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A QUANTITATIVE APPROACH TO FAUNAL PROVINCE ANALYSIS

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ABSTRACT. Provinciality of brachiopods on the North American continent is known to have been strong during Early and Middle Devonian time, but cosmopolitan brachiopod faunas were the rule during the Frasnian. The existence of provinces and the areas they occupied have been predetermined by qualitative methods. The strength of endemism and the contrasting pervasiveness of cosmopolitanism is expressed by degrees of faunal resemblance which can be measured by a Provinciality Index (PI) consisting of a weighted ratio of common and endemic genera. Values obtained, utilizing all brachiopod genera known in North America during Early Devonian to Frasnian time, without exception confirm prior conclusions that provinciality between eastern and western North America was strongest during the late Early Devonian to Middle Givetian interval. Breakdown of east-west provinciality coincident with latest Middle Devonian (Taghanic) onlap, across the continental backbone, is also confirmed by a significant jump in a chronologic series of PI values. Separate regions within the western province provide PI values consistently in accord with east-west comparisons.

Extra-North American PI values strikingly confirm a similar picture reflecting strong Early and Middle Devonian provinciality (between the Appalachian Province and Europe) and Frasnian cosmopolitanism of nearly global extent.

All values computed are consistent with the hypothesis that land barriers were of prime importance to the formation of Devonian provinces. Significant aspects of brachiopod provinciality are not dependent on random factors, so that province analysis can assist in the understanding of the timing and extent of tectonic events.

INTRODUCTION

In recent years increasing attention has been given to the delineation of Paleozoic faunal provinces and realms based on megafauna. Of particular note is attention that has been given to the Ordovician (Spjeldnaes, 1961; Whittington, 1966; Fell, 1968; Williams, 1969; and Ross and Ingham, 1970). Similar work has been conducted for the Devonian (Boucot, Johnson, and Talent, 1969; Johnson, 1970b). Hallam's (1969) work in the Jurassic, Simpson's (1947) dealing with Cenozoic mammals, and Valentine's (1966) work on living molluscan faunas are also noteworthy because of their referential significance.

In the variety of efforts described above various conclusions have been proposed to account for provinciality of the animals studied, or in some cases the published reports were largely descriptive. In any event both qualitative and quantitative procedures have been employed in the analysis of provinciality. The qualitative approach is exemplified by the work of Whittington (1966), Boucot, Johnson, and Talent (1969), and Hallam (1969). The quantitative approach has been employed by Simpson (1947), Valentine (1966), and Williams (1969). In general, it is true that earlier efforts dealing with a particular faunal element and

time span have been of a qualitative nature and that later efforts of numerical analysis have been attempted in order to codify provincial entities and boundaries more rigorously.

In recent work (Johnson, 1970b) I have attempted to demonstrate the waning of provinciality of Devonian faunal provinces, based on brachiopods, coincident with broad onlap of epeiric seas and thus that land barriers have played a major role in the isolation of certain marine regions, allowing increased speciation and divergence of brachiopod lineages at higher levels, to account for the known provincial developments. From this point of view it became evident that a way to express degrees of provinciality and/or cosmopolitanism would be of particular value. The present paper is an attempt to answer that need by providing an easily applied method of quantitative analysis. Except for Simpson's (1947) work the several papers listed above as employing a quantitative approach have used methods of cluster analysis in order to delineate provinces and province boundaries by comparing many separate faunas that constitute the whole mass of unsorted faunal distribution information. The method and results described below reflect a different approach to these problems in which the provinces, believed to be objective realities, are predetermined by qualitative methods. Numerical methods are then employed to demonstrate the degree of provinciality between known provinces and the waning of provinciality or cosmopolitanism through time.

ACKNOWLEDGMENTS

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THE METHOD EMPLOYED

My own work with Devonian provinces, based on brachiopods, has been strictly at the generic level so, for the illustration to follow, the named genera compose the units for quantification. The number of named genera and the degrees of distinction upon which they are based certainly is strongly dependent on the human factors reflecting the predilections of brachiopod workers. Therefore, the genera do not form ideal units for numerical analysis. An attempt to ameliorate this situation has been made by grouping one or more genera together as a unit, whenever it is judged that these genera are based on relatively small distinctions or are so poorly known that problems of recognition hamper their usefulness. Because provinciality is known to wax and wane through time, time intervals form the second group of important parameters—intervals short enough yet with distinct enough boundaries so that they can be utilized on a continental or even a world-wide basis. Intervals varying from about a stage to a series have proved satisfactory in the Devonian. The third entity to be considered comprises the provinces themselves, predetermined according to qualitative evaluations.

In actual practice the fauna of a broad paleogeographic area, which constitutes a province, is often known from a series of monographs and

smaller papers. It is a simple matter to compile a list of genera by the single investigator's perusal of the published illustrations. Search of published illustrations by one person assures that the differing lists, on which the whole study is based, are not the result of taxonomic divergences of investigators studying distant areas. Faunal lists are unsatisfactory unless the investigator has a personal knowledge of the techniques and foibles of the author whose work is being examined. A master compilation for one area is built up in this way and is then reduced to a single alphabetical list for later comparison.

The initial impetus for the present investigation was to compare provinciality east and west of the continental backbone of North America during various periods of the Devonian. Consequently, lists were prepared for the Great Basin and for northwestern Canada and the Arctic Islands, on the west, and for all of the Appalachian area and the central lowlands, east of the continental backbone, which together constitute the Appalachian Province. For these comparisons, restricted to the North American continent where the author has a fairly good grasp of the total Devonian brachiopod fauna, it was possible to define six successive time intervals with which to compare the eastern and western regions. Specifically these are Gedinnian to Early Siegenian, Middle and Late Siegenian, Emsian, Eifelian to Middle Givetian, Late Givetian (or early Taghanic), and Frasnian (including the late Taghanic and the part of the Frasnian that succeeds it). For each of the time intervals involved there are three sets of genera: one is the set endemic to the western areas, second is the set endemic to the eastern areas, and third is the set of genera common to both regions. It is important to realize that these numbers originate from a comparison of two faunas and cannot exist for a single region only. The only remaining necessity is for a method of expressing these three numbers in a way that seems a true measure of the provinciality of the genera, as opposed to other factors which come into play, such as the amount of work done in any given region or how diverse the available communities are in the regions evaluated. A simple percentage of the total which is cosmopolitan somewhat illustrates the degree of provinciality but seems less than satisfactory because it does not weight the factors mentioned above. In response to the data generated and the problems outlined above, a Provinciality Index (PI) was devised in order to express provinciality quantitatively. It is defined as follows:

$$PI = \frac{C}{2E_1}$$

in which C is the number of genera common to both regions being compared. The intent of the ratio is to divide the number of cosmopolitan genera by the total number of endemic genera. E_1 is defined as the smaller of the two available figures for endemic values corresponding to the separate regions with the result that the larger number is discarded when there is a considerable discrepancy. The reason for this is that in a poorly known region the number of genera able to qualify as endemics is usually very low. On the other hand a well studied region or one that

is known to contain many different communities provides a very extensive list of endemics—which, however, are not the result of provinciality. Conversely, when two regions are each well known, because of large efforts in studying the faunas and because a diverse number of communities is sampled in both regions, each list of endemics tends to become long as true provinciality increases. The weighted lower factor of the ratio then becomes insignificant.

As noted in the introduction, similar ratios have been employed by previous workers. Simpson (1947) provided an extensive discussion of the factors involved in defining a ratio with which to express faunal resemblance. The ratio proposed by Simpson was 100 C/N_1 where C is the number of taxonomic units common to both faunas being compared, and N_1 is the total number of taxonomic units in the smaller fauna. Jackson (1969) utilized Simpson's ratio in an evaluation of Ordovician graptolite faunas, and Williams (1969) utilized an almost identical ratio except that he did not multiply it by a factor of 100. The principal reason for use of the PI described above is that the range of values has proved to provide an easy visual evaluation of the results of comparison in which values below 1.0 satisfy the qualitative definition of provinciality and values above 1.0 coincide with cosmopolitan situations. In addition, exclusion of the cosmopolitan genera from the denominator has the effect of spreading extreme values away from a nondecisive figure. Simpson's ratio was also computed and is given in the four tables.

A NORTH AMERICAN EXAMPLE

Recapitulating the substance of my 1970b paper, in its simplest sense, the following can be said: it was apparent that the Middle Devonian faunas of the Great Basin and of western Canada were very different from those of the Appalachian Province. This has long been known and has generally been alluded to by mentioning the distribution of the single important and diagnostic late Middle Devonian brachiopod *Stringocephalus* (Boucot, Johnson, and Struve, 1966). Middle Devonian provincialism was shown to exist when a broad land area separated eastern and western marine areas (fig. 1). It was also known that in the succeeding Frasnian (and especially the later Frasnian) there existed a brachiopod fauna of world-wide extent, perhaps the most cosmopolitan brachiopod fauna ever known. One needs no numbers to convince himself of this fact. Nevertheless, the desire was to measure in time and degree the shift between Middle Devonian provinciality and Late Devonian cosmopolitanism. It had been shown, by analyzing a few sequential zones embraced by the Taghanic Stage (a stage that conveniently bridges the Middle Devonian-Upper Devonian boundary) that provinciality seemed to break down first at a particular time, early in the Taghanic, which was coincident with a great marine onlap forming widespread epicontinental seas across the continental backbone (fig. 2). Yet the Taghanic faunas themselves were not well known in the west—at least not well enough to be truly convincing to all concerned. The result of analysis of

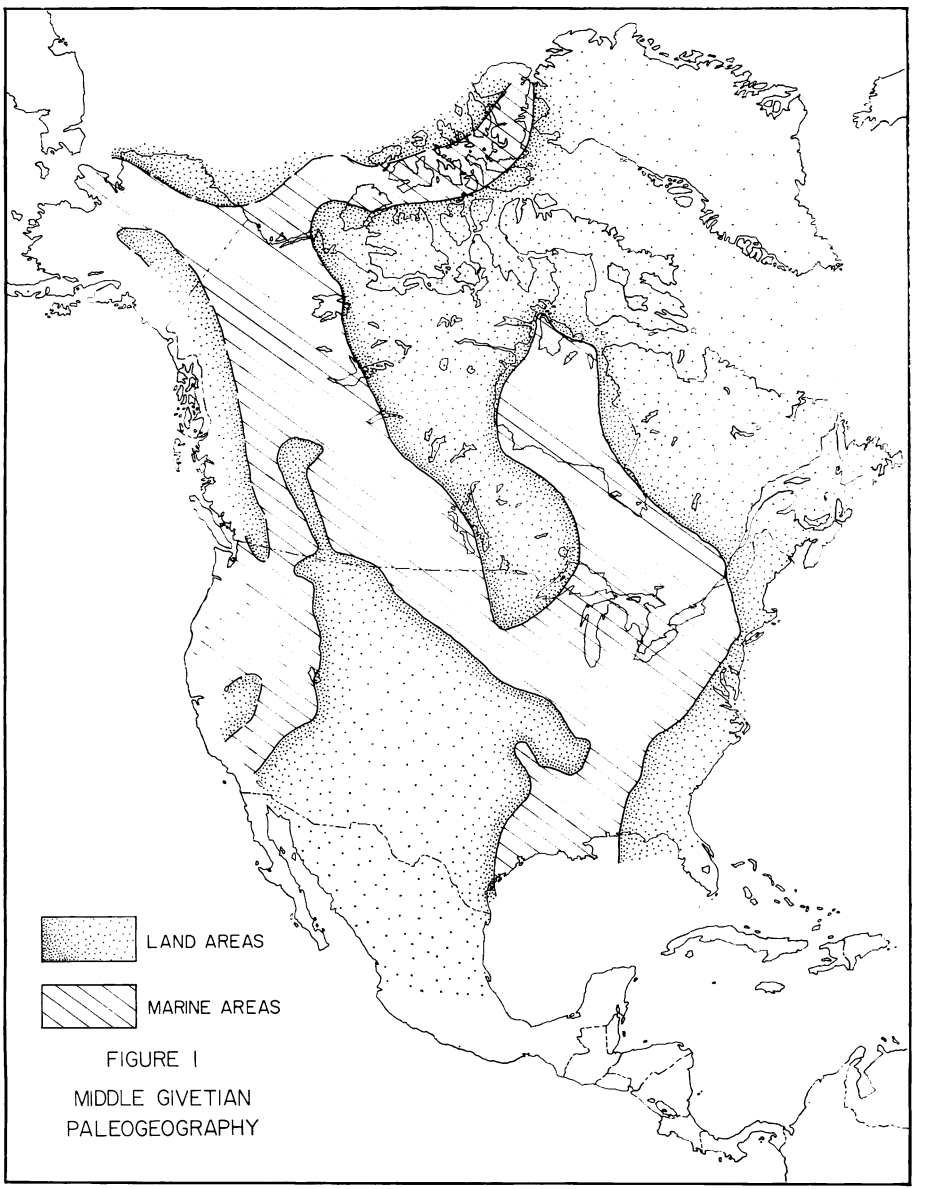

FIGURE 1
MIDDLE GIVETIAN
PALEOGEOGRAPHY

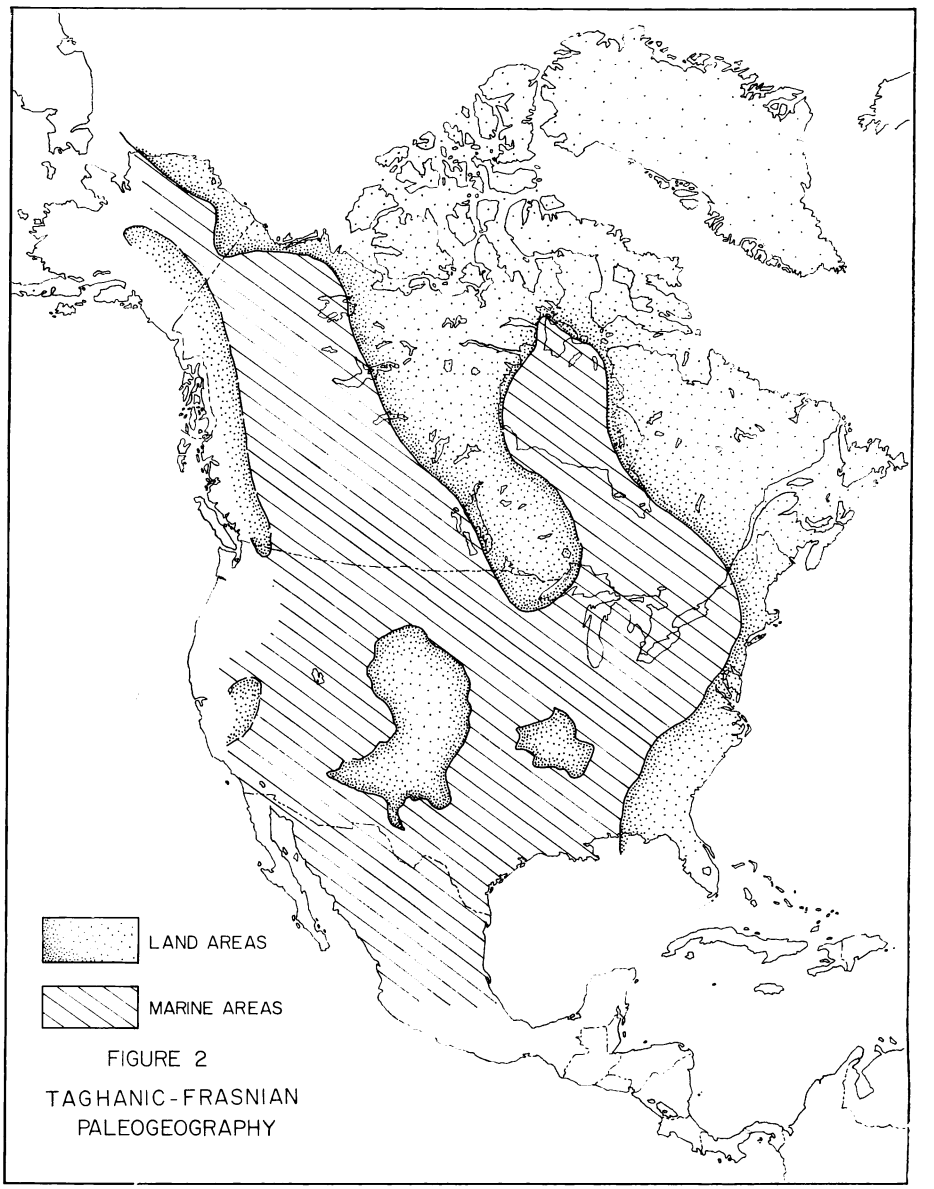

FIGURE 2
TAGHANIC-FRASNIAN
PALEOGEOGRAPHY

the Middle Devonian, the Taghanic, and the Frasnian by application of the Provinciality Index has provided a quantitative confirmation of the provincial shift as outlined earlier (Johnson, 1970b).

Data comparing the Great Basin and the Appalachian Province through the Early and Middle Devonian are listed in table 1. The Gedinnian to Early Siegenian interval (up to and including the *Quadrithyris* Zone of Nevada) is a known time of provinciality and yields a PI of 0.58. The near equal numbers of endemic genera in the two regions (28 and 24) attest to the fact that a comparable sampling is available in both regions.

During the succeeding interval of Middle and Late Siegenian central Nevada was known to contain many Appalachian-type genera of Helderbergian and Oriskany affinity, and it was pointed out elsewhere (Boucot, Johnson, and Talent, 1969) that the Great Basin was an enclave of the Appalachian Province during this time interval. The very strong jump in the PI to a value of 2.06 during this time interval attests to this observation.

TABLE 1

Comparison of Appalachian Province brachiopods with those from the Great Basin

Time interval	A	GB	C	Σ	%	SR	PI
Eifelian-Middle Givetian	51	25	14	90	15	36	0.28
Emsian	28	25	23	76	30	48	0.46
Middle and Late Siegenian	29	8	33	70	47	80	2.06
Gedinnian-Early Siegenian	28	24	28	80	35	54	0.58

A = Appalachian Province endemics
GB = Great Basin endemics
C = Genera common to both regions
Σ = Total of brachiopod genera in both regions
% = Percent of cosmopolitan genera in total brachiopod fauna
SR = Simpson's ratio
PI = Provinciality Index

In the Emsian, provinciality is known to have returned to such an extent that Boucot, Johnson, and Talent (1969) defined a Cordilleran Subprovince of the Old World Province on the basis of the Great Basin brachiopod assemblages. The degree of provinciality in the Emsian is reflected in the relatively low PI of 0.46.

Following the Emsian, the Eifelian to Middle Givetian interval yielded an even smaller PI of 0.28, indicating an increase in provinciality compared to conditions that prevailed during the Early Devonian. This number, when first derived, was something of a surprise because Boucot, Johnson, and Talent (1969) had been of the opinion that the Emsian was the time of greatest Devonian provinciality. Nevertheless, those workers had spent a great deal more time evaluating Emsian faunas than those

of the Middle Devonian. It is also clear that the discrepancy between the Emsian and the Eifelian to Middle Givetian values for the PI are enhanced by the fact that the Emsian fauna carries a number of holdovers from the cosmopolitan Middle and Late Siegenian interval. Genera in the Emsian fauna that can be described as Appalachian Province holdovers include *Anoplia, Coelospira, Leptocoelia, Megakozlowskiella, Metaplasia,* costate *Strophonella, Levenea,* and *Rensselaeria.* If these were removed an Emsian PI of 0.37 would result. Even so, the PI indicates a greater Eifelian to Middle Givetian provinciality, possibly due to the fact that Appalachian Province holdovers occupy niches that might otherwise be occupied by endemic genera. In summary, this initial test of east-west provincial relations shows an early provinciality, probably inherited from the Silurian, giving way to a well-defined Middle and Late Siegenian cosmopolitanism, but which is followed by a strongly provincial situation during the Emsian and most of the Middle Devonian.

To further assess east-west provinciality a set of comparisons was made between western and Arctic Canada and the Appalachian Province. The Early Devonian Canadian data comes from Yukon Territory and the Arctic Islands. The Middle Devonian and Frasnian data are from the shelf and basin-edge deposits of Alberta and Northwest Territories. During the Gedinnian to Early Siegenian interval there was a mild but definite provinciality comparable to that represented by the Great Basin Appalachian Province comparisons of table 1. In the succeeding interval of the Middle and Late Siegenian, provinciality is very strongly developed and is represented by the lowest PI observed in this study. This situation contrasts very strongly with that in the Great Basin which had a prominently cosmopolitan PI, and the great discrepancy is coincident with the faunal shift from an old World type fauna in the *Quadrithyris* Zone and an Appalachian Province fauna in the succeeding *Spinoplasia* Zone in central Nevada. Emsian provinciality was still very strong in Arctic Canada, represented by a PI of 0.18 during the time when Great Basin faunas were resuming a definite provinciality but one that was still influenced by Appalachian Province holdovers which affected the value of 0.46 in table 1. Very likely the still evident disparity of Emsian values is enhanced by the fact that developing Old World elements, established in the Middle and Late Siegenian in the Arctic and continued into the Emsian faunas, had little chance to become a part of Emsian faunas of the Great Basin.

In the interval Eifelian to Middle Givetian western Canadian faunas were still strongly provincial following a continual slow rise in the number of cosmopolitan elements compared to the Early Devonian, to a point where it is almost perfectly comparable to provincial relations in the Great Basin (that is, 0.29 versus 0.28). Table 2 includes two comparisons that were not made for Great Basin faunas due to the fact that they are lesser known at the younger intervals tested. The Taghanic comparison, utilizing Late Givetian faunas only, shows the first very marked depar-

TABLE 2

Comparison of Appalachian Province brachiopods with those from western and Arctic Canada

Time interval	A	WC	C	Σ	%	SR	PI
Frasnian	12	7	35	54	65	83	2.50
Taghanic (Late Givetian only)	30	6	22	58	38	79	1.83
Eifelian-Middle Givetian	54	19	12	85	13	39	0.29
Emsian	36	36	13	85	15	26	0.18
Middle and Late Siegenian	53	36	9	98	9	20	0.12
Gedinnian-Early Siegenian	38	18	17	73	23	49	0.47

A = Appalachian Province endemics
WC = Western and Arctic Canada endemics
C = Genera common to both regions
Σ = Total of brachiopod genera in both regions
% = Percent of cosmopolitan genera in total brachiopod fauna
SR = Simpson's ratio
PI = Provinciality Index

ture from provincial conditions, exemplified by a PI of 1.83. The Frasnian, widely known to be strongly cosmopolitan even on a world-wide scale, is represented by the highest value derived in this study, equaling a PI of 2.50. These last two comparisons of Late Givetian (Taghanic) and Frasnian bear out the conclusions presented elsewhere (Johnson, 1970b) that the breakdown in east-west provinciality in North America first became marked during the Taghanic, a time that was shown to be the time of initial important onlap of epeiric seas over the continental backbone. In retrospect, it is the only logical solution because, given a strongly provincial Middle Devonian situation and a strongly cosmopolitan Late Devonian situation, it is reasonable that stages in the breakdown of provinciality should coincide with the temporal divisions at the transition.

The Great Basin and northern areas in western Canada were compared separately with Appalachian Province faunas, because the separate breakdown was an obvious procedure. In fact, it would take additional steps to compile the combined faunas during any one time interval. Table 3 compares provincial relations between the Great Basin and the western and Arctic faunas through the time intervals of interest. Gedinnian to Early Siegenian time reveals a PI of 1.25, indicating the expected cosmopolitanism. Very likely the lack of detailed knowledge of the Arctic Gedinnian results in the relative lowness of that PI because individual assemblages are so similar between the two regions that they can be correlated zone for zone. However, the situation is vastly different during the Middle and the Late Siegenian, the time when Nevada became an Appalachian Province enclave. The small PI of 0.18 reflects the especially marked differences between Old World-type faunas in Yukon territory and the Arctic Islands compared to the Appalachian assemblages that

TABLE 3
Comparison of Great Basin brachiopods with those from western and Arctic Canada

Time interval	GB	WC	C	Σ	%	SR	PI
Early and Middle Givetian	12	7	22	41	53	76	1.57
Eifelian-Middle Givetian	16	9	23	48	48	72	1.28
Emsian	20	20	28	68	41	58	0.70
Middle and Late Siegenian	30	34	11	75	15	27	0.18
Gedinnian-Early Siegenian	25	10	25	60	42	71	1.25

GB = Great Basin endemics
WC = Western and Arctic Canada endemics
C = Genera common to both regions
Σ = Total of brachiopod genera in both regions
% = Percent of cosmopolitan genera in total brachiopod fauna
SR = Simpson's ratio
PI = Provinciality Index

occur in the Rabbit Hill Limestone and in the lower part of the McColley Canyon Formation in central Nevada. During the Emsian, just as the Nevada faunas were recovering from the cosmopolitan Appalachian situation, the resemblance rises, represented by a somewhat intermediate 0.70 PI and indicating some degree of still maintained provinciality. However, by the Middle Devonian, represented in table 3 by the Eifelian to Middle Givetian interval, cosmopolitanism between the Canadian and Great Basin regions was reinstated. When one compares only the Early and Middle Givetian, cosmopolitanism is indicated by a respectable 1.57 PI. This probably is a more significant figure because the Eifelian faunas of western Arctic Canada are the poorest known of any evaluated here.

The patterns summarized in tables 1 to 3 reveal a consistent picture which numerically seems to reflect accurately the conditions that can be seen from a qualitative analysis. Reasons for the influx of Appalachian Province genera into the Great Basin during the middle and late parts of the Siegenian, thereby upsetting the even cycle of continually heightened provinciality during the late Early Devonian and Middle Devonian followed by a waning of provinciality into the Frasnian, are uncertain. A possible cause suggested earlier (Johnson, 1970b) is that the Middle Siegenian (equals late Helderbergian) corresponded to a time of onlap across the southern part of the continental backbone in the regions of New Mexico and West Texas which resulted in the capability of Appalachian-type faunas to move westward and in a new pattern of marine circulation such that temperature boundaries, which may have been province-limiting, underwent a strong shift northward.

Table 4 presents selected comparisons of intercontinental scope. Comparisons during the Early Gedinnian, between eastern North America and Europe, reveal an intermediate PI value of 1.04, indicating a possible mild but poorly defined cosmopolitanism. This is closely in accord

with the earlier evaluation of Boucot, Johnson, and Talent (1969). However, in the succeeding, relatively long interval of Middle and Late Siegenian plus Emsian a PI of 0.25 indicates well-defined provincial relations, and a test of the whole Middle Devonian between eastern North America and Europe reveals a closely comparable PI of 0.27. These two latter values through the intervals from Middle Siegenian to the end of the Middle Devonian indicate the even strength of continuity of the provincial situation (that is, Middle Devonian provinciality is virtually as strong as late Early Devonian provinciality) that was first noticed in the test of Middle Devonian faunas between the Great Basin and the Appalachian Province. The Frasnian comparison, presented in table 4, is between all Frasnian brachiopod faunas of North America and those of the Russian Platform and Main Devonian Field south of Leningrad. Even for so great a distance a well-defined cosmopolitan situation is revealed by the PI of 1.50, in line with the intra-North American situation and early evaluations which seemed to require a world-wide cosmopolitan Frasnian fauna. A final comparison was made between North America and a distant Frasnian occurrence, that is that of western Australia, and even though the known fauna of western Australia is small, a satisfactorily mild cosmopolitan situation results, as indicated by a PI of 1.14.

COSMOPOLITAN GENERA

Several brachiopod genera appear in almost every comparison. In the ten comparisons composing tables 1 and 2 *Atrypa, Cyrtina,* and *Schizophoria* are ubiquitous. In addition, *Leptaena, Nucleospira, "Schuchertella",* and *"Chonetes"* appear in more than half the lists. Perhaps

TABLE 4

Selected comparisons of intercontinental scope

Time interval	1	2	C	Σ	%	SR	PI
Frasnian	NA38	WA 7	16	61	26	69	1.14
Frasnian	NA24	RP10	30	64	47	75	1.50
Middle Devonian	A51	E81	28	160	17	35	0.27
Middle and Late Siegenian-Emsian	A52	E95	26	173	15	33	0.25
Early Gedinnian	A13	E32	27	72	37	67	1.04

NA = North American endemics
WA = Western Australia endemics
RP = Russian Platform endemics
A = Appalachian Province endemics
E = European endemics
C = Genera common to both regions
Σ = Total of brachiopod genera in both regions
% = Percent of cosmopolitan genera in total brachiopod fauna
SR = Simpson's ratio
PI = Provinciality Index

the most significant thing about these genera is their longevity. Their appearance in successive lists probably has a diluting effect of the numbers, insofar as they bear on true provinciality, because it is not known whether these genera consistently migrate across barriers that blocked migration of the obviously endemic genera or, more likely, whether their slow evolution proceeded in the individual regions, thus masking their true paleogeographic limitations.

Size of generic assemblages.—Theoretically, we would expect, that as cosmopolitanism increases, the total generic assemblage present during any one time interval decreases. The numbers in the various tables bear out this supposition. For instance, in table 1, the cosmopolitan interval of Middle and Late Siegenian provides the smallest number of genera (70), and the most strongly provincial interval of Eifelian to Middle Givetian is characterized by the greatest number of genera (90). The values revealed in table 2 are equally consistent in this regard, varying from a high of 98 genera present in the most provincial interval of Middle and Late Siegenian to a low of only 54 genera for the time of greatest cosmopolitan strength, that is, Frasnian.

TRANSATLANTIC COSMOPOLITANISM

One of the interesting results of comparisons made on the basis of PI in the present study is the determination of a transitional or mildly cosmopolitan situation between the Appalachian Province and Europe during the Early Gedinnian (see table 4). The PI for that comparison is 1.04 which compares markedly with provincial values of 0.58 and 0.47 for the Gedinnian to Early Siegenian comparisons between western North America and the Appalachian Province (see tables 1 and 2). This suggests that migration between eastern North America and Europe during the Gedinnian was more easily accomplished than across the width of the North American continent. Ease of migration between the present continents during Early Gedinnian time was evidently hampered during the later part of the Early Devonian by the increase in size of areas of terrestrial deposition, and in the Middle Devonian by the formation of tectonic lands which arose during the Acadian orogeny. Faunal communication during the Frasnian probably did not result from any east-west communication between the Old and New Worlds but probably resulted from relatively free movement around the northern margins of the Old Red Continent, as emphasized by House (1968). Acadian highlands were still prominent east of the Appalachian geosyncline during that time.

OTHER APPLICATIONS

Because the PI measures faunal resemblance and thus the actual interchange of animals between disparate regions, it is obvious that the higher the PI the more likely it is possible to make satisfactory correlations between any two faunas. The truth of this is evident in the virtual impossibility of transcontinental correlation with brachiopods during

Middle Devonian time and the relative ease of such correlations during the Frasnian. With these ideas in mind it is impossible to overlook the fact that the magnificent Late Devonian correlation scheme based on conodonts comes into being concurrently with the time of important world-wide cosmopolitanism, as indicated by brachiopods.

Procedures such as are used here to evaluate faunal resemblance on a provincial-cosmopolitan basis are probably applicable to community evaluations. However, lists of genera present in an assemblage or group of assemblages judged to represent a community should not be compared in this way for the reason that community definitions realistically hinge on abundances of certain taxa and not on their mere presence or absence.

DIRECTIONS OF MIGRATION

Almost from the beginning of the study of fossils, paleontologists have tried to determine the origin and direction of migration of faunas and of individual genera and species. Two excellent examples are provided by the present collation of distribution data for Devonian brachiopods. The first has to do with the faunal shift within the Siegenian between the *Quadrithyris* and *Spinoplasia* Zones, as noted previously (Johnson, 1970b). During Gedinnian and Early Siegenian the brachiopod faunas of the Great Basin, exemplified by their limestone belt occurrences in central Nevada, were very strongly linked in their faunal resemblance to faunas of western and Arctic Canada. After that time the central Nevada area was occupied by a brachiopod fauna not much different from that of the Appalachian Province. There can be no question that most of the Appalachian elements of the central Nevada Middle and Late Siegenian arrived there by a migration from east to west, because the whole fauna was already established in the Appalachian Province earlier, that is during the Late Gedinnian. The Appalachian Province genera did not penetrate into the Yukon or into the Canadian Arctic Islands, and the reasons for that are uncertain. On the other hand, it is clear that some of the genera that were allowed to migrate westward out of the Appalachian Province followed a circum-North Pacific path to areas as distant as Kazakhstan and eastern Australia (Boucot, Johnson, and Talent, 1969, p. 33, 34). This same time interval saw almost no migration from west to east; at least none of significance has been recognized so far. A genus listed as *Parastrophinella* from the Llano Uplift region of central Texas (Barnes, Cloud, and Warren, 1947, p. 131) and called *"Camerella"* in the *Quadrithyris* and *Spinoplasia* Zones of central Nevada (Johnson, 1970c) may represent an exotic element in an Appalachian Province fauna, but its precursors are not certainly known.

A similar question, on which the present study sheds some light, is the origin of brachiopod genera that compose the widespread Frasnian fauna of North America. H. S. Williams (1890) discussed a part of this question at some length and concluded that a number of the Frasnian and Taghanic brachiopods were invaders from the west and ultimately from an Old World source. Johnson (1970b) also pointed out that west-

ward spread of Appalachian Province elements was indicated by the first wide-spread occurrence of *Mucrospirifer* in areas outside the Appalachian Province in the Frasnian under the name of *Eleutherokomma*. *Eleutherokomma* (also called *Lamellispirifer* by the Russians) appeared all over the northern hemisphere of Europe and Asia for the first time near the beginning of the Late Devonian. It is now possible to provide a somewhat longer list than that discussed by Williams of brachiopod genera that first entered the Appalachian Province during Taghanic time and which are known to be established in the Cedar Valley and Tully faunas of the midcontinent and New York respectively. *Hypothyridina* is the one well-known element discussed at length by Williams, and it appears to have attained an almost world-wide distribution in the late Givetian. Elements that are first known in the Taghanic in either the Cedar Valley or Tully and that are known with certainty in older beds in other regions include *Anathyris, Rhyssochonetes, Leiorhynchus, Rensselandia,* and *Devonoproductus.* In addition, *Leptaena, Schizophoria, Gypidula,* and possibly *Emanuella* or *Ambothyris* and *Xystostrophia* qualify in this regard. *Leptaena, Schizophoria,* and *Gypidula* seem to be virtually absent from pre-Taghanic Middle Devonian faunas in eastern North America, although they were established there during the Early Devonian. Their Taghanic occurrence probably represents a reentry from the outside of the genera listed. *Anathyris* has a large distribution in the Old World as early as the Early Devonian. *Rhyssochonetes* occurs in Nevada and in the Canadian west in Middle Devonian beds that predate the Taghanic. *Leiorhynchus* has an exactly similar distribution. *Rensselandia* also is known to occur in western North America before it occurs in the Appalachian Province (Johnson, 1971), and *Emanuella* or *Ambothyris* has a long history in Old World faunas extending back into the Eifelian. Finally, we know from the evidence provided by Crickmay (1963), and from more recent discoveries in central Nevada, that the supposedly diagnostic Frasnian productid *Devonoproductus* occurs in the Middle and Upper Givetian of the American west. All the genera listed above (with the exception of *Mucrospirifer-Eleutherokomma*) show evidence of having migrated from the west to the east into the Appalachian Province. Some elements of the Frasnian brachiopod fauna, as developed in North America, were already present in Taghanic faunas in the region east of the continental backbone. These include *Centronella, Cranaena, "Cyrtina"* with plications on the fold and sulcus, *Lorangerella* which occurs in the Callaway Formation of Missouri (Cooper, 1945, pl. 63, figs. 24-30), and *Pentamerella* which extends upward from Appalachian Middle Devonian faunas into the Snyder Creek Shale. Also Crickmay (1966, p. 21) has recorded *Charionella* in Early Frasnian age beds in western Canada. Very likely, *Skenidium* spread outward from the Appalachian Province during the Frasnian, because it is known to have reached western Australia during that time. Lastly, the Frasnian cosmopolitan dalmanellid genus *Monelasmina* is a probable derivative of the Appalachian Province Middle Devonian genus *Sphenophragmus.*

SUMMARY AND CONCLUSIONS

Taghanic time, when provinciality was first beginning to break down, seems to have seen migration mostly from west to east. During Frasnian time, when world-wide cosmopolitanism became established, it is clear that both Appalachian Province and Old World Province faunas contributed constituents to the new fauna of world-wide extent. At least for North America quantitative evaluation of brachiopod provincialism is in agreement with a hypothesis that land barriers were of prime importance to province formation.

The consistency of PI values and the well defined trends to which they attest, reflecting degrees of provinciality, require the conclusion that significant migrations of brachiopods are independent of random effects. Some workers believe that, because of the great span of geologic time and the possibility of accidental distributions, "anything can happen". However, the actual existence of well defined marine provinces proves that anything did not happen. Consequently, province analysis based on marine animals holds promise for future understanding of the timing and extent of global tectonic events.

Appendix 1

GENERIC OCCURRENCES

Gedinnian and Early Siegenian, Appalachian Province compared to Great Basin

Appalachian endemics.—*Anastrophia (verneuili* type), *Anoplia, "Chonetes", Chonostrophiella, Cordatomyonia, Costellirostra, Cupularostrum?, Delthyris, Dolerorthis, Eatonia, Hedeina, Leptospira, Merista, Nanothyris* or *Podolella, Obturamentella, Orthostrophia* or *Orthostrophella, Platyorthis, Plectodonta, Plethorhyncha* or *Amsdenella, Plicoplasia, Rensselaerina, Rhynchotreta?, Salopina (lunata* type), *Sieberella* (multiplicate), *Skenidium, Strixella, Strophonella* (costate), *Trematospira.*

Common genera.—*Aesopomum, Ancillotoechia, Atrypa, Atrypina, Coelospira, Cyrtina, Dalejina, Dicaelosia, Gypidula, Howellella, Iridistrophia, Isorthis* or *Tyersella, Leptaena, Leptaenisca, Leptostrophia, Levenea, Machaeraria, Megakozlowskiella, Meristella, Meristina, Mesodouvillina, Nucleospira, Resserella, Reticulariopsis?, Rhynchospirina, Schizophoria, "Schuchertella", Spinoplasia* or *Metaplasia.*

Great Basin endemics.—*Ambocoelia, Anastrophia (magnifica* type), *"Brachyprion", Cryptatrypa, Cyrtinaella, "Dolerorthis", Dubaria, Eoglossinotoechia?, Hebetoechia?, Lepidoleptaena, Lissatrypa, Protocortezorthis, Ptychopleurella, Quadrithyris, Salopina (crassiformis* type), *Sibirispira?, Sieberella* (pauciplicate), *Skenidioides, Spinatrypa, Sphaerirhynchia, Spirigerina, Strophonella* (parvicostellate type), *Toquimaella, Undispirifer.*

Middle and Late Siegenian, Appalachian Province compared to Great Basin

Appalachian endemics.—*Anastrophia (verneuili* type), *Antispirifer, Atrypina, Beachia, Centronella, Chonostrophiella, Cloudella, Costellirostra, Cupularostrum?, Dawsonelloides, Eatonia, Eurythyris, Globithyris, Hedeina, Hipparionyx, Iridistrophia, Isorthis* or *Tyersella, Machaeraria, Megasalopina, Mendathyris, Mesodouvillina, Mutationella, Oriskania, Platyorthis, Plethorhyncha, Prionothyris, Protoleptostrophia, Rhynchotreta?, Salopina.*

Common genera.—*Acrospirifer, Ancillotoechia, Anoplia, Atrypa, Coelospira, Costispirifer, Cyrtina, Discomyorthis, Elytha, Howellella, Leptaena, Leptaenisca, Leptocoelia, Leptostrophia, Levenea, Megakozlowskiella, Megastrophia, Meristella* or *Meristina, Nanothyris* or *Rensselaerina, Nucleospira, Orthostrophia* or *Orthostrophella, Pegmarhynchia, Pholidostrophia, Pleiopleurina, Plicoplasia, Pseudoparazyga, Rensselaeria, Schizophoria, "Schuchertella", Spinoplasia* or *Metaplasia, Stropheodonta, Strophonella* (costate), *Trematospira.*

Great Basin endemics.—"Camerella", Dalejina, Dyticospirifer, Howittia, Leptocoelina, Reticulariopsis, Sieberella (multiplicate), *"Strophochonetes".*

Emsian, Appalachian Province
compared to Great Basin

Appalachian endemics.—Amphigenia, Centronella, Charionella, Charionoides, Chonostrophia, Chonostrophiella, Costellirostra, Costispirifer, Cryptonella, Cupularostrum?, Cyrtinaella, Dawsonelloides, Discomyorthis, Elytha, Eodevonaria, Etymothyris, Fimbrispirifer, Globithyris, Machaeraria, Meganterella, Nanothyris, Pentagonia, Pentamerella, Platyorthis, Plicanoplia, Plicoplasia, Prionothyris, Protoleptostrophia.

Common genera.—Acrospirifer, Anoplia, Atrypa, Brachyspirifer, "Chonetes", Coelospira, Cyrtina, Leptaena, Leptocoelia, Leptostrophia, Megakozlowskiella, Megastrophia, Meristella or *Meristina, Metaplasia* or *Ambocoelia, Mucrospirifer?* or *Hysterolites, Nucleospira, Pholidostrophia, Productella* or *Spinulicosta, Salopina, Schizophoria, "Schuchertella", Stropheodonta, Strophonella* (costate).

Great Basin endemics.—Astutorhyncha, Bifida, Chonetes, Cortezorthis, Corvinopugnax, Cymostrophia, Dalejina or *Rhipidomella, Elythyna, Eurekaspirifer, Gypidula, Gypidula* (aseptate), *Howellella, Katunia?, "Leiorhynchus", Levenea, Mclearnites, Muriferella, Mutationella, Parachonetes, Phragmostrophia, Rensselaeria, Reticulariopsis, Spinella, "Strophochonetes", Trigonirhynchia.*

Eifelian to Middle Givetian,
Appalachian Province compared to Great Basin

Appalachian endemics.—Acrospirifer, Amphigenia, Athyris, Brachyspirifer?, Brevispirifer, Callipleura, Camarospira, Camarotoechia, Centronella, Charionella or *Charionoides, Cranaena, Cryptonella, Cupularostrum, "Cymostrophia", Devonalosia, Devonochonetes, Douvillina, Elytha, Eodevonaria, Fimbrispirifer, Helaspis, Hercostrophia, Heteralosia, Kayserella, "Leiorhynchus", Leptaena, Leptospira?, Levenea, Longispina, Mediospirifer, Megakozlowskiella, Megastrophia, Mucrospirifer, Oligorachis, Orthopleura, Paraspirifer, Parazyga, Pentagonia, Pholidostrophia, Prosserella, Protoleptostrophia, Pustulatia, Rhipidomella, "Rhipidothyris", Sieberella, Sphenophragmus, Spinocyrtia, Stropheodonta, Strophonella, Tropidoleptus, Truncalosia.*

Common genera.—Ambocoelia, Atrypa, "Chonetes", Cyrtina, Echinocoelia, Meristina, Nucleospira, Pentamerella, Schizophoria, "Schuchertella", Spinatrypa, Spinulicosta, Subrensselandia, Warrenella.

Great Basin endemics.—Ambothyris, Anatrypa, Antistrix, Cassidirostrum, Conomimus, Crurithyris, Devonoproductus, Dubaria, Gypidula, Hadrorhynchia, Leiorhynchus, Leptothyris, Mimatrypa, Nemesa?, Parapholidostrophia, Productella, Quadrithyris, Rensselandia, Rhipidothyris, Spinatrypina, Stringocephalus, Teichertina, Undispirifer, Vagrania, Vallomyonia.

Gedinnian and Early Siegenian,
Appalachian Province compared with Yukon and Arctic

Appalachian endemics.—Anastrophia (verneuili type), *Anoplia, Atrypina, Chonostrophiella, Coelospira, Cordatomyonia, Costellirostra, Cupularostrum?, Delthyris, Dolerorthis, Eatonia, Hedeina, Isorthis* or *Tyersella, Leptaenisca, Leptospira, Leptostrophia, Levenea, Megakozlowskiella, Meristina* or *Meristella, Nanothyris* or *Podolella, Obturamentella, Orthostrophia* or *Orthostrophella, Platyorthis, Plectodonta, Plethorhyncha* or *Amsdenella, Plicoplasia, Rensselaerina, Resserella, Rhynchospirina, Rhynchotreta?, Salopina (lunata* type), *"Schuchertella", Sieberella* (multiplicate), *Skenidium, Spinoplasia* or *Metaplasia, Strixella, Strophonella* (costate), *Trematospira.*

Common genera.—Aesopomum, Ancillotoechia, Atrypa, "Chonetes", Cyrtina, Dalejina, Dicaelosia, Gypidula, Howellella, Iridistrophia, Leptaena, Machaeraria, Merista, Mesodouvillina, Nucleospira, Reticulariopsis, Schizophoria.

Yukon and Arctic endemics.—Ambocoelia, Anastrophia? (magnifica), "Astutorhynchia", Cymostrophia?, Katunia?, Leptaenopyxis, Ogilviella, Phragmostrophia, Protathyris, Protocortezorthis, Reticulatrypa, Salopina or *Muriferella, Skenidioides, Sphaerirhynchia, Spinatrypa, Spirigerina, Toquimaella, Undispirifer.*

Middle and Late Siegenian,
Appalachian Province compared with Yukon and Arctic

Appalachian endemics.—Acrospirifer, Anastrophia (verneuili type), *Anoplia, Antispirifer, Atrypina, Beachia, Centronella, Chonostrophiella, Cloudella, Coelospira, Costellirostra, Costispirifer, Cupularostrum?, Dawsonelloides, Discomyorthis, Eatonia,*

Elytha, Eurythyris, Globithyris, Hedeina, Hipparionyx, Howellella, Iridistrophia, Isorthis or *Tyersella, Leptaenisca, Leptocoelia, Leptostrophia, Levenea, Machaeraria, Megakozlowskiella, Megasalopina, Megastrophia, Mendathyris, Meristella* or *Meristina, Mutationella, Nanothyris* or *Rensselaerina, Oriskania, Orthostrophia* or *Orthostrophella, Pegmarhynchia, Pholidostrophia, Platyorthis, Pleiopleurina, Prionothyris, Protoleptostrophia, Pseudoparazyga, Rensselaeria, Rhynchotreta?, Salopina, Spinoplasia* or *Metaplasia, Stropheodonta, Strophonella* (costate), *Trematospira.*

Common genera.—Ancillotoechia, Atrypa, Cyrtina, Leptaena, Mesodouvillina, Nucleospira, Plicoplasia, Schizophoria, "Schuchertella".

Yukon and Arctic endemics.—Aesopomum, Ambocoelia, Anastrophia (magnifica), Anatrypa, "Chonetes", Cortezorthis, Cymostrophia, Dalejina, Davidsoniatrypa, "Dolerorthis", Felinotoechia?, Ferganella, Gypidula, Hebetoechia?, Katunia?, "Kayserella", Latonotoechia, "Leiorhynchus", Linguopugnoides?, Muriferella, Nymphorhynchia, Phragmostrophia, Plicocyrtina, Protathyris, Protocortezorthis, Reeftonia, Reticulariopsis, Reticulatrypa, Sieberella, Skenidioides, Spinatrypa, Thliborhynchia, Trigonirhynchia?, Undispirifer, Vagrania, Warrenella.

Emsian, Appalachian Province
compared with Yukon and Arctic

Appalachian endemics.—Acrospirifer, Amphigenia, Anoplia, Brachyspirifer, Centronella, Charionella or *Charionoides, Chonostrophia* or *Chonostrophiella, Coelospira, Costellirostra, Costispirifer, Cryptonella, Cupularostrum?, Cyrtinaella, Dawsonelloides, Discomyorthis, Elytha, Eodevonaria, Etymothyris, Fimbrispirifer, Globithyris, Leptocoelia, Machaeraria, Megakozlowskiella, Meganterella, Metaplasia* or *Ambocoelia, Mucrospirifer?* or *Hysterolites, Nanothyris, Pentagonia, Pentamerella, Pholidostrophia, Platyorthis, Plicanoplia, Plicoplasia, Prionothyris, Protoleptostrophia, Salopina.*

Common genera.—Atrypa, Cyrtina, "Chonetes", Leptaena, Leptostrophia, Megastrophia, Meristina or *Meristella, Nucleospira, Schizophoria, "Schuchertella", Spinulicosta, Stropheodonta, Strophonella.*

Yukon and Arctic endemics.—Anatrypa, Bifida, Carinatina, Cortezorthis, Cymostrophia, Dalejina, Elythyna, Felinotoechia?, Gorgostrophia, Gypidula, Gypidula (aseptate), *Howellella?, Isorthis, Janius, Katunia?* or *"Pugnax", "Leiorhynchus", Linguopugnoides, Muriferella, Nymphorhynchia, Parachonetes, Phragmostrophia, Quadrithyris?* (smooth), *Quadrithyris* (plicate), *Radiomena, Reticulariopsis, Reticulatrypa, Sieberella, Skenidioides, Skenidium, Spinatrypa, "Strophochonetes", Theodossia?, Toquimaella, Uncinulus?, Vagrania, Warrenella.*

Eifelian to Middle Givetian,
Appalachian Province compared with western Canada

Appalachian endemics.—Acrospirifer, Ambocoelia, Amphigenia, Athyris, Brachyspirifer, Brevispirifer, Callipleura, Camarospira, Camarotoechia, Centronella, Charionella or *Charionoides, Cranaena, Cryptonella, Cupularostrum, "Cymostrophia", Devonalosia, Devonochonetes, Douvillina, Elytha, Eodevonaria, Helaspis, Hercostrophia, Heteralosia, Keyserella, "Leiorhynchus", Leptaena, Leptospira?, Levenea, Longispina, Mediospirifer, Megakozlowskiella, Megastrophia, Meristina, Mucrospirifer, Oligorachis, Orthopleura, Paraspirifer, Parazyga, Pentagonia, Pentamerella, Pholidostrophia, Proserella, Protoleptostrophia, Pustulatia, Rhipidomella, "Rhipidothyris", Sieberella, Sphenophragmus, Spinocyrtia, Stropheodonta, Strophonella, Subrensselandia, Tropidoleptus, Truncalosia.*

Common genera.—Atrypa, "Chonetes", Cyrtina, Echinocoelia, Fimbrispirifer?, Nucleospira, Ribbed Spirifer, *Schizophoria, "Schuchertella", Spinatrypa, Spinulicosta, Warrenella.*

Western Canada endemics.—Ambothyris or *Emanuella, Anatrypa* or *Variatrypa, Carinatina, Cassidirostrum, Devonoproductus, Geranocephalus, Gypidula, Hadrorhynchia, "Hypothyridina", Innuitella, Lazutkinia, Leiorhynchus, Productella, Rhyssochonetes, Rensselandia, Reticulariopsis, Spinatrypina, Stringocephalus, Undispirifer.*

Taghanic (Late Givetian only),
Appalachian Province compared to western Canada

Appalachian endemics.—Allanaria, Ambocoelia, Atribonium, Centronella, Charionella, Cryptonella, Cupularostrum, "Cyrtina", Elytha, Echinocoelia, Eostrophalosia or *Oligorachis, Eosyringothyris, Gypidula, Hamburgia, Tylothyris, Lorangerella, Meristina, Nucleospira, Mediospirifer, Orthopleura, Platyrachella, Protoleptostrophia, Rens-*

selandia, Rhipidomella, Rhipidothyris or *Septothyris, Sphenophragmus, Spinulicosta, Stropheodonta, Tropidoleptus, Truncalosia.*

Common genera.—Athyris or *Anathyris, Atrypa, Cranaena, "Chonetes", Cyrtina, Douvillina, Emanuella, Hypothyridina, Leiorhynchus, "Leiorhynchus", Leptaena, "Leptospira", Mucrospirifer, Nervostrophia, Pentamerella, Pholidostrophia, Productella, Rhyssochonetes, Schizophoria, "Schuchertella"* or *Xystostrophia, Spinatrypa, Spinocyrtia.*

Western Canada endemics.—Ambothyris or *Ladjia, Devonoproductus, Hadrorhynchia, Mimatrypa, Stelckia, Warrenella.*

Frasnian, Appalachian Province
compared with western Canada

Appalachian endemics.—Aulacella, Cariniferella, Hyborhynchella, Hypsomyonia or *Kayserella, Irboskites, Pentamerella, "Schuchertella", Sieberella, Skenidium, Sulcatostrophia, Tropidoleptus, Thiemella.*

Common genera.—Acutatheca or *Eosyringothyris, Allanaria* or *Minutilla, Athabaschia, Atribonium, Atrypa, Calvinaria, Cranaena, "Chonetes" Cupularostrum?, Cyrtina, Cyrtospirifer* or *Regelia, Devonoproductus, Douvillina* and etc., *Elytha, Eostrophalosia* or *Oligorachis, Gypidula, Hypothyridina, Ladogioides, "Anatrypa", Caryorhynchus* or *"Leiorhynchus", Eleutherokomma, Nervostrophia* or *Gamphalosia, Parapugnax, Platyrachella, Productella, Schizophoria, Spinatrypa, Spinatrypina, "Spirifer", Stropheodonta, Strophonelloides, Tenticospirifer, Theodossia* and etc., *Thomasaria, Warrenella.*

Western Canada endemics.—Ambothyris or *Ladjia, Athyris* or *Anathyris, Chonopectoides, "Cyrtina", Maclarenella, Monelasmina.*

Gedinnian and Early Siegenian,
Great Basin compared with Yukon and Arctic

Great Basin endemics.—Atrypina, "Brachyprion", Coelospira, Cryptatrypa, Cyrtinaella, "Dolerorthis", Dubaria, Eoglossinotoechia?, Hebetoechia?, Isorthis or *Tyersella, Lepidoleptaena, Leptaenisca, Leptostrophia, Levenea, Lissatrypa, Megakozlowskiella, Meristella* or *Meristina, Metaplasia* or *Spinoplasia, Ptychopleurella, Quadrithyris, Resserella, Rhynchospirina, Sibirispira?, Sieberella* (pauciplicate), *Strophonella* (parvicostellate type).

Common genera.—Aesopomum, Ambocoelia, Anastrophia (magnifica type), *Ancillotoechia, Atrypa, Cyrtina, Dalejina, Dicaelosia, Gypidula, Howellella, Iridistrophia* or *"Schuchertella", Leptaena, Machaeraria, Mesodouvillina, Nucleospira, Protocortezorthis, Reticulariopsis, Salopina* or *Muriferella, Schizophoria, Skenidioides, Sphaerirhynchia, Spinatrypa, Spirigerina, Toquimaella, Undispirifer.*

Yukon and Arctic endemics.—"Astutorhynchia", "Chonetes", Cymostrophia?, Katunia?, Leptaenopyxis, Merista?, Ogilviella, Phragmostrophia, Protathyris, Reticulatrypa.

Middle and Late Siegenian,
Great Basin compared with Yukon and Arctic

Great Basin endemics.—Acrospirifer, Anoplia, "Camerella", Coelospira, Costispirifer, Discomyorthis, Dyticospirifer, Elytha, Howellella, Howittia, Leptaenisca, Leptocoelia, Leptocoelina, Leptostrophia, Levenea, Megakozlowskiella, Megastrophia, Meristella or *Meristina, Orthostrophia* or *Orthostrophella, Pegmarhynchia, Pholidostrophia, Pleiopleurina, Pseudoparazyga, Rensselaeria, Rensselaerina* or *Nanothyris, Spinoplasia* or *Metaplasia, Stropheodonta, "Strophochonetes", Strophonella* (costate), *Trematospira.*

Common genera.—Ancillotoechia, Atrypa, Cyrtina, Dalejina, Leptaena, Nucleospira, Plicoplasia, Reticulariopsis, Schizophoria, "Schuchertella", Sieberella.

Yukon and Arctic endemics.—Aesopomum, Ambocoelia, Anastrophia (magnifica), Anatrypa, "Chonetes", Cortezorthis, Cymostrophia, Davidsoniatrypa, "Dolerorthis", Felinotoechia?, Ferganella, Gypidula, Hebetoechia?, Katunia?, "Kayserella", Latonotoechia, "Leiorhynchus", Linguopugnoides?, Mesodouvillina, Muriferella, Nymphorhynchia, Phragmostrophia, Plicocyrtina, Protathyris, Protocortezorthis, Reeftonia, Reticulatrypa, Skenidioides, Spinatrypa, Thliborhynchia, Trigonirhynchia?, Undispirifer, Vagrania, Warrenella.

Emsian, Great Basin
compared with Yukon and Arctic

Great Basin endemics.—Acrospirifer, Ambocoelia or *Metaplasia, Anoplia, Astutorhyncha, Brachyspirifer, Chonetes, Coelospira, Corvinopugnax, Eurekaspirifer, Hys-*

terolites, Leptocoelia, Levenea, Mclearnites, Megakozlowskiella, Mutationella, Pholidostrophia, Rensselaeria, Salopina, Spinella, Trigonirhynchia.

Common genera.—Atrypa, Bifida, "Chonetes", Cortezorthis, Cymostrophia, Cyrtina, Dalejina or *Rhipidomella, Elythyna, Gypidula, Gypidula* (aseptate), *Howellella, Katunia?* or *"Pugnax", "Leiorhynchus", Leptaena, Leptostrophia, Megastrophia, Meristella* or *Meristina, Muriferella, Nucleospira, Parachonetes, Phragmostrophia, Reticulariopsis, Schizophoria, "Schuchertella", Spinulicosta* or *Productella, Stropheodonta, "Strophochonetes", Strophonella* (costate).

Yukon and Arctic endemics.—Anatrypa, Carinatina, Felinotoechia?, Gorgostrophia, Isorthis, Janius, Linguopugnoides, Nymphorhynchia, Quadrithyris, Radiomena, Reticulatrypa, Sieberella, Skenidioides, Skenidium, Spinatrypa, Theodossia?, Toquimaella, Uncinulus?, Vagrania, Warrenella.

Eifelian to Middle Givetian,
Great Basin compared with western Canada

Great Basin endemics.—Ambocoelia, Antistrix, Crurithyris, Dubaria, Leptathyris, Meristina, Mimatrypa, Nemesa?, Parapholidostrophia, Pentamerella, Quadrithyris, Rhipidothyris, Subrensselandia, Teichertina, Vagrania, Vallomyonia.

Common genera.—Ambothyris or *Emanuella, Anatrypa* or *Desquamatia, Atrypa, Cassidirostrum, "Chonetes", Conomimus* or *Geranocephalus, Cyrtina, Devonoproductus, Echinocoelia, Gypidula, Hadrorhynchia, Leiorhynchus, Nucleospira, Productella, Rensselandia, Schizophoria, "Schuchertella", Spinatrypa, Spinatrypina, Spinulicosta, Stringocephalus, Undispirifer, Warrenella.*

Western Canada endemics.—Carinatina, Fimbrispirifer?, Helaspis, "Hypothyridina", Innuitella, Lazutkinia, Reticulariopsis, Rhyssochonetes, ribbed spirifer.

Early and Middle Givetian,
Great Basin compared with western Canada

Great Basin endemics.—Ambocoelia, Antistrix, Crurithyris, Leptathyris, Meristina, Mimatrypa, Nemesa?, Parapholidostrophia, Pentamerella, Rhipidothyris, Subrensselandia, Vallomyonia.

Common genera.—Ambothyris or *Emanuella, Anatrypa* or *Desquamatia, Atrypa, Cassidirostrum, "Chonetes", Conomimus* or *Geranocephalus, Cyrtina, Devonoproductus, Echinocoelia, Gypidula, Hadrorhynchia, Leiorhynchus, Nucleospira, Productella, Rensselandia, Schizophoria, "Schuchertella", Spinatrypa, Spinulicosta, Stringocephalus, Undispirifer, Warrenella.*

Western Canada endemics.—Carinatina, Helaspis, "Hypothyridina", Lazutkinia, Rhyssochonetes, ribbed spirifer, *Spinatrypina.*

Early Gedinnian,
Appalachian Province compared with Europe

Appalachian endemics.—Aesopomum, Atrypina, Coelospira, Cordatomyonia, Cupularostrum?, Hedeina, Leptaenisca, Levenea, Orthostrophia, Plicoplasia, Rhynchotreta?, Strixella, Strophonella (costate).

Common genera.—Ancillotoechia, Atrypa, Cyrtina, Dalejina, Delthyris, Dicaelosia, Dolerorthis, Gypidula, Howellella, Iridistrophia, Isorthis, Leptaena, Leptostrophia, Machaeraria, Megakozlowskiella, Merista, Meristina or *Meristella, Mesodouvillina, Nanothyris, Nucleospira, Plethorhyncha, Podolella, Resserella, Rhynchospirina, Salopina, Schizophoria, "Schuchertella".*

European endemics.—Ambocoelia, Anastrophia, Barbaestrophia, Bathyrhyncha, Brachyzyga, Clorinda, Eoglossinotoechia, Eospirifer, Fascicostella, Glossoleptaena, Hebetoechia, Ivanothyris, Lanceomyonia, Linguopugnoides, Lissatrypa, Mesopholidostrophia, Mutationella, Platyorthis, Plectodonta, Proschizophoria, Protathyris, Protochonetes, Protocortezorthis, Retzia?, Septatrypa, Skenidioides, Shaleria, Sphaerirhynchia, Strophochonetes, Strophonella (parvicostellate), *Trigonirhynchia?, Undispirifer.*

Middle and Late Siegenian and Emsian,
Appalachian Province compared with Europe

Appalachian endemics.—Ambocoelia, Anastrophia (verneuili type), *Antispirifer, Atrypina, Beachia, Centronella, Charionella* or *Charionoides, "Chonetes", Chonostrophia, Chonostrophiella, Cloudella, Coelospira, Costellirostra, Costispirifer, Cupularostrum?, Cyrtinaella, Dawsonelloides, Discomyorthis, Eatonia, Elytha, Etymothyris, Eurythyris, Fimbrispirifer, Globithyris, Hedeina, Howellella, Leptocoelia, Levenea, Machaeraria, Megakozlowskiella, Meganterella, Megasalopina, Megastrophia, Mendathyris, Nanothyris* or *Rensselaerina, Oriskania, Orthostrophia* or *Orthostrophella, Pegmarhyn-*

chia, Pentagonia, Pentamerella, Pholidostrophia, Pleiopleurina or *Plethorhyncha, Plicanoplia, Plicoplasia, Prionothyris, Pseudoparazyga, Rensselaeria, Rhynchotreta?, Salopina, Spinoplasia* or *Metaplasia, Strophonella* (costate), *Trematospira.*

Common genera.—Acrospirifer, Amphigenia, Ancillotoechia, Anoplia, Atrypa, Brachyspirifer, Cryptonella, Cyrtina, Eodevonaria, Hipparionyx, Iridistrophia, Isorthis or *Tyersella, Leptaena, Leptaenisca, Leptostrophia, Meristella* or *Meristina, Mesodouvillina* or *Bojodouvillina, Mucrospirifer?* or *Hysterolites, Mutationella, Nucleospira, Platyorthis, Productella* or *Spinulicosta, Protoleptostrophia, Schizophoria, "Schuchertella", Stropheodonta.*

European endemics.—Aesopomum, Alatiformia, Ambocoelia, Amissopecten, Amoenospirifer, Anoplotheca, Areostrophia, Astutorhyncha, Athyris or *Plicathyris, Atrypinella, Biconostrophia, Bifida, Bisinocoelia, Bojothyris, Branikia, Chonetes* or *Plebejochonetes, Clorinda, Coelospirina, Crinistrophia, Cymostrophia, Dalejina, Dalejodiscus, Dicaelosia, Dictyonella, Dinapophysia, Eoglossinotoechia, Eoreticularia, Eospirifer, Euryspirifer, Falsatrypa, Fascicostella, Felinotoechia, Eucharitina, Glossinulus, Gorgostrophia, Gypidula, Hebetoechia, Isopoma, Karpinskia, Latonotoechia, Lepidoleptaena, Leptaenopyxis Leptodonta, Linguopugnoides, Markitotoechia, Merista, Meganteris, Monadotoechia, Multispirifer, Nadiastrophia, Najadospirifer, Papillostrophia, Parachonetes, Paraspirifer, Phoenicitoechia, Plectodonta, Plectorhynchella, Plectospira, Plicocyrtina, Plicostropheodonta, Pradoia, Praegnantenia, Procerulina, Prokopia, Proreticularia, Proschizophoria, Punctatrypa, Quadrithyris, Resserella, Reticulariopsis, Rhenorensselaeria, Rhenostrophia, Rhynchospirina?, Rugoleptaena, Septalaria, Septathyris, Sicorhyncha* or *Zlichorhynchus, Sieberella, Skenidioides, Spinatrypa, "Spirifer" (trigeri,* etc.), *Straelenia, Strophonella* (parvicostellate), *Subcuspidella, Tastaria, Teichostrophia, Tetratomia, Triathyris, Trigonirhynchia, Tropidoleptus, Tubulostrophia, Uncinulus, Warrenella, Xenomartinia, Zdimir.*

Middle Devonian,
Appalachian Province compared with Europe

Appalachian endemics.—Allanaria?, Ambothyris or *Ladjia, Amphigenia, Atribonium, Brachyspirifer?, Brevispirifer, Callipleura, Camarospira, Centronella, Cranaena, Charionella* or *Charionoides, Cryptonella, Cupularostrum, "Cymostrophia", "Cyrtina", Devonalosia, Devonochonetes, Echinocoelia, Elytha, Eodevonaria, Eostrophalosia* or *Oligorachis, Eosyringothyris, Fimbrispirifer, Hamburgia, Helaspis, Hercostrophia, Heteralosia, Leiorhynchus* or *"Leiorhynchus", "Leptospira", Levenea, Longispina, Lorangerella, Megakozlowskiella, Megastrophia, Mucrospirifer, Nervostrophia, Parazyga, Pentagonia, Pholidostrophia, Platyrachella, Prosserella, Protoleptostrophia, Pustulatia, Rhipidomella, Rhipidothyris* or *Septothyris, Rhyssochonetes, Sphenophragmus, Spinulicosta, Strophonella, Tropidoleptus, Truncalosia.*

Common genera.—Acrospirifer, Ambocoelia, Athyris or *Anathyris, Atrypa* s.l., *Chonetes, Cyrtina, Douvillina* or *Mesodouvillina, Drahanostrophia* or *Orthopleura, Emanuella* or *Ambothyris, Gypidula* or *Devonogypa, Hypothyridina, Kayserella, Leptaena, Mediospirifer, Meristina, Nucleospira, Paraspirifer, Pentamerella, Productella, Rensselandia, Schizophoria, Sieberella, Spinatrypa* or *Invertrypa, Spinocyrtia, Stropheodonta, Subrensselandia, Warrenella, Xystostrophia* or *"Schuchertella".*

European endemics.—Alatiformia, Amissopectin, Amoenospirifer, Anatrypa or *Desquamatia, Antirhynchonella, Astutorhyncha, Atrythyris, Aulacella, Bifida, Bornhardtina, Camerophoria, Carinatina, Chascothyris, Chimaerothyris, Cimicinella* or *Cimicinoides, Clorinda, Corvinopugnax, Cryptatrypa, Cyrtinaella* or *Squamulariina, Cyrtinopsis, Dalejina, Davidsonia, Devonaria, Dicamara, Dubaria, Enantiosphen, Eoreticularia, Eurycolporhynchus, Glassia, Gruenewaldtia, Howellella, Ilmenispina, Isopoma, Isorthis, Ivanothyris, Kayseria, Kerpina, Kransia, Ladogifornix, Leptathyris, Leptodontella, Markitotoechia, Merista, Mimatrypa, Moravilla, Mystrophora, Nemesa, Neodelthyris, Nymphorhynchia?, Parastrophonella, Phragmophora, Plectodontella, Plectospira, Procerulina, Prodavidsonia, Prokopia, Pseudocamarophoria, Punctatrypa, Pyramidalia, Quadrithyrina, Quadrithyris, Radiomena, Reticulariopsis, Retzia, Rhynchospirifer, Schnurella, Septalaria, Skenidioides, Spinatrypina, "Spirifer", Stringocelphalus, Stringomimus, Subcuspidella, Teichostrophia, Telaeoshaleria, Tetratomia, Uncinulus* or *Glossinotoechia, Uncites, Undispirifer* or *Pinguispirifer, Xenomartinia, Zdimir.*

Frasnian, North America
compared with Russian Platform

North American endemics.—Acutatheca, Ambothyris or *Ladjia, "Anatrypa", Athabaschia, Atribonium, Aulacella, Cariniferella, Charionella, Chonopectoides, "Cyr-*

tina", Hyborhynchella, Hypsomyonia or *Kayserella, Ladogioides, Lorangerella, Maclarenella, Pentamerella, Platyrachella, Sieberella, Skenidium, Strophonelloides, Sulcatostrophia, Thomasaria* or *Pyramidalia, Tropidoleptus, Warrenella.*

Common genera.—Allanaria or *Minutilla, Athyris* or *Anathyris, Atrypa, Calvinaria, Cranaena, "Chonetes", Cupularostrum, Cyrtina, Cyrtospirifer* or *Regelia, Devonoproductus, Douvillina* and etc., *Eleutherokomma, Elytha, Eostrophalosia* or *Oligorachis, Gypidula, Hypothyridina, "Leiorhynchus"* or *Caryorhynchus, Irboskites, Monelasmina, Nervostrophia* or *Gamphalosia, Parapugnax, Productella, Schizophoria, "Schuchertella", Spinatrypa, Spinatrypina, "Spirifer", Stropheodonta, Tenticospirifer, Theodossia* or *Vandergrachtella.*

Russian Platform endemics.—Adolfia, Anatrypa, Gruenewaldtia?, Ilmenia, Ladogia, Retichonetes?, "Reticularia", Ripidiorhynchus, Steinhagella?, Uchtospirifer.

Frasnian, North America
compared with Western Australia

North American endemics.—Acutatheca, Allanaria or *Minutilla, "Anatrypa", Athabaschia, Athyris* or *Anathyris, Atribonium, Atrypa, Cariniferella, Cranaena, Charionella, "Chonetes", Chonopectoides, Cupularostrum, Cyrtina, "Cyrtina", Cyrtospirifer* or *Regelia, Eleutherokomma, Elytha, Hyborhynchella, Irboskites, Ladogioides, "Leiorhynchus"* or *Caryorhynchus, Lorangerella, Maclarenella, Monelasmina, Pentamerella, Platyrachella, Sieberella, Spinatrypina, "Spirifer", Stropheodonta, Strophonelloides, Sulcatostrophia, Tenticospirifer, Theodossia* or *Vandergrachtella, Thomasaria* or *Pyramidalia, Tropidoleptus, Warrenella.*

Common genera.—Ambothyris or *Ladjia, Aulacella* or *Rhipidomella, Calvinaria, Devonoproductus, Douvillina* and etc., *Eostrophalosia* or *Oligorachis, Gypidula, Hypothyridina, Hypsomyonia* or *Kayserella, Nervostrophia* or *Gamphalosia, Parapugnax, Productella, Schizophoria, "Schuchertella", Skenidium, Spinatrypa.*

Western Australian endemics.—Crurithyris or *Emanuella, Fitzroyella, Retichonetes, Steinhagella?, Teichertina, Uncinulus?, Zophostrophia.*

Appendix 2

MAJOR DATA SOURCES

Gedinnian.—Boucot and Johnson (1967); Johnson, Boucot, and Murphy (1967); Johnson, unpublished; Lenz (1967); Barrois, Pruvost, and Dubois (1922); Kozlowski (1929); Dahmer (1951); Chlupác (1953); Boucot (1960); Havlícek (1959, 1961, 1967).

Siegenian and Emsian.—Boucot and Johnson (1967); Johnson (1970c and unpublished); Lenz (1967); Ludvisen (1970); Asselberghs (1946); Comte (1938); Havlícek (1956, 1959, 1961, 1967).

Eifelian to Middle Givetian.—Boucot and Johnson (1967); Hall (1867); Imbrie (1959); Johnson (1969, 1970a, 1971, and unpublished); Crickmay (1960, 1963); Warren and Stelck (1956); McLaren, Norris, and McGregor (1962); Norris (1967); Krömmelbein and others (1965); Biernat (1959, 1964, 1966); Havlícek (1956, 1959, 1961, 1967).

Taghanic (Late Giventian only).—Cooper and Williams (1935); Cooper and Cloud (1938); Cooper (1945, 1967); Branson (1923); Griesemer (1965); Imbrie (1959); Muir-Wood and Cooper (1960); Stainbrook (1938a and b, 1940, 1942a, 1943a and b); Cloud (1942); Grant (1965); Johnson (1970b); Crickmay (1963); McLaren and Norris (1964).

Frasnian.—Hall (1867); Williams (1913); Belanski (1928a and b); Fenton and Fenton (1924); Branson (1923); Stainbrook (1945, 1942b, 1948); Cooper (1945); McLaren (1954, 1962); Crickmay (1963, 1966); Warren and Stelck (1956); McLaren, Norris, and McGregor (1962); Pedder (1959, 1960); Liashenko (1959); Nalivkin (1941); Veevers (1959); Muir-Wood and Cooper (1960); Grant (1965); Cloud (1942).

REFERENCES

Asselberghs, Etienne, 1946, L'Éodévonien de l'Ardenne et des Régions voisines: Louvain Univ., Inst. Géol. Mém., v. 14, 598 p.

Barnes, V. E., Cloud, P. E., Jr., and Warren, L. E., 1947, Devonian rocks of Central Texas: Geol. Soc. America Bull., v. 58, p. 125-140.

Barrois, Charles, Pruvost, P., and Dubois, G., 1922, Description de la faune Siluro-Dévonienne de Liévin: Soc. géol. Nord Mém., v. 6, pt. 2, p. 65-234.

Belanski, C. H., 1928a, Pentameracea of the Devonian of northern Iowa: Iowa Univ. Studies Nat. History, v. 12, no. 7, p. 1-34.

———— 1928b, Description of some typical fossils of the Shellrock Stage: Am. Midland Naturalist, v. 11, no. 5, p. 171-212.

Biernat, Gertruda, 1959, Middle Devonian Orthoidea of the Holy Cross Mountains and their ontogeny: Palaeont. Polonica, no. 10, 78 p.

———— 1964, Middle Devonian Atrypacea (Brachiopoda) from the Holy Cross Mountains, Poland: Acta Palaeont. Polonica, v. 9, no. 3, p. 277-356.

———— 1966, Middle Devonian brachiopods of the Bodzentyn syncline (Holy Cross Mountains, Poland): Palaeont. Polonica, no. 17, 162 p.

Boucot, A. J., 1960, Lower Gedinnian brachiopods of Belgium: Louvain Univ., Inst. Géol. Mém., v. 21, p. 283-324.

Boucot, A. J., and Johnson, J. G., 1967, Paleogeography and correlation of Appalachian Province Lower Devonian sedimentary rocks: Tulsa Geol. Soc. Digest, v. 35, p. 35-87.

Boucot, A. J., Johnson, J. G., and Struve, Wolfgang, 1966, *Stringocephalus,* Ontogeny and Distribution: Jour. Paleontology, v. 40, p. 1349-1364.

Boucot, A. J., Johnson, J. G., and Talent, J. A., 1969, Early Devonian brachiopod zoogeography: Geol. Soc. America Spec. Paper 119, 113 p.

Branson, E. B., 1923, General account of Missouri Devonian, *in* The Devonian of Missouri: Missouri Bur. Geology, Mines, v. 17, 2nd ser., p. 1-129.

Chlupác, Ivo, 1953, Stratigraphical investigation of the border strata of the Silurian and the Devonian in central Bohemia: Ustred. Ustavu Geol. Sborník, v. 20, p. 277-380.

Cloud, P. E., Jr., 1942, Terebratuloid Brachiopoda of the Silurian and Devonian: Geol. Soc. America Spec. Paper 38, 182 p.

Comte, Pierre, 1938, Brachiopodes Dévoniens des gisements de Ferroñes (Asturies) et de Sabero (Léon): Ann. Paléont., v. 27, p. 41-87.

Cooper, G. A., 1945, New species of brachiopods from the Devonian of Illinois and Missouri: Jour. Paleontology, v. 19, p. 479-489.

———— 1955, New genera of Middle Paleozoic brachiopods: Jour. Paleontology, v. 29, p. 45-63.

———— 1967 (1968), Age and correlation of the Tully and Cedar Valley formations in the United States: Alberta Soc. Petroleum Geologists, Internat. Symposium Devonian System, Calgary, 1967, v. 2, p. 701-709.

Cooper, G. A., and Cloud, P. E., Jr., 1938, New Devonian fossils from Calhoun County, Illinois: Jour. Paleontology, v. 12, p. 444-460.

Cooper, G. A., and Williams, J. S., 1935, Tully Formation of New York: Geol. Soc. America Bull., v. 46, p. 781-868.

Crickmay, C. H., 1960, The older Devonian faunas of the Northwest Territories: Calgary, Alberta, published by the author, 21 p.

———— 1963, Significant new Devonian brachiopods from western Canada: Calgary, Alberta, published by the author, 31 p.

———— 1966, Devonian time in western Canada: Calgary, Alberta, published by the author, 38 p.

Dahmer, Georg, 1951, Die Fauna der nach-Ordovizischen Gleider der Verse-Schichten mit Ausschluss der Trilobiten, Crinoiden, und Anthozoen: Palaeontographica Abt. A, v. 101, 152 p.

Fell, H. B., 1968, The biogeography and paleoecology of Ordovician seas, *in* Drake, E. T., ed., Evolution and environment: New Haven, Conn., Yale Univ. Press, p. 139-162.

Fenton, C. L., and Fenton, M. A., 1924, The stratigraphy and fauna of the Hackberry Stage of the Upper Devonian: Michigan Univ., Contr. Mus. Geology, v. 1, 260 p.

Grant, R. E., 1965, The brachiopod superfamily Stenoscismatacea: Smithsonian Misc. Colln., v. 148, no. 2 (4569), 192 p.

Griesemer, A. D., 1965, Middle Devonian brachiopods of southeastern Wisconsin: Ohio Jour. Sci., v. 65, no. 5, p. 241-295.

Hall, James, 1867, Descriptions and figures of the fossil Brachiopoda of the upper Helderberg, Hamilton, Portage and Chemung Groups: New York Geol. Survey, Palaeontology, v. 4, pt. 1, 428 p.

Hallam, A., 1969, Faunal realms and facies in the Jurassic: Palaeontology, v. 12, pt. 1, p. 1-18.

Havlícek, Vladimír, 1956, The brachiopods of the Braník and Hlubocepy Limestones in the immediate vicinity of Prague: Ustred. Ustavu Geol. Sborník, v. 22, p. 535-665.

———— 1959, Spriferidae v ceském siluru a devonu: Ustred. Ustavu Geol. Rozpravy, v. 25, 275 p.

———— 1961, Rhynchonelloidea des böhmischen alteren Paläozoikums (Brachiopoda): Ustred. Ustavu Geol. Rozpravy, v. 27, 211 p.

———— 1967, Brachiopoda of the suborder Strophomenidina in Czechoslovakia: Ustred. Ustavu Geol. Rozpravy, v. 33, 235 p.

House, M. R., 1968, Continental drift and the Devonian System: Univ. Hull, Inaugural Lectures, 24 p.

Imbrie, John, 1959, Brachiopods of the Traverse Group (Devonian) of Michigan. Part 1, Dalmanellacea, Pentameracea, Strophomenacea, Orthotetacea, Chonetacea, and Productacea: Am. Mus. Nat. History Bull., v. 116, p. 345-410.

Jackson, D. E., 1969, Ordovician graptolite faunas in lands bordering North Atlantic and Arctic oceans, *in* Kay, G. M., ed., North Atlantic-Geology and Continental Drift: Am. Assoc. Petroleum Geologists Mem. 12, p. 504-512.

Johnson, J. G., 1969, Some North American Rensselandiid brachiopods: Jour. Paleontology, v. 43, p. 829-837.

———— 1970a, Early Middle Devonian brachiopods from central Nevada: Jour. Paleontology, v. 44, p. 252-264.

———— 1970b, Taghanic onlap and the end of North American Devonian Provinciality: Geol. Soc. America Bull., v. 81, p. 2077-2105.

———— 1970c, Great Basin Lower Devonian Brachiopoda: Geol. Soc. America Mem. 121, 421 p.

———— 1971, Lower Givetian brachiopods from central Nevada: Jour. Paleontology, v. 45, p. 301-326.

Johnson, J. G., Boucot, A. J., and Murphy, M. A., 1967 (1968), Lower Devonian faunal succession in central Nevada: Alberta Soc. Petroleum Geologists, Internat. Symposium Devonian System, Calgary, 1967, v. 2, p. 679-691.

Kozlowski, Roman, 1929, Les Brachiopodes Gothlandiens de la Podolie Polonaise: Palaeont. Polonica, v. 1, 254 p.

Krömmelbein, Karl, Hotz, E. E., Kräusel, Wolfgang, and Struve, Wolfgang, 1955, Zur Geologie der Eifelkalkmulden: Beihefte Geol. Jahrb., v. 17, 204 p.

Lenz, A. C., 1967 (1968), Upper Silurian and Lower Devonian biostratigraphy, Royal Creek, Yukon Territory, Canada: Alberta Soc. Petroleum Geologists, Internat. Symposium Devonian System, Calgary, 1967, v. 2, p. 587-599.

Liashenko, A. I., 1959, Atlas of the brachiopods and stratigraphy of the Devonian deposits of the central part of the Russian Platform: Minist. Geol. Okhran Nedr. SSSR, Vsesoyuzny Nauchno-Issledov. Geol. Neftianoy Inst., 451 p.

Ludvigsen, Rolf, 1970, Age and fauna of the Michelle Formation, northern Yukon Territory: Canadian Petroleum Geologists Bull., v. 18, no. 3, p. 407-429.

McLaren, D. J., 1954, Upper Devonian rhynchonellid zones in the Canadian Rocky Mountains *in* Clark, L. M., ed., Western Canada Sedimentary Basin: Tulsa, Ok., Am. Assoc. Petroleum Geologists, p. 159-181.

———— 1962, Middle and early Upper Devonian rhynchonelloid brachiopods from western Canada: Canada Geol. Survey Bull. 86, p. 1-122.

McLaren, D. J., and Norris, A. W., 1964, Fauna of the Devonian Horn Plateau Formation, District of Mackenzie: Canada Geol. Survey Bull. 114, 74 p.

McLaren, D. J., Norris, A. W., and McGregor, D. C., 1962, Illustrations of Canadian fossils—*Devonian of Western Canada*: Canada Geol. Survey Paper 62-4, 34 p.

Muir-Wood, H. M., and Cooper, G. A., 1960, Morphology, classification, and life habits of the Productoidea (Brachiopoda): Geol. Soc. America Mem. 81, 447 p.

Nalivkin, D. V., 1941, Brachiopods of the Main Devonian Field, *in* Batalina, M. A., and others, Fauna glavnogo devonskogo polia, v. 1: Akad. Nauk. SSSR, Paleont. Inst., p. 139-226.

Norris, A. W., 1967 (1968), Devonian of northern Yukon Territory and adjacent District of Mackenzie: Alberta Soc. Petroleum Geologists, Internat. Symposium Devonian System, Calgary, Alberta, 1967, v. 1, p. 753-780.

Pedder, A. E. H., 1959, *Monelasmina besti*, a new schizophoriid brachiopod from the Upper Devonian of western Canada: Geol. Mag., v. 96, p. 470-472.

———— 1960, New species of brachiopods from the Upper Devonian of Hay River, western Canada: Palaeontology, v. 3, pt. 2, p. 208-216.

Ross, R. J., Jr., and Ingham, J. K., 1970, Distribution of the Toquima-Table Head (Middle Ordovician Whiterock) faunal realm in the northern Hemisphere: Geol. Soc. America Bull., v. 81, p. 393-408.

Simpson, G. G., 1947, Holarctic mammalian faunas and continental relationships during the Cenozoic: Geol. Soc. America Bull., v. 58, p. 613-687.

Spjeldnaes, Nils, 1961, Ordovician climatic zones: Norsk geol. tidsskr., v. 41, p. 45-77.

Stainbrook, M. A., 1938a, *Atrypa* and *Stropheodonta* from the Cedar Valley beds of Iowa: Jour. Paleontology, v. 12, p. 229-256.

———— 1938b, Pentameridae of the Cedar Valley beds of Iowa: Am. Midland Naturalist, v. 19, no. 3, p. 723-739.

———— 1940, Orthoid brachiopods of the Cedar Valley Limestone of Iowa: Am. Midland Naturalist, v. 23, no. 2, p. 482-492.

———— 1942a, Brachiopoda of the Cedar Valley beds of Iowa; Inarticulata, Rhynchonellacea and Rostrospiracea: Jour. Paleontology, v. 16, p. 604-619.

———— 1942b, The brachiopoda of the High Point Sandstone of New York: Am. Jour. Sci., v. 240, p. 879-890.

———— 1943a, Strophomenacea of the Cedar Valley Limestone of Iowa: Jour. Paleontology, v. 17, p. 39-59.

———— 1943b, Spiriferacea of the Cedar Valley Limestone of Iowa: Jour. Paleontology, v. 17, p. 417-450.

———— 1945, Brachiopoda of the Independence shale of Iowa: Geol. Soc. America Mem. 14, 74 p.

———— 1948, Age and correlation of the Devonian Sly Gap beds near Alamagordo, New Mexico: Am. Jour. Sci.. v. 246, p. 765-790.

Valentine, J. W., 1966, Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf: Limnology and Oceanography, v. 11, p. 198-211.

Veevers, J. J., 1959, Devonian brachiopods from the Fitzroy Basin, Western Australia: Australia Bur. Mineral Resources, Geology, Geophys. Bull. 45, 220 p.

Warren, P. S., and Stelck, C. R., 1956, Reference fossils of Canada, Part 1, Devonian faunas of western Canada: Geol. Assoc. Canada Spec. Paper 1, p. 1-15.

Whittington, H. B., 1966, Phylogeny and distribution of Ordovician trilobites: Jour. Paleontology, v. 40, p. 696-737.

Williams, Alwyn, 1969, Ordovician faunal provinces with reference to brachiopod distribution, *in* Wood, Alan, ed., The Pre-Cambrian and Lower Palaeozoic Rocks of Wales: Univ. Wales, p. 117-154.

Williams, H. S., 1890, The Cuboides zone and its fauna; a discussion of methods of correlation: Geol. Soc. America Bull., v. 1, p. 481-500.

———— 1913, Recurrent *Tropidoleptus* zones of the Upper Devonian of New York: U. S. Geol. Survey Prof. Paper 79, 103 p.