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PALEOBIOGEOGRAPHY OF DEVONIAN BRYOZOA IN LAURUSSIA

By

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ABSTRACT

PALEOBIOGEOGRAPHY OF DEVONIAN BRYOZOA IN LAURUSSIA

By

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During the Devonian, the continents of Baltica and Laurentia collided, creating Laurussia. Biogeographic data provide information on the configuration of epeiric seas and land barriers permitting or barring taxonomic dispersal of marine animals. Bryozoan generic data are analyzed using Parsimony Analysis of Endemicity and Simpson's Index of Overall Faunal Similarity to identify biomes and provinces that existed during the Devonian Period. Endemic and shared genera are combined with lithologic data and time scales to present a picture of geodispersal and vicariance over time. Forty-four local areas contain significant diversity to be used in the analyses, and eight biomes are described: Appohimchi II, Old World II, Michigan, Ohio II, Appohimchi Ia, Appohimchi Ib, Ohio I, and Old World I. Two provinces are proposed, Laurussia I and Laurussia II, which are distinguished temporally. A major extinction event occurred within Bryozoa during the Devonian, and a lack of endemic taxa makes both biomes and provinces indistinguishable after the Givetian. The North American biomes were more heavily affected by the Givetian mass extinction than the European areas.

For CMH, JEH, and MAH

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Introduction

The Devonian Period was a stage of great geological change. The continents of Baltica and Laurentia were colliding, producing the Acadian Orogeny. Biogeographic analyses have utilized numerous marine taxa, but a thorough study has yet to be focused upon the Bryozoa. The purpose of this study is to delineate patterns of endemism in Devonian bryozoans in North America and Europe, and to suggest hypotheses for the development of biogeographic regions during the period. The strategy employed in this research is to create a more complete database of bryozoan distributions by adding geographic data to the Horowitz and Pachut (1993) generic and specific database, focusing on Laurussia, which is comprised of modern day North America, Europe, and Russia west of the Urals.

Devonian marine rocks are widespread within North America, with extensive outcrops in New York and Ontario. In Europe, the Devonian outcrops in Germany, the Czech Republic, Poland, Spain, France, and in the Ukraine. I analyze patterns of generic endemism through the Devonian, facilitating comparisons between endemic associations across stadial boundaries. Identifying areas that have similar faunal makeup allows for relationships to be established between provinces and biomes. Shared endemicity can provide information on the configuration of epeiric seas and land barriers permitting or barring taxonomic dispersal of marine animals and the historical subdivision of these regions through vicariance. Here I propose two time based provinces, Laurussia I and Laurussia II. I also look at the Givetian mass extinction and how it affects the endemism of the succeeding stages; investigating whether some endemic associations were differentially affected and whether these survive the extinction event or events, testing the hypothesis that mass extinction leads to biogeographic reorganization during recovery and rebound.

Background Information

The paleobiogeography of the Devonian Period has been studied using a number of different taxa, including trilobites (Lieberman 1993; Eldredge and Ormiston, 1979), brachiopods (Johnson and Boucot, 1973; Koch, 1981), corals (Oliver, 1976; Oliver and Pedder, 1979), and ammonites. In their study of brachiopods, Johnson and Boucot (1973) recognized three major realms or provinces that for the Late Silurian Early Devonian (see Table 1 for Devonian stadial nomenclature). Their Old World Realm covered Western North America, the American Arctic, Australia, Eurasia, and North Africa. South America and Africa were contained within the Malvinokaffric Realm, and Central and Eastern North America within the Appalachian Realm. Each of these realms was divided into a number of provinces.

Table 1. Devonian Relative Time Scale

System	Series	Stage
Devonian	Upper	Fammenian
		Frasnian
	Middle	Givetian
		Eifelian
	Lower	Emsian
		Pragian
		Lochkovian

The Emsian showed the highest level of endemism within all of the realms. The Eifelian and majority of the Givetian also exhibited high levels of endemism, but in the late Givetian and into the Frasnian, provincial distinctions virtually disappeared. In the Fammenian, the Malvinokaffric Realm disappeared as there are no marine strata to study, and a cosmopolitan fauna was established everywhere else. Oliver (1976; Oliver and Pedder, 1979) analyzed rugose corals in North America, and found major differences in faunas between Western and Eastern North America (corresponding approximately to the

Old World Realm and the Appalachian Realm, respectively) with high levels of endemism in the Emsian declining to complete cosmopolitanism by the Frasnian. Koch (1981) identified the brachiopod affinities in the early Eifelian Onondaga Limestone and other units of the same age. He identified the Eastern Americas and Old World Realms as well as the Michigan-Hudson Bay Lowland and Appohimchi Provinces within the Eastern Americas Realm.

Lieberman (1993) was the first to use any kind of quantitative analysis to identify Devonian provinces. He used both cluster analysis and Brooks Parsimony Analysis (BPA); the latter uses phylogenetic data along with geographic data to identify biogeographic provinces. Lieberman and Eldredge (1996) studied Middle Devonian trilobite geography and found similar patterns to those seen in brachiopod and coral distributions, with areas easily recognizable as corresponding to the Appalachian and Old World Realms. They also hypothesized locations of land barriers and incorporated sea level changes to explain variations in provincial locations and faunas. Lieberman and Stigall Rode (2005) also used BPA, looking at a variety of taxa and focusing on the Frasnian-Fammenian crisis. They found that singular tectonic events had more influence on Devonian extinctions than cyclic sea level changes, and that using cross-faunal analysis allowed for a broader view of marine biogeography in comparison with to single taxon studies.

Bryozoan paleobiogeography in the Devonian is not discussed in the Treatise on Invertebrate Paleontology Volume A (House, 1979; Norris, 1979). Bigey (1985; 1986) published a first attempt at Devonian bryozoan distributions, but based provincial divisions on those of other marine organisms instead of looking for differing patterns within Bryozoa themselves. She also did not present a global database for Devonian Bryozoa nor did she quantitatively or numerically analyze any data that might corroborate the previously published patterns. Bigey (1985) suggested that in the Early Devonian an Old World Realm encompassed much of Europe and North Africa, a Malvinokaffric Realm covered most of South America and Southern Africa, and an Eastern Americas Realm existed that was a smaller region and not yet subdivided. Middle Devonian Bryozoa have not been found in the Malvinokaffric Realm, and in the Old World Realm, a decline in provinciality has been seen in the Givetian. The Eastern Americas Realm became more diverse and subdivided, and she recognized two provinces within it named by Koch (1981) for brachiopods, the Appohimchi and Michigan-Hudson Bay Lowland Provinces. Bigey noted that Late Devonian Bryozoa were found in the Frasnian in Europe and North America. She recognized two low diversity faunas in western North America (Montana and New Mexico) that are dated as Fammenian. These low diversity Frasnian/Fammenian faunas exhibit no endemism. In Russia and the far east, bryozoan faunas continued into the Fammenian, but while more numerous, were again low in diversity.

Horowitz and Pachut (1993) compiled a specific, generic, and familial diversity database of all Devonian Bryozoa that was later analyzed in terms of extinctions, originations, and biogeography by Horowitz et al. (1996). This database is reasonably complete (up to 1993) as a taxonomic list of all named bryozoan species extant in the global Devonian, but lacks information on the specific local areas or regions in which each species occurs. The resulting paper (Horowitz et al., 1996) included a brief biogeographical analysis in which they found that the Appohimchi Province was disproportionately affected by the Givetian mass extinction, with 41% of all generic extinctions confined to the Eastern Americas Realm. They linked the development of a high diversity biome to the progradation of the Catskill clastic wedge, and the extinction to a rise in sea level coupled with an influx of anoxic waters over the eastern portion of Laurentia.

Materials and Methods

The database created for this study included taxonomic data (order, suborder, family, genus, species), locality data (country, region/state, local area), and geology (stratigraphy, lithology) for 1,874 records. This study focuses on locating published descriptions of bryozoan faunas in what is currently North America and Europe. Included within the European localities were Russia west of the Urals, Novaya Zemlaya, and the Transcaucasus. These areas comprise the current locations of Baltica and Laurentia. Faunal lists and descriptions were compiled into a data file at the genus level, along with other higher taxonomic assignments, locality information, and stratigraphic and lithologic descriptions where possible. The database is too large to be included here and is available from R.L. Anstey, Michigan State University.

Bryozoan species tend either to be geographically local or tenuously identified in different regions if widespread. Therefore, the genus level is usually the lowest taxonomic rank that can be used confidently in biogeographic studies. The original database contains species-rank data, but species were not reliably determined in many 19^{th} century publications that did not use thin sections; therefore the fossils are almost certainly assigned to the correct genus, but species identifications are more likely to be doubtful. Also, there is little consensus in the literature on the species concept in Bryozoa; numerical-quantitative protocols for recognizing fossil species are rarely consistently followed (Anstey and Pachut, 2004). In this study, only generic data are analyzed (Appendix A).

The smallest operational biogeographic unit (OBU), the local area, is both a region and a stratigraphic unit identified as having Bryozoa within its boundaries. In this study, composite listings were tabulated for counties and/or county-sized areas in the United States and Canada, while sites in Europe were most often single exposures. These were identified within approximately county sized areas (voivodeships in Poland, oblasts in Russia, etc.) in which they occurred. Where possible, the local areas were also defined by formations, so a local area would thus represent not only a definite geographic area but would also have definite lithostratigraphic boundaries. However, this was not possible for some local areas due to many of the faunal listings' lack of resolution to formation. The Hamilton Group in New York and the Traverse Group in Michigan could be geologically distinguished in some cases, but a number of sources did not subdivide the data on the basis of stratigraphic units and thus some local areas (Alpena-Traverse Group, Grand Traverse-Traverse Group, and the New York-Hamilton areas) represent a slightly longer time scale and thus more composite faunas. Local areas that were adjacent to one another and from the same rock unit were combined to create slightly more diverse faunas in those areas (Coal and Haragan Counties, Oklahoma and many of the Maryland and West Virginia localities). While this reduces the number of local areas, it ncreases the number of genera per locality and is more biogeographically informative. Counties were chosen due to the ease of mapping, and being somewhat arbitrary allows for the reconstruction of local area borders more easily than other methods. Similarly, local areas that were adjacent and contained homogeneous faunas were combined in order to streamline the results. None of the local areas in Figure 1 amalgamate nonadjacent or non-homogeneous faunas.

Many of the areas Bryozoa are found in do not contain diverse faunas. This may reflect the bias of poor sampling or may be a realistic reflection of low diversity in the area. In a study of Ordovician and Silurian biogeography, Anstey et al. (2003) found that it was necessary to have at least ten genera in the faunal list of each local area in order to produce a tree in a reasonable amount of time and to reduce the number of equally parsimonious trees. They based their decision on the idea that low diversity faunas were often composed of cosmopolitan genera and provided little to no biogeographic information. Here, only local areas containing a minimum of nine or more genera were used.

To indicate faunal linkage, a genus must be found in at least two local areas. While genera reported in only one locality support patterns of endemism, they do not add to information on the relationships between areas. The strength of the data can be inferred in a number of ways. The consistency index (CI) provided in parsimony analysis is an indicator of how well the cladogram differs from completely random information. Another indication is how well the data confirm previously developed hypotheses of provinces based on other taxonomic groups, and in this case, to those of Bryozoa from Bigey (1985). Table 2 contains a seriated distribution that shows the biomes/provinces in my inferred cladogram order. Taxa should be found continuously throughout contiguous areas of the cladogram. If one area is skipped, shown here as a hyphen, it is considered a

Table 2. Patterns of endemism among genera within each biome. Genera extending over four or more biomes are excluded. Documented occurrences are marked with an X, expected occurrences with a -.

	Appohimchi II	Michigan	Old World II	Ohio II	Appohimchi Ib	Appohimchi Ia	Ohio I	Old World I
Acrogenia	X							
Bactropora	X							
Glauconome	X							
Ceramella	X	X						
Nematopora	X	-	X					
Taeniopora	X	X	-	X				
Stictoporina	X	X	-	X				
Eliasopora	X	-	X	X				
Allonema	X	-	X	X				
Reptaria	X	-	-	X				
Semiopora	X	-	-	X				
Paleschara	X	-	-	X	-	X		
Callotrypa	X	-	-	-	X	X		
Ceramopora	X	-	-	-	X	X		
Ptilodictya	X	-	-	-	-	X		
Callopora	X	-	-	-	-	X		
Coscinium	X	X	-	-	-	-	X	
Fenestrapora	X	-	-	X	-	-	X	
Thamniscus	X	-	-	-	-	X	X	
Prismopora	X	-	-	-	-	-	X	
Trematopora	X	-	-	-	-	-	X	
Clonopora	X	-	-	-	-	-	X	
Trematella	X	-	-	-	-	-	X	
Nemataxis	X	-	-	-	-	-	X	
Ptilopora	X	-	-	-	-	-	-	X
Anomalotoechus		X						
Eridocampylus		X						
Dyoidophragma		X						
Microcampylus		X						
Calacanthopora		X						
Callocladia		X						
Atactotoechus		X	X	X				
Fenestrellina		X	-	X				
Anastomopora		X	-	X				
Fistuliphragma		X	-	X				
Helopora		X	-	X				
Lyropora		X	-	X				
Euspilopora		X	-	-	X			
Monticulipora		X	-	-	X			
Cyphotrypa		X	-	-	X	X		
Trachytoechus		X	-	-	-	X		
Cystodictya		X	-	X	-	-	X	
Hernodia		X	-	X	-	-	X	
Discotrypa		X	-	-	-	-	X	
Phyllopora		X	-	-	-	-	X	
Phractopora		X	-	-	-	-	X	
Cyclopora		X	-	-	-	-	X	
Chondraulus		X	-	-	-	-	X	X
Petaloporella		X	-	-	-	-	-	X
Sulcoretepora		X	-	X	-	-	-	X

Table 2. (cont'd).

	Appohimchi II	Michigan	Old World II	Ohio II	Appohimchi Ib	Appohimchi Ia	Ohio I	Old World I
Ptiloporina		x	-	x	-	-	-	x
Isotrypa		x	-	-	-	-	-	x
Vinella			x	x				
Rhopalonaria			x	x	x			
Cheilotrypa			x	-	x			
Eridotrypa			x	-	x	x		
Cyclotrypa			x	-	-	x		
Reteporidra			x	-	-	-	x	
Alternifenestella			x	-	-	-	-	x
Paralioclema			x	-	-	-	-	x
Rectifenestella			x	-	-	-	-	x
Spinofenestella			x	-	-	-	-	x
Corynotrypa			x					
Fistuliramus			x					
Leptotrypa			x					
Saffordotaxis			x					
Primorella			x					
Canutrypa			x					
Fistuliporella				x	x	x		
Monotrypella				x	-	x		
Coscinotrypa				x	-	-	x	
Scalaripora				x	-	-	x	
Pinacotrypa				x	-	-	-	x
Stenopora					x			
Stromatotrypa					x	x		
Batostomella					x	x		
Diplostenopora					x	x		
Coelocaulis						x		
Cyclopelta								x
Filites								x
Laxifenestella								x

missing occurrence. For the 82 most endemic taxa, namely those found in 3 or fewer biomes, the ratio of absences where expected to total occurrences is 158 to 321, or 49%, giving a 51% estimation of biogeographic completeness in the available data.

Using Hammer et al.'s (2001) program PAST (PAlaeontological STatistics), parsimony analysis was run with the local areas being defined by the genera present in each. The local areas are used as "taxa" with the genera performing as "character states" and the analysis groups areas based upon their shared endemic genera. With the locality data, character states in the data sheet are presence/absence. Parsimony analysis looks for the shortest tree which describes the relationships between all of the local areas. Therefore, areas with more endemic genera in common with each other would be more likely to group together than those with fewer shared endemic genera. Parsimony analysis also searches for the shortest tree, that with the smallest number of branching events. When used as a biogeographic cladistic technique, this is called Parsimony Analysis of Endemicity (PAE) (Rosen and Smith, 1988; Fortey and Cocks, 1992). Errors in the tree represent "homoplasy," which is calculated as one minus the Consistency Index of the tree, and reflects the degree of "false" results caused by either incomplete sampling and/or disjunct distributions of genera.

For this study, the Wagner algorithm (which gives equal weight to both forward and reverse character state transitions) was used; because I only coded for presence/absence data as 1 and 0, the Fitch algorithm, which is used for datasets where there are more than two character states, was inappropriate. Heuristic branch reordering was also chosen, with a reordering number of 75. Due to the large size of the data set, heuristic Tree Bisection and Reconnection (TBR) was most appropriate. TBR adds OBUs to a tree in the order from the data matrix that will add the shortest number of branching events. Then the tree is divided into two subsets and the sets switched to find a shorter tree. This is repeated after each local area is added and for all divisions of the tree. While TBR takes longer than the other heuristic analyses, it often results in a shorter, more parsimonious tree. The resulting tree from this study was divided into clusters first by obvious branching (Figure 1). Next, those genera with CIs of 1 or 0.5 (the two highest CIs) were plotted on the cladogram to identify the groups that were most strongly supported by particular endemic genera (Figure 2). Clusters were divided further based upon the age of the faunas.

Hierarchical cluster analysis (Figure 3) was also run on the data using Simpson's Index of Faunal Similarity. This method groups the areas by overall similarity, and gives equal weight to both endemic and cosmopolitan taxa. The cluster diagram uses the overall similarity between faunas to relate them, whereas the cladogram reflects only endemic genera. Whereas faunal provinces are defined entirely by the percentage of endemic genera, biomes are better defined by overall faunal similarity. Therefore the Simpson's cluster diagram (Fig. 3) better reflects the biomes, whereas the cladistic area tree better (Fig. 1) better reflects the time-variant provinces.

The biogeographic terminology used in this paper are those set forth in Anstey et al. (1996). A province is therein defined as a biotically distinct geographic area that is separated by barriers (physical or climatic) from adjacent provinces. Endemic taxa should constitute 25-50% of overall taxa. A biome, as used here, is a smaller unit, characterized by a distinctive overall biota, substrate (lithology) and bathymetry.

Results

Forty-four OBUs were identified from the database that have sufficient generic diversity to be of use in analysis. The PAE method requires an artificial Hypothetical Ancestral Area, coded as all 0s, with presumably bryozoan genera present. All of these areas were run through the cladistic algorithm of PAST (see Table 3 for a list of all local areas; complete datafile found in Appendix A). PAST found one most parsimonious tree

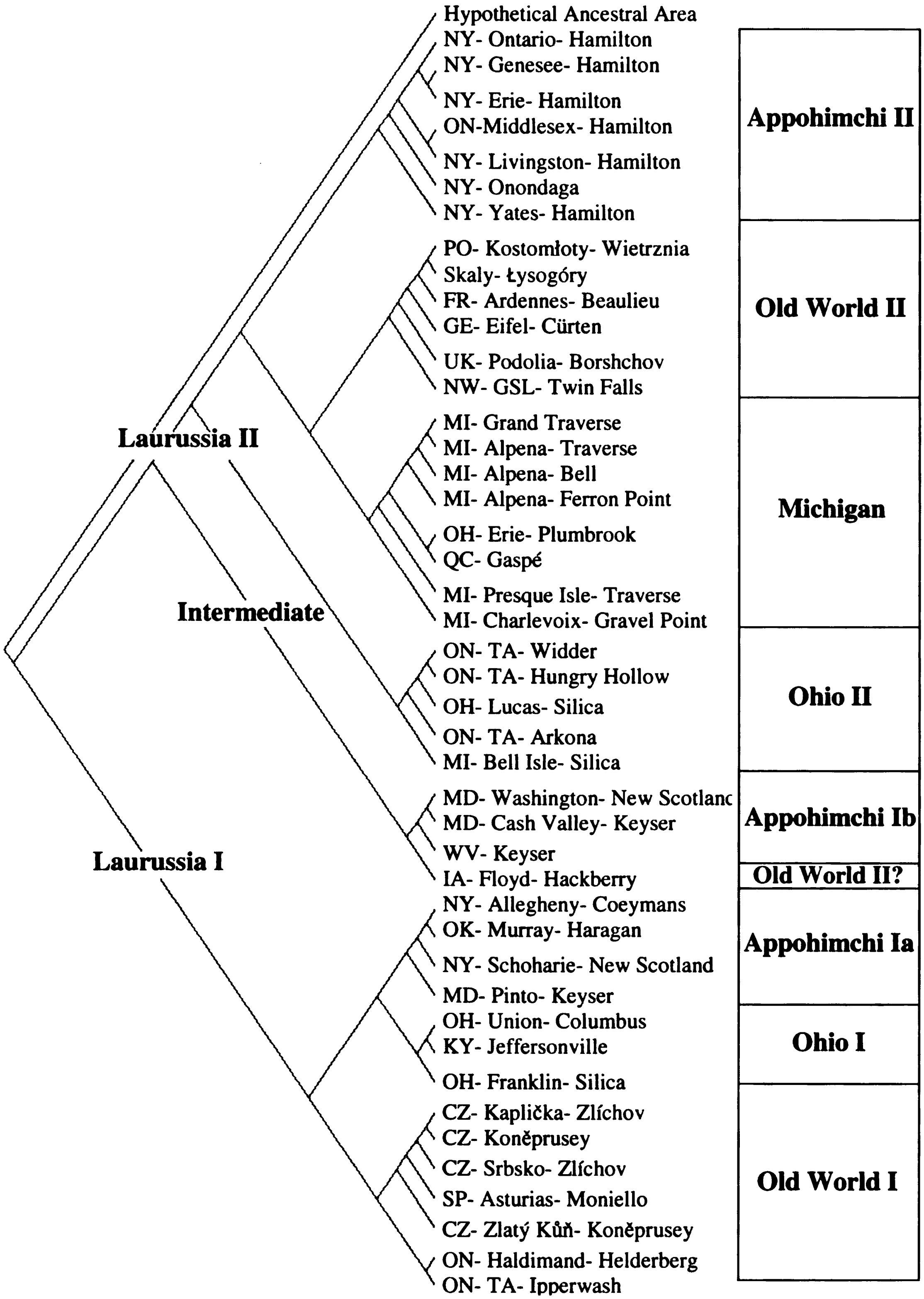


Figure 1. Most parsimonious tree with length of 308 run with heuristic Tree Bisection - Reconnection (TBR) with 75 reorderings. CI= 0.2865, HI= 0.7135. Hypothetical Ancestral Area indicates a local area in which all the taxa were absent. Postal code abbreviations are used for states, the rest as follows: ON= Ontario, Canada, PO= Poland, UK= Ukraine, NW= Northwest Territories, Canada, GSL= Great Slave Lake, QC= Quebec,Canada TA= Thedford-Arkona, CZ= Czech Republic, SP= Spain.

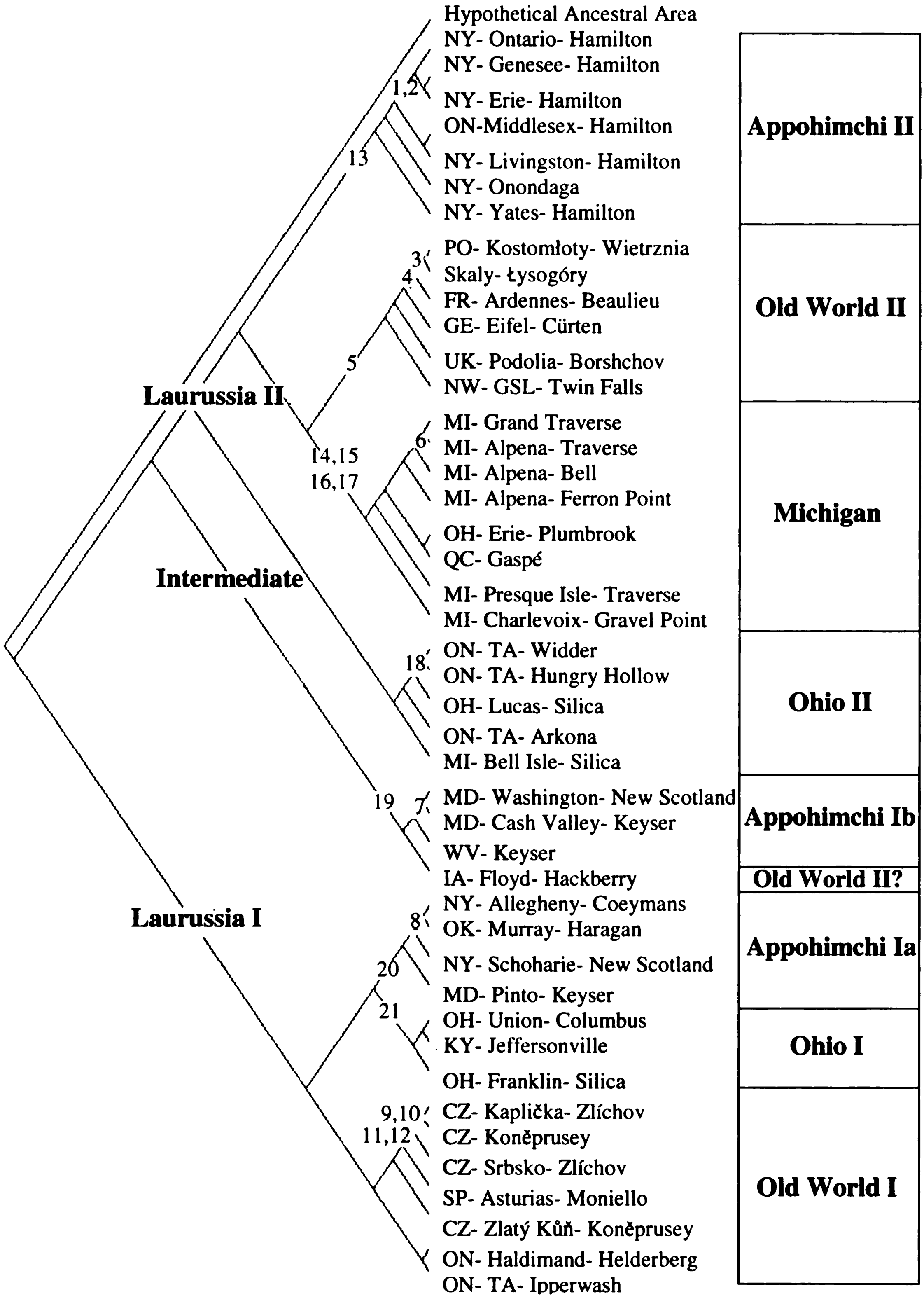


Figure 2. Cladogram showing generic support for each biome. Genera with a CI of 1.0 are 1. *Bactropora*, 2. *Glauconome*, 3. *Primorella*, 4. *Canutrypa*, 5. *Leptotrypa*, 6. *Callocladia*,7. *Stenopora*, 8. *Coelocaulis*, 9. *Utropora*, 10. *Laxifenestella*, 11. *Filites*, 12. *Cyclopelta*. Genera with a CI of 0.5 = 13. *Acrogenia*, 14. *Anomalotoechus*, 15. *Calacanthopora*, 16. *Dyoidophragma*, 17. *Eridocampylus*, 18. *Coscinotrypa*, 19. *Cheilotrypa*, 20. *Ptilodictya*, 21. *Prismopora*.

(Figure 1). The tree length was 380 and the ensemble CI was 0.2865. The Homoplasy Index (HI) is 0.7135. The CI for a random set of data of this size is 0.0839, which shows that the CI is greater than the random CI by 0.2026, indicating that the data are biogeographically informative (Klassen, et. al, 1991).

Ensemble (average) CIs for each biome are shown in Table 3; the most strongly supported areas are the Old World I and II Biomes. The relationships from the area cladogram were compared with Paleozoic continental reconstructions of Scotese (2002). Table 2 shows the distributions of the 82 most endemic genera across each biome. There are 21 genera endemic to a single biome. Table 4 shows genera endemic to each biome and ten genera that are found in both the same biome in both the Laurussia I and Laurussia II Provinces (for example, Appohimchi Ia, Ib, and II) as well as those contained within a time unit. These genera must persist through time in their linked biomes, and their separation on the cladogram represents a false disjunction.

Discussion of Biomes

Old World I (Pragian to Eifelian) – Lower Devonian in age, these strata primarily come from the Prague Basin of the Czech Republic and are all limestones (Figure 5). The Moniello Formation along the northern border of Spain also belongs in the biome. The group is strongly supported by the presence of *Utropora*, *Laxifenestella*, *Filites*, and *Cyclopelta* (Figure 2).

Two localities in Ontario, Canada appear on the tree to be closely related to the Old World I biome (Figure 1). While Haldimand, Ontario is part of the Helderberg Group and Emsian aged and thus overlaps with Old World I, the Ipperwash Limestone of

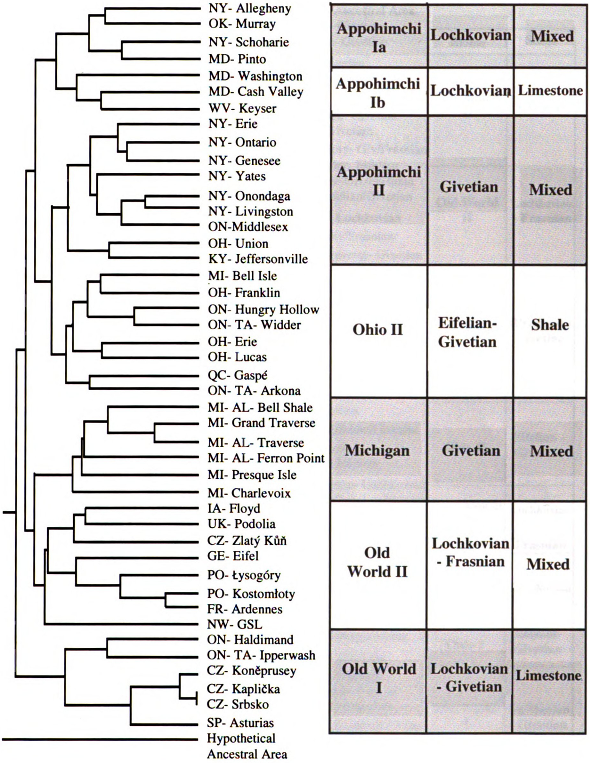
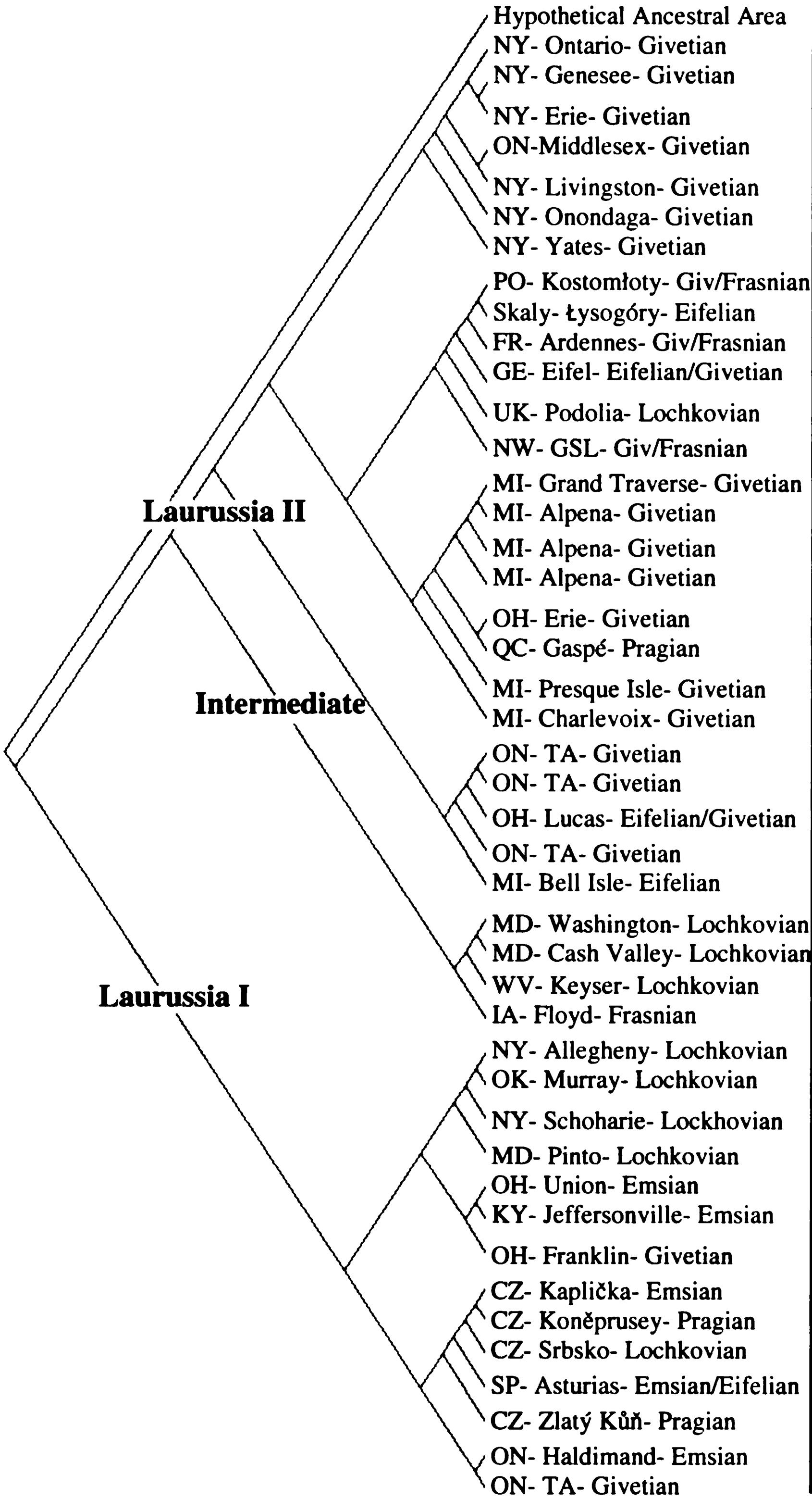


Figure 3. Cluster analysis of Simpson's Index of Faunal Similarity between each local area. * denote the OBUs that do not cluster within their Parsimony Analysis of Endemicity (PAE) groupings.



Biome	Stage
Appohimchi II	Givetian
Old World II	Lochkovian - Frasnian
Michigan	(Pragian) - Givetian
Ohio II	Eifelian - Givetian
Appohimchi Ib	Lochkovian
Old World II	Frasnian
Appohimchi Ia	Lochkovian
Ohio I	Emsian-Givetian
Old World I	Lochkovian - Givetian

Figure 4. Area Cladogram showing the stage occurrences of each OBU. See Table 1 for Devonian stages.

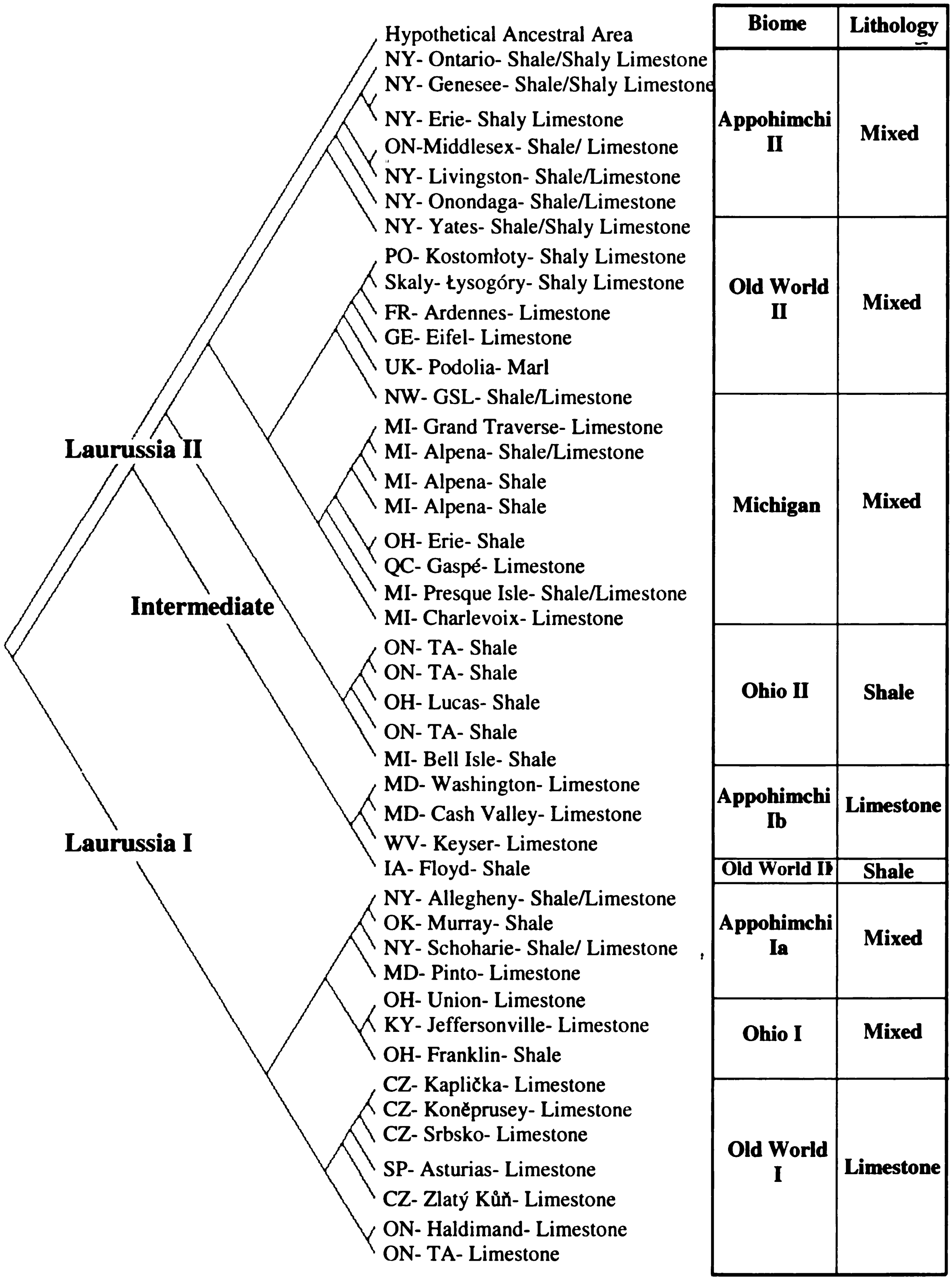


Figure 5. Area Cladogram showing the lithology of each local area. Mixed lithotypes include areas receiving deposition of both carbonate and siliciclastic materials.

Table 3. Local areas with the average Consistency Index (CI) of each and the average CI for each cluster

Area	Area CIs
Hypothetical Ancestral Area	0.000
NY- Ontario	0.340
NY- Genessee	0.396
NY- Erie	0.305
ON- Middlesex	0.164
NY- Livingston	0.184
NY- Onondaga	0.205
NY- Yates	0.243
Appohimchi II	**0.262**
MI- Grand Traverse	0.322
MI- Alpena- Traverse	0.296
MI- Alpena- Bell	0.269
MI- Alpena- Ferron Point	0.281
OH- Erie	0.218
QC- Gaspé	0.201
MI- Presque Isle	0.231
MI- Charlevoix	0.302
Michigan	**0.265**
PO- Wietrznia	0.381
PO- Skaly	0.379
FR- Ardennes	0.360
GE- Eifel	0.348
UK- Podolia	0.303
NW- Great Slave Lake	0.361
Old World II	**0.355**

Area	Area CIs
ON- TA- Widder	0.212
ON- TA- Hungry Hollow	0.216
OH- Lucas	0.247
ON- TA- Arkona	0.223
MI- Bell Isle	0.151
Ohio II	**0.210**
MD- Washington	0.312
MD- Cash Valley	0.343
WV- Keyser	0.238
IA- Floyd	0.208
Appohimchi Ib	**0.275**
NY- Allgheny	0.335
OK- Murray	0.346
NY- Schoharie	0.233
MD- Pinto	0.250
OH- Union	0.253
KY-Jeffersonville	0.287
OH- Franklin	0.165
Appohimchi Ia	**0.267**
CZ- Kaplička	0.520
CZ- Koněprusey	0.468
CZ- Srbsko	0.520
SP- Asturias	0.401
CZ- Zlatý Kůň	0.251
ON- Haldimand	0.208
ON- TA- Ipperwash	0.176
Old World I	**0.364**

Thedford-Arkona, Ontario is Givetian and younger than all of the Old World I faunas (although it is of the same age as Old World II faunas). In the cluster diagram (Figure 3), both of these local areas group with the Old World Fauna, and are also less argillaceous limestones than the other Ontario rock units. This leads to the conclusion that the

Ipperwash and Haldimand represent a less argillaceous lithotope that has Old World affinities that are conserved into the Emsian and Givetian. Koch (1981) found Old World brachiopod faunas in Quebec in the Eifelian and noted that they were near the borders of both the Michigan-Hudson Bay Province and the Appohimchi Province, as well as those of the Eastern Americas and Old World Realms. This could partially explain the difficulty in placing the Quebecois Gaspé fauna in any cluster or area clade with any certainty. Koch's (1981) recognition of the Old World fauna in Quebec represents the only support for such affinities in Eastern North America, but it does offer a link to the Ontario faunas.

Ohio I (Emsian to Givetian) – This region was considered part of the Michigan-Hudson Bay Lowland province by Bigey (1985). Comprising of the Jeffersonville Limestone of Kentucky (mainly exposed at the Falls of the Ohio), and Union and Franklin Counties, Ohio, the biome is partially supported by the presence of the genus *Prismopora*. Franklin County reflects a Silica Shale exposure, and is younger than the other two local faunas (Eifelian/Givetian vs. Emsian) which are found in limestones. In the faunal cluster analysis (Figure 3) these areas are absorbed by other clusters, namely the Appohimchi II and Ohio II biomes. Because of this, and because of its lack of purely endemic genera, its designation as a separate biome is not strongly supported.

Appohimchi Ia (Lochkovian) – This Early Devonian biome contains faunas from some of the same rock units as Appohimchi Ib, the New Scotland and Keyser Limestones. It includes areas in New York, Maryland, and a fauna in Oklahoma. The Oklahoma fauna indicates that this biome is geographically widespread reflecting its large size. Faunally, this biome is supported by the genus *Ptilodictya*, with a CI of 0.5, and *Coelocaulis* is endemic to the two Maryland localities.

Appohimchi Ib (Lochkovian) – This biome is located in West Virginia and Maryland limestones. It is of similar age as that of Appohimchi Ia, but is more closely related faunally with the younger biomes of the Laurussia II branches. The most obvious disjunct fauna is found in this cluster, in the Frasnian Hackberry Shale fauna of Floyd County, Iowa. This fauna appears to cluster with Old World faunas in terms of overall similarity, age, and it also differs from its area clade in lithology. Regardless, in further discussion it will be assumed that this area is disjunct and that Appohimchi Ib only contains those local areas in the Appalachian region. Apart from the Hackberry area, this biome was strongly supported faunally and geologically, with the genera *Stenopora* and *Cheilotrypa* defining the group. Appohimchi Ib and Ia cluster together in terms of overall faunal similarity (Figure 3), and could possibly be combined into one biome. I am choosing to leave them separate due to the clear branching event that separates them on the cladogram and signifies a difference in endemic taxa (Figure 1).

Ohio II (Eifelian to Givetian) – This biome represents the northward expansion of the Ohio I biome. This biome is confined to southeastern Michigan, northwestern Ohio, and southern Ontario. The fauna occurs in shaly facies. Its only partially endemic genus is *Coscinotrypa*, which is confined to the two Thedford-Arkona, Ontario units, the Widder and Hungry Hollow Shales. It also contains a number of genera only found in one other biome, sharing some endemic genera with the nearby Michigan Biome In the cluster analysis (Figure 3), this biome takes in the Franklin County Silica Shale fauna, as well as the Gaspé Limestone.

Table 4. Endemic genera for each biome. Genera listed in biomes with both Roman numerals (i.e. Old World I/II) are those that occur in both Provinces, but are geographically endemic to the corresponding Operational Biogeographic Unit (OBU). * denotes genera that became extinct in the Givetian.

Appohimchi II
*Acrogenia**   *Bactropora**   *Glauconome*
Appohimchi I
Stenopora   *Stromatotrypa*   *Batostomella*   *Diplostenopora*   *Coelocaulis*
Appohimchi I/II
*Callotrypa**   *Cerampora*   *Callopora*   *Ptilodictya**
Michigan
*Anomalotoechus**   *Eridocampylus*   *Dyoidophragma*   *Microcampylus*   *Calacanthopora*   *Callocladia**
Ohio I/II
*Coscinotrypa**   *Scalaripora**
Old World II
*Corynotrypa**   *Fistulirama**   *Leptotrypa*   *Saffordotaxis*   *Primorella*   *Canutrypa*
Old World I
Cyclopelta   *Filites*   *Laxifenestella*   *Utrapora*
Old World I/II
*Alternifenestella**   *Paralioclema*   *Rectifenestella*   *Spinofenestella**

Old World II (Eifelian to Frasnian) – Comprised mainly of Middle to Late Devonian faunas, the Old World II biome covers Poland, Germany, France, and Western Canada. These findings support the Old World Biome recognized by Bigey (1985) . *Leptotrypa* is endemic to the entire biome, *Primorella* to Poland, and *Canutrypa* to Poland and France. The lithology of the units is predominantly limestone, with the Polish and Canadian units being shaly limestones. Also included here is a fauna from the Lochkovian of the Ukraine, which while faunally similar, is temporally disjunct. The Ukraine faunais also the only location in this study in which the lithology was not described as a shale or a limestone, but as a marl. The Northwest Territories of Canada is only an apparent disjunction; the extension of the Old World Province to Western Canada is supported by other taxa that show similar affinities (Johnson and Boucot, 1973; Oliver, 1976); Johnson and Boucot suggested that this pointed to an open seaway along the Northern Coast of Laurussia through which Old World taxa migrated, and Oliver noted that the only apparent barrier between the Western United States and Canada faunas was distance. He also saw that for corals, the linked Old World faunas include sites in the

Russian platform as well (see Figure 7 for Middle Devonian paleogeographic reconstructions and biome placements).

In the cluster analysis (Figure 3) the Koněprusey limestone fauna at Zlatý Kůň, Czech Republic grouped together with the Old World II cluster. However, due to age (Pragian), and the fact that both the Zlatý Kůň fauna and the other Koněprusey fauna are in the same area clade in Old World I, it is here considered to be an Old World I fauna.

Michigan (Givetian) – Bigey (1985) proposed a Michigan-Hudson Bay region that covered Southern Canada, the Michigan Basin, Ohio, and Kentucky, but my findings suggest that the Northern Michigan faunas are distinct enough from those further south to warrant separation. This biome is Givetian except for the area of Gaspé, in Quebec, which is Pragian and Emsian. The Michigan biome also contains a number of sites along the northern lakeshore of the lower peninsula of Michigan, along with the Plumbrook Shale in Erie County, Ohio. Faunal lists were used for the Traverse Group in the Alpena and Grand Traverse regions (Stumm, 1942) and primary literature was also used (Duncan, 1939; McNair, 1942) that contained more specific stratigraphic and locality data. There may be overlap in genera between the areas of Alpena-Traverse and Alpena-Bell Shale, Alpena-Ferron Point, and Presque Isle-Traverse local areas, and between the Grand Traverse-Traverse and Charlevoix-Gravel Point areas. The composite areas of the Traverse Group contain both shale and limestone units, whereas Charlevoix and Gaspé are limestones and Erie, Alpena-Bell Shale, and Alpena-Ferron Point are shales. Alpena-Traverse and Grand Traverse-Traverse branches are supported by the presence of *Stenopora*, and the entire clade is partially supported by *Anomalotoechus*, *Calacanthopora*, *Dyoidophragma*, and *Eridocampylus*.

Table 5. Genera that disappear after the Givetian with their respective Orders.

Order	Genus
Cheilostomata	*Fistulicella*
Cryptostomida	*Acanthoclema*
	Bactropora
	Coscinella
	Euspilopora
	Helopora
	Intrapora
	Nemataxis
	Nematopora
	Paleschara
	Petaloporella
	Ptilodictya
	Stictopora
	Streblotrypa
Ctenostomata	*Allonema*
	Ascodictyon
	Eliasopora
	Heteronema
	Ropalonaria
	Vinella
Cyclostomata	*Corynotrypa*
	Stomatopora
Cystoporida	*Acrogenia*
	Buskopora
	Ceramella
	Ceramoporella
	Coscinium
	Coscinotrypa
	Cyclotrypa
	Cystodictya
	Eridopora
	Favositella
	Fistuliphragma
	Fistulicella
	Fistulipora
	Fistuliporella
	Fistuliporina
	Fistuliramus
	Lichenalia
	Pinacotrypa
	Scalaripora
	Semiopora
	Taeniopora

Order	Genus
Fenestrida	*Alternifenestella*
	Anastomopora
	Bashkirella
	Fenestrapora
	Fenestrellina
	Hemitrypa
	Loculipora
	Penniretepora
	Polypora
	Prolixicella
	Reteporina
	Semicoscinium
	Spinofenestella
	Unitrypa
Hederellida	*Diversipora*
	Hernodia
	Reptaria
Trepostomatida	*Anomalotoechus*
	Callocladia
	Callotrypa
	Monotrypa
	Monticulipora

This biome is strongly supported by cluster analysis (Figure 3), but Gaspé, Quebec, and Erie County, Ohio (Plumbrook Shale) do not group cladistically with the others (Figure 1). Their overall fauna links them to the Ohio cluster rather than the Michigan biome. Gaspé is older than all of the areas in Michigan, and does not fit well into any of the designated biomes. It is of a similar age to the Old World faunas, and further east geographically, but does not appear to be related faunally.

Appohimchi II (Givetian) – The Appohimchi II fauna is contained entirely within New York and Ontario, and the Givetian aged Hamilton Group (For ages of local areas, see Figure 4). The Hamilton is one of the units where a number of formations are combined, but the overall lithology is comprised of shales and shaly limestones (Figure 5). The genera *Bactropora* and *Glauconome* are found only within this biome's Erie, Genessee, and Ontario local areas, and *Acrogenia* is another endemic genus of the region with a CI of 0.5. Appohimchi II is slightly younger and north of the other Appohimchi areas, which are Lochkovian outcrops in Maryland and West Virginia as well as New York. The Jeffersonville Limestone in Kentucky and the Columbus Limestone in Ohio are additions to Appohimchi II during cluster analysis (Figure 3). Both are older (Emsian) than the other OBUs in Appohimchi II but are closely related faunally. Both of the localities contain a large number of genera, however, and thus the overall similarity may be a reflection of their inclusion of a number of cosmopolitan taxa.

Biome Relationships

Geographically, the bryozoan biogeographic data do not suggest a separate Eastern Americas and Old World Realm. The data clearly cluster both European and American faunas together in both of the major branches of the cladogram. Instead, two provinces, Laurussia I and Laurussia II, can be distinguished temporally. This allows for comparison between the two major branches of the cladogram, and allows one to notice patterns of vicariance in the data. The Appohimchi I biomes are geographically very large, and it is most likely that one of them is the vicariant predecessor to the Michigan Biome of Laurussia II (Figures 6 and 7).

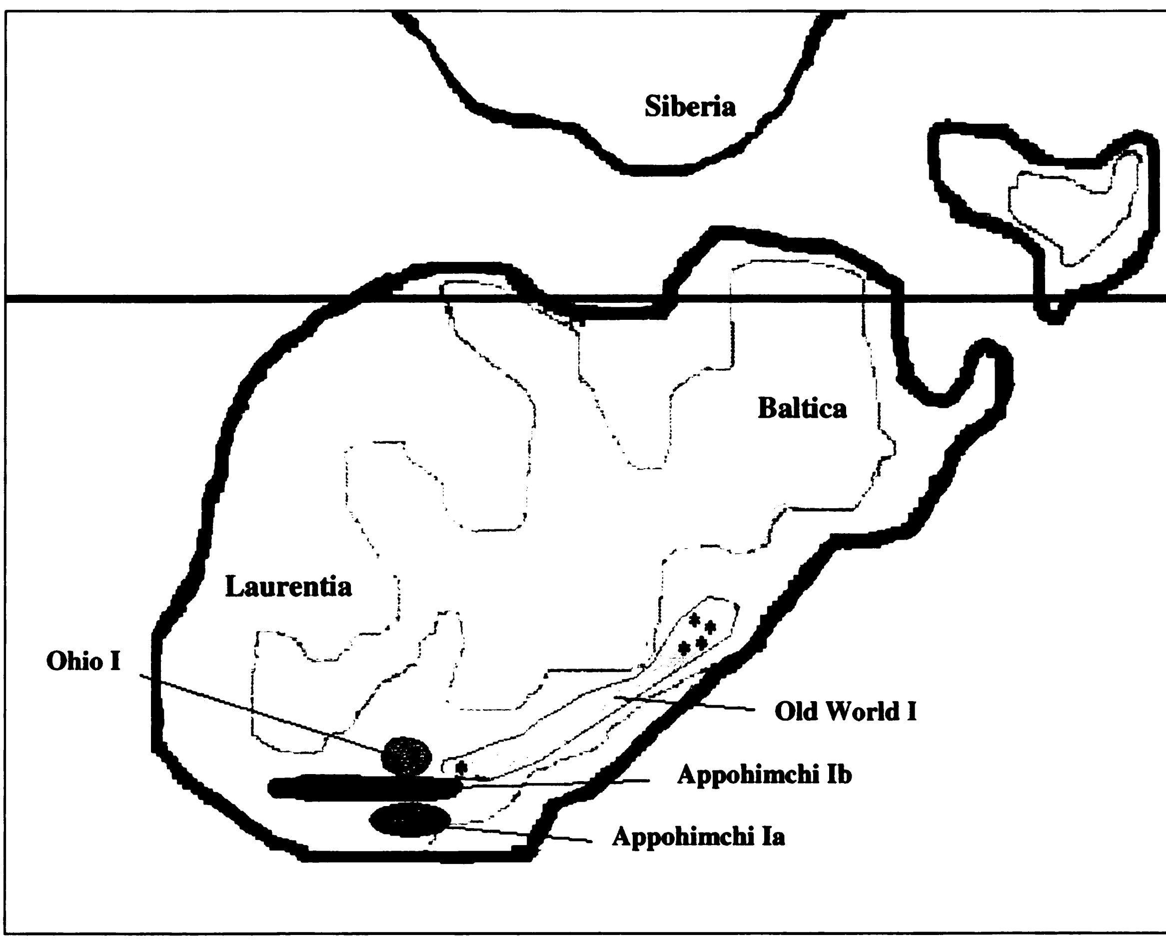


Figure 6. Paleobiogeographical reconstruction of Laurussia showing biome placement in the Early Devonian. Bold line = paleoequator. Base map modified from Scotese, 2002.

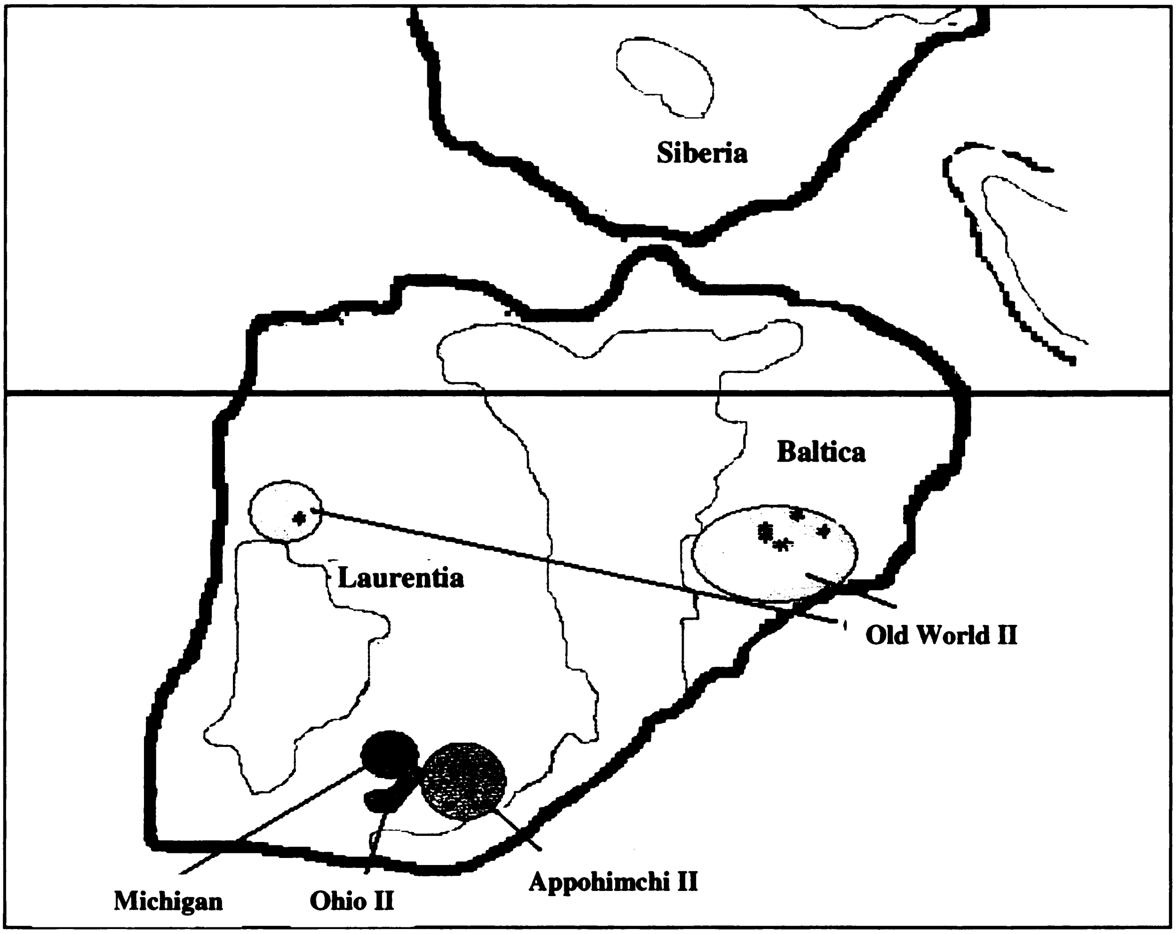


Figure 7. Paleobiogeographical reconstruction of Laurussia showing biome placement in the Middle Devonian. Bold Line = paleoequator. Base map modified from Scotese, 2002.

Givetian Mass Extinction

Although many other taxa experienced mass extinction during the Fammenian, Bryozoa lost more genera in the Givetian. Horowitz et al. (1996) regarded the Givetian event as the largest bryozoa extinction of the Paleozoic. Of 79 genera present in the Givetian of Laurussia, only 17 survive into the Frasnian, and only five of these are found in the Fammenian, which has no significantly diverse faunas. This loss is reflected in the lack of any local area from the Fammenian in Figure 1. Cystoporids and fenestrids contributed over half of the extinctions, 30% (20 genera) and 21% (13 genera), respectively. Twenty seven percent (17 genera) of the extinctions were fistuliporines.

The majority of the extinct genera were present in the Hamilton Group of New York, the Thedford-Arkona region in Southern Ontario, and to a lesser extent, the Traverse Group in Northern Michigan. The Hamilton Group has one of the largest outcrops of the Middle Devonian and is one of the best studied. While this might cause a bias in sampling (because more genera have been identified from the group, there are more available in the data to disappear) the preferential extinction in this area is supported by losses among other taxa (Oliver, 1976). The beginning of the Acadian Orogeny caused by the collision of Baltica and Laurentia has been dated to the late Emsian or early Eifelian (Naylor, 1971). Horowitz et al. (1996) suggested that the progradation of the Catskill siliciclastic wedge over the Laurentian craton led to changes in deposition environments that caused the biomes to diversify over time. One can see that between the Early and Middle Devonian there is a decrease in land surface area over Laurentia (Figs. 6 and 7). Horowitz et al. (1996) noted that this is caused by a sea level transgression that was coupled with an influx of anoxic waters. This event, indicated by the deposition of black shales over the Tully formation in the Hamilton Group was set forth as the major cause of extinction in the Eastern Americas Realm.

Conclusions

1. Analyses of both endemic and overall similarities between local faunas are biogeographically informative. In this study, Parsimony Analysis of Endemicity (PAE), which places more emphasis upon endemic genera, identified two major provinces, Laurussia I and Laurussia II, which existed during the Early and Middle Devonian, respectively. The eight biomes within these two provinces were more clearly defined by

Simpson's Index of Overall Faunal Similarity. The Laurussia I biomes are named Appohimchi Ia, Appohimchi Ib, Old World I, and Ohio I; the Laurussia II biomes are Appohimchi II, Old World II, Ohio II, and Michigan.

2. Provinces are defined by shared endemic genera. Biomes are usually supported by overall faunal similarity, endemic taxa, geographically contiguous distributions, common lithotopes, and restricted temporal ranges. .

3. Bryozoa experienced a mass extinction at the end of the Givetian that significantly reduced the number of genera in Laurussia. Few significantly diverse faunas have been found in the Frasnian and none in the Fammenian compared with the highest Devonian levels of diversity in the Givetian. North American faunas were affected more heavily than their Western European counterparts.

4. Vicariance can be seen in the change in faunas from the Lower to the Middle Devonian; Appohimchi Ia or Ib are candidates for the predecessor of the Michigan biome, which developed vicariantly within the Appohimchi I Biome.

5. The Gaspé region of Quebec does not fit well into a biome in either analysis, with PAE placing it in the Michigan biome and Simpson's Index placing it in the Ohio II biome. Koch (1981) also noted this phenomenon when studying brachiopods, and this discrepancy highlights the difficulty of correctly placing border localities in biogeographical studies. Because of Gaspé's location and age, it shared endemic genera with both provinces, and was faunally related to multiple biomes. This creates an ambiguity in its overall biogeographical affinity.

APPENDIX

Database of Bryozoan Generic Occurrences

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
NY- Ontario	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
NY- Genessee	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0
NY- Erie	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0
ON- Middlesex	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
NY- Livingston	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Onondaga	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Yates	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Grand Traverse	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0
MI- Alpena- Traverse	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0
MI- Alpena- Bell	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
MI- Alpena- Ferron Point	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
OH- Erie	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0
QC- Gaspé	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
MI- Presque Isle	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
MI- Charlevoix	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
PO- Wietrznia	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
PO- Skaly	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1
FR- Ardennes	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
GE- Eifel	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
UK- Podolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NW- Great Slave Lake	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ON- TA- Widder	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
ON- TA- Hungry Hollow	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0
OH- Lucas	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0
ON- TA- Arkona	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Bell Isle	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MD- Washington	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
MD- Cash Valley	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
WV- Keyser	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IA- Floyd	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Allgheny	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
OK- Murray	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
NY- Schoharie	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
MD- Pinto	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
OH- Union	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KY-Jeffersonville	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
OH- Franklin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CZ- Kaplička	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CZ- Koněprusey	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CZ- Srbsko	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SP- Asturias	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CZ- Zlatý Kůň	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ON- Haldimand	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ON- TA- Ipperwash	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
NY- Ontario	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Genessee	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
NY- Erie	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ON- Middlesex	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Livingston	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Onondaga	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Yates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Grand Traverse	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
MI- Alpena- Traverse	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Alpena- Bell	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Alpena- Ferron Point	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
OH- Erie	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
QC- Gaspé	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
MI- Presque Isle	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
MI- Charlevoix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PO- Wietrznia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PO- Skaly	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
FR- Ardennes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GE- Eifel	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
UK- Podolia	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NW- Great Slave Lake	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ON- TA- Widder	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
ON- TA- Hungry Hollow	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
OH- Lucas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ON- TA- Arkona	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Bell Isle	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
MD- Washington	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
MD- Cash Valley	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WV- Keyser	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
IA- Floyd	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Allgheny	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
OK- Murray	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0
NY- Schoharie	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MD- Pinto	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
OH- Union	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
KY-Jeffersonville	0	0	0	1	1	0	0	0	1	1	0	1	0	0	1	1	1	0	0
OH- Franklin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
CZ- Kaplička	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
CZ- Koněprusey	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
CZ- Srbsko	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
SP- Asturias	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
CZ- Zlatý Kůň	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ON- Haldimand	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ON- TA- Ipperwash	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
NY- Ontario	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1
NY- Genessee	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
NY- Erie	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1
ON- Middlesex	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
NY- Livingston	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
NY- Onondaga	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
NY- Yates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
MI- Grand Traverse	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	1	0	0	1
MI- Alpena- Traverse	0	0	0	1	0	1	1	0	0	0	1	0	0	1	0	1	0	1	1
MI- Alpena- Bell	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
MI- Alpena- Ferron Point	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0
OH- Erie	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1
QC- Gaspé	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
MI- Presque Isle	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1
MI- Charlevoix	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
PO- Wietrznia	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1
PO- Skaly	0	0	0	0	1	1	0	1	0	1	0	0	1	0	0	0	0	0	1
FR- Ardennes	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1
GE- Eifel	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0
UK- Podolia	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1
NW- Great Slave Lake	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
ON- TA- Widder	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	1
ON- TA- Hungry Hollow	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1
OH- Lucas	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1
ON- TA- Arkona	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	1
MI- Bell Isle	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1
MD- Washington	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1
MD- Cash Valley	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
WV- Keyser	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
IA- Floyd	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0
NY- Allgheny	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
OK- Murray	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
NY- Schoharie	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
MD- Pinto	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
OH- Union	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
KY-Jeffersonville	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1
OH- Franklin	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1
CZ- Kaplička	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
CZ- Koněprusey	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
CZ- Srbsko	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
SP- Asturias	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
CZ- Zlatý Kůň	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
ON- Haldimand	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
ON- TA- Ipperwash	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0

	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
NY- Ontario	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
NY- Genessee	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
NY- Erie	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
ON- Middlesex	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
NY- Livingston	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
NY- Onondaga	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
NY- Yates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
MI- Grand Traverse	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0
MI- Alpena- Traverse	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0
MI- Alpena- Bell	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0
MI- Alpena- Ferron Point	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0
OH- Erie	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
QC- Gaspé	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
MI- Presque Isle	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Charlevoix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
PO- Wietrznia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
PO- Skaly	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
FR- Ardennes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
GE- Eifel	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1
UK- Podolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
NW- Great Slave Lake	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
ON- TA- Widder	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
ON- TA- Hungry Hollow	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0
OH- Lucas	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	1	0
ON- TA- Arkona	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
MI- Bell Isle	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
MD- Washington	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
MD- Cash Valley	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
WV- Keyser	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
IA- Floyd	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
NY- Allgheny	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0
OK- Murray	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
NY- Schoharie	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
MD- Pinto	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
OH- Union	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
KY-Jeffersonville	0	0	0	0	1	0	1	1	0	1	1	0	0	0	1	0	0	1	0
OH- Franklin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CZ- Kaplička	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0
CZ- Koněprusey	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0
CZ- Srbsko	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0
SP- Asturias	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
CZ- Zlatý Kůň	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
ON- Haldimand	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
ON- TA- Ipperwash	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0

	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94
NY- Ontario	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
NY- Genessee	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
NY- Erie	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0
ON- Middlesex	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
NY- Livingston	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
NY- Onondaga	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
NY- Yates	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Grand Traverse	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0
MI- Alpena- Traverse	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
MI- Alpena- Bell	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Alpena- Ferron Point	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
OH- Erie	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
QC- Gaspé	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Presque Isle	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Charlevoix	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
PO- Wietrznia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
PO- Skaly	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FR- Ardennes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GE- Eifel	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
UK- Podolia	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0
NW- Great Slave Lake	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ON- TA- Widder	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
ON- TA- Hungry Hollow	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
OH- Lucas	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0
ON- TA- Arkona	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Bell Isle	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MD- Washington	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
MD- Cash Valley	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
WV- Keyser	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
IA- Floyd	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Allgheny	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
OK- Murray	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Schoharie	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0
MD- Pinto	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
OH- Union	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
KY-Jeffersonville	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
OH- Franklin	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
CZ- Kaplička	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
CZ- Koněprusey	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
CZ- Srbsko	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
SP- Asturias	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
CZ- Zlatý Kůň	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
ON- Haldimand	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ON- TA- Ipperwash	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113
NY- Ontario	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
NY- Genessee	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
NY- Erie	0	0	0	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	0
ON- Middlesex	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
NY- Livingston	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
NY- Onondaga	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Yates	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
MI- Grand Traverse	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
MI- Alpena- Traverse	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
MI- Alpena- Bell	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
MI- Alpena- Ferron Point	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
OH- Erie	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
QC- Gaspé	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Presque Isle	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Charlevoix	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PO- Wietrznia	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0
PO- Skaly	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
FR- Ardennes	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
GE- Eifel	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
UK- Podolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
NW- Great Slave Lake	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
ON- TA- Widder	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0
ON- TA- Hungry Hollow	0	0	1	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1
OH- Lucas	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1
ON- TA- Arkona	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
MI- Bell Isle	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
MD- Washington	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
MD- Cash Valley	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
WV- Keyser	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IA- Floyd	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Allgheny	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
OK- Murray	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
NY- Schoharie	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
MD- Pinto	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
OH- Union	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0
KY-Jeffersonville	1	1	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0
OH- Franklin	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
CZ- Kaplička	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
CZ- Koněprusey	0	0	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0
CZ- Srbsko	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
SP- Asturias	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
CZ- Zlatý Kůň	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
ON- Haldimand	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
ON- TA- Ipperwash	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0

	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130
NY- Ontario	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0
NY- Genessee	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0
NY- Erie	0	0	0	1	0	1	0	0	1	1	0	0	0	1	1	0	0
ON- Middlesex	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Livingston	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0
NY- Onondaga	0	0	0	1	0	0	0	0	1	1	0	0	1	1	0	0	0
NY- Yates	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0
MI- Grand Traverse	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
MI- Alpena- Traverse	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
MI- Alpena- Bell	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
MI- Alpena- Ferron Point	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
OH- Erie	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
QC- Gaspé	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
MI- Presque Isle	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MI- Charlevoix	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PO- Wietrznia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PO- Skaly	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
FR- Ardennes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GE- Eifel	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
UK- Podolia	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NW- Great Slave Lake	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ON- TA- Widder	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
ON- TA- Hungry Hollow	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	1
OH- Lucas	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0
ON- TA- Arkona	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
MI- Bell Isle	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
MD- Washington	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MD- Cash Valley	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WV- Keyser	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
IA- Floyd	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NY- Allgheny	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0
OK- Murray	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
NY- Schoharie	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0
MD- Pinto	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0
OH- Union	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
KY-Jeffersonville	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	0	0
OH- Franklin	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
CZ- Kaplička	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
CZ- Koněprusey	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
CZ- Srbsko	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
SP- Asturias	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CZ- Zlatý Kůň	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ON- Haldimand	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
ON- TA- Ipperwash	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	

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