Famennian boundary but the Upper and Lower Kellwasser Kalk levels are two which represent an acme of the spread of a distinctive facies and which are in many sections precisely constrained by conodont dating.

In parallel with the work of the SDS in recent years has been the recognition of an important extinction event near the Frasnian/Famennian boundary. Some of these extinctions were listed in section 2 above. The recommendations of the Subcommittee for a GSSP fall at the level thought to mark the acme of extinctions which is at the base of the *Lower triangularis* Zone. The most precise documentation for this (Becker *et al.* 1989) has been followed by data assembled for the Subcommittee and shown here on Figures 6-11. Following especially the work of Sandberg *et al.* (1988) this level has been widely traced internationally.

There has, however, been much debate on the cause of the the sedimentary perturbation

represented by the Upper Kellwasser Kalk. The matter cannot be said to be resolved. Indeed, some members of the Subcommittee earlier took the view that a more accurate boundary might be chosen away from the sudden faunal and sedimentary change at the base of the Lower *triangularis* Zone but in the end, the ease of international correlation based on the faunal changes led to this boundary being recommended.

Three main groups of hypotheses have been invoked to explain the faunal and sedimentary changes around the base of the Lower *triangularis* Zone. Firstly, causes related to a bolide impact or impacts (McLaren & Goodfellow 1990, Sandberg *et al.* 1988). Secondly, events, probably tectonic, producing a spread of anoxic conditions on continental shelves associated with ocean overturn (Buggisch 1991, Wilde & Berry 1984). Thirdly, a peak of cold climatic conditions, resulting in a rise of the pycnocline (Copper 1986).

Whatever the cause may be, the Subcommittee is of the opinion that the hypoxic perturbations below the base of the Lower *triangularis* Zone have resulted in a considerable faunal changeover and an horizon which may be correlated internationally with perhaps more precision than any other in the Devonian. It is in the light of this view that the Subcommittee wishes to recommend Coumiac for the GSSP to define the base of the Famennian Stage.

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Michael R. House & Raimund Feist
October 1992

Figure 1. Maps showing the position in the Montagne Noire of south-eastern France of the proposed GSSP for the base of the Famennian at the Upper Quarry at Coumiac (inset map A). Modified from Becker *et al.* (1989).

Figure 2. The local stratigraphy and goniatite and conodont zones around the boundary in the Montagne Noire. From Feist (Ed.) 1990.

Figure 3. Plan and profile of the succession in the Upper Quarry at Coumiac showing the position of the proposed GSSP at the boundary between Bed 31 and Bed 32. Modified from House *et al.* (1985).

Figure 4. The detailed succession of beds around the proposed GSSP boundary at the junction of Bed 31g and Bed 32a in the Upper Quarry at Coumiac.

Figure 5. The sequence between Beds 2 and 39 in the Upper Quarry at Coumiac showing bed numbering and bed thicknesses. From Feist (Ed.) 1990.

Figure 6. The succession of goniatites known from Bed 23 to Bed 39 in the Upper Quarry at Coumiac. From Becker *et al.* (1989).

Figure 7. The conodont record from Beds 23 to Bed 39 in the Upper Quarry at Coumiac. Data of G. Klapper *in* Feist (Ed.) 1990.

Figure 8. The trilobite record from Bed 23 to Bed 39 in the Upper Quarry at Coumiac. Data of R. Feist *in* Feist (Ed.) 1990.

Figure 9. Record of brachiopods and bivalve molluscs in the Upper Quarry at Coumiac. Data of C. Babin and P.R. Rachebouf *in* Feist (Ed.) 1990.

Figure 10. Record of homoctenids in the Upper Quarry at Coumiac. Data of Truyols-Massoni *in* Feist (Ed.) 1990.

Figure 11. Record of ostracoda in the Upper Quarry at Coumiac. Data of F. Lethiers *in* Feist (Ed.) 1990.

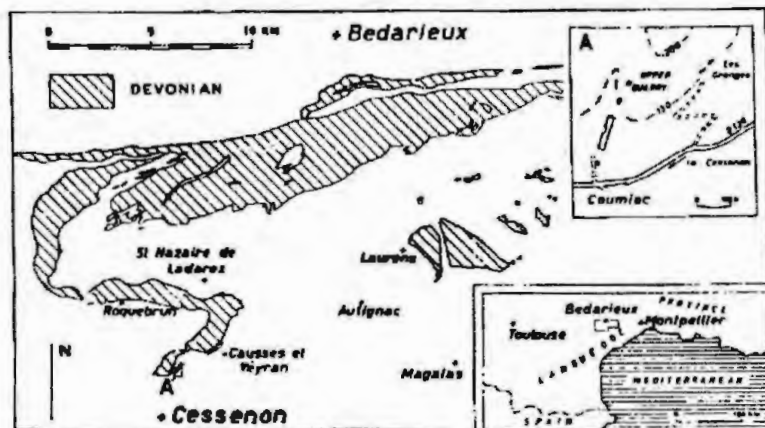


Figure 1. Maps showing the position in the Montagne Noire of south-eastern France of the proposed GSSP for the base of the Famennian at the Upper Quarry at Coumiac (inset map A). Modified from Becker *et al.* (1989).

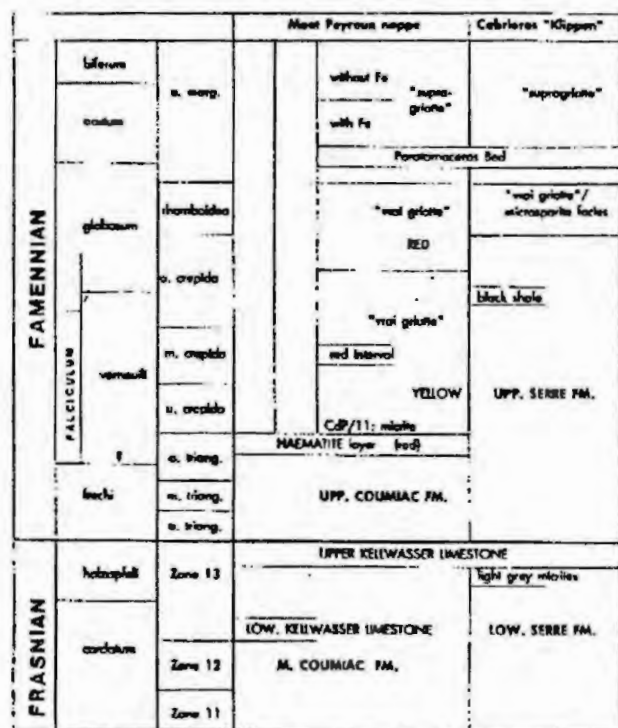
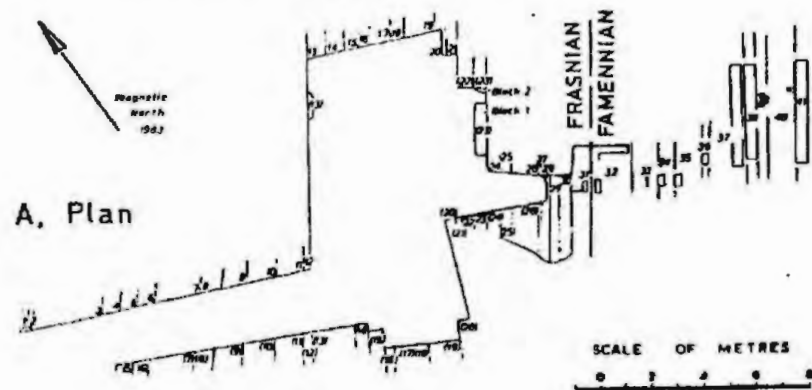


Figure 2. The local stratigraphy and graptolite and conodont zones around the boundary in the Montagne Noire. From Feist (Ed.) 1990.

COUMIAC: Upper Quarry



A. Plan

B. Profile

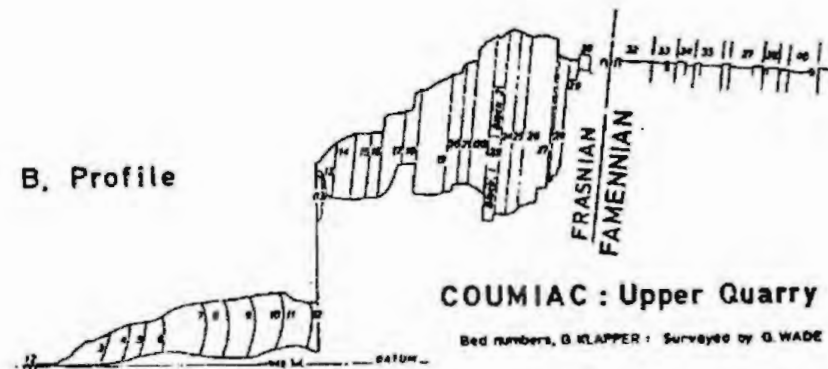


Figure 3. Plan and profile of the succession in the Upper Quarry at Coumiac showing the position of the proposed GSSP at the boundary between Bed 31 and Bed 32. Modified from House *et al.* 1985).

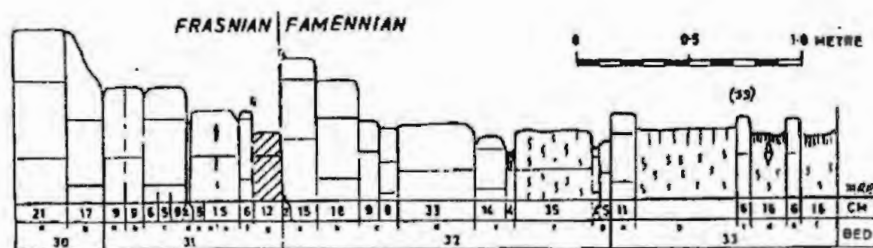


Figure 4. The detailed succession of beds around the proposed GSSP boundary at the junction of Bed 31g and Bed 32a in the Upper Quarry at Coumiac.

COUMIAC: Upper Quarry

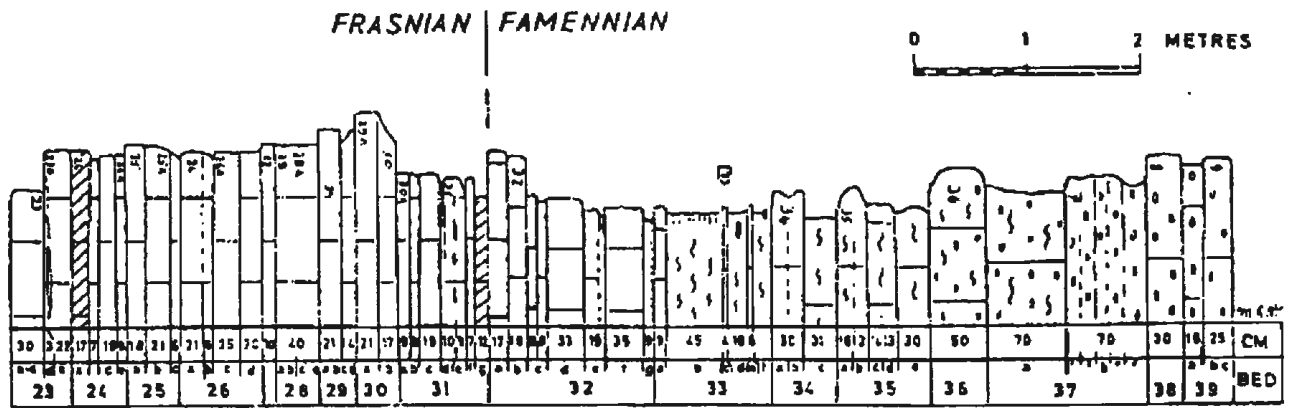


Figure 5. The sequence between Beds 2 and 39 in the Upper Quarry at Coumiac showing bed numbering and bed thicknesses. From Feist (Ed.) 1990.

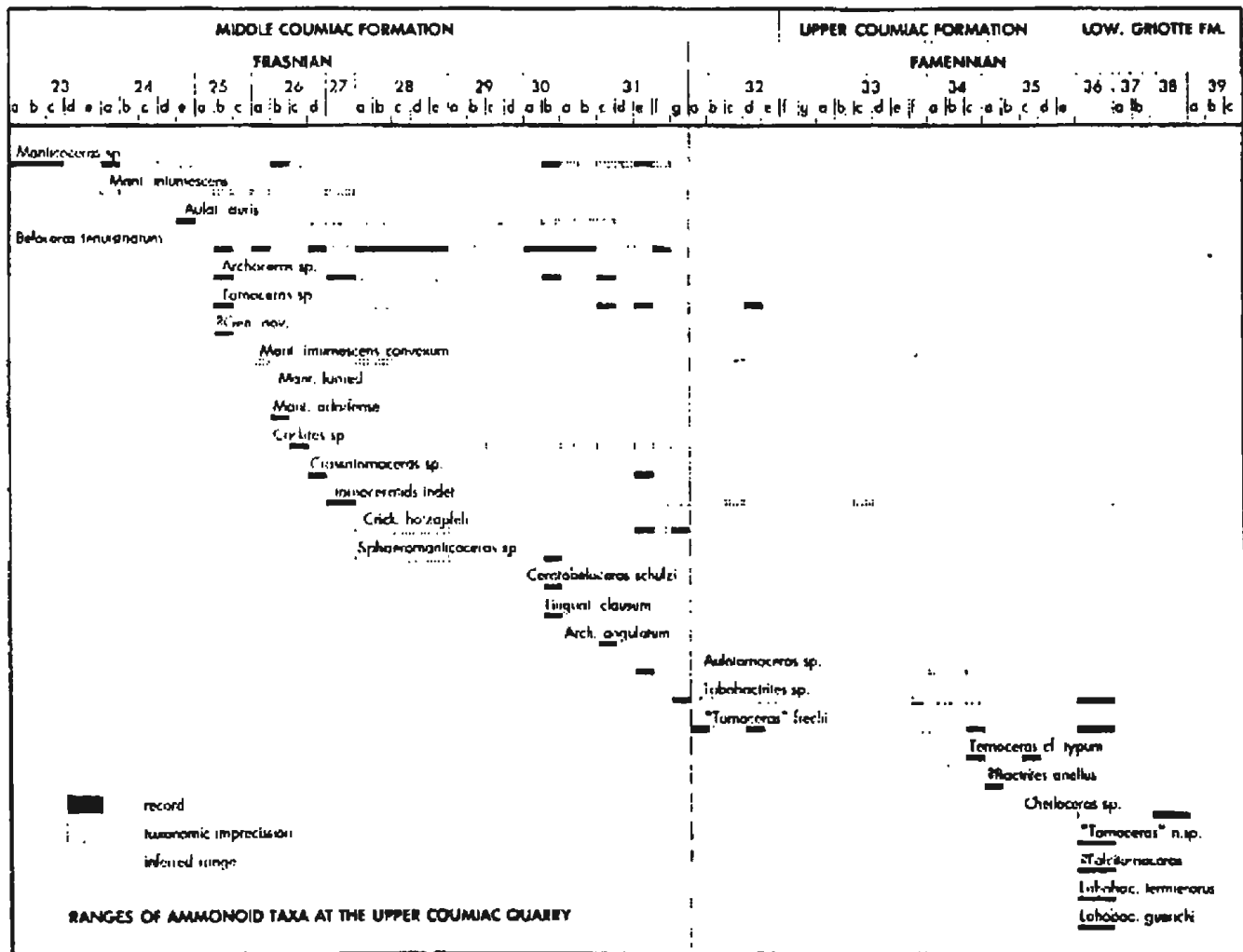


Figure 6. The succession of goniatites known from Bed 23 to Bed 39 in the Upper Quarry at Coumiac.

COUMIAC: Upper Quarry

conodonts

- Ancyrognathus triangularis* Youngquist
- A. asymmetricus* (Ulrich & Bassler)
- Ancyrodella curvata* (Branson & Mehl) late from
- Palmatolepis* sp. indet.
- P. kireevae?* Ovnatanova
- Polygnathus webbi* Stauffer
- P. pacificus* Savage & Funai
- Icriodus alternatus* Branson & Mehl
- I. symmetricus* Branson & Mehl
- Palmatolepis bogartensis* (Stauffer)
- P. hassi* Müller & Müller form 4
- Polygnathus decorosus* Stauffer
- Ancyrodella nodosa* Ulrich & Bassler
- P. cf. P. brevis* Müller & Youngquist
- P. winchelli* (Stauffer) [= *P. subrecta* Miller & Youngquist]
- Ancyrognathus amana* Müller & Müller
- A. sp. indet.*
- P. cf. P. rhenana* Bischoff
- Mehlina* sp.
- P. rhenana*
- P. n. sp. T.*
- P. lodinensis* Pölsler
- A. uliquitus* Sandberger et al. [one specimen]
- P. triangularis* [one specimen]
- Palmatolepis triangularis* Sannemann
- Polygnathus brevilaminus* Branson & Mehl.
- P. n. sp.*
- Branmehla* sp.
- P. aff. "delicatula delicatula"* Ziegler, 1962
- P. prorhomboidea*
- Palmatolepis minuta minuta* Branson & Mehl
- P. tenuipunctata* Sannemann
- P. quadrantinodosalobata* Sannemann
- Ancyrognathus sinelaminus* (Branson & Mehl)
- P. cf. P. regularis* Cooper
- P. crepida?* Sannemann [one specimen]
- Polygnathus glaber glaber* Ulrich & Bassler
- Pelekysgnathus planus* Sannemann

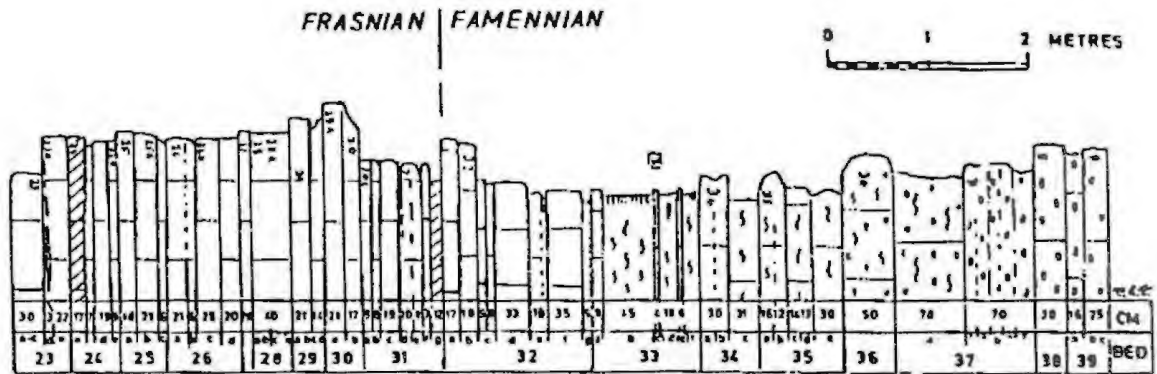
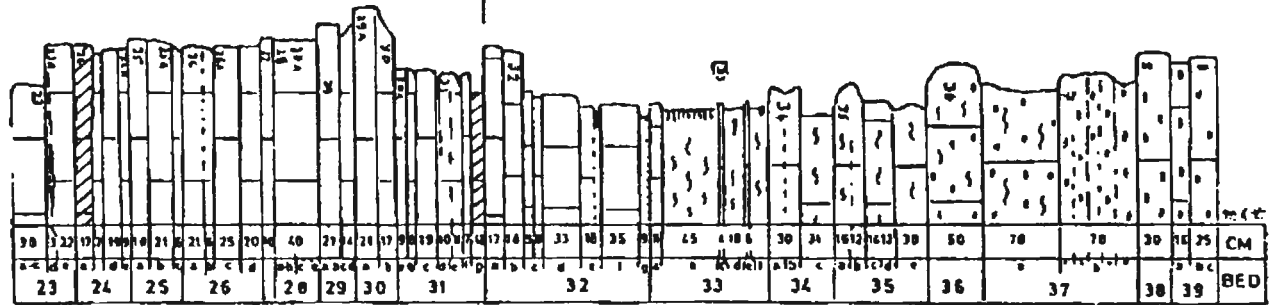


Figure 7. The conodont record from Beds 23 to Bed 39 in the Upper Quarry at Coumiac. Data of G. Klapper in Feist (Ed.) 1990.

COUMIAC: Upper Quarry

FRASNIAN | FAMENNIAN



- Harpes neogracilis* —
- Radiaspis* n.sp. —
- Scutellum costatum* —
- Pteroparia coumiacensis* —
- Cyphaspis stigmatophthalmus* —
- Palpebralia palpebralis* —
- Cryphops acuticeps* —
- Cryphops* aff.*acuticeps* —
- Palpebralia* aff.*nodannulata* —
- Harpes neogracilis* group —
- Cryphops acuticeps* group —
- Cyphaspis* aff.*stigmatophthalmus* —
- Palpebralia* aff.*palpebralis* —
- Palpebralia brecciae* —
- Cryphops* n.sp. —
- Radiaspis* sp. —
- Bradocryphaeus* sp. —
- Nephranops* sp. —
- Nephranops incisus dillanusi* —

Figure 8. The trilobite record from Bed 23 to Bed 39 in the Upper Quarry at Coumiac. Data of R. Feist in Feist (Ed.) 1990.

Bed n°	31e1: <i>Strophodontacea</i> sp. 1 (4vv) " <i>Striatochonetes</i> " sp. 1 (3vv) Rhynchonellid undet. (2ca) <i>Buchiola</i> sp. ? <i>Cypricardina</i> sp.
21c: " <i>Striatochonetes</i> " sp. 1 (1vv, 1dv) <i>Dualina</i> sp.	31e2: <i>Strophodontacea</i> sp. 1 (7vv, 2ca) " <i>Striatochonetes</i> " sp. 1 (1vv, 3dv) Rhynchonellid undet. (2ca) " <i>Cyrtina</i> " sp. (1vv) <i>Buchiola</i> sp. ? <i>Cypricardina</i> sp. Pectinid undet.
21e: ? <i>Cypricardina</i> sp. <i>Buchiola</i> sp.	31f: " <i>Lingula</i> " sp. " <i>Striatochonetes</i> " sp. 1 (3vv, 1dv) Bivalve undet.
23a: <i>Buchiola</i> sp.	32b: Bivalve undet.
24b: cf. <i>Monelasma</i> sp. (1dv)	32c: <i>Buchiola</i> sp.
26b: Pectinacea undet.	32d: <i>Buchiola</i> sp. Bivalve undet. (large shells)
26d: " <i>Striatochonetes</i> " sp. 1 (1vv) <i>Strophodontacea</i> sp. 1 (2vv)	35: Bivalve undet. (large shells)
28a: <i>Buchiola</i> sp.	
31a: " <i>Striatochonetes</i> " sp. 1 (1vv) Rhynchonellid undet. (1ca)	
31b: cf. <i>Skenidium</i> sp. (1vv) <i>Strophodontacea</i> sp. 1 (1vv) " <i>Striatochonetes</i> " sp. 1 (1dv) <i>Buchiola</i> sp. <i>Leptopora</i> undet.	
31c: cf. <i>Skenidium</i> sp. (1vv) <i>Strophodontacea</i> sp. 1 (1ca) Rhynchonellid undet. (2ca) <i>Buchiola</i> sp. ? <i>Kralovna</i> sp. (1) <i>Leptopora</i> undet. (1) ? <i>Cypricardina</i> sp.	

vv = ventral valve
dv = dorsal valve
ca = complete shell

Figure 9. Record of brachiopods and bivalve molluscs in the Upper Quarry at Coumiac. Data of C. Babin and P.R. Rachebouf in Feist (Ed.) 1990.

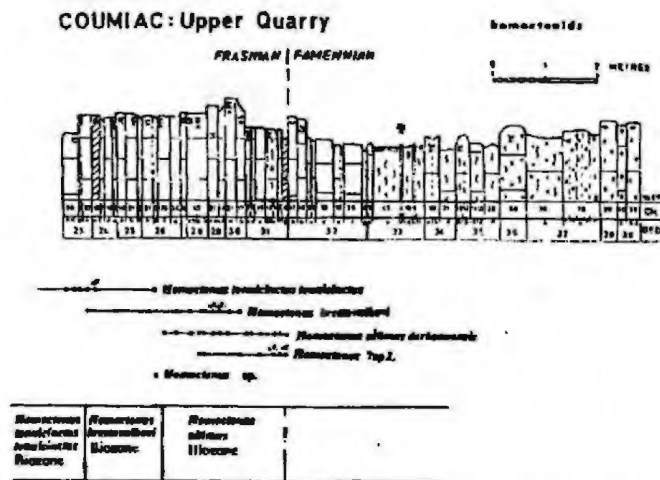


Figure 10. Record of homotertoids in the Upper Quarry at Coumiac. Data of Truyols-Masson in Feist (Ed.) 1990.

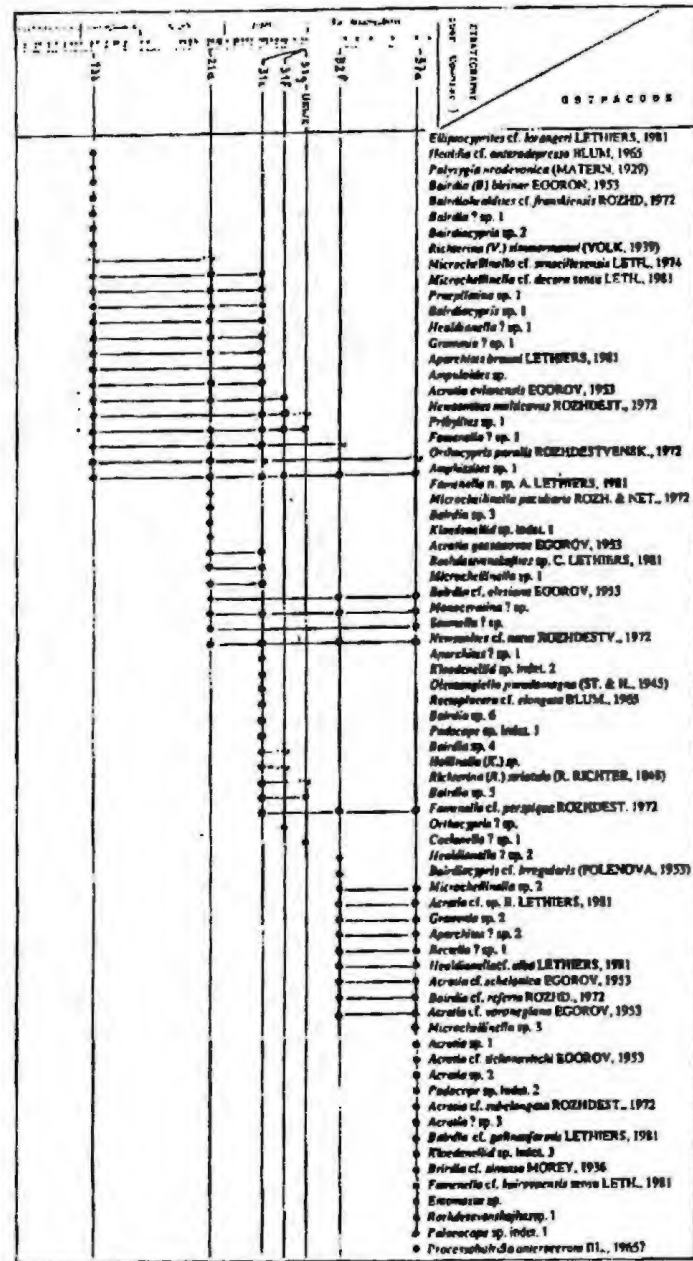


Figure 11. Record of ostracoda in the Upper Quarry at Coumiac. Data of F. Lethiers in Feist (Ed.) 1990.

INTERNATIONAL UNION OF GEOLOGICAL SCIENCES
(IUGS)
INTERNATIONAL COMMISSION ON STRATIGRAPHY

Subcommission on Devonian Stratigraphy

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[Bureau elected August 1992]

CONCERNING: Proposal for the Global Stratotype Section and Point (GSSP) for the Eifelian - Givetian boundary.

FROM: Subcommission on Devonian Stratigraphy

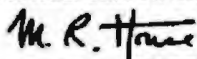
TO: ICS and IUGS for acceptance and ratification

15 March 1993

(1) The Subcommission on Devonian Stratigraphy (SDS) wishes to recommend an horizon and locality for a basal Givetian GSSP. The Final Postal Ballot naming only the base of Bed 123 at Jebel Mech Irdane, Morocco was held on 30 March 1992. The voting in the final ballot was as follows: Yes votes; Bultynck, Chlupáč, Dineley, Feist, Garcia-Alcalde, Hou, House, Menner, Morzadec, Oliver, Sandberg, Streef, Talent, Yolkin, Ziegler. No replies counted under the Rules as Yes votes; Hünicken, Klapper, Pedder, Walliser, Yu. Vote against; Richardson. This gave 20 votes in favour and 1 against and shows 95% of Titular Members in favour of Mech Irdane.

(2) In earlier phases of the deliberations of the SDS potential GSSPs had been considered in Belgium, Germany and Morocco. It had been agreed that a boundary related to conodont lineages would be used. Formal submissions had been received for three localities in Morocco (Ou Driss, Bou Tchrafine and Mech Irdane). At a Business Meeting held in Morocco on 4 December 1991, following field visits to these three localities, all proposals other than Mech Irdane were withdrawn and this was unanimously accepted by the TMs present. It was decided that the entry of *Polygnathus hemiansatus* (as defined by Plate 4, figs 2a,b in the Appendix C) in Bed 123 be the reference marker.

(3) In accordance with the requirements for submission to the ICS of a candidate for a GSSP, details regarding the motivation and factual data on the locality and horizon are given in Appendices A-C.



M.R. House, Chairman

CONCERNING: Proposal for the Global Stratotype Section and Point (GSSP) for the Eifelian - Givetian boundary.

FROM: Subcommission on Devonian Stratigraphy

TO: ICS and IUGS for acceptance and ratification

APPENDICES A-C

Appendix A comprises the statements required under the *Guidelines and Statutes* for Submission to ICS of a Global Stratotype section and Point (GSSP). It refers where appropriate to details in later appendices, namely, Appendix B, taken from Walliser (Ed. 1991) is a document by Bultynck, Walliser & Weddige giving the critical conodont criteria for the boundary and Appendix C, taken from Walliser (Ed. 1991), which is a document by Walliser describing the proposed section at Jebel Mech Irdane.

APPENDIX A

1. Motivation for choice of boundary level

Historically several different levels have been used to define the base of the Givetian. In the type area for the naming of the stages in southern Belgium, the boundary has for many years been taken at the base of the Givet Limestone which falls within the conodont *ensensis* Zone, but some have placed the lowest 5-6 m of dark-bluish limestone in the Couvinian (Bultynck 1987). Another boundary has been the entry of *Stringocephalus*, which appears above the base of the Givet Limestone in the type area and in the Loogh Formation in the Eifel (Struve 1982). Largely resulting from work in the first half of this century in Germany another boundary has been that based on the Zone of *Cabrieroceras crispiforme*, but that is in pelagic facies. It is now known that this goniatite species group occurs in the *kockelianus* Zone and ranges up into the the *ensensis* Zone.

In parallel with the SDS work on international correlation about this level has been the recognition of an important hypoxic sedimentary perturbation near the Eifelian/Givetian boundary which has been named the Kačák Event (House 1985). It is represented by black shales. Their onset has been named the *otomari* or *rouvillei* Event (Walliser 1985). Also the upper limit of the black shale intercalation has turned out to correspond to a global here provisionally named Basal Givetian Event. The Subcommission has sought a level which is close to these events, and to the base of the Givet Limestone, but which can be defined in terms of a lineage of conodont evolution. The recommended level of the Subcommission lies at a faunal marker level just below the top of this sedimentary perturbation. It became clear after the published work of Bultynck (1987) that Morocco offered many advantages for stratotype definition because of the range of facies developments over the desired interval and the excellent exposures and faunal representation.

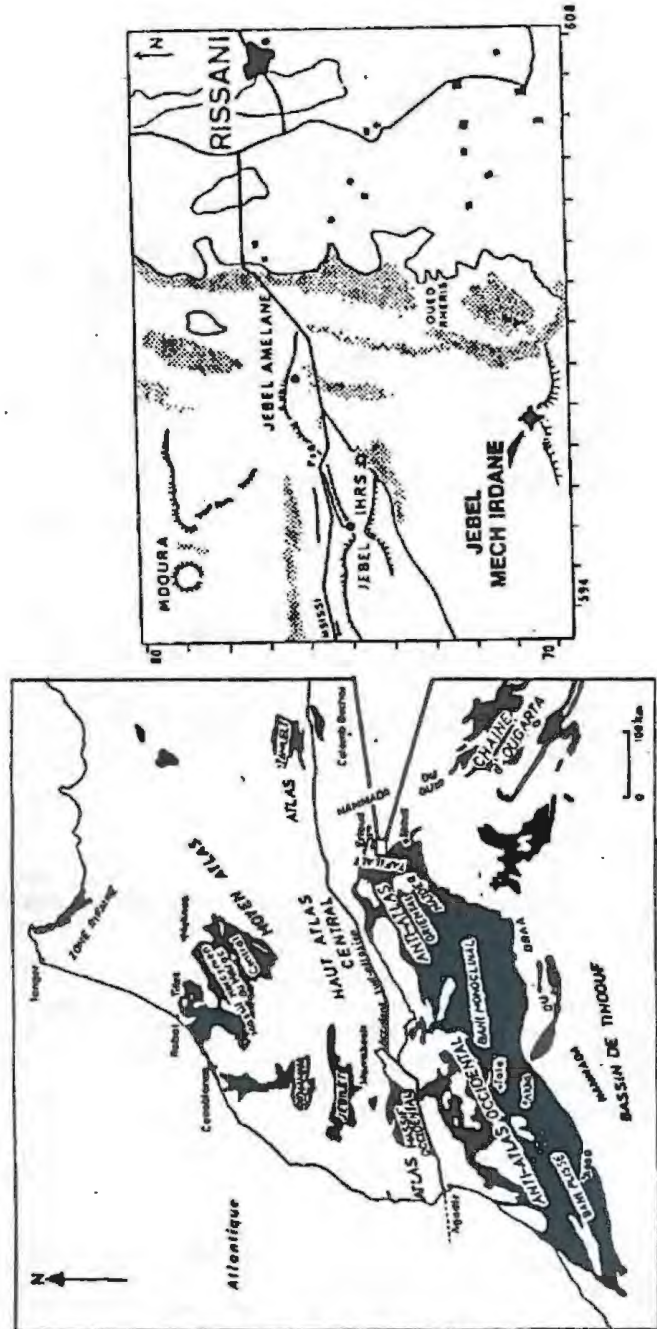


Figure 1. Maps showing the position of the proposed GSSP for the base of the Givetian SW of Rissani, Tafilalet, Morocco.

2. Correlation of the proposed boundary level

The boundary proposed represents the level at which *Polygnathus pseudofoliatus* changes to *Polygnathus hemiansatus* by a change from a steep outer anterior platform margin to an obliquely declining one and in particular the new form recognised as *Polygnathus hemiansatus*; this level, of Bed 123 at Mech Irdane, is at about the Freilungen/Ahbach boundary in the Eifel. The *Stringocephalus* entry level in the Eifel lies at the overlying Ahbach/Loogh boundary, thus the range of the true *Stringocephalus* is wholly within the Givetian under the proposed definition. The main development of black limestones in the Odershausen Formation of the eastern Rhenish Schiefergebirge lies below the new boundary, as does much of the Kačák shale of the Srbsko Formation in the Prague Basin; these units correspond to the entry of *Nowakia otomari* and mark the *otomari* Event (Walliser 1985) or Kačák Event (House 1985), and hence to the *crispiforme* (= *rouvillei*) Zone, the top of which represents a marked extinction event for goniatites (House 1985, 1993, Becker & House 1991). This event would be between beds 119 and 123 in the Mech Irdane section. The proposed level appears to be just above the entry of *Maenioceras undulatum* Holzzapfel Group and hence close to the base of the widely used *Maenioceras* Stufe of the goniatite terminology but now to be used excluding the *Cabrioceras crispiforme* levels.

For spores it is the entry of the *Geminospora lemurata* which is a very important tie into terrestrial facies although subsequently the species is very long ranging. No spores have yet been obtained from the Mech Irdane section, but *Geminospora lemurata* occurs in Algeria (Blumendjel *et al.* 1988). In the Eifel this spore enters in the Möllert division of the Ahbach. The entry has been widely used elsewhere in spore-bearing regions as a guide to the Givetian (Richardson & McGregor 1986, Streef *et al.* 1987) and this usage is unaltered by the definition proposed.

Because of the wide range of faunal and floral changes at the proposed level, it is considered that the international correlation possible at the entry of *Polygnathus hemiansatus* is superior to any other level considered by the Subcommittee for this GSSP.

3. Motivation for choice of the stratotype

It has been the view of the Subcommittee that sections in pelagic realm facies are likely to be more complete than those in neritic facies and it has sought potential stratotype sections which are in pelagic facies with good conodont records and with as many other faunal and floral groups represented as possible. Following work by Bultynck and Hollard (1980) it was clear that sections in the Tafilalet area of Morocco were much superior to those known elsewhere. Three proposals were received for potential stratotypes there, at Jebel Ou Driss (Bultynck 1989, in Walliser (Ed.) 1991, p.17-23), Bou Tcharfine (Bultynck & Walliser in Walliser (Ed.) 1991, p.49-57) and Jebel Mech Irdane (Walliser (Ed.) 1991, 25-29, included as Appendix C). Jebel Ou Driss, although a thicker section, and containing more neritic elements than Jebel Mech Irdane, was poorer in goniatites. Bou Tcharfine raised problems because there are no limestone beds intercalated in the corresponding upper part of the *otomari* black shales and the cliff exposures are less accessible. Jebel Mech Irdane, in the event, was preferred because of the greater abundance of pelagic and hemipelagic faunas and excellence of the sections above and below the boundary. Whilst a spore record is not available, it seems probable

that this will be forthcoming in readily correlatable localities in view of the records in southern Algeria (Boumendjel *et al.* 1988). In addition the section at Mech Irdane provides high potential for other fossil groups, especially trilobites and ostracods, but also pelecypods gastropods, thin-shelled brachiopods and even corals.

4. Location of type section and point

The recommended level for the GSSP to define the base of the Givetian is at Jebel Mech Irdane, 25 km SSW of Erfoud and 12 km SW of Rissani (Figure 1). The proposed level is at the base of Bed 123 (1:100,000 Carte du Maroc, Feuille NH-30-XX-2, Erfoud, Lambert's coordinates: $x = 599,2, y = 470,6$). The ridge there gives continuous exposure. The locality is about 6 km from the metalled Mssisi road west of Rissani (Figure 1) and easily reached by four-wheel drive vehicles.

Protection. The area is isolated and unlikely to be threatened in any way. Access is available to scientists but authorisation papers should be sought from the Bureau of Mines, Rabat.

5. Description of type section

The ridge of Jebel Mech Irdane is 4 km long and exposes a full succession from the Emsian into the Frasnian. Exposure is complete and each bed may be examined in numerous places along the ridge. The actual proposed stratotype sequence is on the gently-sloping western side of a knoll which gives easy access to all beds. Around the GSSP the section is primarily one of pelagic calcilitites and micrites with shales at the Kacak Event level. The detailed faunal record of the section is given in Appendix C (taken from Walliser (Ed.) 1991) where the detailed succession is shown on p.28.

6. Relation to marker horizons

The proposed boundary coincides with the upper boundary of the *crispiforme* Zone and is near to the entry of *Stringocephalus* which has been the Belgian standard. However, it is now recognised that a sedimentary hypoxic perturbation is recognisable preceding the proposed definition. This *otomari* or Kačák Event has been increasingly recognised as important in the last few years and it is now recognised in Germany, Spain, North Africa and Central Asia. One of us (MRH) thinks it may be represented in the Old Red Sandstone by the Sandwich and Achanarass Fish beds of Scotland. Neither conodont nor goniatite evidence places it precisely in eastern North America, but the acme of the event may be the deepening and entry of black shales associated with the Chittenango Shale of the early Hamilton Group in New York. Very little work has been done on the precise documentation of faunas across the boundary in other regions, especially when compared with the interest generated by the Frasnian/Famennian extinction event. Nevertheless it does appear to be an extinction event of some importance and, as has been shown, it falls within definitions used in Belgium and Germany hitherto. However it is to be expected that the precision of the new conodont data will enable it to be placed with accuracy in many areas of the globe. The Subcommission recommends the new GSSP and anticipates it will do much to stabilise terminology and encourage further study internationally.

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Michael R. House & Otto H. Walliser
January 1993

CONODONT BASED PROPOSAL
FOR THE
EIFELIAN-GIVETIAN BOUNDARY

by F. Bultynck, O. H. Walliser & K. Weddige

It is proposed to base the definition of the Eifelian-Givetian Boundary on the entry of a definite form of the conodont species *Polygnathus hemiansatus* BULTYNCK 1987.

The *Polygnathus hemiansatus* lineage

Appearance

This lineage derived most probably from the *Polygnathus pseudofoliosus* Group. The critical point in the development from *Polygnathus pseudofoliosus* WITTEBANDT 1966 to *P. hemiansatus* is the transformation from a steep outer anterior platform margin to an obliquely declining one.

Varieties

Within the succeeding development of *P. hemiansatus* the outer adcarial trough in front of the genalation point is flattening progressively. Variations of this flattening can be used for the morphotypic differentiation of *P. hemiansatus*. Two extremes are obvious.

One is represented for instance by the holotype (BULTYNCK 1987: pl. 7 fig. 26). It demonstrates a flat convex expansion of the anterior outer platform which is strongly bowed outwards, thus forming a spoon-like shelf. This spoon-like structure can even be stronger pronounced in late varieties (fig. 4 e) and less pronounced in early ones (fig. 4 d). A further characteristic feature is a distinct constriction of the outer platform just posterior to the genalation point. There, its upper margin forms a high "shoulder" which arises above the general platform surface.

The contrary variation also shows a flat slope of the anterior outer platform. The shelf structure, however, is narrower - without a distinct spoon-like expansion, a constriction of the outer platform, or a prominent "shoulder" (fig. 4 c). It occurs at the beginning of the range of *P. hemiansatus*, and is - in our samples from pelagic facies realms - already accompanied by the first specimens of the *P. hemiansatus* morphotype with moderately developed spoon-like structure (sensu fig. 4).

Ancestors

Ancestors of *P. hemiansatus*, which are still present with the just mentioned early *P. hemiansatus*

APPENDIX B

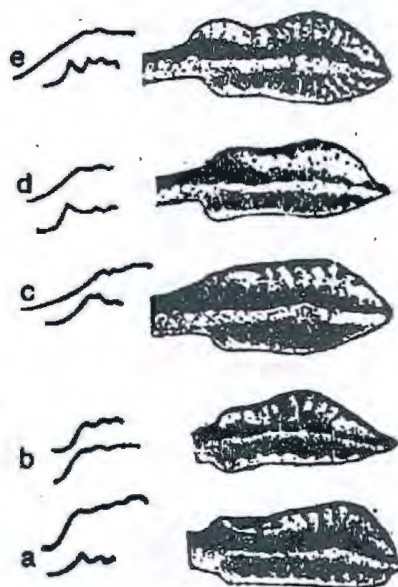


Fig. 4: Morphotypes of the *Polygnathus pseudofoliosus* - *Polygnathus hemiansatus* lineage.

a + b: *P. pseudofoliosus* with steep outer anterior platform margin; in b, the outer anterior adcarial trough is already less narrow than in a.

c - e: *P. hemiansatus* with obliquely declining outer anterior platform margin forming a spoon-like structure; the latter becomes gradually more evident from c to e; d coincides with the holotype.

morphotypes, have a steep outer anterior platform margin (figs. 4 a, b). They are included in the *P. pseudofoliosus* Group of which typical representatives are characterized by deep and narrow anterior adcarial troughs. Immediate ancestors, however, already demonstrate a slight expansion of the outer anterior platform (e.g. in BULTYNCK 1987: pl. 2 fig. 5). Also the slope of the anterior outer margin of such *P. pseudofoliosus* specimens tends to become shallower, thus indicating the transition to real *P. hemiansatus* types. Formerly, these transitional forms have partly been regarded as early varieties of *P. hemiansatus* (e.g. BULTYNCK 1987: pl. 7 fig. 22; WEDDIGE 1988: range chart of Freilingen Fm.).

Reference sections

The *P. hemiansatus* evolution can be demonstrated in two sections of Southern Morocco ("Jbel Ou Driss" and "Jbel Mech Irdene") as well as in Germany ("Blauer Bruch"). In the Ou Driss Section, the two earliest morphotypes (sensu fig. 4 c, d) occur in sample ODE 7-11 and specimens similar to the holotype in sample ODE 7-13. In the Mech Irdene Section, specimens of *P. hemiansatus* are first recognized in sample 123, equivalents of the holotype in samples 125, 127, and 129, and youngest morphotypes with extremely developed "spoon" in sample 131. In the Section of the Blauer Bruch, *P. hemiansatus* has its inception within the uppermost part of the Odenhausa Formation: in sample a of collection WALLISER, in sample D2 of collection WEDDIGE. Underlying less calcareous limestones contain poor conodont faunas but one fragment of a very early *P. hemiansatus* representative has been recorded from sample D1 of WEDDIGE. The first "spoon morphotypes" occur within the first massive limestone bed of the overlying *discolides* Limestones (sample d of WALLISER, sample C4 of WEDDIGE).

Comparisons

Accompanying indicative conodonts

After our intensive studies of different conodont sequences in Morocco and Central Europe we decided to prefer the lineage of *P. hemiansatus* instead of that of *Polygnathus ensensis* ZIEGLER & KLAPPER 1976 which formerly has also been taken into consideration as a boundary index (e.g. WEDDIGE 1989). In the studied sections, however, the latter species is distinctly less frequent than *P. hemiansatus*. That is the reason that the understanding of the evolution of *P. ensensis* is not yet as progressed as that of *P. hemiansatus*. Till now, it has been recognized that the typical representatives of *P. ensensis*, the anterior platform of which are strongly serrated on both sides, are relatively frequent in levels with "spoon morphotypes" of *P. hemiansatus*.

Further correlative indications are given by conodonts of the genus *Icriodus*, particularly of the lineage *Icriodus regularis* BULTYNCK 1970 to *Icriodus obliquimarginatus* BISCHOFF & ZIEGLER 1957. Transitional forms of both species and early morphotypes of *I. obliquimarginatus* occur with the earlier representatives of *P. hemiansatus*. But the more typical morphotypes of *I. obliquimarginatus*, which are characterized by oblique posterior denticles, accompany the "spoon morphotypes" of *P. hemiansatus*.

Geographic distribution

The main advantage of *P. hemiansatus* as an index of the Eifelian-Givetian Boundary in comparison with other conodont taxa is its world-wide geographic distribution.

Occurrences are known from Morocco, Tafilalet, Ma'der (BULTYNCK 1987, 1989; WALLISER 1988) Spain, Cantabrian Mts. (GARCIA-LOPEZ 1987) France, Montagne Noire, Pic de Bissous (WALLISER 1990) Belgium, Ardennes, Corvin (BULTYNCK 1970; pl. 45 fig. 5) Germany, Eastern Rhenish Mts., Blauer Bruch (WEDDIGE 1989; WALLISER & WEDDIGE, in prep.) Germany, Eifel (WEDDIGE, in prep.) China, Guangxi Province (ZIEGLER & WANG 1985; BULTYNCK 1987) Australia, North Queensland, Broken River (MAWSON & TALENT 1989)

Interfacial correlative aspects

Event stratigraphy

In respect to event stratigraphy the proposed boundary is somewhat below that global event which is characterized by the change from black *otomari* Shales and Limestones to lighter "normal" pelagic facies. In the section Blauer Bruch, the entry of *P. hemiansatus* is within the upper still black coloured Odenhausa Level, 15 cm below the lighter, predominantly grey basal (nearly *discolides* Limestones which obviously represent a gradual transition from dark to light sedimentation. This coincidence quite well with the entry of *P. hemiansatus* in Morocco, where it is positioned 11 cm below the mentioned event boundary in Section J, Mech Irdene.

Traditional Eifelian-Givetian boundaries

In the pelagic realm the traditional Eifelian/Givetian boundary has been drawn at the base of the Odenhausa Formation (eastern Rheinische Schiefergebirge) or Kacsk Formation (Bohemia), respectively, thus the traditional pelagic boundary coincides with the *otomari*- or Kacsk Event, which most probably happened at the boundary of the *lockhartensis/ensensis* conodont zones.

In the neritic realm the traditional boundary has been drawn distinctly higher in the sequence. In the Eifel, it is regarded within the lowermost Ahabach Formation the top of which has marked the Eifelian-Givetian boundary till now, e.g. by the entry of the typical *Stringocephalus*. Even higher is the traditional Couvinian-Givetian boundary in the

Ardenes whereas the actually proposed level is positioned distinctly lower, i. e. most probably in the lower part of the uppermost Couvianian Hanozet Formation (Co 2d) and about 42 m below the base of the Givet Limestone. Both boundaries appear to be characterized by the inceptions of typical representatives of *P. hemiansatus* ("spoon morphotype"), of *P. ensensis* (with strongly "serrated" anterior platform), and of *I. obliquimarginatus* (with oblique posterior margin). Within these highest Eifelian or lower Givetian levels of the neritic facies realm, however, the documentation of the conodonts, particularly of the two *Polygnathus* species, is aggravated by the wide-spread increase of reefal biostromal limestones, mostly barren of conodonts. On the contrary, the neritic limestones around the "hemiansatus level" originated even in open-marine facies. Therefore, they are usually productive in indicative conodonts.

Conclusion

Because of the better documentation in regard to the conodont stratigraphy and of further stratigraphic correlations, we gave preference to the conodont based "hemiansatus level" instead of the levels of traditional boundaries.

Moreover and finally, we want to stress our main intention that the new definition of the Eifelian-Givetian boundary must be orientated at that global event that marks a "natural" middle of the Middle Devonian.

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Section JEBEL MECH IRDANE (Mapsheet Erfoud, NH-30-XX-3)

by O.H. Walliser

Introduction

The section is situated in the Tafilalet region, 25 km SSW of Erfoud, 12 km SW of Riassani. It is near by the western track to Tabhet el Rhir.

The Jebel Mech Irdane is part of an East-West orientated, synclinal structure, the Emsian to Upper Devonian sequences of which form the 4 km long and 1,5 km broad Jebel.

Most parts of the sequences, especially the Middle Devonian ones, are excellently exposed and can be traced for hundreds of meters or found at numerous places.

The sequence under discussion, i.e. the late Eifelian and early Givetian, belongs to the pelagic to hemipelagic facies realm. It is relatively fossiliferous with orthocone cephalopods and goniatites. Tabulate and rugose corals are present, but rare. Very abundant is the pelocypode "*Panetia*". A large collection of this fossil group has been made in order to examine its biostratigraphical value. Conodonts are frequent, i.e. hundreds of specimens per kilogramme. Because the SDS decided to fix the boundary on the basis of the conodont sequence, conodonts have been studied intensively.

M: 220 cm limestones of the Middle *Po. varcus* Zone. In the uppermost 50 cm, there have been recorded *Maenioceras terabrutum*, *Pharcoceras amplexum* and conodonts from the Middle *varcus* Zone as well as from the upper *M. asymmetrica* Zone.

K + L: 220 cm limestones, at the base and top layers with "*Terabrutula pumilio*".

J: 1070 cm platy and nodular limestones; lower *Po. varcus* Zone and upper part of the *Po. ensensis* Zone.

I: 37 cm dark shales with intercalated marly limestones and nodular limestones; lower part of the *Po. ensensis* Zone.

G + H: 800 cm platy or nodular limestones, in the upper part, i.e. the *Po. kockelianus kockelianus* Zone, *Cabrioceras crispiforme* is frequent; in the lower part *Subanarcestes macrocephalus* is abundant.

F: 280 cm dark platy limestones with *Fidelites* and *Pinctes*.

E: 1040 cm nodular limestones with *Sellanarcestes*.

D: Marls with intercalated marly limestone beds.

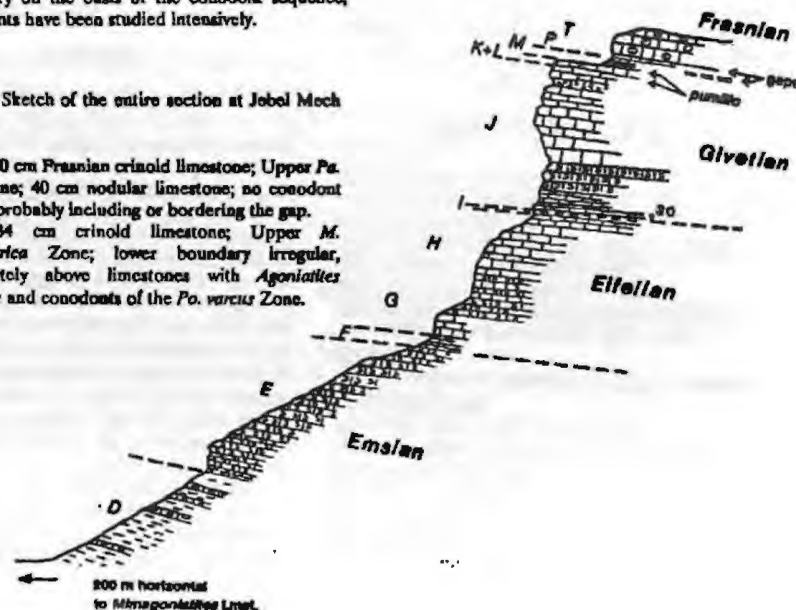
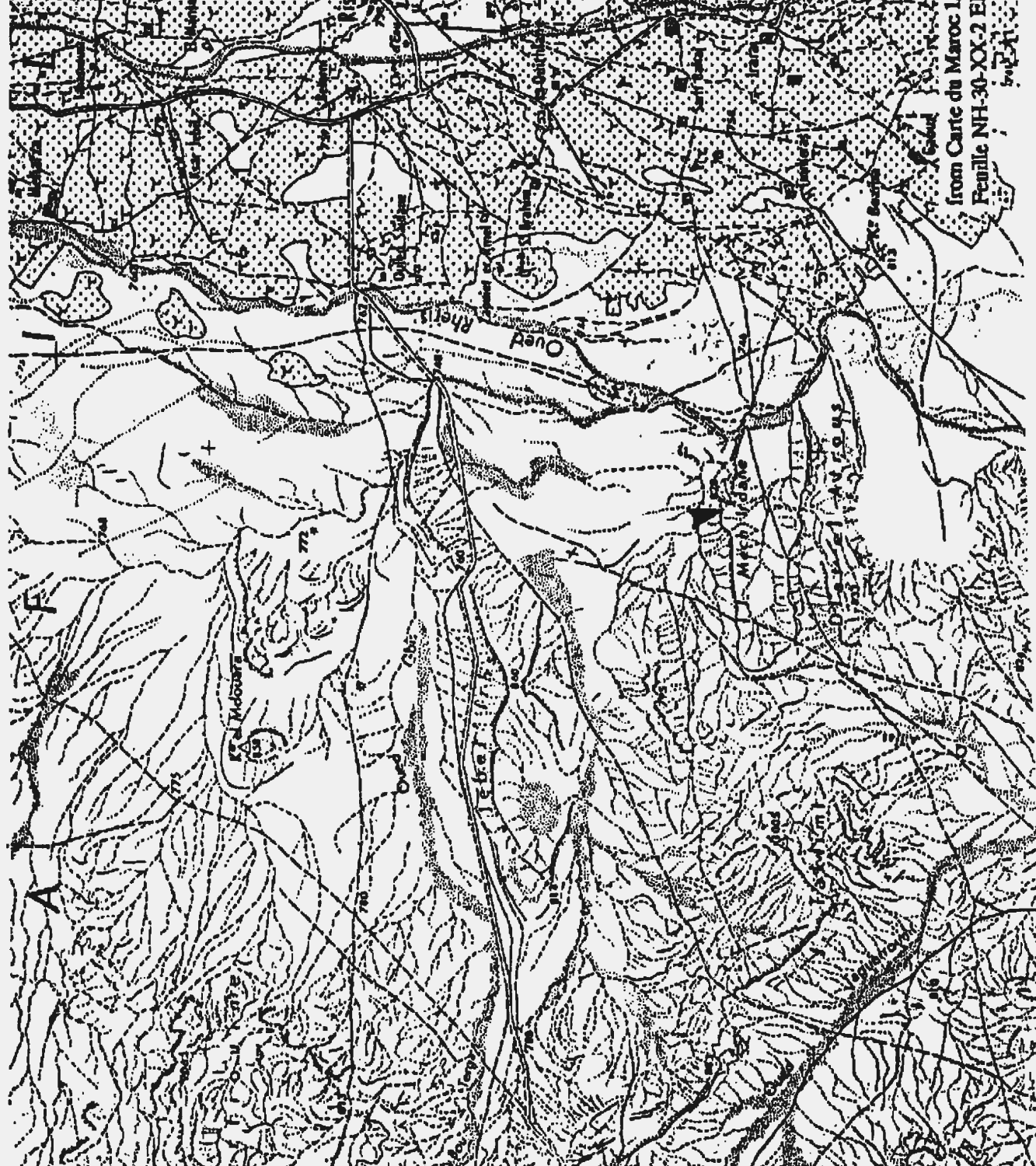


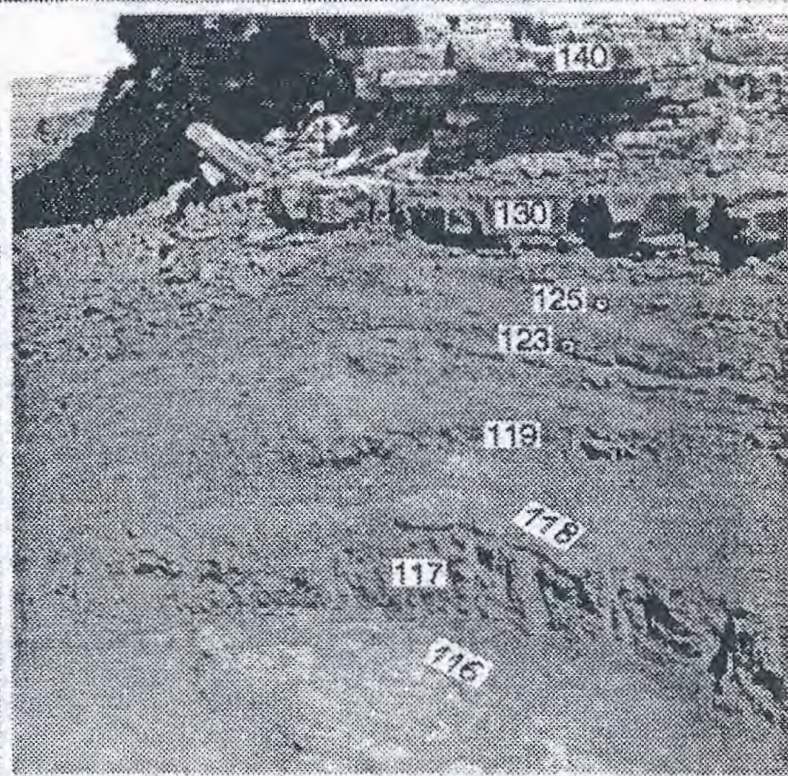
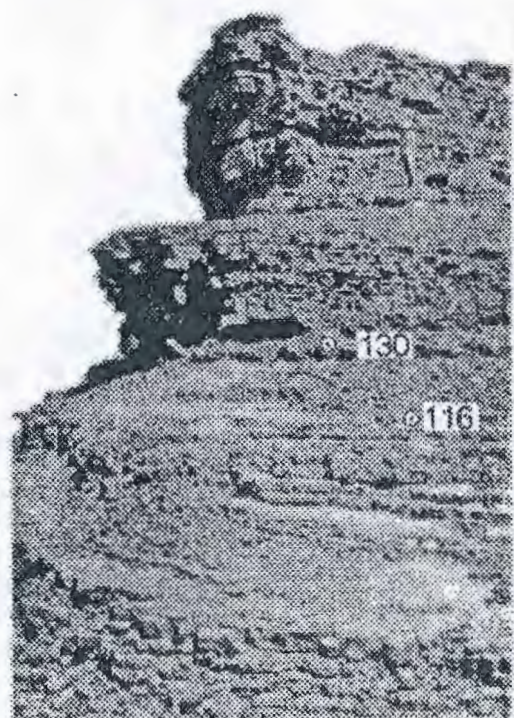
Fig. 1: Sketch of the entire section at Jebel Mech Irdane.

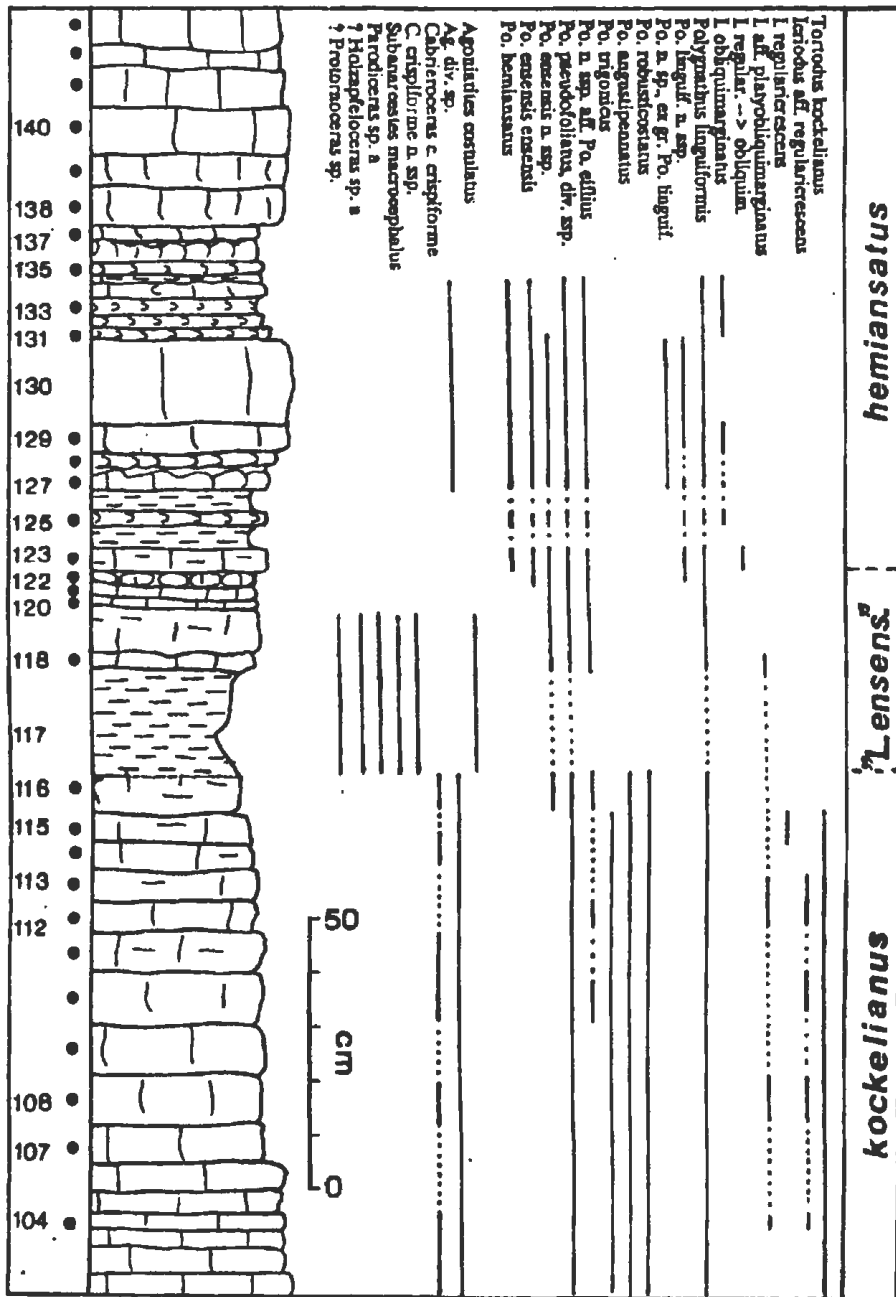
T: 250 cm Frasnian crinoid limestone; Upper *Po. gliger* Zone; 40 cm nodular limestone; no conodont record; probably including or bordering the gap.

P: 34 cm crinoid limestone; Upper *M. asymmetrica* Zone; lower boundary irregular, immediately above limestones with *Agoniatites discoides* and conodonts of the *Po. varcus* Zone.



from Carte du Maroc 1
Feuille NH-30-XX-2 E
1:50,000





Conodont succession

Because *Po. hemiansatus*, the proposed index species for the Eifelian/Givetian boundary, belongs to the evolutionary lines of the *Po. effilius*/*Po. pseudofolius* and *Po. ensensis* groups, only they are figured in the attached plates. All other taxa will be figured in the mentioned forthcoming publication.

In the list of the fauna, page 28, one major faunal change is visible between layers 116 and 118. In layer 116 *Po. robusticosatus* and *Po. angusticostratus* disappear. *T. kockelianus* has already in layer 115, and *Po. trigonus* in layer 113 its last record. In comparison with other sections, it is assumed that *T. kockelianus* should still be present in layer 116. Its absence may be due to the rarity of this species in section Meck Irdano. A further characteristic taxon for the *T. kockelianus* Zone is that morphotype of *Po. pseudofolius* which coincides with the holotype by having gently downward bent anterior ends of the platform margins (e.g. the specimen pl. 1, fig. 1); the last occurrence of this morphotype is in layer 116.

Then, in layer 118 are only those morphotypes of *Po. pseudofolius* present, in which the anterior end of the platform margin has a steep slope; of course, they also occur already before. In layer 118 occur also for the first time morphotypes which lead to the higher up occurring *Po. ensensis*. The characteristic feature of this morphotype is the absence of denticulation at one of the anterior platform margins. At the other margin the denticulation is very weak; they are here mentioned as *Po. ensensis* n. sp. Typical morphotypes of *Po. ensensis*, i.e. those with strong serration at both anterior platform margins, occur not earlier than in layer 122.

Also in layer 122, the first tendency in the evolution to *Po. hemiansatus* can be recognized. This taxon then occurs immediately above in layer 123. In the

following layers this taxon shows a further evolution to a more pronounced spoon-like structure at the anterior end of the outer platform margin and, in addition, a general widening of the adcarinal trough. This indicates an evolution to a feature as it is characteristic for *Po. ensensis*.

In summarizing the evolution of the *pseudofolius/effilius* group, we can emphasize two points: (1) The boundary between the *T. kockelianus* Zone and the *Po. ensensis* Zone is a very remarkable boundary. It coincides with a globally recognizable facies change as well as with the traditional Eifelian/Givetian boundary in the pelagic realm. (2) The mentioned evolutionary lines show a gradual development, thus indicating that there is no recognizable gap in the succession despite the intercalation of the dark shales in the lower part of the *Po. ensensis* Zone. Thus, the gradual morphological development within one evolutionary line provides us with an excellent possibility to recognize the boundary under the condition of a high time resolution.

The evolution of some other taxa also help to recognize the boundary and to trace it into other facies realms. Thus, e.g. the gradual evolution from *I. regulariterosus* to *I. obliquimarginatus* can be exactly correlated with the above-mentioned changes. A certain morphotype of *I. obliquimarginatus* has its first occurrence in the same layer just as *Po. hemiansatus*.

Goniatites

As to be seen in the list of the fauna, page 28, goniatites have been recorded. They are not as abundant and not as numerous in taxa as in the section Bos Tcharfina. In contrast to that section, they are not pyritized at the section Jebel Meck Irdano.

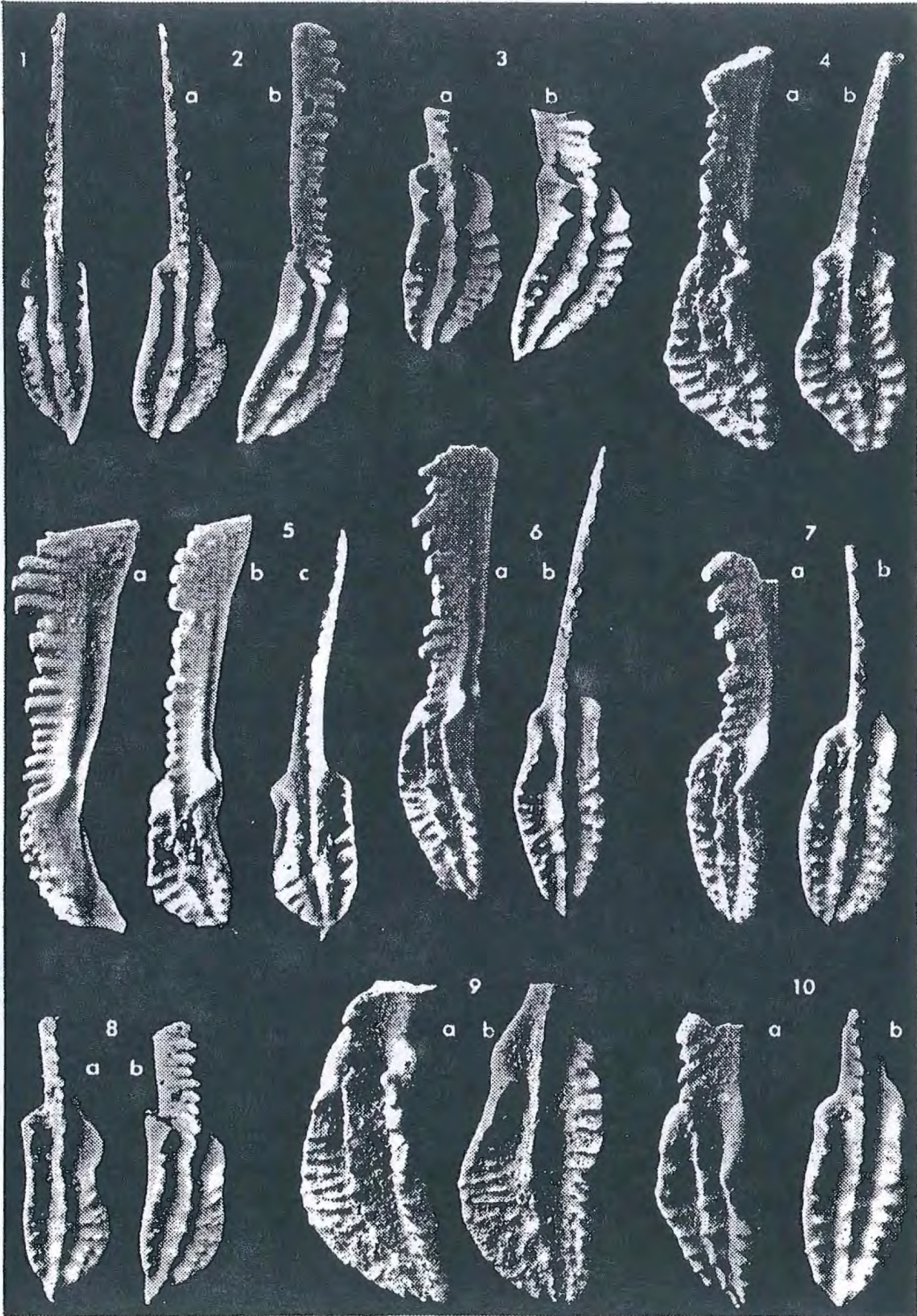
Plate 4

Variation of certain pterygote species in the lowermost layer (123) with *Po. hemiansatus*.

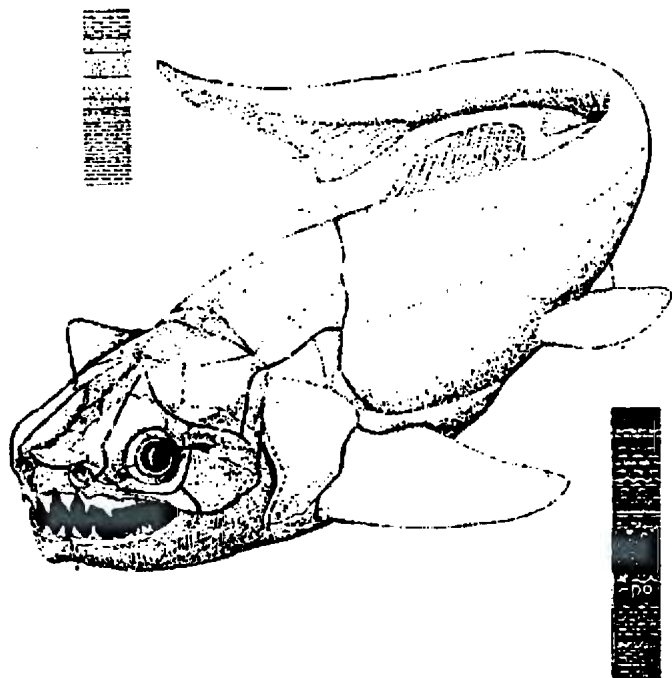
Figs. 1, 2, 5 and 6: *Po. hemiansatus*. All specimens well serrated at the lower anterior platform margin. With regard to the sculpture and outline of platform, the specimen of fig. 6 shows a special, but very characteristic pattern.

Figs. 3, 7-9: Morphotypes with steep anterior end of the platform margin, thus showing the characteristic of *Po. pseudofolius*, but probably representing an ancient morphotype of the now developing species of *Po. hemiansatus*.

Fig. 4: *Po. n. sp. aff. po. effilius*



PALAEOZOIC VERTEBRATE BIOSTRATIGRAPHY and BIOGEOGRAPHY



Edited by

John A. Long

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EDITED BY JOHN A. LONG
PALAEOZOIC VERTEBRATE BIOSTRATIGRAPHY AND BIOGEOGRAPHY

PROGRAM SUMMARY AND ABSTRACTS WITH DEVONIAN CONTENT FROM NORTH
AMERICAN PALEONTOLOGICAL CONVENTION (JULY 1992, CHICAGO, ILLINOIS)

**Fifth North American Paleontological Convention
(NAPC.V)**

Field Museum of Natural History, Chicago

Summary of Program

Monday, June 29 th , 1991	Tuesday, June 30 th , 1991	Wednesday, July 1 st , 1991	Location
1. <i>The Meaning of Higher Taxa in Macroevolutionary Studies</i> ¹ D. E. Fastovsky & J. M. Clark	6. <i>Early Mesozoan Evolution</i> S. Conway Morris	16. <i>Paleobiogeography: Global Change and Evolution</i> R. E. Crick, A. Raymond & C. Scotese	James Simpson Theater
2. <i>Phylogenetics and Rates of Evolution: Morphologic, Genomic and Taxic Rates</i> R. Cloutier & D. K. Elliott	7. <i>Early Mesozoan Evolution</i> continued with contributed papers	17. <i>Paleobiogeography: Global Change and Evolution</i> continued with contributed papers	James Simpson Theater
3. <i>Paleontology Applied to Geologic Problem Solving (Part 1)</i> L. E. Edwards & S. R. Jacobson	8. <i>Implications of Sequence Stratigraphy for Evolutionary and Biostratigraphic Patterns</i> R.W. Scott and A.R. Ormiston	18. <i>Environmental and Biological Change in Neogene and Quaternary Tropical America</i> J. B. C. Jackson, A. G. Coates & A. F. Budd	Montgomery Ward Lecture Hall
3. <i>Paleontology Applied to Geologic Problem Solving (Part 2)</i>	9. <i>Long Records of Land Biotas: A Comparison of Wyoming-Montana Paleogene and Siwalik Miocene Sequences</i> A. K. Behrensmeyer & C. E. Badgley, with contributions from T. M. Bown	19. <i>Origination and Extinction</i> contributed papers	Montgomery Ward Lecture Hall
4. <i>Environmental Patterns in the Origins and Fates of Major Groups (Part 1)</i> D. J. Botjter & D. Jablonksi	10. <i>Origin of Modern Terrestrial Ecosystems: Late Mesozoic and Cenozoic</i> G. R. Upeharch & R. K. Stocky	20. <i>Palaeozoic and Post-Palaeozoic Benthos: Comparative Ecology and Physiology</i> ¹ M. C. Rhodes & G. J. Vermeij	Founders' Room
4. <i>Environmental Patterns in the Origins and Fates of Major Groups (Part 2)</i>	11. <i>Origin of Modern Terrestrial Ecosystems: Late Mesozoic and Cenozoic</i> continued with contributed papers	21. <i>Evolution and Functional Morphology</i> contributed papers	Founders' Room
5. <i>Advances in Deep Sea Paleocology (Part 1)</i> W. C. Miller	12. <i>Conquering Shape and Form: Quantitative Morphometrics</i> ² B. T. Huber & D. Bravin	22. <i>Molecular Paleontology and Exceptional Preservation</i> D. E. G. Briggs	Dining Room E
5. <i>Advances in Deep Sea Paleocology (Part 2)</i>	13. <i>Morphological Evolution</i> contributed papers	23. <i>Taphonomy</i> contributed papers	Dining Room E
	14. <i>Biomolecular and Isotopic Paleontology: An Integrated Approach</i> ⁴ J. D. Hudeon, J. M. Hayes & D. M. Martill	24. <i>Late Palaeozoic and Early Mesozoic Circum-Pacific Events and their Global Correlation: A Comparison of the Permian and Triassic of the North American and East Asian Pacific Regions</i> ³ M. Dickins, D. W. Boyd & G. D. Stanley	Lecture Hall II
	15. <i>Paleocology</i> contributed papers	25. <i>Lagerstätten</i> H. R. Feldman	Lecture Hall II

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³Sponsored by International Geological Correlation Project 272

⁴Sponsored by Organic Geochemistry Division of the Geochemical Society of America

FUNCTIONAL SIGNIFICANCE OF VARIATIONS IN THE CENTRAL FOLD OF SHELLS OF LATE ORDOVICIAN THROUGH DEVONIAN BICONVEX BRACHIOPOD GENERA

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Flume experiments with models of Mid-Paleozoic atrypids, orthids, rhynchonellids, and spiriferids indicate that the central fold functions efficiently to separate lateral-margin incurrents from the anterior-medial margin excurrent in five of nine possible life orientations of the shell relative to the current direction and substrate. Anterior-medial incurrents and lateral excurrents are effectively separated in four of the nine orientations used with models of spiriferids and atrypids, but non-pediculate brachiopods drawing in water anterior-medially could not take advantage of reversing tidal currents to feed. The risk of refiltration of medial excurrent water is reduced with increasing relief of the central fold above the commissural plane. Downcurrent turbulence increases with increasing relief of the central fold. Eddies with a large radius of curvature are generated by large chevron-shaped central folds at low current velocities (5 cm/sec) and boomerang against the downcurrent lateral margin of models. Flume experiments on models also reveal that a well-developed sinus accelerated erosion of the supporting sediment around the weight-bearing posterior of the valves. Shells with high relief in the sinus destabilized comparatively quickly from valves-erect orientations when subjected to moderate current velocities (25 cm/sec).

Morphospace (ternary) diagrams of sinus shape for Late Ordovician (Caradocian) through Devonian (Famennian) genera show the realized field among the potential morphotypic extremes, namely, 1) rectimarginate (no fold), 2) isoclinal, chevron-shaped, and 3) M-shaped anterior commissural outlines. Morphospace plots through successive stages suggest centripetal selection for taxa with moderately developed folds in the atrypids and spiriferids, with occasional evolution of "outlier" genera with chevron-shaped central folds. Orthids display progressive loss of rectimarginate genera through the Devonian. Weak directional selection is suggested by the successive stage-level plots of the rhynchonellid genera which expanded toward the extremes of chevron- and M-shaped central folds in potential morphospace during the Devonian.

TROPHIC LEVEL & EVOLUTION IN PALEOZOIC GASTROPODS

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Although trophic position or level is one of the most basic aspects of a benthic marine species' ecology, its evolutionary significance remains obscure. Gastropods offer a suitable model for examining the relationship between trophic level and evolution since they exhibit a wide variety of trophic strategies and their mode of life is often reflected in their shell form. We examined 196 genera of Paleozoic gastropods ($\approx 1/3$ of known genera) for which first appearance and last appearance could be specified to stage level and for which trophic strategy could be inferred with a reasonable degree of confidence. We classified these genera into four trophic categories on the basis of shell characters relating to locomotion and clamping. These trophic categories are: Suspension feeders, Grazers on firm substrata, Soft substrate Grazers/Detritivores, and Carnivores. Suspension feeders are the most unambiguously recognizable category, marked by clear indicators of a sessile mode of life such as a radial apertures and planispiral shell forms. Our central observation from these data is that suspension feeders have shorter generic longevities than the other three trophic groups. This pattern is robust to a variety of methods of analysis. The mean generic longevity of the suspension feeders is 15 MY less than the other trophic categories. Cumulative frequency of genera within trophic categories versus log duration shows suspension feeders to be statistically significantly shorter lived than the other three trophic categories. The other three categories are not distinguishable. This pattern is unchanged by the removal of taxa dying out at mass extinctions. Suspension feeders have lower origination rates and higher extinction rates than the other trophic classes. This is not a taxonomic artifact produced by ornamentation and the number of characters available. This background pattern is also present in the end Ordovician and Late Devonian mass extinctions. Suspension feeders lose about half their genera in these extinctions, the two classes of grazers lose about 1/3 of their genera, and the carnivores suffer almost no extinctions. Suspension feeding appears to carry a significant evolutionary detriment in both mass extinctions and background times. This may be reflected in the change in trophic distribution of gastropods from the Ordovician to the Recent. The end Permian extinction shows a different pattern of selectivity; detritivores suffer the least.

EVOLUTION OF BIOLOGICAL COMPLEXITY: A CASE STUDY OF AMMONOID SUTURES

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The evolution of ammonoid sutures has long been cited as an example of the evolution of increased biological complexity. The complexity of sutures has increased, on average, but the exact nature of this increase, and any benefit associated with this increase has yet to be documented. We measure the fractal dimension of >600 ammonoid species and document the change in complexity of sutures between and among seven orders: Ammonitida, Anarcestida, Ceratitida, Clymeniida, Goniatitida, Phylloceratitida, and Prolecanitida. The average complexity of sutures and range of complexity of sutures increased from the Devonian to the Triassic. With the rise of the Ammonitida, average complexity of sutures remained constant or dropped slightly through the Mesozoic. However, the simplest sutures continue to originate over that same interval. The evolution of increased complexity is the result of increased number of complex forms, not selective loss of simple ones. (See figure 1)

We then compare the stratigraphic ranges (longevity) of a genus with the fractal dimension of a member of the genus. Increased sutural complexity does not significantly increase or decrease the susceptibility of a genus to extinction. In other words, there is no differential survival among simple and complex forms. We also show that in ancestor-descendant pairs, descendants do not demonstrate a propensity to become either more complex or more simple than their ancestors. These observations suggest that it may be difficult to demonstrate that the evolution of biological complexity is the result of natural selection. Increased complexity may be the result of experimentation with other anatomical features or the result of an evolutionary random walk.

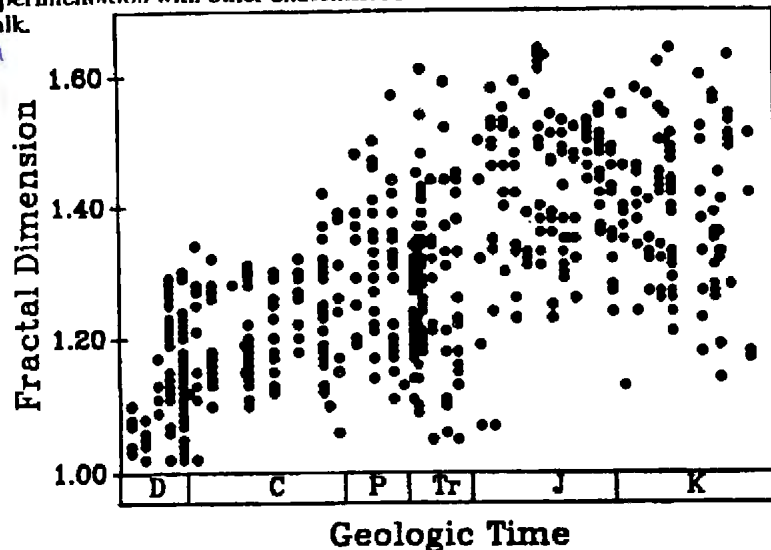


Figure 1. The fractal dimension of >600 ammonoid genera plotted at the time of their origination.

TAPHOFACIES AND BIOEVENTS IN MARINE SEQUENCES OF THE APPALACHIAN BASIN MIDDLE DEVONIAN

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The Middle Devonian (Givetian) Hamilton Group is composed of widespread, time-stratigraphic, discontinuity-bounded depositional cycles which correspond to sequences and sub-sequences. Not only do recurrent lithofacies and biofacies units correlate predictably with given parts of cycles, distinctive taphonomic features also correlate with appropriate parts of transgressive-, early highstand-, and late highstand (regressive) systems tracts within sequences. Transgressive systems tracts (TSTs) are marked by widespread, thin (0.5 to 3 m), winnowed, shelly sandstones or skeletal wacke- to grainstones. Bases are typically heavily burrowed with a distinctive firmground ichnofacies. Internally, the beds display mixtures of variably disarticulated and corroded skeletal fragments, especially pelmatozoan debris. Condensed intervals are typified by sharp diastemic contacts between TSTs and overlying maximum highstand shales. These surfaces of maximum starvation may have thin (centimeters) lags of phosphatic, concretionary, or pyritic diacasts, bones and conodonts as well as corroded carbonate skeletal debris. Early highstand deposits are characterized by an alternation of discrete storm beds with mudstones which may yield exceptionally well-preserved faunas. Late highstand- and regressive taphofacies display greater evidence of sediment-shell disturbance by bioturbation and repeated storms. The decrease in accommodation space dictates sediment-bypass and mixing with increased evidence of skeletal disarticulation and shell abrasion.

A recurring, and somewhat enigmatic phenomenon consists of widespread (to 100s of km) shell and reworked concretion layers, associated with diastems, which occur at the late highstand or early sea level-fall position within offshore, low energy mudstones. These "precursor beds" are sediment-starved lags, which mark abrupt shoaling events followed by a return to deeper-water deposits below the transition to lowstand conditions. These lags either represent the overprint of condensed smaller cycles superimposed on larger ones or they may record a fundamentally new, little-understood, process associated with abrupt sea level drop.

Most of the typical Givetian "Hamilton fauna" appears abruptly in the second major sub-sequence (4th order cycle) of the Hamilton Group. The Hamilton fauna was partitioned into distinctive biofacies which were remarkably stable in terms of taxonomic composition, guild structure and relative abundance. These biofacies tracked favored environments and recur through 10 or more basinwide cycles (including sub-sequences) during some 6-7 my. Surprisingly, relative lowstands, represented by sequence-bounding unconformities, appear to have had very little disruptive influence on tracking Hamilton biotas. Very few species became extinct, immigrated, or underwent significant morphological change during the entire Givetian interval. Instead, both the initiation and termination of the Hamilton fauna correspond with major deepening events (Marcellus and Genesee transgressions) of combined eustatic/tectonic origin. In both cases, the major faunal changes (extinctions, immigrations, species evolution) appear to be associated with widespread anoxic black shales in condensed early highstands of sequences. Both of these correspond to global bioevents (Kacac-otoman and Pharciceras events) that have been related to climatic change. This observation suggests that the major transgressions may have been associated with widespread environmental restructuring.

mean extinction: difficult for complex forms
normal fits: longevity of Bifurcans

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The historical and prevailing view regarding the distribution of nautiloid cephalopods is one of cosmopolitanism. There are several objections to such a sweeping view of this major group of marine invertebrates, but only the most significant are addressed here. First, unlike endemism, there is no clear agreement on the meaning of the term cosmopolitanism as used in biogeography. It is thus extremely difficult to gain a historical perspective without access to original data. I have found the term used for as few as four occurrences on four modern landmasses without reference to the paleogeographic relationships of these landmasses. Second, while a few nautiloid groups did compile impressive dispersal statistics, the fossil record clearly reveals that such periods of dispersal were generally brief in geological terms and that the group or groups involved did not colonize all available landmasses. Third, nautiloids were incapable of developing cosmopolitan distributions unless climatic constraints were removed by changes in the global system or by positioning all landmasses within the sub-tropical to tropical latitudes. Since there is no convincing evidence that either event occurred during the 520 million years of nautiloid evolution, it is perhaps more appropriate to view the distribution of nautiloids in terms of the number of landmasses colonized relative to the number of landmasses available for colonization. For nautiloids, the number of landmasses available for colonization was always fewer than the number of landmasses comprising the global paleogeography during any one slice of geologic time. Nautiloid genera restricted to one landmass are considered endemic, a condition exhibited by 65% of the Ordovician and Silurian genera and 81% of the Devonian genera. The maximum number of landmasses colonized by any one nautiloid genus for any one particular period of time was four, two fewer than the six available landmasses.

The basic biogeographic unit for nautiloid cephalopods is the genus. This is so because the dispersive potential of nautiloids was low when compared with true pelagic groups such as conodonts. Thus for nautiloid groups capable of dispersal among landmasses, the time needed to effect dispersal and insure permanence in the stratigraphic record was something greater than the longevity of the typical nautiloid species but less than the longevity of most genera. It seems reasonable that the best chance for the occurrence of cosmopolitan nautiloid genera would be at or near the zenith of those groups with attributes most suitable for dispersal. However, the fossil record for nautiloids shows that such periods rarely coincide with the peak intervals of total nautiloid diversity for the Lower and Middle Paleozoic (Arenig, Wenlock and Eifelian) occurring instead during succeeding intervals of time. Such events are generally confined to periods of modal diversity within each group. The lowest percentages of endemic genera and the intervals in which they occurred for the major nautiloid groups are: Ellesmerocerida (57%) and Endocerida (60%) for the Llanvirn, Actinocerida (36%) and Tarphycerida (45%) in the Llandovery, Orthocerida (52%, 47%, 55%) and Oncocerida (66%, 66%, 75%) for the Caradoc, Ludlow, and Givetian, Discosorida (67%) in the Wenlock and Nautilida (62%) for the Givetian. While the low percentage of endemics for the Actinocerida and Tarphycerida translate into the highest percentages of genera found on more than three separate landmasses (20%), similar percentages of endemics for the Orthocerida do not. Nonendemic members of the Orthocerida are more common to two or three of the available landmasses with approximately 20% occurring in either of these configurations. The fossil record also shows that Devonian nautiloids were the most restricted with the majority occurring on no more than two landmasses.

These and other criteria indicate that the distributions of nautiloid cephalopods do not conform to the general perception of cosmopolitanism. At the generic level the group is largely endemic with reasonably large numbers of genera occurring on two or three landmasses with no genus occurring on all available landmasses during a given interval of time. Because of the type and manner of biogeographic barriers imposed on nautiloids, their distributions or patterns tend to have well defined limits with considerable predictive powers.

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Paleozoic acritarch and marine phytoplankton associations clearly interpret paleoenvironments within marine shelf and oceanic depositional areas. Marginal marine sediments are characterized by low diversity acritarch assemblages, while shelf areas contain a higher diversity of forms. Areas with significant terrestrial runoff tend to have higher phytoplankton abundance together with terrestrial palynomorphs in contrast to restricted circulation carbonate shelf areas with distinctive low abundance acritarch associations. Deep water basinal and oceanic areas with low phytoplankton nutrient availability are characterized by very low diversity acritarch associations of moderate to very low abundance. Within the Paleozoic, changes in relative sea level are indicated by the record of a series of acritarch associations reflecting changing depositional environments comparable to depositional sequences and parasequences.

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The gastropod superfamily Subulitoidea first appeared during the Early-Middle Ordovician gastropod radiation, seemingly from within the pleurotomarid family Lophospiridae, and persisted with low diversity and generally low abundance through the Paleozoic. One species survived the end-Permian mass extinction, but like many other Paleozoic remnants, the clade became extinct in the mid-Triassic. Many members of the clade are homomorphic with later 'neogastropods' and have frequently been fingered as the ancestors of these later, predatory gastropods. There is however, no direct evidence for an ancestor-descendent relationship. Addressing this possibility and understanding of the systematics and evolutionary history of the clade has been complicated by relatively simple shell form and apparent paucity of shell characters. The strength of the morphological and probable ecologic similarities between subulitids and 'neogastropods' raises the question why this clade was unable to capitalize on their position as perhaps the only predatory gastropods during the Paleozoic. Such questions of evolutionary history are best addressed within the context of a combination of morphometric and phylogenetic analyses which may resolve the systematic questions and reveal something of the evolutionary relationships of the clade.

Morphometric analyses were performed on some 40 specimens covering the 13 described genera (and several undescribed forms). Both linear and angular measurements of external shell form and internal structure from axial thin sections were measured and apertures were analyzed using elliptical Fourier analysis (EFA). The number of specimens analyzed was intentionally limited because of difficulties obtaining specimens with sufficient preservation of the aperture. The results demonstrate the necessity, for this clade at least, of including a more complex description of apertural morphology than simple maximum length and width. Principle component analyses of the EFA data distinguishes complexity of the columellar folds along the first axis and basal rounding along the second - both biologically meaningful aspects of apertural form. Moreover, the occupation of a taxon-specific apertural space defined by the PCA increases through the Paleozoic. Further, the analyses suggest that the two traditionally recognized subfamilies of the Subulitidae (Ordovician-Devonian and Devonian-Triassic) each exhibit increased variance in the occupation of morphologic space, but additional data is required to confirm this pattern and determine if any temporal trends exist.

Analyzing patterns of occupation of morphologic space requires a rigorously constructed phylogeny. A cladistic (parsimony) analysis of the superfamily was performed using 16 taxa and over 30 discrete morphologic characters. The resulting cladograms were plotted within the taxon-specific morphospaces produced by the morphometric analyses.

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The names proposed world-wide for Devonian bryozoans have been evaluated with respect to replaced names, synonyms, and nomina dubia [Horowitz and Pachut (1993), *Journal of Paleontology*, in press]. The resulting list contains 1738 specific names assigned to 199 genera in 45 families. Approximately 75% of Devonian bryozoan species are reported from a single stage. Not more than 10%, and usually 4-6%, of the species reported in any Devonian stage are also reported in the succeeding stage.

The largest decrease in observed bryozoan diversity occurs between the Givetian and Frasnian stages, reducing the number of species by 77%, genera by 64%, and families by 42%. These values are less than those reported for the range-through method for the entire fauna of the Permian mass extinction (Raup, 1979) but larger than percentage extinctions (presumably based on range-through data) for four other Phanerozoic mass extinctions tabulated by Valentine and Walker (1987).

The range-through method dampens the observed differences in taxonomic diversity among Devonian stages at all taxonomic levels. The range-through number of species/stage is based upon both direct applications of the range-through method and on the assignment of ranges known only to early, middle and late Devonian to include appropriate Devonian stages. Generic and familial diversity increases monotonically from Lochkovian through Givetian stages. Thereafter (Givetian to Frasnian), range-through values for specific (69%), generic (31%), and familial diversity (10%) decrease. Specific and familial decreases across the Givetian-Frasnian boundary are comparable to those reported for non-Permian mass extinctions by Valentine and Walker, but the generic decrease is not as great. These results are consistent with Valentine and Walker's random mass extinction model.

Observed bryozoan diversity across the Frasnian-Famennian boundary increases while values calculated using the range-through method decrease by approximately 5-15%. This does not suggest a major bryozoan extinction event. Conversely, the decrease in bryozoan diversity across the Givetian-Frasnian interval is similar to an important Devonian extinction among rugose corals. The reason(s) for these extinctions is not yet clear. With respect to Devonian bryozoans, our inadequate understanding of the cause(s) of mass extinctions and the relatively coarse resolution of the stadial timescale does not permit differentiating between gradual or catastrophic scenarios.

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In recent years it has been recognised as a result of careful field work that there are a series of extinction events affecting goniatites and clymenids during the Devonian and early Carboniferous which can be confirmed in many parts of the world. Many have been given names, such as the Daleje, Chotec, Kacák, Pumlilo, Taghanic, Kellwasser, Nebden, Condroz, Annulata, Hangenberg and Alum Shale Events. The Taghanic Event, which falls within the Givetian stage, is a major extinction event, as is the Upper Kellwasser Event at the end of the Frasnian and the Hangenberg Event near the end of the Devonian. At major events many familial and generic taxa are lost and few stocks, often of a particular type, survive; at smaller events, lower taxon levels are affected. The events are usually associated with sedimentary perturbations of some sort. These are usually linked with transgression, or regressive/transgressive couplets, and frequently with anoxia or hypoxic conditions; it has given emphasis to the concept of the ammonoid record as a *biostratigraphic* of environmental events. Where documented in detail a gradual decline before the event is noticeable, and although this may appear stepped on diagrams, this results from the time-blocks used in analysis. Probably gradual extinction events occurred at Milankovitch band interval culminations. There is usually a trauma period of very low diversity, but not necessarily of abundance. Subsequent innovation and diversity is gradual. There is no evidence for sudden events such as might be caused by bolides or large meteorites, however much they might be expected.

A programme of research has studied these events in Europe, North America, North Africa and Western Australia, that is, on separate continents where sealevel changes can be documented by movements over stable shelf or cratonic areas. This has suggested that many are linked with eustatic events. The association with hypoxia is not universal although that is common in the eastern North America-Europe-North Africa area, then closely juxtaposed after the initiation of the docking of Gondwanaland against Laurussia. Comparisons of the Australian sealevel curves with those of North America and other areas suggest a correlation of pulses, especially for the Frasnian. But anoxic events have not been located at the Kellwasser and Hangenberg events in Western Australia, for example, to match those of other areas.

Since there are at least ten of these events, not all of the same power, in the interval from the late Lower Devonian to the basal Carboniferous, and since only two of them closely conform to stage boundaries (end Frasnian and end Famennian) it is misleading to plot these as stage or series blocks and to suggest there are extinctions at stage boundaries. Only in two cases (Upper Kellwasser and Hangenberg) would this be approximately true, but the staged decline at both would make even those misleading.

It is too early to speculate whether the events are periodic, or result from episodic culminations of different orbitally forced periodicities. However, many successions show small-scale rhythmic repetitions of facies which, when well developed, are the hallmark of some events. This might suggest a climatic control. The Taghanic Event, however, seems well correlated with the Taghanic Onlap (formerly known as the basal Upper Devonian transgression) suggesting a (plate) tectonic cause. It is important as a next stage to document the paleoecological changes of other groups over these events; already it is clear that other invertebrate groups are significantly affected by some. Precise documentation of tectonic events is also needed in the search for a cause.

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Though long suspected to be critical to the understanding of the evolution of the pelecypod subclass Pteriomorpha, the mid-Palaeozoic family Rhombopteriidae was too poorly known to allow clarification of its relationships. Furthermore, numerous species were assigned to the nominate genus, *Rhombopteria*, many of which belong in other genera or even other subclasses. Consequently, the morphologic concept entailed by *Rhombopteria* was confused as were functional morphologic investigations.

Silicified rhombopteriids discovered in the Lower Devonian of Australia are referred to a new genus, and reveal internal shell characters essential for understanding rhombopteriid relationships. The family Rhombopteriidae is revised to include only three genera, *Rhombopteria*, *Prantliella* and the new Australian genus.

New data provided by the Australian material indicate that rhombopteriids were non-byssate, dimyarian pteriomorphs that lived pleurothetically on the left valve as do gryphaeid oysters. The Rhombopteriidae are assigned to the Ostreina and are the sister group of all other ostreins including the Ostreoidea, Pseudomonotidae and Terquemidae. Important characters common to rhombopteriids and gryphaeid oysters include: 1) left-sided pleurothetic habit; 2) absence of byssal notch or sinus throughout ontogeny; 3) Quenstedt muscle scar; 4) proximal gill weal; 5) circumferential curb; 6) commissural shelf; and 7) posteroventral palliobranchial fusion as evidenced by a branchitellum and posterior radial fold and sulcus. Outgroup comparison with Umburridae indicate that characters 1-4 are symplesiomorphic for the Order Ostreoidea. Characters 5-7 are autapomorphies for a clade including the Rhombopteriidae, Pseudomonotidae, Terquemidae and Ostreoidea.

Rhombopteriids were probably derived from left-sided pleurothetic, umburrid-like ancestors which, in turn, descended from primitive, equivalved, orthothetic prionodonts. Thus, a right-sided pleurothetic stage was never part of the evolutionary pathway of oysters. The inequivalved shell of eupteriomorphs evolved initially for a left-sided pleurothetic semi-infaunal habit. Retained as an adaptation in rhombopteriids and oysters, the inequivalved shell is an exaptation in Pterioidea (winged shells), Pectinina (scallops) and Pseudomonotidae, having been coopted for a right-sided pleurothetic orientation, and having the effect of enhancing stability in an epifaunal habit. Evolution of right-sided pleurothetic pteriomorphs, including the Pseudomonotidae, Pectinina and Pterioidea, from separate left-sided pleurothetic rhombopteriid-like or umburrid-like ancestors, is explicable by paedomorphic retention of the byssus and epifaunal habit of the early post-larva. A right-sided pleurothetic orientation would follow 'automatically' owing to hydrodynamic and mechanical constraints on the already evolved, inequivalved shell, byssally attached by the anterior margin on the substrate surface.

BIOSTRATIGRAPHY AND BIOGEOGRAPHY OF FRASNIAN, UPPER
DEVONIAN CONODONTS

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Analysis of Frasnian conodont sequences in the Montagne Noire, southern France, results in the recognition of a conventional zonation consisting of thirteen zones. Graphic correlation of eight Montagne Noire sections with a total of 11 sections in the Alberta Rockies, the Hay River-Trout River areas of the southern Northwest Territories, Canada, the Midcontinent and New York sequences in the United States, and the Canning Basin, Western Australia divides the Frasnian into 34 composite standard units. Most of these sections are dominated by conodonts of the outer-shelf to basinal *Palmatolepis* biofacies, but those of Hay River-Trout River are occupied by the quite contrasting inner-shelf *Polygnathus* biofacies. Correlation of the latter with the Montagne Noire zonation is effected only through graphic correlation. The taxonomy of many of the critical species involved in the correlations is based on shape analysis and multielement taxonomy of *Palmatolepis*.

Prevailing opinion is that the Frasnian was a time of cosmopolitanism as exemplified both by benthic organisms, especially corals and brachiopods, as well as conodonts. This contrasts with the Early and Middle Devonian which was a time of significant endemism in benthic fossils and in conodonts. The high point in conodont endemism according to the zone-by-zone analysis of the Early and Middle Devonian (Klapper and Johnson, 1980) was the early Eifelian when there were about 70% endemic species. Although endemism did not reach this high in the Frasnian, analysis of a limited number of intensively collected and studied sections in the Montagne Noire, U.S. and Canada, Western Australia, and the Russian Platform demonstrates levels of endemism ranging from about 30 to 45% in three composites of two zones each. Endemic species occur in both the *Palmatolepis* and *Polygnathus* biofacies. Using the Probabilistic Index of Similarity of Raup and Crick (1979), the null hypothesis of randomness is rejected for some paired comparisons between localities representing different biofacies, as would be expected, but it is also rejected between some localities representing the same biofacies on different continents. Although the explanation of significantly dissimilar faunas can be accepted at 95% confidence levels in only a limited number of instances, there are dissimilarities of somewhat lesser magnitude among various paired comparisons. This seems to indicate that the Frasnian was not a time of conodont cosmopolitanism even within the *Palmatolepis* biofacies.

SPINE FUNCTION IN THE ODONTOLEURID TRILOBITES *LEONASPIS* AND
DICRANURUS FROM THE DEVONIAN OF OKLAHOMA

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The Lower Devonian Haragan Formation of Oklahoma has well preserved odontoleurid trilobites found in repeated calcareous mudstones. These layers (5-9cm. thick) represent distal tempestites that rapidly buried and preserved completely articulated odontoleurids which provide important paleobiological information. The genal and pleural spines of *Leonaspis williamsi* and *Dicranurus hanatus elegantus* of the Haragan Formation are examined and compared.

In *Leonaspis* the ventrally directed genal and pleural spines are straight and lay flat. The first pleural spine is the longest followed by progressively shorter pleural spines. Several collected and prepared enrolled specimens have the spines radiating outward. In an enrolled position the spines would protect *Leonaspis* from a large predator.

The pleural spines of *Dicranurus* have a very different pattern from *Leonaspis*. The first three spines are short and laterally directed, the fourth, sixth and seventh are very long, curved and directed ventrally, the eighth, ninth and pygidial spines are short and decrease in length toward the pygidium. There is no pleural spine on the fifth thoracic segment and the genal spine is very long and curved. On these spines at many growth stages there is direct and indirect evidence of being encrusted based on the following: (1) Epibionts such as bryozoans, brachiopods and a crinoid; 2) Endoliths (25-150 microns in diameter) of unknown origin are found all over *Dicranurus* but are predominantly on the spines; 3) Pyrite (now limonite) coating the spines apparently formed from the decay of organic matter. If the source of the organic matter came from the trilobite, then pyrite would be found all over *Dicranurus*. However, it is only found randomly on the spines. This pattern is like some of the encrusting bryozoans suggesting that the source of the organic matter may be from an encrusting organism.

It is doubtful that the pleural spines of *Dicranurus* would be adapted for resting on the bottom when bryozoans are found encrusting the entire surface of the spine. However, the very long pleural and genal spines with attached organisms would break up the outline of *Dicranurus* making it less conspicuous to a predator.

THE ISOTOPIC RECORD OF OXYGEN IN PHOSPHATES OF FOSSIL FISH - DEVONIAN TO RECENT.

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The isotopic composition of oxygen in the phosphate ($\delta^{18}\text{O}_p$) was determined in 159 fish bones and teeth from museum collections throughout the world. The fossils were both marine and fresh-water ranging in age from the Devonian to the Recent. In 45 of those we also determined the isotopic composition of oxygen and carbon of the lattice carbonate in apatite ($\delta^{18}\text{O}_c$ and $\delta^{13}\text{C}$). In most cases the isotopic results are compatible with previously available geological information: the difference between marine and fresh water, the indication of previously known warm and cold time periods, and the ranking of fishes from warm to cold according to their inferred life habitat.

Three fish specimen from the Devonian of the Orcadian Basin in Scotland yield results which are compatible with the thermal structure of a stratified lake. The isotopic analysis of *Inoceramus vulgaris*, a fish found inside Cretaceous inoceramids, yields normal marine $\delta^{18}\text{O}_p$. Hence we favor the suggestion of Tourtelot and Rye (1969) that ^{18}O depleted inoceramids did not deposit their shells in isotopic equilibrium with sea water.

The relationship between $\delta^{18}\text{O}_p$ and $\delta^{18}\text{O}_c$ suggests early diagenetic replacement of an originally phosphatic phase by carbonate fluor apatite (CFA). This conclusion is in accord with REE studies of fish fossils. The correlated latitudinal variation in $\delta^{18}\text{O}$ of meteoric water and temperature should result in a small variation of $\delta^{18}\text{O}_p$ in fresh water fish. The large range in $\delta^{18}\text{O}_p$ of Recent fish is the outcome the "altitude effect" (Dansgaard, 1964) i.e. of the existence of Recent high altitudes, and sharp morphological gradients.

PALEOBIOGEOGRAPHIC SIGNIFICANCE OF FAMENNIAN ECHINODERM FAUNAS FROM NORTHWESTERN CHINA

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A diverse (>200 specimens representing more than 20 taxa) Famennian echinoderm fauna has been collected from the Hongguleleng Formation, Junggar Basin, Xinjiang, Uygur Autonomous Region, Peoples Republic of China. Famennian faunas are relatively poorly known on a global basis, Famennian echinoderm faunas in general are very poorly known, and echinoderm faunas of any age from China are virtually unstudied. Echinoderms are highly endemic, which makes them relatively poor for global biostratigraphy, but excellent for use in biogeographic studies. Because Frasnian and Famennian faunas are noted for their general lack of endemism, echinoderms may be critical, sensitive indicators of Famennian biogeographic provinces. Preliminary analysis indicates that this Chinese Famennian echinoderm fauna is dominated by blastoids and inadunate, small-calyx camerate, and flexible crinoids, many of which show morphological characters that are intermediate in nature at higher classificatory levels between older Devonian and younger Carboniferous taxa. The taxonomic composition of this fauna clearly indicates that diversification and re-radiation in the aftermath of the Frasnian-Famennian extinction event was well underway before the close of the Famennian. The most similar faunas are from Famennian rocks of England and, possibly, Germany. Brachiopods, corals, and trilobites of this age also show similarities between northwestern China and western Europe. These two areas were high latitudinal and tropical, respectively, during deposition, therefore their similar composition may represent latitudinal contraction associated with global cooling or a nearshore migratory pathway between the two areas via Kazakhstan and Poland.

PALEOCLIMATE, CONTROLS ON UPPER DEVONIAN SOURCE ROCK SEQUENCES AND STACKED EXTINCTIONS.

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High quality (>2% TOC) Upper Devonian source rocks are developed in several sequence types. The commonest type, accounting for 70% of the studied examples is the transgressive sequence with a basal hiatus. Others include shallowing upward sequences (12%), lacustrine sequences in fault-controlled basins (7%), distal slope sequences (7%), and evaporite capped sequences (4%).

Starting from the synthesis of Johnson, Klapper, and Sandberg (1985) it has been possible to demonstrate correlativity of Upper Devonian transgressive episodes globally. The marked association of epeiric sea Upper Devonian source rocks with transgressions heightens interest in their causation. Could they have been produced by glacio-eustatic sea-level change as Stanley (1984; 1988) implies? Quantitative paleoclimate modeling and isotopic paleotemperatures for the Upper Devonian suggest not. Modeling using CCM₁ at NCAR, including five year seasonal cycles, suggests the absence of any large southern hemisphere ice volume. Because much of the Upper Devonian land mass was either in equatorial or high latitude regions, there was little development of monsoonal climates. Midlatitude cyclonic activity was also much less than at present, meaning less polar transport of moisture and drier polar areas. Precipitation maxima largely coincided with topographic elevations. In contrast to the Late Ordovician to earliest Silurian, there was no Upper Devonian perennial snow cover even over the high latitude southern land mass. This was in spite of winter land temperatures as low as -40°C. in eastern Gondwana. In that area and elsewhere, there was thin winter snow cover which melted in late spring resulting in no build-up of snow cover to produce glaciation. This was mainly the consequence of low winter precipitation in Gondwana. High latitude sea surface temperatures were certainly cold enough to displace or exclude some organisms. However, in low latitude areas where Upper Devonian extinctions also took place, modeled sea surface temperatures range between 27° and 34°C. Such areas would have been refuges for any organisms displaced by cold, high latitude waters. The higher temperature values of low latitudes are convergent with the isotopic paleotemperatures determined by Brand (1989) using well preserved Upper Devonian brachiopods. Brand's determinations suggest temperatures even reaching lethal values for many plankton (37°C). The extinction of reefs by the close of Frasnian time could have been partly a result of such elevated temperatures. Stacked extinctions of conodonts (Ziegler and Lane, 1987) and acritarchs may have been a further result. The loss of reefs, an important consumer of plankton, may have permitted a relative increase in plankton abundance crossing from more oceanic areas into epeiric seas, possibly contributing to high quality source rock deposition.

VASCULAR LAND PLANT DIVERSITY IN A BIOGEOGRAPHIC CONTEXT

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The history of vascular land plant diversity from the late Silurian to the Early Carboniferous has two major features: a pronounced diversity peak in the late Siegenian-Emsian (Devonian), approximately 12 million years after the appearance of vascular land plant body fossils; and a diversity low in the late Frasnian-early Famennian (Devonian), which coincides with the Frasnian-Famennian mass extinction of marine invertebrate faunas. Because the diversity of fossil land plants depends in part on sampling intensity, this diversity history requires evaluation. Biogeographic data are useful for assessing diversity histories because they incorporate one of the best measures of sampling intensity, the number of localities known from a time interval, and because the amount of biogeographic differentiation present during an interval may influence global diversity.

The data for this study consist of compression-impression genera from 394 Late Silurian-Devonian and 64 Tournaisian (Early Carboniferous) floral assemblage lists. Most of these assemblage lists represent florules: defined as the compression-impression genera found in a single formation, member, or other narrow stratigraphic horizon at a single outcrop. However the data include some regional lists from China and parts of the former U.S.S.R., because we could not obtain florules for all time intervals from these regions. Regional lists consist of the genera found in one formation from a limited geographic region. All of the Laurussian assemblage lists used in this study (244 Late Silurian-Devonian and 49 Tournaisian lists), including those from the Russian platform, represent florules. Linear regression of both the total diversity and the standing diversity of vascular land plant genera against the number of floral assemblage lists from each interval suggests that the number of floral assemblage lists correlates strongly and significantly with generic diversity ($r = 0.88$). Thus, the late Siegenian-Emsian diversity peak is probably an artifact of sampling: there are more florules described from the late Siegenian-Emsian than from the Eifelian and Givetian combined. The late Frasnian - early Famennian diversity low may be an artifact of sampling: few reliably-dated assemblages exist for this interval. However, late Frasnian - early Famennian assemblages show no biogeographic differentiation between 'equatorial' Laurussian assemblages from the United States and Europe and northern 'non-equatorial' assemblages from Arctic Canada and Siberia. This biogeographic differentiation is a persistent feature of floral assemblages from all other Devonian time intervals, and from the Early Carboniferous. Low numbers of florules could cause an apparent loss of biogeographic differentiation for an interval. Conversely, all three phenomena (low diversity, low numbers of florules, and loss of biogeographic differentiation) may indicate that the Frasnian-Famennian mass extinction affected terrestrial land plants.

The diversity history of Late Silurian through Early Carboniferous land plants suggests that three major evolutionary innovations: heterospory, which appeared in the late Emsian; arborescence, which appeared in the Givetian; and seeds, which appeared in the late Famennian had little effect on land plant diversity.

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At Miguasha, Québec (earlier referred to as Scaumenac Bay), the Escuminac Formation, lowermost Upper Devonian, yields an abundant and diverse fish fauna and flora. Both vertebrates and plant fossils from the locality are renowned throughout the world. The excellent preservation, including that of endocranial anatomy, enabled Jarvik to describe and illustrate fine anatomical details of the osteolepiform *Eusthenopteron*. That gives the wrong impression that Miguasha is throughout the Escuminac Formation an outstanding Conservat Fossil-Lagerstätte.

The cliffs at Miguasha bear fishes throughout the approximately 120 m thick Escuminac Formation. The lithology of the sediments changes throughout the sequence. Close to the base of the formation, acanthodians and anaspid-like agnathans occur in laminites, sometimes hundreds on one horizon. In these laminites, soft tissue preservation may occur (anaspid-like agnathans), and diagenetic transformations of acanthodians into organic substance led to misinterpretations and recognition of the "larval chordate *Scaumenella*." Most common within the sequence are limy concretions with different fish fossils, most commonly *Bothriolepis*. Three-dimensionally preserved fishes occur within the sandstone-siltstones and sometimes within the concretions. In all these cases, dermal bone is preserved, and in few cases chondral bone too, as in *Eusthenopteron*. One can characterize these fossiliferous sections of the Escuminac Formation as Concentration Fossil-Lagerstätte, whereas the laminites are Conservat Fossil-Lagerstätten.

The depositional environment was previously interpreted as an intermontaneous basin, based on tectonic and paleogeographic position. More recent paleogeographic reconstructions show a connection with Scottish deposits and to marine deposits in the present day North Sea. The lack of invertebrates and of marine plant remains, and the occurrence of vertebrates in other localities were used as additional indicators for freshwater deposition.

The sedimentological features are ambiguous, the turbidites, such as those found at Miguasha, can occur in marine or large freshwater bodies. Conchostracans occur, sometimes in the thousands on a single plane, in the basal part of the Escuminac Formation. They occur today in freshwater or brackish environments; the same species as the one in the Escuminac Formation is reported from lower Upper Devonian marine deposits in the Baltic (Koknese, Latvia). A detailed comparison of the fish fauna with other lower Upper Devonian fish faunas indicates a coastal marine environment. That is supported by rare trace fossils and by different chemical analyses of the sediments and $^{87}\text{S}/^{34}\text{S}$ analysis of *Bothriolepis* bones.

In conclusion, earlier interpretations of the paleogeographic position of the Escuminac Formation at Miguasha and chemical and faunal indicators contradict each other in the interpretation of the paleoenvironment of the formation.

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Five distinctive vertebrate faunas characterised by endemic taxa can be recognised for the Early Devonian (Euramerica, Siberia, Tuva, China, and East Gondwana). By Late Devonian time these faunal provinces are obscured by widespread taxa which also inhabited nonmarine aquatic environments, but indicate faunal communication between Gondwana, Euramerica and China. This marked change in pattern between the Early and Late Devonian may be attributed to intrinsic (evolutionary) or extrinsic causal factors. Dispersal capabilities of aquatic vertebrates may have increased during the initial gnathostome radiation of the Devonian, but a predominantly extrinsic cause (e.g. global change in geography or climate) is suggested by the similar pattern for marine invertebrate faunas of Early Devonian endemism and Late Devonian cosmopolitanism. Outstanding problems of Devonian vertebrate biogeography include faunal differentiation on the largest landmass of the time (Gondwana), and the nature of barriers and connections between East and West Gondwana, East Gondwana and South and North China, and West Gondwana and Euramerica. A vertebrate equivalent of the cool-water Malvinokaffric invertebrate faunal realm of the Siluro-Devonian is not clearly identified, but vertebrate data from southern Africa and south America are sparse.

Wide latitudinal distributions for some Late Devonian vertebrate taxa appear anomalous, and could indicate either reduced global climatic gradients, or erroneous paleogeographic base maps. There are difficulties in formulating a hypothesis of global warming and/or major paleogeographic change in a way which clearly distinguishes basic from interpreted data. Three major subdisciplines (paleomagnetism, paleoclimatology, paleobiogeography) contribute to Paleozoic paleogeographic reconstructions. Their data tend to be organised and represented in different ways, but each relies on the same principle of concordance with a general pattern (Young 1990). Degree of consistency of a hypothesis based on one data set (the extent to which it explains patterns within an unrelated set of data) is a primary criterion for accepting or rejecting the hypothesis. Apparent polar wander path representation facilitates testing of paleomagnetic data against those paleoclimatic or paleobiogeographic data which provide evidence of paleolatitude. However, as well as the simple indication of paleolatitude, biogeographic and some other qualitative data sets provide more complex evidence concerning connections or barriers between regions, for which APWP representation is not appropriate. Cladistic analysis of hierarchically organised data sets (Young, 1986, 1987) provides a means of integrating qualitative paleobiogeographic, paleoclimatic, and paleogeographic data such that inconsistencies in the evidence are emphasised, and the hypothesis is exposed to falsification. These ideas are illustrated using Devonian examples.

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ZLICHOVIAN--GIVETIAN BIVALVE FAUNA FROM THE PLANKTONIC
FACIES (NANDAN FACIES) OF NANDAN, GUANGXI, SOUTH CHINA

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A large amount of pteriomorphs of bivalve have been found in the Zlichovian--Givetian black mudstone-siltpelite in the trough in basin facies-zone of Luofu, Nandan, north-west Guangxi, South China. This fauna consists of 20 species, placed in 11 genera and 6 families, of which 1 family, 2 genera and 8 species are new. It has a very low diversity while compared with the contemporaneous fauna of Xiangzhou facies. This fauna is characterized by: a. Only 2 subclasses, the Pteriomorphia and Cryptodonta of 6 subclasses of Bivalvia were presented in the Nandan facies fauna; b. Among the occurred 6 families: Praecardiidae, Antipleuridae, Lunulacardiidae, Pterineidae, Posidoniidae, and Guangxiconchiidae, the Guangxiconchiidae (fam. nov.) is the most flourishing one. About 80% of individuals of bivalves belong to it. In contrast, the Pterineidae which was very flourish in the Xiangzhou facies, is represented by a small amount of specimens. In the generic level, the Guangxiconcha is mostly developed and distributed from Zlichovian to Givetian; c. This is a basically cosmopolitan fauna, and may compare with the contemporaneous bivalve fauna of the same facies of western Europe and North America. Among 11 genera of this fauna, 7 genera: Ptychopteria(Actinopteria), Cheiopteria, Pterochaenia, Posidonia, Lunulacardium and Buchiola are the cosmopolitan or basically cosmopolitan taxa, while Guangxiconcha, Nandannia and Opisthonia are the endemics to South China. 62% of the species are the endemics; d. This fauna is dominated by the small-sized, thin-shelled and fragile taxa. Except for Buchiola and Ptychopteria, most taxa are ornamented by fine concentric line, or acrossed by very weakly radial line; e. About 54% of taxa and 90% of total individuals of this fauna may be the byssal attached epifauna, most of them may be the pseudoplanktonic bivalves.

Seven bivalve zones of Zlichovian--Givetian of Nandan, Guangxi have been recognized, and compared with the associated tentaculitid zones.