

Paleobiology

Paleolongitudinal estimates for paleocontinents derived from interplate distances based on Late Ordovician bivalves

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Abstract.—The geographic distribution of 293 Modern bivalve genera has been analyzed and found to be statistically correlated with distance. In particular, a least-squares regression analysis of the data indicates that the distance between faunal realms (D) in kilometers can be estimated using the equation $D = (\ln(d) + 0.4233) / -0.00013$, where d is the Dice coefficient of faunal similarity. Analysis of 59 genera of Late Ordovician bivalves indicates that the above equation also describes their biogeographic distribution.

Using this formula, the distance between Laurentia and Scotland/Northwest Ireland was estimated to be 5500 kilometers. This is consistent with the reconstruction of a connection among these areas during the Late Ordovician based on brachiopod and graptolite biogeographic data.

Paleomagnetic and paleoclimatic data also suggest that Avalonia, Baltica, and Laurentia were at tropical latitudes. Distances between these paleocontinents can therefore be used to estimate paleolongitudes. If the location of England on the eastern side of Avalonia is used as zero degrees paleolongitude for the Late Ordovician as it is today, the paleolongitude for South America, Laurentia, Scotland and northwest Ireland, and Baltica would be 125°W, 45°W, 10°W, and 15°E, respectively. Because of drifting of the Avalonia plate, these paleolongitudes probably do not coincide with the longitudinal grid used today. The paleolongitudes indicate only the relative spacing between continents in the past. The methodology in this study should be useful for improving the accuracy of paleogeographic reconstructions for the Late Ordovician throughout the Cenozoic, and especially the Paleozoic periods for which magnetic seafloor anomaly data are not available.

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Introduction

The longitudinal spacing between continents can be easily established for the past 100 Myr using magnetic seafloor anomaly data. Beyond 100 Myr, subduction has destroyed these data. Rotation of apparent paleomagnetic poles can determine past latitudinal position of the continents and their angular orientation, but because of the symmetry of the earth's magnetic field, longitudinal data cannot be determined using this method (Smith and Briden 1977; Kent and Opdyke 1978; Smith et al. 1981). Scheltema (1977) has shown that bivalve larvae are planktotrophic and can stay in the water column for weeks. Thus, some species can be transported great distances by current systems. But studies of Modern mollusks have shown that the greater the longitudinal separation between faunal areas, the greater the faunal dissimilarity of those areas (Campbell and Valentine 1977). This led paleo-

geographers to use faunal similarity as a way of qualitatively gauging longitudinal separation between plates in the past (Fortey and Cocks 1992; Harper et al. 1996). Schmachtenberg (2008) has shown that longitudinal separation between the North American and European plates can be estimated quantitatively on the basis of bivalve species similarity for the Cretaceous, using an equation derived from an analysis of Modern bivalve faunas. This separation was shown to be consistent with magnetic seafloor anomaly data.

The purpose of the current paper is to derive a formula showing the relationship between distance in kilometers between faunal regions and Modern faunal generic similarity. Paleomagnetic and paleoclimatic data will then be used to show that Laurentia, Avalonia, and Baltica were located at tropical latitudes during the Late Ordovician. Once the latitude of a paleocontinent is established, the formula mentioned above can then be

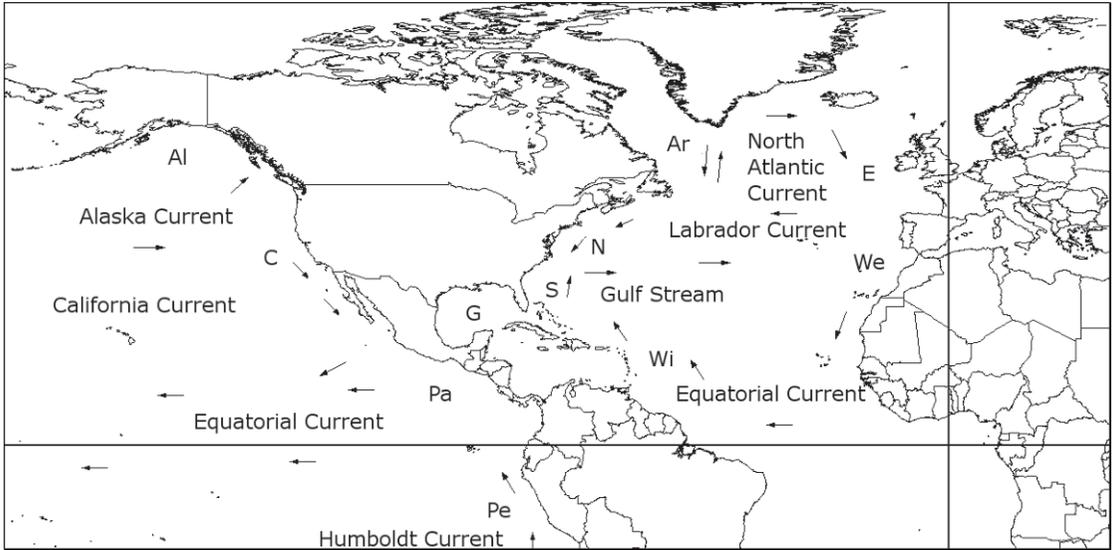


FIGURE 1. Biogeographic realms used in this study. Abbreviations: Al, Alaska; C, California; Pa, Panama; Pe, Peru; Wi, West Indies; G, Gulf of Mexico; S, South Atlantic; N, North Atlantic; Ar, Arctic; E, England; We, western Europe. Currents are based on those of Schopf (1980). This map is based on data sources from ESRI Data and Maps, 2002. Used with permission of ESRI.

used to estimate longitudinal distances in kilometers and degrees between Laurentia, Avalonia, and Baltica. Bevens et al. (1992) have proposed, on the basis of brachiopod and graptolite data, that Scotland and north-west Ireland were attached to Laurentia in the Late Ordovician. This interpretation is tested with the bivalve data. Scotese and Barrett (1990) inverted South America and positioned the current northern part of South America at the South Pole by using climate sensitive rocks. The distance between Laurentia and central South America has been estimated from the bivalve data and converted to a paleolongitude for South America. Although an equation based on species-level data was used in the Cretaceous study, a formula based on genera of bivalves is necessary because many Late Ordovician fossil data are identified only to the genus level.

Methods

Modern Bivalve Faunal Data.—Data on the geographic distribution of 293 Modern bivalve genera were compiled for 11 regions (Fig. 1). These regions were defined by Schopf (1980) on the basis of convergence of ocean current systems and land and deep ocean barriers. The Alaska region (Al) is a

cold-water area, whose southern boundary is Oregon. This boundary is defined by the area where the Alaska Current becomes the California Current. The California region (C) includes the shelf off California and the Gulf of California. The Panama region (Pa) is a tropical warm-water region extending from Mexico south to Ecuador. The Peru region (Pe), comprising the shelf off Peru and Chile, includes the cold-water Humboldt Current. The West Indies region (Wi) includes the warm-water Caribbean area; the northern boundary is the Yucatán peninsula and Cuba. North of this region is the Gulf of Mexico region (G). On the east side of Florida, extending north to Cape Hatteras, North Carolina, is the South Atlantic region (S). The North Atlantic region (N) extends from Cape Hatteras to Newfoundland. Cape Hatteras was chosen as a biogeographic boundary because it is where the north-flowing warm-water Gulf Stream meets the south flowing cooler-water Labrador Current. The Arctic region (Ar) includes the Canadian shelf north to the Arctic. The shelf surrounding England encompasses the English region (E), and the shelf to the west of France and the Iberian Peninsula is the West Europe Region (We). The Arctic data were obtained from

Lubinsky (1980), whereas information for England and West Europe is based on Moller (1978). Biogeographic data in Abbott and Morris (1995) were used for the Atlantic, Gulf, and West Indies regions. The data for the Peru, Panama, California, and Alaska regions are primarily from Olsson (1961). Attempts were made to standardize the taxonomy in these references to that of Abbott and Morris (1995), and in general the systematics in these studies were consistent. As noted in Schmachtenberg (2008), endemism in these data tends to be low, indicating that the regions in Figure 1 are on the order of realms rather than provinces.

The Dice Similarity Coefficient.—Faunal similarity can be measured in a variety of ways (see Cheetham and Hazel 1969; Raup and Crick 1979; and Lees et al. 2002). The Dice similarity index (d) can be calculated using the following formula:

$$d = 2c / (n_1 + n_2) \quad (1)$$

where c is the number of genera in common between the two realms and n_1 and n_2 are the number of genera in the smaller and larger realms, respectively. This index varies from 0 representing totally different faunas to 1 indicating identical faunas in two realms, and takes into account both differences in composition and diversity between the realms. The statistical program PAST was used to calculate d for each of the realm pairs in this study.

ArcView 9.2 from ESRI was used to measure the geodesic distance between the centroids of realms within an ocean basin. This geodesic distance takes into account the curvature of the earth. The centroid was calculated by finding the midpoint between the boundaries of each realm. Piccoli et al. (1991) recommended using the shortest or most direct route between realms, and I have followed this convention as well. Similarities were calculated only for realm pairs in which both realms were in the same ocean basin. Land barriers can create very low similarities for marine faunas even though the distance between realms is low. Some realm pairs, such as Panama and Peru, were also omitted from the analysis because they reflect much

higher diversities than existed in the past. A least-squares linear regression was used to obtain a linear equation between Dice similarity index (d) and distance (D).

Late Ordovician Faunal Data.—Generic bivalve data were downloaded from the online Paleobiology Database between November 2008 and December 2009 for the paleocontinents of Laurentia, Avalonia, Baltica, South America, and Scotland and northwest Ireland. Scotland and northwest Ireland were on the same plate in the Late Ordovician. The bivalve data include the Caradocian and Ashgillian Stages. Late Ordovician bivalve genera that could be identified only questionably were omitted. Faunal data were requested from all lithologies, environments, and environmental zones in the database. The data were sorted first by paleocontinent, and the plate ID field was used to make sure the faunal data for each paleocontinent came from the same tectonic plate. The data were also disaggregated into nearshore sand fauna and an offshore shale-limestone fauna. A field trip during the fall of 2008 to the Late Ordovician Martinsburg Formation in southwest Virginia produced bivalve data similar to those downloaded for Laurentia in the Paleobiology Database. The geographic distribution of sampling localities for the Late Ordovician is shown in Figure 2.

Results

Modern bivalve diversities varied greatly among the realms (Table 1). In particular, diversity decreased toward higher latitudes. A plot of the Dice similarity index (d) for the Modern bivalve data versus distance is given in Figure 3, and a natural logarithmic transformation of the Dice indices before the regression is given in Figure 4. A regression of the points on Figure 3 produced the following equation:

$$d = -0.000043(D) + 0.583, \quad (2)$$

where D is distance in kilometers. The correlation coefficient (r) for equation (2) is -0.757 . A regression of the data in Figure 4 produces equation (3):

$$\ln(d) = -0.00013D - 0.4233. \quad (3)$$

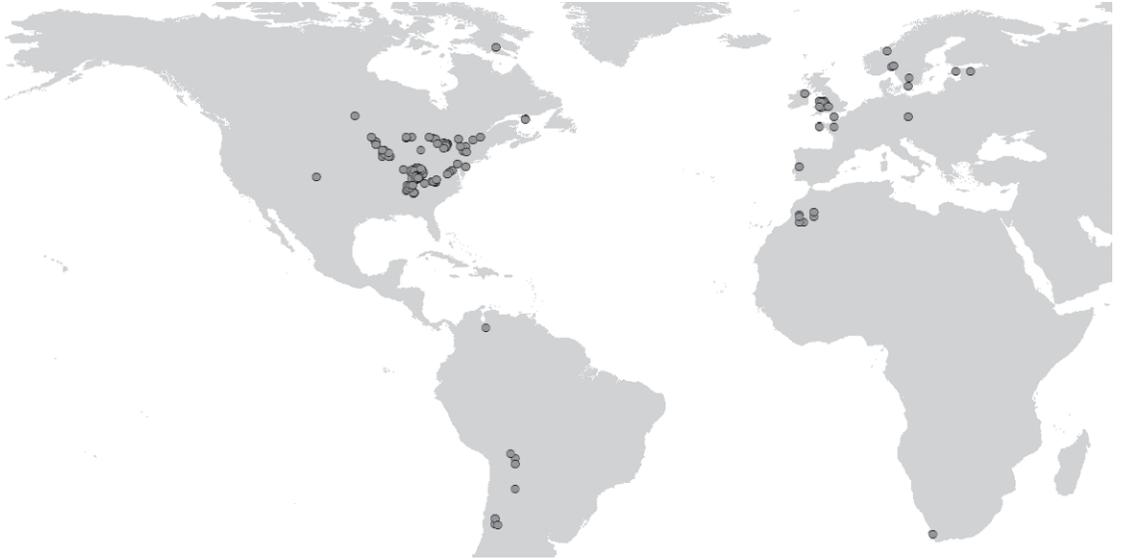


FIGURE 2. Location of samples of Late Ordovician bivalves used in the study. This map is based on data sources from ESRI Data and Maps, 2002. Used with permission of ESRI.

The correlation coefficient (r) for equation (3) is -0.749 . Both of these correlation coefficients are statistically significant at the 0.01 level.

Rearranging equation (2), the distance in kilometers can be calculated from d using equation (4):

$$D = (d - 0.583) / -0.000043. \quad (4)$$

Rearranging equation (3) gives the distance from the logarithmically transformed Dice indices:

$$D = ((\ln(d) + 0.4233) / -0.00013). \quad (5)$$

The statistical program PAST was used to calculate d both for onshore sand and for offshore shale-limestone bivalve faunas of Laurentia and England. Equations (4) and

(5) were used to convert the Dice indices to distances in kilometers. The distance between Laurentia and England based on equation (4) was 4610 km for the onshore fauna and 5943 km for the offshore fauna, for a difference of 1333 km. The distance based on equation (5) produced a distance of 4094 km for onshore fauna and 5336 km for offshore fauna, for a difference of 1242 km. Ideally, the distance based on the onshore fauna should be the same as for the offshore fauna. Because equation (5) gave the lower difference in distances, it was used to estimate the distance between Laurentia and the rest of the paleocontinents. The diversity for each paleocontinent, Dice index, and distance based on equation (5) are given in Table 2. Offshore faunas for each paleocontinent were used rather than onshore faunas because the diversities were higher.

TABLE 1. Modern bivalve generic diversity for each of the realms.

Realm	Generic diversity
Alaska	22
Arctic	43
England	88
North Atlantic	79
West Europe	74
California	131
South Atlantic	129
Gulf of Mexico	58
Panama	175
West Indies	113
Peru	140

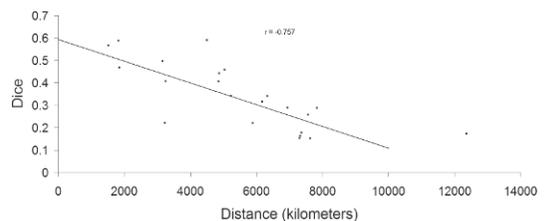


FIGURE 3. Plot of the Dice fauna similarity index of Modern bivalve data versus distance.

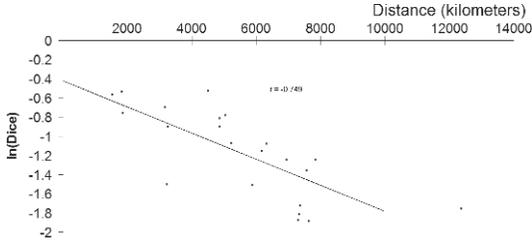


FIGURE 4. Plot of the natural logarithm of the Dice faunal similarity index for Modern bivalve data versus distance.

Discussion

There is some concern that the low generic diversity of Baltica, South America, England, and Scotland and northwest Ireland compared with Laurentia in Table 2 may affect the distances between paleocontinents. The low diversities may reflect different sampling intensities by workers on different continents. Raup and Crick (1979) proposed an index of faunal similarity that is designed to compensate for sampling problems. Unfortunately, when the Raup-Crick index was used to analyze the Modern and Late Ordovician bivalve data, the distances between Laurentia and England/Wales based on nearshore faunas and on offshore faunas differed by 6518 km. This is a much larger difference than $\ln(d)$ gave. It is also possible that the difference in diversities reflects differences in marine area of the paleocontinents. Disaggregating the data by facies may partly compensate for area differences by reducing the area of Laurentia. Valentine (1971) has argued that there are longitudinal as well as latitudinal diversity gradients in Modern marine faunas, and that they are caused by environmental variations such as stability, upwelling, and productivity. If this is the case, then faunal similarity indices that measure diversity as well as compositional differences in faunas may be appropriate. The Jaccard index of faunal similarity, which is similar to the Dice index, was also used to analyze the Modern and Late Ordovician bivalve data. The difference in nearshore-offshore faunal distance, 1335 km, was slightly higher than that given by $\ln(d)$, using the Dice index.

MacNiocail et al. (1997) have summarized the paleomagnetic data for the Early Ordovi-

TABLE 2. Generic diversity, Dice index, and distance in kilometers from Laurentia for paleocontinents in this study. Dice indices were calculated for offshore faunas between Laurentia and each paleocontinent. Equation (5) was used to calculate the distances. The generic diversity for the offshore fauna of Laurentia was 41.

Paleocontinent	Generic diversity	Dice index (d)	Distance ($\times 10^3$ km)
Baltica	9	0.32	5.5
South America	7	0.208	8.8
England	15	0.327	5.3
Scotland/ Ireland	9	0.32	5.5

cian through the Early Silurian. During this period, South America, Africa, and the Precordillera terrane were joined to form Gondwanaland, which was located near the South Pole. Laurentia was positioned at the equator throughout Ordovician time, while Avalonia and Baltica drifted from 60°S to collide with Laurentia in the Early Silurian. Baltica and Avalonia were at about 30°S or lower latitudes in the Late Ordovician. Barnes and Stone (1999) have summarized faunal and paleomagnetic data showing that England was separated from Scotland and northern Ireland during the Late Ordovician. Bevins et al. (1992) have cited brachiopod and graptolite data that show that Scotland and northwest Ireland were attached to Laurentia in the Late Ordovician. In fact, the distance of 5500 kilometers between Laurentia and Scotland/northwest Ireland is consistent with a connection between those paleocontinents. The distance of 5500 km is only assumed accurate to the hundreds place as shown in Table 2.

Combined with the paleogeographic information above, the distances in Table 2 were used to reconstruct the position of the paleocontinents in Figure 5. A land barrier probably existed along the northeast side of Laurentia from Virginia to central Greenland. Distances were measured around that land barrier to reconstruct the paleocontinents. Measurements were also taken from the center of the data points in Figure 2 to position the continents. Modern bivalve faunas in general show decreasing generic diversity from the equatorial realms to the higher latitudes. Some of these diversity changes may reflect sampling error, but this

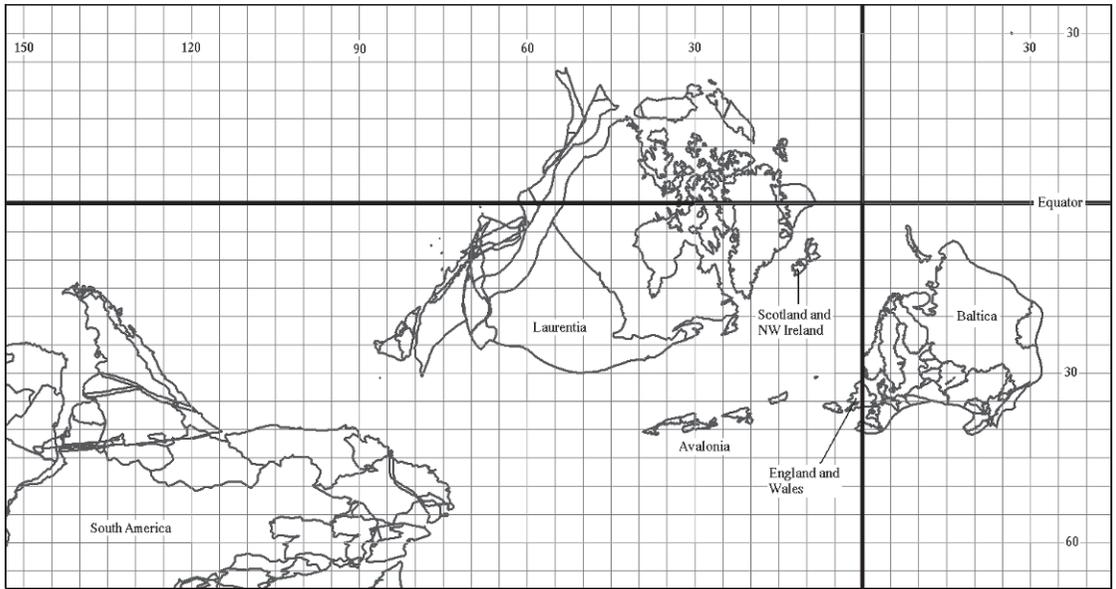


FIGURE 5. Reconstructed Late Ordovician paleogeography. The map is based on data from C. Scotese.

latitudinal gradient has also been interpreted as a result of temperature changes (Valentine 1966; Jablonski et al. 1985; Jablonski and Valentine 1990) or decrease in solar input (Roy et al. 1998).

The generic diversity data for bivalves (Table 2) supports the paleogeographic reconstruction of Figure 5. Just as in the Modern bivalve data, Late Ordovician generic diversity was greatest in Laurentia at the equator, and low in the Gondwanaland continent of South America.

Because paleomagnetic, biogeographic, and paleoclimatic data constrain Laurentia, Baltica, Avalonia, and Scotland and northwest Ireland to tropical latitudes, the distance between Laurentia and the other paleocontinents can be used to estimate paleolongitudes for the Late Ordovician. England is at 0° today, so I have set the paleolongitude for the centroid of East Avalonia, which contains England at 0° in Figure 5. That would place the centroids of Laurentia, Scotland and northwest Ireland, and Baltica at 45°W, 10°W, and 15°E, respectively. Scotese and McKerrow (1990) indicated that Avalonia may have collided with Baltica in the Late Ordovician, so those two paleocontinents may have been connected. It is no surprise that distances between Laurentia/Baltica and

Laurentia/England in eastern Avalonia are similar. Also, Scotese and Barrett (1990), using climatically sensitive rock data, have shown that South America was upside-down relative to the position of South America today, with the northern part of the paleocontinent near the poles while the southern tip was at a low latitude. With the paleolatitude of South America so constrained latitudinally, it was possible to estimate the paleolongitude of South America from the distance data in Table 2. South America would have been approximately 8800 km from Laurentia, which would have placed it at 125°W. Again the data centroids of the paleocontinents were used for the calculations. Unfortunately, the paleocontinents of Africa, Kazakstania, Australia, South China, North China, and Siberia have few or no bivalve data for the Late Ordovician, and as a result cannot be accurately placed using the methodology in this study.

Conclusions

This study has presented a new way of quantitatively estimating interplate distances based on bivalve similarity. When constrained latitudinally by paleomagnetic and paleoclimatic data, these distances can be converted to paleolongitudes. Because the Avalonian plate, which contains England,

has drifted over geologic time, these paleo-longitudes do not correspond to the Modern longitudinal grid, but they do indicate relative longitudinal spacing between plates in the past. The method is limited only to the time periods in which bivalves were sufficiently abundant in the fossil record. Sepkoski's (2002) bivalve data indicate that the method should work well for geologic time periods from the Late Ordovician through the Quaternary, and will be most useful for the Paleozoic, for which seafloor anomaly data are not available.

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