A REINTERPRETATION OF THE CONODONT ATLANTIC REALM IN THE LATE EARLY ORDOVICIAN (EARLY LLANVIRN)

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Two major Ordovician faunal realms have usually been distinguished around the Iapetus Ocean. The Midcontinent Realm included Laurentia and Siberia, whereas the (North) Atlantic Realm included Baltoscandia and the easternmost part of Laurentia (the Appalachians and western Newfoundland). This study is based on published and unpublished data from the basal Llanvirn (*L. variabilis–E. suecicus* zones in Baltica and *H. holodentata–P. harrisi* zones in Laurentia). Cluster analyses demonstrate that the relatively close similarity between Baltica and eastern Laurentia was mainly due to the coexistence of pandemic, deeper-water taxa of the *Protopanderodus–Periodon* Biofacies. Therefore, it is suggested that the Atlantic Realm was restricted to the areas south-east of the Iapetus, while Laurentia, including its easternmost parts, belonged to the Midcontinent Realm. The contemporary pandemic faunas of the *Protopanderodus–Periodon* Biofacies were not restricted to a specific realm, but occurred in the Iapetus as well as in the neighbouring platform-margin areas.

Key words: Conodonta, paleobiogeography, cluster analysis, biofacies, Early Llanvirn, Early Ordovician, Iapetus Ocean, Laurentia, Baltica, Atlantic Realm.

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INTRODUCTION

Quantitative statistical methods have been playing an increasing role in paleobiogeographical analyses during the past two decades because of the readily available and increasingly powerful personal computers. The advantage of the computer-based methods is that paleobiogeographical patterns can be explored more rigorously. It is important to keep in mind, however, that the conclusions still will be much more dependent on the taxonomical interpretations than on the choice of statistical methods.

The classical view is that two major conodont provinces existed around the Iapetus Ocean throughout the most of the Ordovician (e.g. BARNES *et al.* 1973; BERGSTRÖM 1973; FORTEY and BARNES 1977) (Fig. 7A). The Midcontinent Realm (or Province) characterized Laurentia and Siberia, while the North Atlantic Realm (or Province) included Baltoscandia and the easternmost part of Laurentia. LINDSTRÖM (1976) refered to the two realms as "faunas", and distinguished between the typical Baltic *Periodon* Fauna and the typical North American *Histiodella* Fauna. In the circum-Iapetus area, BERGSTRÖM (1990) subdivided the Midcontinent Realm (Midcontinent Faunal Region *sensu* BERGSTRÖM) into the "North American Interior Province" and the "Siberian Province", while the Iapetus-near part of the Atlantic Realm (Atlantic Faunal Region) was separated into the "Baltic Province" and the "Mediterranean Province" (Fig. 7B). BERGSTRÖM (1990) included both Baltoscandian and North American (mainly Appalachian) localities in the Baltic Province, whereas POHLER and BARNES (1990) distinguished between the Baltoscandian Province and the Appalachian Province (Fig. 7C). This general pattern occurred already in the mid-Arenig, for which BAGNOLI and STOUGE (1991) subdivided the Midcontinent Realm into the Midcontinent Province and the China Province and the Atlantic Realm into the Balto-Scandic Province and the Precordilleran Province. The latter province corresponds roughly to the Appalachian Province of POHLER and BARNES (1990), but was extended to include the east and west coasts of Gondwana together with the Laurentian margin.

The division into two major conodont realms around the Iapetus Ocean is widely accepted, but there has been a lot of disagreement concerning the classification of the biogeographic units. In most early studies on conodont provincialism, in the 1970's, the term "province" was used as the principal unit. Recently, BERGSTRÖM (1990) followed BERRY (1979) and used "faunal region" as the major unit that can be further subdivided into "provinces". POHLER and BARNES (1990) used "realm" as the larger unit and "province" as the smaller one. This procedure has been followed here. None of the papers mentioned above gave any clear definitions explaining the differences between a realm or faunal region and a province. MCKERROW and COCKS (1986) used realms for climatically controlled faunas and floras, and provinces for regions separated by physical barriers. This definition was not recommened by HALLAM (1994) who thought that the terms should be purely descriptive. In the present paper no precise definitions have been used, other than realm has been used for the larger units and province for the smaller ones. The present study confirms the widely accepted view that two major conodont realms existed around the Iapetus Ocean in the Early Llanvirn. However, thanks to a better understanding of the conodont paleoecology gained in the last decade, there is now growing evidence that call for a modification of the previous paleobiogeographical models.

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CONODONT PALEOECOLOGY

Since the early 1960's, it has been known that the occurrence and relative abundance of certain conodont genera and species were related to the surrounding environments (e.g. MÜLLER 1962), but it was not until the early 1970's that the first proper paleoecological models were proposed (see review by POHLER and

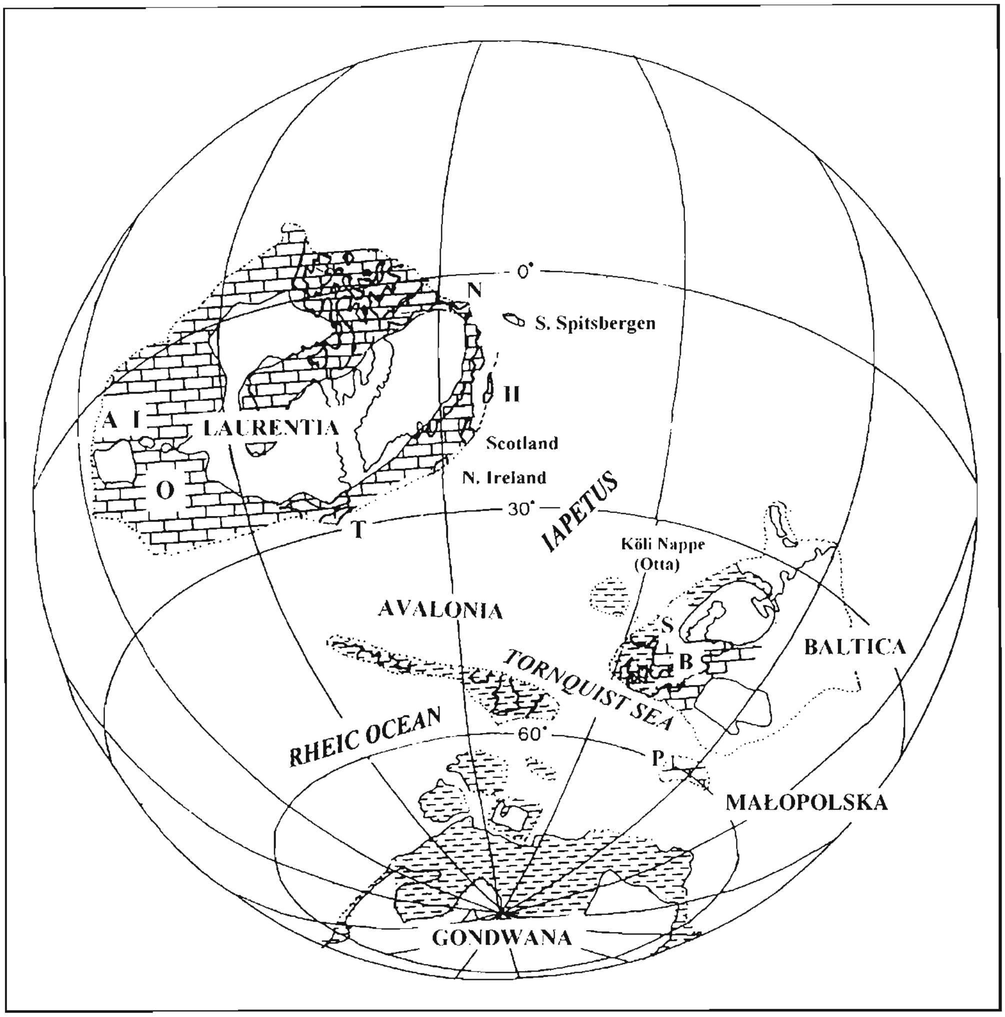

Fig. 1

Locality map based on a modification of the Middle Ordovician palaeogeographic reconstruction of DZIK and PISERA (1994). A – Antelope Valley (eastern Nevada), I – Ibex (western Utah), O – Eastern Oklahoma, T – Table Head (western Newfoundland), H – Hølonda (Upper Allochthon, Scandinavian Caledonides), N – eastern North Greenland, S – Stein (Lower Allochthon, Scandinavian Caledonides), B – Baltica (inner stable platform), P – Poland (Małopolska microcontinent, southern Poland).

BARNES 1990: table 1). SEDDON and SWEET (1971) proposed a depth-stratified pelagic mode of life for the conodonts, whereas BARNES and FÅHRÆUS (1975) suggested that most conodonts were nectobenthic and only few were pelagic. DRUCE (1973) proposed an intermediate model. Finally, STOUGE (1984) was of the opinion that some conodonts were pelagic and others were benthic in their mode of life.

The SEDDON and SWEET (1971) model – which is an example of the "additive model for plankton distributions" (TIPPER 1980) – implies that shallow-water species are ubiquitous, whereas those from deeper waters are more spatially restricted. As a result the diversity increases away from the shore line. Conversely, the nectobenthic and benthic model of BARNES and FÅHRÆUS (1975) suggests a distinctive lateral segregation of conodont biofacies, controlled by depth-related limiting factors such as temperature, salinity, current energy, and oxygen. The model is an example of the "seriative model for benthic species distributions" of TIPPER (1980). Recently, it was further confirmed that most conodont species seem to fit the latter model: their distribution is mainly related to depth and distance from shore, that is, oceanicity *sensu* TIPPER (1980). Accordingly, RASMUSSEN and STOUGE (1995) distinguished between five biofacies on and off the Baltic platform, each characterized by a certain environment related to oceanicity. A few taxa, however, were observed in equal numbers from a variety of environments, and therefore were apparently pelagic. POHLER (1994) showed in detail how Arenig conodont biofacies may change with time in certain environments at the Laurentian south-eastern margin (Cow Head, western Newfoundland).

TOTAL FAUNA

	B-S	B-P	B-H	B-T	B-A	B-I	B-O	B-N
C	24	16	0	9	3	1	0	1
n1	26	26	26	26	26	26	26	26
n2	39	18	8	44	8	15	14	11

	S-P	S-H	S-T	S-A	S-I	S-O	S-N
C	16	3	19	4	1	1	1
n1	39	39	39	39	39	39	39
n2	18	8	44	8	15	14	11

	P-H	P-T	P-A	P-I	P-O	P-N
C	0	5	0	0	0	0
n1	18	18	18	18	18	18
n2	8	44	8	15	14	11

	H-T	H-A	H-I	H-O	H-N
C	7	2	2	1	1
n1	8	8	8	8	8
n2	44	8	15	14	11

	T-A	T-I	T-O	T-N
C	6	7	6	6
n1	44	44	44	44
n2	8	15	14	11

	A-I	A-O	A-N
C	5	3	5
n1	8	8	8
n2	15	14	11

	I-O	I-N
C	9	10
n1	15	15
n2	14	11

	O-N
C	7
n1	14
n2	11

SHELF FAUNA

	B-S	B-P	B-H	B-T	B-A	B-I	B-O	B-N
C	16	10	0	5	2	1	0	1
n1	18	18	18	18	18	18	18	18
n2	22	12	7	30	5	13	13	10

	S-P	S-H	S-T	S-A	S-I	S-O	S-N
C	10	2	8	3	1	1	1
n1	22	22	22	22	22	22	22
n2	12	7	30	5	13	13	10

	P-H	P-T	P-A	P-I	P-O	P-N
C	0	2	0	0	0	0
n1	12	12	12	12	12	12
n2	7	30	5	13	13	10

	H-T	H-A	H-I	H-O	H-N
C	6	1	2	1	1
n1	7	7	7	7	7
n2	30	5	13	13	10

	T-A	T-I	T-O	T-N
C	3	6	5	5
n1	30	30	30	30
n2	5	13	13	10

	A-I	A-O	A-N
C	4	2	4
n1	5	5	5
n2	13	13	10

	I-O	I-N
C	8	9
n1	13	13
n2	13	10

	O-N
C	6
n1	13
n2	10

Fig. 2

Comparison of Early Llanvirn faunas of the nine selected areas. C is the number of taxa in common, n_1 is the total number of taxa in the first locality, and n_2 is the total number of taxa in the second locality. Abbreviations as in Fig. 1. The total fauna (that is the platform genera/species together with the oceanic and marginal fauna) is shown to the left and the shelf fauna is shown to the right. The figure shows, for example that Baltica (B) and Stein (S) contained 26 and 39 taxa respectively, and that the two localities have 24 taxa (genera or species) in common.

In conclusion, there is good evidence for the assumption that the spatial distribution of conodonts was very much dependent on paleoecological factors. The importance of considering biofacies before identifying faunal provinces was already shown by FORTEY (1975), who gave an elegant example based on Early Ordovician trilobites.

DATA ACQUISITION

The fauna includes 80 different conodont taxa (69 species belonging to 36 genera in addition to 11 genera which have not been subdivided into species) from nine localities (or areas) situated on both sides of the Iapetus Ocean (Fig. 1). It should be noted that the selected localities represent key areas for the topic in discussion. However, they represent only a limited fraction of the total amount of data available in the areas surrounding the Iapetus Ocean.

All faunas included are of Early Llanvirn age and correlate with the Baltic *Lenodus variabilis* and *Eoplacognathus suecicus* zones or the Laurentian *Histiodella holodentata* and *Phragmodus harrisi* zones.

TOTAL FAUNA

	Dice	Jaccard	Simpson
	2C/(N1+N2)	C/(N1+N2-C)	C/N1
B-S	0.74	0.59	0.92
B-P	0.73	0.57	0.89
B-H	0.00	0.00	0.00
B-T	0.26	0.15	0.35
B-A	0.18	0.10	0.38
B-I	0.05	0.03	0.07
B-O	0.00	0.00	0.00
B-N	0.05	0.03	0.09
S-P	0.56	0.39	0.89
S-H	0.13	0.07	0.38
S-T	0.46	0.30	0.49
S-A	0.17	0.09	0.50
S-I	0.04	0.02	0.07
S-O	0.04	0.02	0.07
S-N	0.04	0.02	0.09
P-H	0.00	0.00	0.00
P-T	0.16	0.09	0.28
P-A	0.00	0.00	0.00
P-I	0.00	0.00	0.00
P-O	0.00	0.00	0.00
P-N	0.00	0.00	0.00
H-T	0.27	0.16	0.88
H-A	0.25	0.14	0.25
H-I	0.17	0.10	0.25
H-O	0.09	0.05	0.13
H-N	0.11	0.06	0.13
T-A	0.23	0.13	0.75
T-I	0.24	0.13	0.47
T-O	0.21	0.12	0.43
T-N	0.22	0.12	0.55
A-I	0.43	0.28	0.63
A-O	0.27	0.16	0.38
A-N	0.53	0.16	0.63
I-O	0.62	0.45	0.64
I-N	0.77	0.63	0.91
O-N	0.56	0.39	0.64

SHELF FAUNA

	Dice	Jaccard	Simpson
	2C/(N1+N2)	C/(N1+N2-C)	C/N1
B-S	0.80	0.67	0.89
B-P	0.67	0.50	0.83
B-H	0.00	0.00	0.00
B-T	0.21	0.12	0.28
B-A	0.17	0.10	0.60
B-I	0.06	0.03	0.15
B-O	0.00	0.00	0.07
B-N	0.07	0.04	0.00
S-P	0.59	0.42	0.83
S-H	0.14	0.07	0.29
S-T	0.31	0.18	0.36
S-A	0.22	0.13	0.60
S-I	0.06	0.03	0.08
S-O	0.06	0.03	0.08
S-N	0.06	0.03	0.10
P-H	0.00	0.00	0.00
P-T	0.10	0.05	0.17
P-A	0.00	0.00	0.00
P-I	0.00	0.00	0.00
P-O	0.00	0.00	0.00
P-N	0.00	0.00	0.00
H-T	0.32	0.19	0.86
H-A	0.17	0.09	0.14
H-I	0.20	0.11	0.29
H-O	0.10	0.05	0.14
H-N	0.12	0.06	0.14
T-A	0.17	0.09	0.60
T-I	0.28	0.16	0.46
T-O	0.23	0.13	0.38
T-N	0.25	0.14	0.50
A-I	0.44	0.29	0.80
A-O	0.22	0.13	0.40
A-N	0.53	0.13	0.80
I-O	0.62	0.44	0.62
I-N	0.78	0.64	0.90
O-N	0.52	0.35	0.60

Fig. 3
Computed Dice, Jaccard and Simpson coefficients for the total faunas and shelf faunas respectively. Abbreviations as in Fig. 1. A higher number indicates a higher similarity.

The investigation has been restricted to this interval to minimalize the possibility of comparing faunas of different age. It is impossible, however, to avoid the problem of diachronism completely when faunas from different realms are being compared and the correlation of the conodont zones is still debatable.

The south-eastern Iapetus margin areas are represented by data from (1) the proximal part of the Baltic shelf (data from Viira 1974; Löfgren 1985; Stouge and Bagnoli 1990; Rasmussen 1991); (2) Stein (south-central Norwegian Caledonides), which was situated on the western, outer margin of Baltica (Rasmussen and Bruton 1994; Rasmussen in press); and (3) Małopolska, Holy Cross Mountains, southern Poland (Dzik 1994). Data from areas on the western side of the Iapetus Ocean (Laurentia) were obtained from (1) Ibex, Utah (Ethington and Clark 1982); (2) Antelope Valley, eastern Nevada (Harris *et al.* 1979); (3) eastern Oklahoma (Bauer 1987); (4) Table Head, western Newfoundland (Stouge 1984); and (5) Kronprins Christian Land, eastern North Greenland (Ineson *et al.* 1986, Peel and Smith 1988, Rasmussen unpublished). An ancient intra-Iapetus island setting is represented by data from Hølonda, central Norway (Bergström 1979). For the faunal list, taxonomic interpretations of the original authors have been used whenever possible (in most cases), whereas the present author's interpretation has been favored in cases of disagreement.

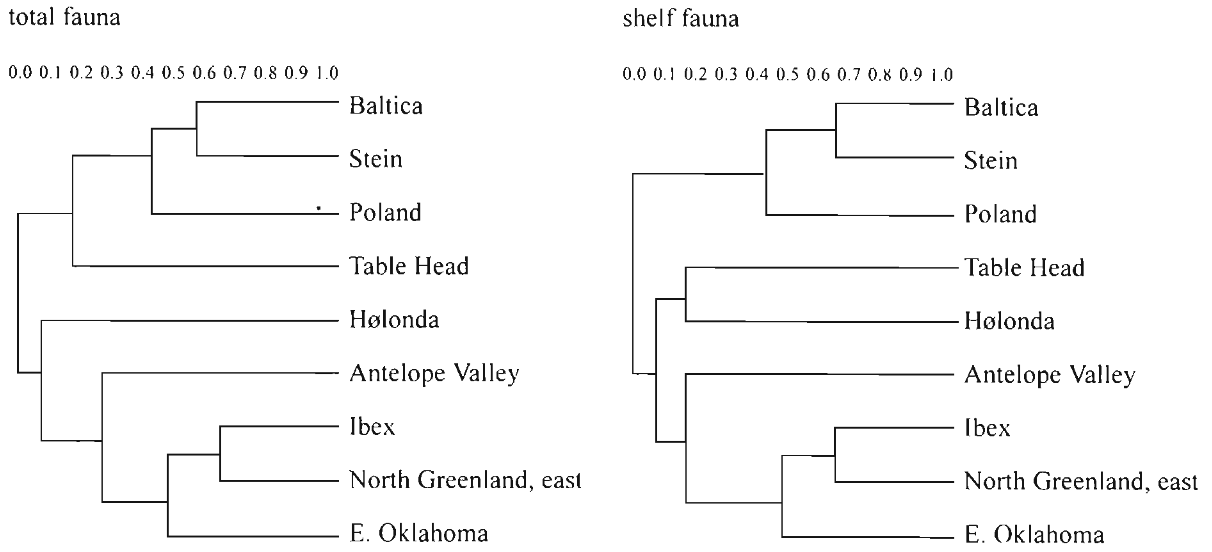

Fig. 4

Dendrogram showing average pair group clustering based on the Jaccard coefficients (see Fig. 3). The horizontal axis represents the degree of likeness; clusters with values close to 1.0 indicate high similarity levels. Note that clustering based on the Jaccard coefficients, which mainly tend to underline differences between the compared faunas, produced dendrograms that are very similar to the dendrograms based on the Dice coefficient (Fig. 5). The latter coefficient tends to accentuate similarities.

The nine localities have been compared one to one with respect to their individual faunas (Fig. 2). The values for the total fauna are shown on the left and those for the shelf fauna only on the right. It was shown by RASMUSSEN and STOUGE (1995) that taxa of the *Protopanderodus–Periodon* Biofacies are pandemic, typically occurring in the outer shelf, slope and basin settings. Characteristic taxa of this biofacies include *Ansella* spp., *Dapsilodus viruensis, Paroistodus horridus, Periodon* spp., *Protopanderodus* spp., and "*Walliserodus*" spp. The shelf fauna, that is the total fauna with the deep-water species of the *Protopanderodus–Periodon* Biofacies excluded, includes 59 taxa (50 species classified into 31 genera and 9 additional genera that have not been subdivided into species) and is listed on the right side of Figs 2 and 3.

An overview of the number of taxa (genera and/or species) in common (C), the total number of taxa in a given first locality (n_1), and the total number of taxa in a given second locality (n_2) are listed in Fig. 2. For example, as shown in the upper left corner, that the inner shelf of Baltica contains 26 taxa, Stein 39 taxa, and that the two localities have 24 taxa in common.

QUANTITATIVE METHODS

The paleobiogeographical analysis presented here is based on computer-aided, multivariate analysis, typically used to examine many variables simultaneously (KOVACHS 1988). These techniques include two major groups – ordination and cluster analysis – which both aim to simplify multidimensional data by reducing the number of dimensions.

Ordination methods rearrange the original data-points in a multidimensional space, along new dimensions (principal axes) that explain maximum possible amount of variation. The outcome of an ordination is typically a two or three dimensional scatter plot, where the First Axis (or first dimension) is the axis representing the direction of the most significant variation among the data-points, the Second Axis represents the direction of the second-most significant variation, etc.

Cluster analysis organizes the objects in a two-dimensional dendrogram by forcing the data into discrete groups. Before the actual clustering takes place, a correlation between the original data points is computed by use of a similarity or distance coefficient. Accordingly, it is the calculated correlation matrix that

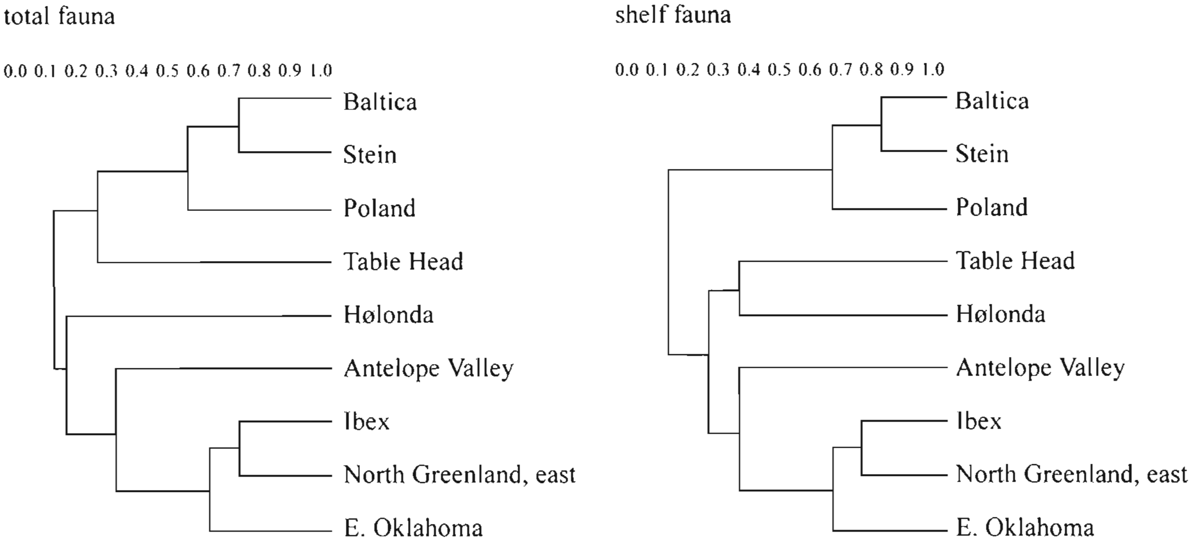

Fig. 5
Dendrogram showing average pair group clustering based on the Dice coefficients. See comments in Fig. 4.

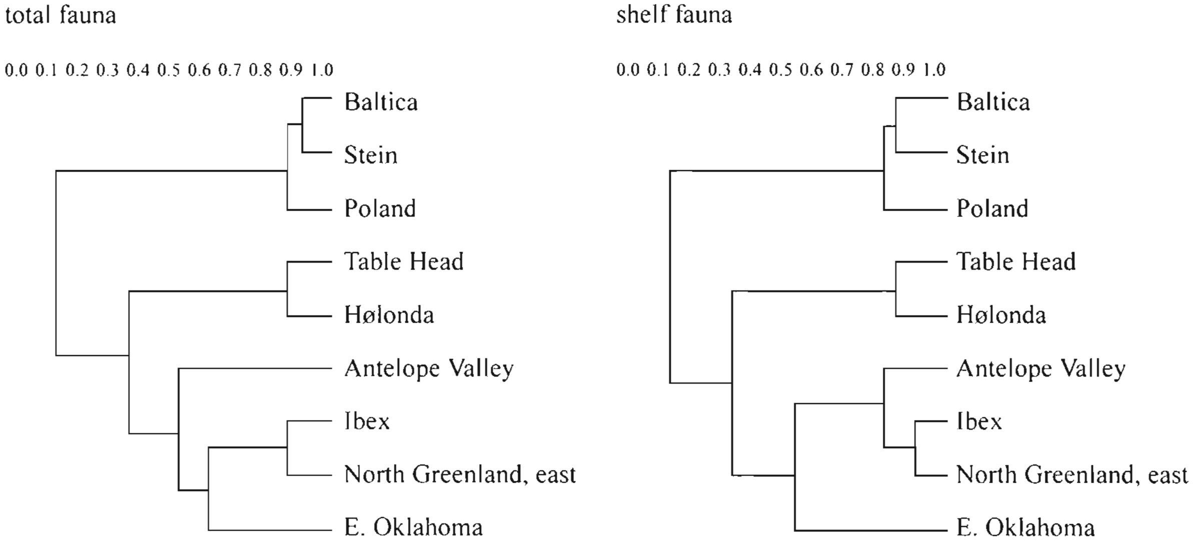

Fig. 6
Dendrogram showing average pair group clustering based on the Simpson coefficients. Note, that both the clustering of the shelf fauna and the total fauna produce three distinct clusters: A Baltoscandian Province cluster, a North America Interior Province cluster and a marginal Laurentian cluster.

determines the position of the individual objects in the dendrogram. A similarity coefficient gives a value for likeness between two samples. Among the most accepted coefficients for biogeographical analyses are the Jaccard, Dice, Otsuka and Simpson indices (see e.g. CHEETHAM and HAZEL 1969) and the Provinciality Index of JOHNSON (1971). Various ordination methods are also popular, e.g. Correspondence Analysis and Principal Component Analysis. For biogeographical analyses, the methods give the most convincing results when they are based on binary data because it is the actual presence or absence of a certain species or genus that is important rather than the relative abundance (see e.g. SHI 1993). In contrast, the relative abundance is essential in paleoecological analyses, meaning that the precise (absolute or relative) number of specimens of each species in each sample or locality forms the database.

The present investigation has focused on clustering of the Jaccard ($C/(N_1+N_2-C)$), Dice ($2C/(N_1+N_2)$), and Simpson (C/N_1) coefficients (Fig. 3) using the MVSP software (KOVACHS 1990), where C is the number of taxa the two faunas (or areas) share in common, N_1 is the number of taxa for the fauna with fewer taxa, and N_2 the number of taxa for the fauna with greater number of taxa. The Jaccard coefficient expresses the similarity as the number of taxa in common between the faunas divided by the number of taxa limited to one of the two faunas, or more simply, the percentage of taxa in common if the coefficient is multiplied with 100. It is often a problem, however, that one of the two faunas is better known or investigated than the other, which may cause a significant, "false" difference between the two faunas. It is also important to keep in mind that this method will give low values if there is a significant difference in diversity between the two faunas, even if the taxa from the less diverse fauna do occur in the more diverse fauna. The Dice (or Sørensen) coefficient expresses the similarity as the number of taxa in common divided by the average total number of taxa. Hence, faunal similarities play a relatively more important role here, than in the Jaccard coefficient. In a comprehensive study of the changing conodont provinces during the Early Paleozoic, BERGSTRÖM (1990) used an identical coefficient named "Coefficient of Similarity". The Simpson coefficient is suitable when two faunas differ notable in diversity. This is because the coefficient is normalized to the less diverse fauna: the coefficient will be high if the less diverse fauna has most taxa in common with the more diverse fauna. A disadvantage is, however, that a possible high number of endemic taxa within the more diverse fauna will be hidden, and therefore, will have no influence on the computed degree of similarity. The final dendrograms (Figs 4–6) were obtained by unweighted average pair group clustering of the computed coefficients.

INTERPRETATION

All the computed coefficients result in dendrograms with two distinct clusters: the Baltoscandian cluster comprising faunas from the inner platform of Baltica, Stein, and the Małopolska area in Poland, and the Midcontinent cluster comprising Ibex, North Greenland, and eastern Oklahoma, and Antelope Valley. These two main clusters are distinct both when the total faunas and the shelf faunas are used as input matrix. The distinct similarity between the two Baltoscandian faunas (Baltica and Stein) and Poland (Małopolska) is related to the position of the latter area, which either was situated on the southern margin of Baltica, or, what seems more likely, represented a small microcontinent situated just south of Baltica (DZIK and PISERA 1994) (Fig. 1). The close similarity between Ibex, North Greenland, and, in most cases, also east Oklahoma, is a result of the equal shallow-water, tropical depositional environments that characterized these areas. The significant distance (probably more than 4000 km) between eastern North Greenland and Ibex, apparently did not hinder free migration of conodonts around the Laurentian craton in the Early Llanvirn times. Antelope Valley is linked more distantly to the other Laurentian localities, probably because it was deposited in a deeper (outer shelf or slope) environment. It seems clear, however, that a notable faunal communication with the neighbouring, shallower parts of the shelf (Ibex) existed.

In case of the localities situated on and off the south-eastern margin of Laurentia, the situation is quite different. When the dendrograms are based on the Jaccard and Dice coefficients of the total faunas, Table Head clusters more closely to the Baltoscandian localities than to the Laurentian ones. This is obviously why Table Head and related areas on the western Laurentian margin were incorporated in the former "North Atlantic Province" (or Baltic Province of BERGSTRÖM 1990) (Fig. 7B). In contrast, Table Head clusters closely together with Hølonda when the pandemic taxa of the deeper-water *Protopanderodus–Periodon* Biofacies are excluded from the data matrix. In both the Dice and Jaccard dendrograms based on the cratonic taxa, the Table Head – Hølonda cluster is linked more closely to the Laurentian sites than to the Baltoscandian ones.

Cluster analysis based on Simpson coefficients does not indicate any notable differences between the two input matrices. In both cases (for shelf and for total faunas), three distinct clusters occur: (1) Baltoscandian or Baltic cluster comprising Baltica, Stein, and Poland; (2) Laurentian comprising Ibex, North Greenland, Antelope Valley, and eastern Oklahoma, and finally (3) a marginal, ocean-near cluster comprising Table Head and Hølonda. In both analyses, the Table Head – Hølonda cluster is linked more closely to the Laurentian cluster than to the Baltoscandian. The reason for the closer similarity of shelf faunas of Table Head and Hølonda samples is, most likely, the fact that Hølonda was an ocean island situated relatively close to the Laurentia's margin (BERGSTRÖM 1979), and that the two areas displayed similar environmental conditions. In comparison, it is interesting to note that *Multioistodus* spp. (*Neomultioistodus* sp. here) and *Histiodella* aff. *tableheadensis* have been documented from the Hornsundtind Limestone, southern Spitsbergen (SZANIAWSKI 1994). *Neomultioistodus* is not known from Baltica, but is

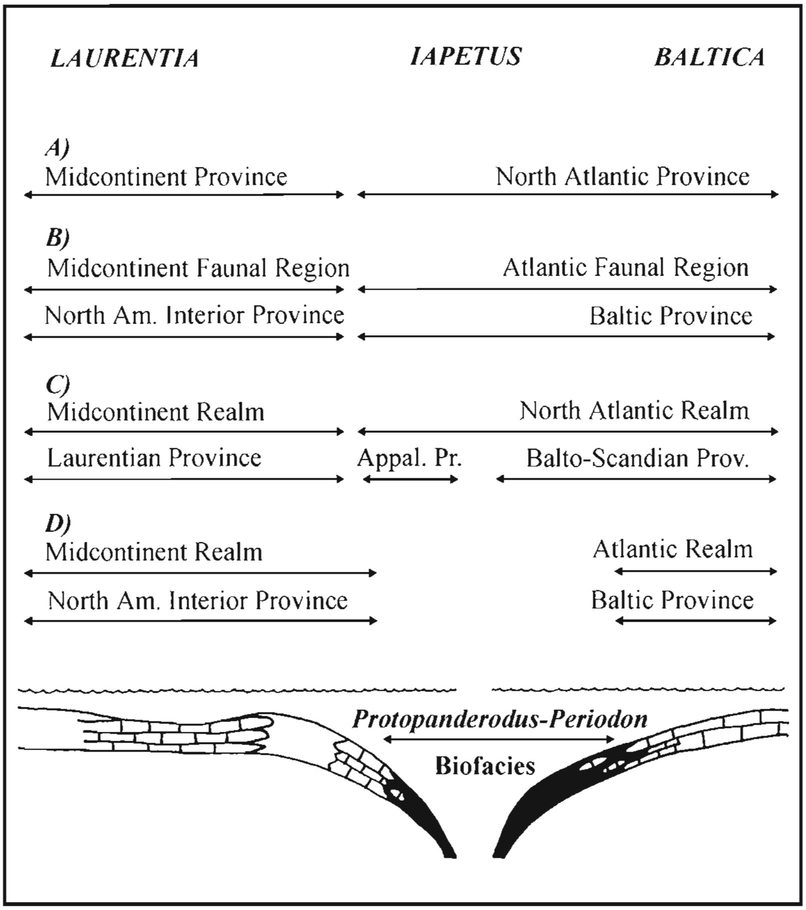

Fig. 7

A. The "classical" conodont province model for the Iapetus region (e.g., Barnes *et al.* 1973; Bergström 1973; Fortey and Barnes 1977). The North Atlantic Province typifies Baltica as well as the marginal areas of Laurentia. **B**. The model by Bergström (1990) differs from model **A** by a subdivision of the two major faunal regions into provinces. The Atlantic Faunal Region includes the Baltic Province (Baltica and parts of the Laurentian marginal areas) and the Mediterranean Province. **C**. A further subdivision of the North Atlantic Realm was made by Pohler and Barnes (1990), who subdivided it into the Balto-Scandian Province (Baltica) and the Appalachian Province (south-eastern margin of Laurentia). **D**. The combined province-biofacies model. The general outline is somewhat similar to (**B**) and (**C**), but with one important difference: that is, the conodont faunas of the Iapetus Ocean and the surrounding marginal platform areas are not regarded as members of a certain conodont realm, but instead as a suite of genera and species of the pandemic *Protopanderodus–Periodon* Biofacies. Future studies may confirm the existence of the Appalachian Province, but possibly as a subdivision of the Midcontinent Realm.

common in Laurentia. Thus, the assumption that, in the Early Llanvirn, Spitsbergen was situated relatively close to Laurentia (Northeast Greenland) (see review by Harland *et al.* 1988) is further supported.

Pohler (1994) divided the upper Arenig sections at Cow Head, Western Newfoundland (Bed 13/14), into two different biofacies: the *Periodon–Parapanderodus* Biofacies typical of the shelf edge environment and the *Periodon* Biofacies characterizing the lower slope environment. Moreover, she distinguished the *Trigonodus–Tetraprioniodus* Biofacies (= *Trigonodus–Eoneoprioniodus*? Biofacies of Stouge [1984]) characterizing the contemporary shelf environment. She followed the opinion of Stouge (1984) and referred the latter to the Midcontinent Realm, while the *Periodon–Parapanderodus* Biofacies was shown to constitute "typical North Atlantic Realm" species (80%) mixed with a minor content of typical Midcontinent species (9%), endemic species (3%) and Argentinian elements (0.5%). Seven percent of the fauna was characterized as cosmopolitan. The *Periodon–Parapanderodus* Biofacies of Pohler corresponds to the *Acodus*? *combsi* Biofacies of Stouge (1984), that was interpreted as reflecting a carbonate buildup environment between the outer shelf and the upper slope. Both the *Periodon–Parapanderodus* and the *Periodon* Biofacies were regarded as being members of a subprovince of the North Atlantic

Province (POHLER 1994: p. 22) (compare with Fig. 7C). All the species that were mentioned as typical for the Lower Slope Biofacies (*Periodon* Biofacies) in Bed 13 occur also at the western margin of Baltica (RASMUSSEN in press) as well as in other ocean-facing settings. The faunas described by POHLER (1994) are slightly older than the faunas analyzed in this paper. However, it is the present author's interpretation that the *Periodon* Biofacies of POHLER (1994) corresponds to the *Periodon–Cordylodus*? Biofacies (STOUGE 1984) and the pandemic (cosmopolitan) *Protopanderodus–Periodon* Biofacies (RASMUSSEN and STOUGE 1995), which is not restricted to a certain realm. In contrast, the faunas of the shelf edge *Periodon–Parapanderodus* Biofacies should possibly be regarded as members of a province (probably the Appalachian Province) of the Midcontinent Realm rather than members of the Atlantic Realm. The reason for this is that the *Periodon–Parapanderodus* Biofacies apparently did not contain any species restricted to the Baltic craton but did contain species endemic to the Laurentian craton.

CONCLUSION

When the pandemic, deeper-water faunas of the *Protopanderodus–Periodon* Biofacies is excluded from the input data set, faunas of the Table Head and related sites on the western, Laurentian margin have more in common with the Midcontinent rather than Baltoscandian faunas. This may question the current interpretation of the conodont provinces in the Iapetus region, and lead to a revision of the "classic" paleobiogeographic model for the Iapetus Ocean. As a concequence, the Atlantic Realm did not occur on the north-western side of the Iapetus Ocean (Fig. 7D). It was restricted to the south-eastern side of the Iapetus Ocean and did probably extend to the areas east of Baltica (BERGSTRÖM 1990). The Baltoscandian Province was restricted to Baltica and the neighbouring areas (e.g. Małopolska). Taxa belonging to the *Protopanderodus–Periodon* Biofacies (RASMUSSEN and STOUGE 1995) were pandemic and occurred within the Iapetus Ocean as well as on the surrounding continental slopes and outer shelves of Laurentia, Baltica, and other continents (e.g. South America and South China). The faunas do not indicate relationships to a specific conodont realm. Cluster analysis based on the Simpson coefficients may indicate that the shelf faunas from Table Head and Hølonda belonged to a separate conodont province, probably the Appalachian Province of POHLER and BARNES (1990), but more analyzes need to be carried out to confirm this. If this separate province is correctly identified, the Appalachian Province should likely be regarded as a subdivision of the Midcontinent rather than Atlantic Realm.

In conclusion, it is necessary to exclude pandemic, deeper water conodont faunas from a data-set, before paleobiogeographic models can be tested. When deep-water faunas are included, the calculations and conclusions can be significantly distorted. This problem has already been recognized for other fossil groups, e.g. trilobites (FORTEY 1975), but has been difficult to apply for conodonts, because of the, hitherto, relatively poor knowledge of their paleoecology.

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