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Paleotethyan faunal/floral evidence in the Mississippian Maritimes Basin of Canada: An overview

Pedro Cózar^{1*}  and Ian D. Somerville²

¹Instituto de Geociencias (CSIC, UCM), Ciudad Universitaria, 28040 Madrid, Spain <p.cozar@igeo.ucm-csic.es>

²UCD School of Earth Sciences, University College Dublin, Belfield, Dublin 4, Ireland <ian.somerville@ucd.ie>

Abstract.—In this study, middle to late Mississippian microfossil assemblages from the Maritimes Basin of eastern Canada (Nova Scotia, SW Newfoundland, and New Brunswick) are closely compared to those from Western Paleotethys basins. The comparison is focused mainly on foraminifers and calcareous algae. Most foraminifers and algae described from the Maritimes Basin are considered cosmopolitan, and the occurrence in western Europe and northern Africa of taxa previously considered endemic to the North America Realm suggests a close paleobiogeographic relationship. This European/African correlation is further supported by other foraminiferal/algal taxa, the importance of which were previously overlooked, including: *Plectogyranoopsis* ex gr. *P. hirosei* (Okimura, 1965), *Mikhailovella* Ganelina, 1956, *Koktjubina windsorensis* (Mamet, 1970), *Polysphaerina bulla* Mamet, 1973, *Mstinia* Dain in Dain and Grozdilova, 1953, *Haplophragmina* Reitlinger, 1950, *Omphalotis* Shlykova, 1969, *Pseudolituotuba* Vdovenko, 1971, *Pseudoendothyra* Mikhailov, 1939, *Saccaminopsis* (Sollas, 1921) Vachard and Cózar, 2003, *Kamaenella* Mamet and Roux, 1974, and *Anthracoporellopsis* Maslov, 1956. Some species recorded in the Maritimes Basin have been typically recorded in Britain and Ireland in the southern platform of Laurussia. This implies a connection via the Rhenohercynian Ocean, whereas statistical analyses suggest that Maritimes Basin assemblages are closer to those of the Gondwana platform, which could have been established via the Paleotethys Ocean, and also with terranes northwest of the Variscan Front, in which its most logical connection should be with a still-open Rheic Ocean during the Viséan and early Serpukhovian. Those taxa demonstrate a more-or-less continuous faunal and microfloral interchange between the Maritimes Basin and the Western Paleotethys paleobiogeographic realm. Furthermore, the width of the Paleotethys and Rheic oceans separating these regions is not considered excessive, particularly during the late Viséan and early Serpukhovian.

Introduction

The Maritimes Basin of Atlantic Canada comprises Middle Devonian to early Permian strata (Gibling et al., 2019) and includes SW Newfoundland, Nova Scotia, and New Brunswick (Fig. 1). Its underlying substrata are composed of a series of amalgamated terranes of peri-Gondwanan affinity that drifted from Gondwana during Ordovician times (e.g., Waldron et al., 2015; Gibling et al., 2019) or even from the Proterozoic/early Cambrian (e.g., Landing, 2005). By the Middle Devonian, these terranes were supposedly attached to the North American craton (e.g., van Staal et al., 1998; Murphy et al., 2004). This episode is related to the closure of the Rheic Ocean (Fig. 2) that started in the Early Devonian and by the early Carboniferous was considered according to some authors essentially closed (e.g., Nance et al., 2012, and references therein). McKerrow et al. (2000) considered that the Rheic Ocean was open during the Devonian and the collision occurred during the early Carboniferous. During the Devonian, the ocean was not wide enough to prevent the migration of key fauna. A similar scenario was adopted by Torsvik and Cocks (2004, 2013), although they

considered the relatively narrow Rheic Ocean was located northward of Armorica. South of Armorica, Torsvik and Cocks (2004, 2013) interpreted a wide Paleotethys Ocean, with Gondwanaland displaced to a more southerly position. Since the Middle Devonian, Stampfli and Borel (2002) only considered a vast Paleotethys Ocean to the south, and the Rhenohercynian Ocean to the north, separated by the macro-European Hunic terrane. In contrast, Stampfli et al. (2013) considered a wide Rheic Ocean during the Frasnian and Famennian (Upper Devonian) between the Meguma/Avalonia terranes and the newly formed continent (Laurussia). Stampfli et al. (2013) considered that closure of the Rheic Ocean occurred during the Tournaisian, coincident with opening of the Paleotethys Ocean to the south.

It must be taken into consideration that tectonic models developed for the Maritimes Basin by North American researchers are usually related to the Alleghenian orogeny, and that this zone is typically compared with the Appalachian style (e.g., Waldron et al., 2015; Gibling et al., 2019). This is illustrated by the postulated collision of the terranes with the North American part of Laurussia during Devonian times. Eastern Appalachian tectonic units have been correlated with those in Britain and Ireland, suggesting a pre-collision (Devonian) separation of ~800 km between Newfoundland and Ireland (Waldron et al., 2018).

*Corresponding author

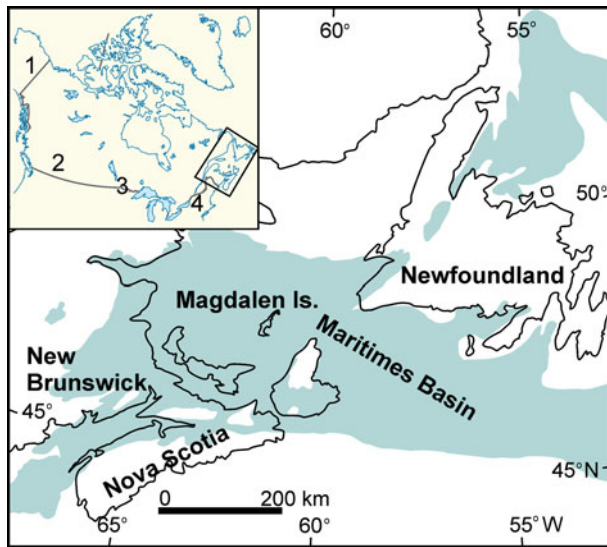


Figure 1. The Maritimes Basin of Atlantic Canada (shaded). Inset map shows location of the Maritimes Basin in North American craton and other regions/basins cited in the text. 1 = Alaska; 2 = Alberta (Western Cordillera); 3 = Mid-Continent; 4 = Appalachians.



Figure 2. Late Viséan-Serpukhovian paleogeography and paleobiogeography (modified from 340–325 Ma map of Blakey, 2013).

Facies and tectonic models reflecting similarities between Mississippian rocks in Ireland and the Maritimes Basin were first claimed by Belt (1929, 1944, 1969), and the first faunal arguments corroborating this hypothesis based on rugose corals were published contemporaneously (Lewis, 1935). Nevertheless, the general paleogeographic models disagree, and the idea has not been unanimously accepted by all authors who have studied the diverse fauna and microflora. These later authors supported the hypothesis that the Maritimes Basin was closer to the American Appalachians than to Europe (e.g., Globensky, 1967; Mamet, 1968, 1970; Jansa and Mamet, 1984). Other authors have progressively revealed new data that disagree with this distant paleogeographic position for the

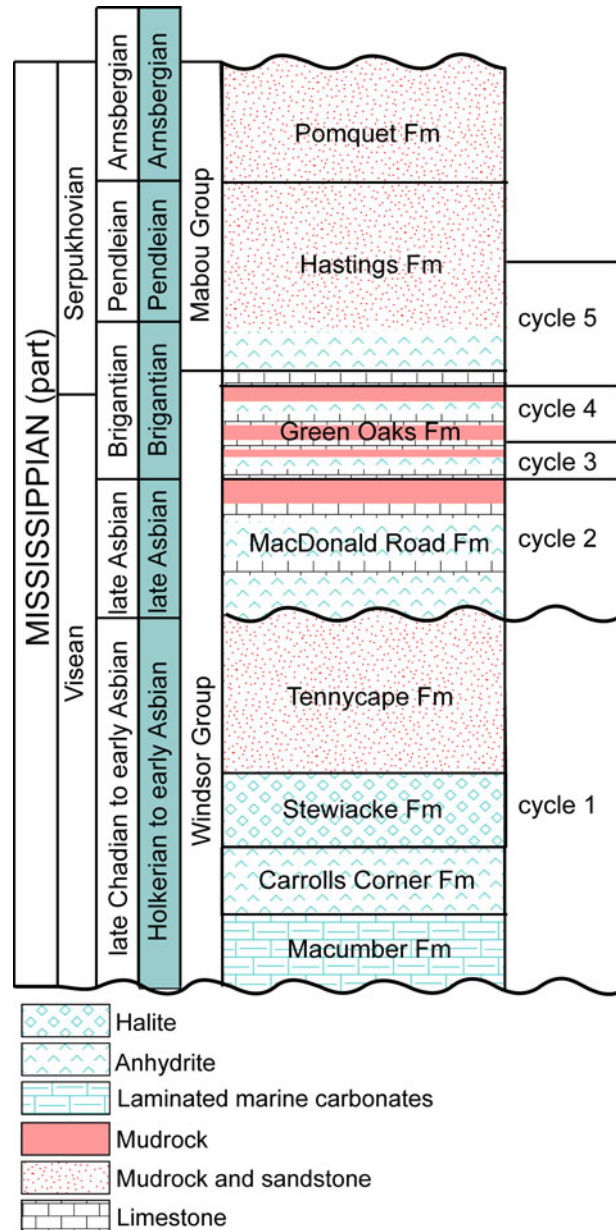


Figure 3. Simplified stratigraphic succession for the Windsor Group in Nova Scotia. Biostratigraphic age determinations: shaded column from Jutras et al. (2015); white column according to von Bitter et al. (2007). Cycles 1–5 as defined by Giles (1981). Fm = Formation.

Maritimes Basin and Europe, showing additional sedimentological similarities between the Maritimes Basin and Ireland/Britain (Giles, 1981, 2009; Mitchell, 1992; von Bitter et al., 2007). Transgressive-regressive events have been recognized in the Viséan Windsor Group (e.g., Giles, 1981, 2009; Fig. 3), which were compared with the major cycles defined in northern England by Ramsbottom (1973). Mitchell (1992) showed unconformities with similar timing and duration, and similar fault control for basin initiation and subsidence, and thus, stratigraphic similarities between the Maritimes Basin and Northern Ireland. All of those previous studies, as well as some faunal and floral similarities, were summarized by von Bitter et al. (2007).

Giles (1981) described five cycles in the Windsor Group (A–E or 1–5 auct.; Fig. 3), of which cycles 2–5 show similarities with the cycles defined in the Asbian–Brigantian of Ireland and northern England (von Bitter et al., 2007). However, cyclic sedimentation interpreted as glacioeustatic-driven transgressive-regressive sequences for the late Visean and Serpukhovian, as shown in detail by Giles (2009), are not exclusive to Ireland and England (Yoredale cyclothems) being common in Belgium/northern France (e.g., Hance et al., 2001), the North American Midcontinent (e.g., Smith and Read, 2000), and even in Saharan basins of the Gondwana platform (e.g., Bourque et al., 1995; Cózar et al., 2014, 2016b).

Faunal and floral similarities between the Maritimes Basin and Ireland/Britain have been highlighted in previous publications (von Bitter, 1976; von Bitter and Plint-Geberl, 1982; Clayton, 1985; Utting, 1987; Purnell and von Bitter, 1992; Poty, 2002; Utting and Giles, 2004; von Bitter and Legrand-Blain, 2007). Most data are based on rugose corals, conodonts, brachiopods, and miospores.

This study is primarily focused on two groups of microfossils: foraminifers and calcareous algae (including problematic algae). Both groups are widespread in most carbonate platform facies during the Mississippian and are distributed over a vast geographic area suitable for paleobiogeographic comparisons. The aim of this study is to highlight species of foraminifers and calcareous algae that are recorded in western Europe/northern Africa and the Maritimes Basin, and those recorded in the North American Realm, whose migration routes might have passed through the Maritimes Basin.

Material and methods

A revision of individual foraminiferal/algal taxa is included for which plausible paleobiogeographical affinities are discussed. This section is based purely on the presence/absence of different taxa in the Maritimes Basin as well as in other basins in Europe, North Africa, or North America.

To compare the paleobiogeography of the Maritimes Basin, foraminifers (excluding unilocular genera) and algae (including problematic algae) of the late Visean and Serpukhovian were selected from the following regions: Midcontinent/Appalachians, Britain/Ireland, SW Spain (including basins in the northern Ossa-Morena and southern Central Iberian zones), Moroccan Meseta (mostly western Meseta), NW Spain (Cantabrian Mountains), southern France (including Montagne Noire, Mouthoumet, and Pyrenees), and the Saharan basins of Morocco and Algeria (including the Tindouf and Béchar basins). The database from the Maritimes Basin is mostly based on Mamet (1968, 1970), Brisebois (1979), Jansa and Mamet, (1984), Poty (2002), and von Bitter and Legrand-Blain (2007) (see Tables 1, 2).

To avoid a long list of publications, recent studies that have previously compiled taxonomic databases are preferred herein, and thus the database on foraminifers contains 110 genera based on Davydov and Cózar (2019, and references therein). The database on algae contains 74 genera compiled from Mamet (1991, 1992, 1995b, 2002), Cózar and Vachard (2003, 2005), Pille (2008), Vachard and Cózar (2010), and Vachard et al. (2016).

A binary presence/absence database was analyzed using the PAST v.3.14 software (Hammer, 2016). The Jaccard and Raup and Crick similarity indices were calculated in the cluster using paired linkage (UPGMA). Nonmetric multidimensional scaling (NMDS) was also applied to graphically express the similarity indices among the regions. The Raup-Crick coefficient was used because it minimizes the result of overweighting widely distributed species and is less affected by sampling bias (Raup and Crick, 1979). The database was analyzed at the generic level, because (as demonstrated by Cózar et al., 2018 and Davydov and Cózar, 2019) there was no significant difference with the analysis at the specific level, and it prevents more frequent contradictory interpretations resulting from the species comparison due to more uneven data.

Repositories and institutional abbreviations.—The algal and foraminiferal collections of thin sections used for the statistical analysis are deposited in the following institutions: Royal Ontario Museum, Canada (studies by P. von Bitter); National Museum of Natural History, Washington DC, USA (studies by R.G. Browne, D.E. N. Zeller, and M. Rich); University of Colorado Museum, Boulder, USA (studies by P. Brenckle; part of the collection from northern Arkansas is still in the possession of the author); Institut Royal des Sciences Naturelles de Belgique, Brussels (part of the studies after 2000 by B.L. Mamet); Université de Liège, Belgium (studies by R. Conil and M. Laloux); Université Paul-Sabatier, Toulouse, France (studies by L. Pille); Université de Lille 1, France (studies by D. Vachard); British Geological Survey, Keyworth, UK (studies by I. Burgess and by A.R.E. Strank, C.N. Waters, I. Burgess, and P. Cózar from boreholes in northern England); British Geological Survey, Edinburgh, UK (studies by P. Cózar from boreholes in the Midland Valley of Scotland); University College Dublin, Ireland (studies by I.D. Somerville and S. Gallagher); Université Moulay Ismail, Meknès, Morocco (studies by M. Berkli); Institut Scientifique de Rabat, Morocco (studies by A. Tahiri); Université Cadi Ayyad, Marrakech, Morocco (studied by A. Tourani); Paleontological Collection, Universidad Complutense de Madrid, Spain (studies by P. Cózar = PC). The collection of M.-F. Perret is lost (personal communication, M.-F. Perret, 2015). The repository of B. Mamet's pre-2000 samples referred to in this study is unknown (personal communication, A. Prétat, 2021).

Algae and problematic algae

A detailed revision of the Carboniferous calcareous algae was published by Mamet (1991), with the main paleobiogeographic aspects more extensively developed by Mamet (1992). These studies summarized knowledge of the calcareous algae in the twentieth century and include a vast paleobiogeographic and biostratigraphic database. However, as Mamet (1991) recognized, the algal nature of numerous taxa used in his paleobiogeographic analysis is rather questionable (e.g., *Cylindrofolia* Brenckle and Groves, 1987, and *Eolithoporella* Johnson, 1966). He recognized 135 valid genera with 276 species distributed in three major realms (Fig. 2)—North America, Paleotethys, and Arctic (= Boreal)—subdivided into eight

Table 1. Revised late Viséan-Serpukhovian algae and problematic algae from the Maritimes Basin, Midcontinent/Appalachian, and western Paleotethys. 0 = absent; 1 = present.

Genus	North America	Maritimes Basin	Britain/Ireland	Moroccan Meseta	SW Spain	Southern France	NW Spain	Sahara
<i>Amarellina</i> Mamet, 1995a	0	0	1	1	0	0	0	0
<i>Anatolipora</i> Konishi, 1956	1	0	1	1	1	1	1	1
<i>Anthracoporellopsis</i> Maslov, 1956	0	1	1	1	1	1	1	1
<i>Aoujgalia</i> Termier and Termier, 1950	1	0	1	1	1	1	1	1
<i>Aphralysia</i> Garwood, 1914	1	0	1	1	1	1	1	1
<i>Archaeolithophyllum</i> Johnson, 1956	1	0	1	1	1	1	1	1
<i>Asphaltina</i> Mamet in Petryk and Mamet, 1972	1	0	1	1	1	1	0	1
<i>Asphaltinella</i> Mamet and Roux, 1978	1	0	1	1	1	1	0	1
<i>Asphaltinoides</i> Devera, 1987	1	0	0	0	0	0	0	0
<i>Asteroaoujgalia</i> Brenckle, 2004	0	0	0	1	0	1	0	0
<i>Atractyliopsis</i> Pia, 1937	1	1	1	1	1	1	1	1
<i>Borladella</i> Cózar et al., 2007	0	0	0	0	1	0	1	0
<i>Cabrieropora</i> Mamet and Roux, 1975a	0	0	1	1	1	1	1	1
<i>Cabrieroporellopsis</i> Pille and Vachard, 2011	0	0	0	1	0	1	1	0
<i>Calcifolium</i> Shvetsov and Birina, 1935	0	0	1	1	1	1	1	1
<i>Claracrusta</i> Vachard in Vachard and Montenant, 1981	1	0	1	1	1	1	0	1
<i>Coelosporella</i> Wood, 1940	1	1	1	1	1	1	1	1
<i>Costacheoides</i> Vachard and Cózar, 2010	0	0	1	1	1	0	0	1
<i>Crassikamaena</i> Brenckle, 1985	1	0	0	0	0	0	0	0
<i>Cribrokamaena</i> Brenckle, 1985	1	0	0	0	0	0	0	0
<i>Eovelebitella</i> Vachard, 1974	0	0	0	0	0	1	1	0
<i>Epistacheoides</i> Petryk and Mamet, 1972	1	1	1	1	1	1	1	1
<i>Evlania</i> Bykova, 1952	0	0	1	1	0	1	0	0
<i>Exvotarissella</i> (Elliot, 1970) Mamet and Roux, 1974	1	1	1	1	1	1	1	1
<i>Falsocalcifolium</i> Vachard and Cózar, 2005	0	0	1	1	1	1	1	1
<i>Fasciella</i> Ivanova, 1973	1	0	1	1	1	1	1	1
<i>Fascifolium</i> Vachard and Cózar, 2010	0	0	0	1	0	1	0	0
<i>Fourstonella</i> Cummings, 1955a	1	1	1	1	1	1	1	1
<i>Frustulata</i> (Saltovskaya, 1984) Vachard and Cózar, 2005	0	0	1	1	1	1	1	1
<i>Garwoodia</i> Wood, 1941	1	0	1	1	1	1	1	1
<i>Girvanella</i> Nicholson and Etheridge, 1878	1	1	1	1	1	1	1	1
<i>Guadiatella</i> Cózar et al., 2007	0	0	0	0	1	1	0	0
<i>Hedstroemia</i> Rothpletz, 1913	1	0	1	1	1	1	1	1
<i>Hortonella</i> Mamet, 1995b	1	1	1	1	1	1	0	1
<i>Issinella</i> Reitlinger, 1954	1	1	1	1	1	1	0	1
<i>Kamaena</i> Antropov, 1967	1	1	1	1	1	1	1	1
<i>Kamaenella</i> Mamet and Roux, 1974	0	1	1	1	1	1	1	1
<i>Koninckopora</i> Lee, 1912	1	1	1	1	1	1	1	1
<i>Kulikia</i> Golubsov, 1961	1	1	1	1	1	1	1	1
<i>Lemosquetella</i> Mamet and Sebbar, 1998	0	0	1	0	0	0	0	1
<i>Maimonachaetetes</i> Cózar and Vachard, 2006	0	0	0	0	1	0	0	0
<i>Mitcheldeania</i> Wethered, 1886	1	1	1	1	1	1	1	1
<i>Moravammina</i> Pokorný, 1951	0	0	1	1	1	1	1	1
<i>Murvielipora</i> Pille and Vachard, 2011	0	0	0	0	0	1	1	0
<i>Nanopora</i> Wood, 1964	1	1	1	1	1	1	1	1
<i>Neoprincipia</i> Cózar and Vachard, 2003	0	0	1	1	1	1	1	1
<i>Neoradiosphaeaporella</i> Vachard and Cózar in Vachard et al., 2016	0	0	0	0	1	1	0	0
<i>Orthriosiphon</i> Johnson and Konishi, 1956	1	0	1	1	1	1	1	1
<i>Ortonella</i> Garwood, 1914	1	1	1	1	1	1	1	1
<i>Ortonellopsis</i> Vachard and Cózar in Vachard et al., 2016	1	0	0	0	0	1	1	0
<i>Palaeoberesella</i> Mamet and Roux, 1974	1	1	1	1	1	1	1	1
<i>Palaeopimastoporella</i> Cózar and Vachard, 2004	0	0	1	1	1	1	0	0
<i>Paraepimastopora</i> Roux, 1979	0	0	1	1	1	1	1	1
<i>Pekiskopora</i> Mamet, 1974a	1	1	0	0	0	0	0	0
<i>Pokorninella</i> Vachard in Perret and Vachard, 1977	1	0	1	1	1	1	1	1
<i>Poncetellina</i> Mamet and Roux, 1984	0	0	0	0	1	1	0	0
<i>Praedonezella</i> Kulilk, 1973	0	0	0	1	1	1	1	1
<i>Principia</i> Brenckle in Brenckle et al., 1982	1	1	0	0	1	1	0	0
<i>Pseudokulikia</i> Mamet, 1997	0	0	1	1	1	0	0	0
<i>Pseudonanopora</i> Mamet and Roux, 1975b	0	0	0	1	0	0	0	0
<i>Pseudostacheoides</i> Petryk and Mamet, 1972	1	0	1	1	1	1	1	1
<i>Renalcis</i> (Vologdin, 1932) Mamet and Roux, 1983	1	0	1	1	1	1	1	1
<i>Richella</i> Mamet and Roux in Mamet et al., 1987	1	0	0	1	1	0	1	0
<i>Roquesselsia</i> Termier, Termier, and Vachard, 1977	0	0	1	1	1	1	1	1
<i>Saccaminopsis</i> (Sollas, 1921) Vachard and Cózar, 2003	0	1	1	1	1	1	1	1
<i>Sinustacheoides</i> Termier, Termier, and Vachard, 1977	1	0	1	1	1	0	0	0
<i>Sparaphralysia</i> Vachard in Vachard and Beckary, 1991	0	0	1	1	1	1	1	0
<i>Stacheia</i> Mamet and Roux, 1983	1	1	1	1	1	1	1	1

Table 1. Continued.

Genus	North America	Maritimes Basin	Britain/Ireland	Moroccan Meseta	SW Spain	Southern France	NW Spain	Sahara
<i>Stacheoides</i> Cummings, 1955b	1	1	1	1	1	1	1	1
<i>Ungdarella</i> Maslov, 1950	1	0	1	1	1	1	1	1
<i>Valuzieria</i> Termier, Termier, and Vachard, 1977	0	0	0	1	0	1	0	0
<i>Wetheredella</i> Wood, 1948	1	0	1	1	1	1	1	1
<i>Windsoporella</i> (Mamet and Rudloff, 1972) Vachard, 1980	1	1	1	1	1	1	1	1
<i>Zidella</i> Saltovskaya, 1984	0	0	1	1	1	1	1	1
Total	42	23	54	60	59	61	49	49

subrealms. Approximately half of the calcareous algae were considered cosmopolitan (49 genera) or of generalized dispersion (16 genera), but more important for the paleobiogeographic studies, are the endemic taxa to these three realms. The Paleotethys is the most diverse realm containing up to 38 endemic genera.

The geographic distribution of several genera has been updated since Mamet's (1991, 1992) database, resulting in modification of the distribution of some taxa. Mamet (1968, 1970) and mostly Jansa et al. (1978) identified a total of 31 taxa from different localities in the Maritimes Basin, of which *Windsoporella* (Mamet and Rudloff, 1972) Vachard, 1980 and *Pekiskopora* Mamet, 1974c were considered endemic to the North American Realm, with the rest of the assemblages as cosmopolitan or of generalized distribution. Similar taxa were also recorded by Brisebois (1979). The diversity and richness of algae in the Maritimes Basin are difficult to assess because: (1) the possible influence of deep oceans and cold water platforms/currents that did not permit a widespread settlement of the dasycladales (Jansa and Mamet, 1984); (2) limited documentation of these algal assemblages available in only a few publications, even in the absence of illustrations; and (3) variable but often-poor preservation in most of the carbonates in the Windsor Group of Nova Scotia and Codroy Group of Newfoundland, which are often dolomitized or composed of evaporites (Mamet, 1970; Jansa et al., 1978).

Windsoporella was originally considered as an algal genus endemic to the North American Realm, but has been recorded, rarely, in the eastern Paleotethys realm (Vachard, 1980) and subsequently commonly recorded in western European/northern African basins (see revision of the genus *Windsoporella* by Cózar et al., 2009; Pille and Vachard, 2011).

Jansa et al. (1978) illustrated *Pekiskopora* sp. (endemic to the North American realm), although it cannot be unquestionably attributed to that genus because of its poor preservation. In those specimens, only the outer morphology is preserved, a feature that does not allow a reliable identification of *Pekiskopora*, and in general, of any dasycladal algae. Furthermore, the outer morphology is rather like that of other coeval dasycladal algae, e.g., *Kulikia* Golubsov, 1961. *Pekiskopora* was also documented (but not illustrated) by Brisebois (1979) in limestones of Brigantian age on the Magdalen Islands in the central Gulf of St. Lawrence (Fig. 1). Although the identification cannot be confirmed at either of these widely separated localities in the Maritimes Basin, its reported presence continues to signal an American connection.

Additional remarks on the algal assemblages need to be highlighted. First, the Maritimes Basin is notable for the

occurrence of *Kamaenella* Mamet and Roux, 1974, a typical Western Paleotethyan genus that does not occur in other regions of North America. *Kamaenella* thickets are common in many upper Viséan platforms from Ireland and England (Gallagher, 1996; Horbury and Adams, 1996; Cózar and Somerville, 2005b). Nevertheless, quantification of the calcareous algae listed by Jansa et al. (1978) was not documented, and thus, it is not possible to precisely establish whether it contributes to similar thickets. Second is the occurrence (although rare) of *Saccaminopsis* (Sollas, 1921) Vachard and Cózar, 2003 in the Maritimes Basin. This problematic alga was attributed to the Udoteacea algal reproductive organs by Vachard and Cózar (2003), although it was previously attributed to the dasycladal algae (Skompski, 1986), and recorded only in the Paleotethys realm (see distribution of Vachard and Cózar, 2003). In Ireland and northern England, this taxon commonly occurs as 'floods,' i.e., rich concentrations in bands in upper Viséan limestones (e.g., Hallett, 1971; Gallagher and Somerville, 1997; Cózar and Somerville, 2005b). Its occurrence in the Maritimes Basin has never been documented as flood-like deposits, but its occurrence 'outside' of the Paleotethys realm is significant enough by itself. Third is the presence of the problematic alga *Anthracoporellopsis* Maslov, 1956, a taxon reported by both Jansa et al. (1978) and Brisebois (1979), and restricted to the Paleotethys realm and the Canadian Arctic (Vachard and Cózar, 2010).

As a consequence of the above data, the assemblages of the Maritimes Basin do not contain unquestionable algal or problematic algal genera endemic to the North American Realm in the assemblages of the Maritimes Basin, because the identification of *Pekiskopora* could not be confirmed and the recrystallized specimens are more similar to the outer morphology of *Kulikia* (a cosmopolitan taxon). In addition, *Pekiskopora* is recorded only in the Tournaisian, and thus its occurrence in the late Viséan of the Maritimes Basin seems implausible. In contrast, there are at least three typical Paleotethyan genera present: *Kamaenella*, *Saccaminopsis*, and *Anthracoporellopsis*.

Another significant algal taxon for paleobiogeographic interpretations is *Albertaporella* Johnson, 1966, described as an early Viséan endemic genus in the North American Cordillera (Johnson, 1966; Mamet, 1991) and New Mexico (Armstrong et al., 1992); it has also been recorded in the early Viséan of SE Ireland (Cózar and Somerville, 2005a). The most logical explanation is that the taxon migrated via the Rheic corridor (Fig. 2), because there is no record of *Albertaporella* in the Arctic realm (Mamet and Preat, 2010), and thus, migration by the Franklinian corridor in the Boreal Ocean is discarded (Fig. 2). The apparent absence of *Albertaporella* in the Maritimes Basin can be explained by the absence of more

Table 2. Revised late Viséan-Serpukhovian foraminifers from the Maritimes Basin, Midcontinent/Appalachian, and western Paleotethys (unilocular genera excluded). 0 = absent; 1 = present.

GENERA	North America	Maritimes Basin	Britain/Ireland	Moroccan Meseta	SW Spain	Southern France	NW Spain	Sahara
<i>Ammarchaediscus</i> Conil and Pirlet in Pirlet and Conil, 1977	0	0	0	1	0	1	0	0
<i>Ademassa</i> Vachard in Vachard et al., 1993	1	0	1	1	1	1	1	1
<i>Ammovertella</i> Cushman, 1928	1	0	1	1	1	1	0	0
<i>Archaediscus</i> Brady, 1873	1	1	1	1	1	1	1	1
<i>Asteroarchaediscus</i> Miklukho-Maklay in Kiparisova et al., 1956	1	1	1	1	1	1	1	1
<i>Bibradya</i> Strank, 1983	0	0	1	0	0	0	0	1
<i>Biseriella</i> Mamet in Armstrong and Mamet, 1974	1	0	1	1	1	1	1	1
<i>Bradyina</i> Möller, 1878	0	0	1	1	1	1	1	1
<i>Brenckleina</i> Zaninetti and Altiner, 1979	1	0	1	1	1	0	1	1
<i>Brownediscus</i> Brenckle, Ramsbottom, and Marchant, 1987	0	0	1	0	1	0	0	0
<i>Brunsia</i> Mikhailov, 1935	1	0	1	1	1	1	1	1
<i>Calciornella</i> Cushman and Waters, 1928	1	0	1	1	1	0	1	1
<i>Calcivertella</i> Cushman and Waters, 1928	1	0	1	1	1	1	1	1
<i>Cepekia</i> Vašíček & Růžicka, 1957	1	1	1	1	1	1	1	1
<i>Chomatomediocris</i> Vdovenko in Brazhnikova and Vdovenko, 1973	0	0	1	1	0	0	0	0
<i>Climacammina</i> Brady in Etheridge, 1873	1	1	1	1	1	1	1	1
<i>Conilidiscus</i> Vachard, 1988	0	0	0	1	0	0	0	1
<i>Consobrinellopsis</i> Krainer and Vachard, 2015	1	1	1	1	1	1	1	1
<i>Criboospira</i> Möller, 1878	0	0	1	1	1	1	1	1
<i>Cribrastomum</i> Möller, 1879	1	1	1	1	1	1	1	1
<i>Earlandia</i> Plummer, 1930	1	1	1	1	1	1	1	1
<i>Eblanaia</i> Conil and Marchant in Conil, 1977	0	0	1	0	0	1	0	0
<i>Endospiroplectammina</i> Lipina, 1970	0	0	1	1	1	1	1	1
<i>Endostaffella</i> Rozovskaya, 1961	1	0	1	1	1	1	1	1
<i>Endostaffellopsis</i> Cózar et al., 2016a	0	0	1	1	0	1	1	1
<i>Endotaxis</i> Bogush and Brazhnikova in Aizenverg et al., 1983	1	0	1	1	0	1	1	0
<i>Endothyra</i> Phillips, 1846	1	1	1	1	1	1	1	1
<i>Endothyranella</i> Galloway and Harlton in Galloway and Ryniker, 1930	1	0	0	1	0	0	1	0
<i>Endothyranopsis</i> Cummings, 1955a	1	1	1	1	1	1	1	1
<i>Eoendothyranopsis</i> Reitlinger and Rostovzeva in Reitlinger, 1966	1	1	0	0	0	0	0	0
<i>Eolasiodiscus</i> Reitlinger, 1956	1	0	1	0	0	0	1	1
<i>Eoparastaffella</i> Vdovenko, 1954	0	0	0	1	1	0	0	0
<i>Eosforschia</i> Mamet in Mamet et al., 1970	1	0	0	0	0	0	0	0
<i>Eosigmoilina</i> Ganelina in Kiparisova et al., 1956	1	0	1	1	1	1	1	1
<i>Eostaffella</i> Rauzer-Chernousova, 1948a	1	1	1	1	1	1	1	1
<i>Eostaffellina</i> Reitlinger, 1963	1	0	1	1	1	1	1	1
<i>Euxinita</i> Conil and Dřil in Conil et al., 1980	0	0	1	1	1	1	1	1
<i>Florenella</i> Conil in Groessens et al., 1982	0	0	1	0	0	0	0	0
<i>Forschia</i> Mikhailov, 1935	0	0	1	1	1	1	1	1
<i>Forschiella</i> Mikhailov, 1939	0	0	1	1	1	1	0	1
<i>Globispiroplectammina</i> Vachard, 1977	0	0	0	1	0	1	0	0
<i>Globivalvulina</i> Schubert, 1921	1	0	1	1	1	1	1	1
<i>Globoendothyra</i> Bogush and Juferev, 1962	1	1	1	1	1	1	1	1
<i>Globoomphalotis</i> Bogush, 1987	0	0	0	1	0	0	1	0
<i>Glomodiscus</i> Malakhova, 1973	0	0	1	1	1	1	0	0
<i>Haplophragmina</i> Reitlinger, 1950	0	1	1	1	1	1	1	1
<i>Hemidiscopsis</i> Cózar in Cózar et al., 2015	0	0	1	1	0	1	1	1
<i>Holkeria</i> Strank, 1982	0	0	1	0	0	0	0	0
<i>Howchinia</i> Cushman, 1927	0	0	1	1	1	1	1	1
<i>Insolentitheca</i> Vachard in Bensaid et al., 1979	0	0	1	1	0	1	1	1
<i>Janischewskina</i> Mikhailov, 1939	1	0	1	1	1	1	1	1
<i>Kasachstanodiscus</i> Marfenkova, 1978	1	0	0	0	1	0	1	1
<i>Koktjubina</i> Marfenkova, 1991	1	1	1	1	1	1	1	1
<i>Koskinobigenerina</i> Eickhoff, 1968	1	1	1	1	1	1	1	1
<i>Koskinotextularia</i> Eickhoff, 1968	1	0	1	1	1	1	1	1
<i>Litotubella</i> Rauzer-Chernousova, 1948b	0	0	1	1	1	1	1	1
<i>Loeblichia</i> Cummings, 1955a	1	0	1	1	1	0	1	1
<i>Magnitella</i> Malakhova, 1975	0	0	1	0	0	1	0	0
<i>Mediocris</i> Rozovskaya, 1961	1	0	1	1	1	1	1	1
<i>Mikhailovella</i> Ganelina, 1956	0	1	1	1	1	1	1	1
<i>Millerella</i> Thompson, 1942	1	0	0	1	1	0	0	0
<i>Millerella</i> Thompson, 1942	1	0	1	1	0	1	1	1
<i>Mirifica</i> Shlykova, 1969	0	0	1	0	0	1	0	0
<i>Monotaxinoides</i> Brazhnikova and Yartseva, 1956	1	0	1	1	0	1	1	0
<i>Mstina</i> Dain in Dain and Grozdilova, 1953	1	1	1	1	1	1	1	1

Table 2. Continued.

GENERA	North America	Maritimes Basin	Britain/Ireland	Moroccan Meseta	SW Spain	Southern France	NW Spain	Sahara
<i>Neoarchaediscus</i> Miklukho-Maklay in Kiparisova et al., 1956	1	1	1	1	1	1	1	1
<i>Nodasperodiscus</i> Conil and Pirlet in Pirlet and Conil, 1977	1	0	1	1	1	1	1	1
<i>Nodosarchaediscus</i> Conil and Pirlet in Pirlet and Conil, 1977	1	0	1	1	1	1	1	1
<i>Omphalotis</i> Shlykova, 1969	0	1	1	1	1	1	1	1
<i>Palaeotextularia</i> Schubert, 1921	1	1	1	1	1	1	1	1
<i>Parabiseriella</i> Cózar and Somerville, 2012	0	0	0	1	0	0	1	0
<i>Parabadyina</i> Mamet and Pinard, 1992	0	0	1	0	0	0	0	1
<i>Pirletidiscus</i> Vachard, 1988	0	0	0	0	1	0	1	1
<i>Planoarchaediscus</i> Miklukho-Maklay in Kiparisova et al., 1956	1	0	1	1	1	1	1	1
<i>Planoendothyra</i> Reitlinger in Rauzer-Chernosova and Fursenko, 1959	1	0	1	1	1	1	1	1
<i>Planohowchinia</i> Cózar and Mamet, 2001	0	0	0	0	1	1	1	0
<i>Planospirodiscus</i> Sosipatrova, 1962	1	0	1	1	1	1	1	1
<i>Plectogyransopsis</i> Vachard, 1977	1	1	1	1	1	1	1	1
<i>Plectogyrina</i> Reitlinger in Rauzer-Chernosova and Fursenko, 1959	1	0	0	0	1	0	0	0
<i>Plectomediocris</i> Brazhnikova and Vdovenko in Aizenverg et al., 1983	0	0	0	0	0	0	1	0
<i>Plectostaffella</i> Reitlinger, 1971	1	0	1	1	1	1	1	0
<i>Pojarkovella</i> Simonova and Zub, 1975	0	0	1	0	1	1	1	1
<i>Praeastaffellina</i> Cózar et al., 2008	1	0	1	0	0	1	1	1
<i>Praeplectostaffella</i> Cózar et al., 2008	0	0	1	1	0	1	1	1
<i>Protoinsolentitheca</i> Vachard and Cózar, 2004	0	0	1	0	1	1	1	1
<i>Pseudoammodiscus</i> Conil and Lys in Conil and Pirlet, 1970	1	1	1	1	1	1	1	1
<i>Pseudoendothyra</i> Mikhailov, 1939	0	1	1	1	1	1	1	1
<i>Pseudoglomospira</i> Bykova, 1955	1	1	1	1	1	1	1	1
<i>Pseudolituotuba</i> Vdovenko, 1971	0	1	1	1	1	1	1	0
<i>Pseudotaxis</i> Mamet, 1974b	1	1	1	1	1	1	1	1
<i>Quasiarchaediscus</i> Miklukho-Maklay, 1960	1	0	1	0	0	0	0	0
<i>Rectocornuspira</i> Warthin, 1930	1	0	0	1	0	1	0	0
<i>Rectoendothyra</i> Brazhnikova in Aizenverg et al., 1983	1	0	0	1	0	1	1	0
<i>Scalebrina</i> Conil and Logerstaey in Conil et al., 1980	0	0	1	1	1	1	1	0
<i>Semiendothyra</i> Reitlinger, 1980	1	0	1	0	0	1	1	0
<i>Spinobrunsiina</i> Conil and Longerstaey in Conil et al., 1980	1	0	1	0	1	1	0	0
<i>Spinothyra</i> Mamet, 1976	0	0	1	0	1	1	1	1
<i>Spireitlina</i> Vachard in Vachard and Beckary, 1991	0	0	0	0	0	1	0	0
<i>Tetrataxis</i> Ehrenberg, 1854	1	1	1	1	1	1	1	1
<i>Tournayella</i> Dain in Dain and Grozdilova, 1953	1	0	0	0	0	0	0	0
<i>Trepeilopsis</i> Cushman and Waters, 1928	1	1	1	1	1	0	1	0
<i>Tubispirodiscus</i> Browne and Pohl, 1973	1	0	1	1	1	1	1	1
<i>Turrispiroides</i> Reitlinger in Rauzer-Chernosova and Fursenko, 1959	0	0	1	1	1	0	0	0
<i>Uralodiscus</i> Malakhova, 1973	0	0	0	0	1	1	1	0
<i>Vachardites</i> Cózar et al., 2016a	0	0	0	0	0	0	1	0
<i>Valvulinella</i> Schubert, 1908	0	0	1	1	1	1	1	1
<i>Viseidiscus</i> Mamet, 1975	1	0	1	1	1	0	1	0
<i>Vissarionovella</i> Cózar and Vachard, 2001	0	0	1	1	1	1	1	1
<i>Vissariotaxis</i> Mamet, 1970	0	0	1	1	1	1	1	0
<i>Volgella</i> Reitlinger in Reitlinger and Melnikova, 1977	0	0	0	0	1	0	0	1
Total	53	26	76	71	64	68	70	65

diverse and richer assemblages due to limited documentation to date, but also because the presence of early Visean strata in the Windsor Group is still debated; if present, these are mostly composed of thick evaporite deposits in cycle 1 (e.g., Jutras et al., 2015; Waldron et al., 2017; Fig. 3) that would themselves have formed an unfavorable environment.

Foraminifers

Despite the presence of numerous endemic genera, a clear exclusively worldwide provincialism does not seem to have existed within the Mississippian Fusulinata foraminifers. Mamet and

Skipp (1970a) and Mamet (1977) documented continuous interchange between the three main realms—Paleotethys, North American, and Boreal (Fig. 2)—but not exclusive provincialism. Ross (1995) introduced a fourth realm, called Panthalassa or Sonomia, including some terranes in parts of Japan, the southern Russian Far East, British Columbia, and New Zealand. In the Mississippian, geographic and stratigraphic distribution of foraminifers are better known than those of calcareous algae.

Previous data on Fusulinata foraminifers from the Maritimes Basin are restricted to a limited number of publications (Mamet, 1968, 1970; Brisebois and Mamet, 1974; Jansa et al., 1978; Brisebois, 1979; Jansa and Mamet, 1984). It is

noteworthy that taxa recorded by Brisebois (1979) are rather similar to those of Jansa et al. (1978) and Mamet (1970), and they do not contribute to new occurrences of taxa. In total, ~50 taxa have been listed by the previous authors. Mamet (1970) based his attribution of the fauna to the North American Realm on the occurrence of *Zellerinella* Mamet, 1981, and mostly by the absence of some typical Paleotethyan taxa, e.g., *Loeblichia* Cummings, 1955 (Cummings, 1955a), *Valvulinella* Schubert, 1908, *Omphalotis omphalota* (Rauzer-Chernousova and Reitlinger in Rauzer-Chernousova et al., 1936), and *Archaeodiscus karreri* Brady, 1873. Jansa and Mamet (1984) further extended the comparison, including more detailed paleobiogeographic maps of the geographic distribution of *Howchinia* Cushman, 1927, *Bradyina* Möller, 1878, *Lituotubella* Rauzer-Chernousova, 1948 (Rauzer-Chernousova, 1948b), and *Omphalotis* Shlykova, 1969 (all absent in the Maritimes Basin), and consideration that the distance between Newfoundland and Ireland was at least 1,000 km separated by a deep ocean, which did not permit faunal interchange, and rejecting contemporaneous paleogeographic reconstructions locating the Maritimes Basin close to Spain or the Moroccan Meseta.

Although most foraminifers recorded in the Viséan-early Serpukhovian Windsor Group are cosmopolitan, their relative abundance is distinct in the different paleobiogeographic domains (Mamet, 1970, fig. 15), but could also be subject to paleoecological constraints (e.g., Mamet and Skipp, 1979). The basal Windsor Group strata comprises a thick interval of evaporites resting on a single marine carbonate unit (Macumber Formation), which defines the base of the group (Fig. 3) and provides the single potential source of foraminiferal data that have proven rare at this stratigraphic level. Thick lower Windsor Group evaporites imply a lack of open marine connections, which would necessarily be reflected in the benthic fauna and result in a limited foraminiferal population. These ‘reduced’ suites are not themselves similar, but they are similarly reduced, as in other apparently better-connected marine basins, e.g., in SW Spain (Cózar, 2003) where the foraminiferal assemblages show many dissimilarities (in diversity, abundance, and first occurrences of taxa) compared with neighboring basins in Morocco, France, and England. In a similar manner, the Maritimes Basin is notable for the rarity of one of the most diagnostic North American taxa, *Eoendothyranopsis* Reitlinger and Rostovzeva in Reitlinger, 1966, which is widespread in Viséan North American successions (e.g., Mamet and Skipp, 1970a, b), but it is also common in Boreal and northwestern Paleotethyan realms (e.g., Loeblich and Tappan, 1987).

Another constraint is that the most diverse and richer realms (both in terms of numbers of genera and species, and also number of specimens) are the Paleotethyan and Boreal realms (Mamet and Skipp, 1970a, 1979; Mamet, 1977; Davydov, 2014) as well as realms with more endemic taxa. Thus in the Maritimes Basin, the absence of more numerous Paleotethyan taxa is more likely for North American affinities. A final constraint is the established migration routes for foraminifers. According to Mamet and Skipp (1970a) and Mamet (1977), most foraminifers are Euroasiatic in origin and migrated westward to western Europe and later to American and Arctic realms. This migration route was established on the basis of: (1) the earliest Late Devonian Endothyridae flourished in Eurasia but

are rarely observed in North America; (2) the presence of complete phylogenetic lines in Europe but incomplete ones in North America; (3) impoverished microfauna in North America in regard to Eurasian assemblages, and with few endemic taxa; and (4) heterochronism of the base of the acmes and first occurrences (the oldest forms always occur first in Eurasia, then in the Arctic, and finally in the North American Cordillera). This direction in essence suggests that a communication route had to have existed between western Europe and eastern North America, and those taxa recorded in basins such as the Midcontinent had to have crossed using the Rheic Ocean and then via regions with more similarities with western Europe, i.e., the Maritimes Basin. However, some taxa must have migrated via the northern Boreal Ocean through the Franklinian corridor and Alaska (Harris et al., 1997; Davydov and Cózar, 2019; Fig. 2).

A distinctive feature of the Maritimes Basins, as noted by Mamet (1970) and Jansa and Mamet (1984), is the absence of typical large foraminifers recorded in the Paleotethys realm (e.g., *Omphalotis omphalota*, large *Archaeodiscus* Brady, 1873, *Bradyina*, *Janischewskina* Mikhailov, 1939). The absence of these taxa in the Maritimes Basin is significant, but even in better-connected marine basins in SW Europe, they can show a similar phenomenon. For instance, in Sierra Morena in SW Spain, which should be paleogeographically relatively close to the Maritimes Basin, a typical late Viséan-early Serpukhovian succession occurs (Cózar, 2003). Currently, from this succession, more than 4,000 thin sections have been studied, and only one specimen of *Bradyina* has been recorded, and no more than five specimens of *Janischewskina*. In addition, only sparse specimens of the large species of *Archaeodiscus* have been recorded, and the largest species are absent, compared to successions in Britain and Ireland. Thus, the absence of certain taxa, although at first glance might seem to provide a solid paleogeographic argument, could on the other hand be explained by responses to paleoecological constraints. Hence, the absence of some species is not exclusive to the Maritimes Basin, and needs to be further investigated due to similar patterns in unquestionable Paleotethyan basins. Furthermore, Jansa and Mamet (1984) considered the poor assemblages of the Maritimes Basin as being themselves characteristic and caused by a certain isolation from the main region of marine sedimentation and migration routes.

The second main argument in the comparison of Maritimes Basin foraminifers with those of the North American Realm, is the genus *Zellerinella* (= *Zellerina* Mamet in Mamet and Skipp, 1970b, preoccupied), which was formerly considered endemic to this realm (Mamet, 1974c; Armstrong and Mamet, 1977). Equatorial sections might be confused with *Eostaffella* Rauzer-Chernousova, 1948 (Rauzer-Chernousova, 1948a), *Endostaffella* Rozovskaya, 1961, or other similar planispiral genera, but the axial sections are more distinctive. Since these earlier studies, the taxonomy of this taxon has progressed notably, and species originally interpreted as a primitive *Millerella* Thompson, 1942 by Zeller (1953) (e.g., *Millerella tortula* Zeller, 1953 and *Millerella designata* Zeller, 1953) were included in the genus *Zellerina*/*Zellerinella* by Mamet in Mamet and Skipp (1970b) and Mamet (1981), and was later reassigned to *Paramillerella* Thompson, 1951 (Brenckle and Groves, 1981), *Plectomillerella* Brazhnikova and Vdovenko in Aizenverg et al., 1983 (van Ginkel, 2010), or simply ‘*Millerella*’

(Gibshman, 2001). The type species of the genus, *Endothyra discoidea* Girty, 1915, is now considered an *Endostaffella* (Brenckle, 2005). Independently of the preferred genus name, the same species have been recognized from China (e.g., Groves et al., 2012), eastern Europe (e.g., Gibshman, 2003), western Europe (e.g., Cózar and Somerville, 2016), and northern Africa (Cózar et al., 2011, 2016b). Thus, the genus is now considered as cosmopolitan and it cannot be used to ascribe the foraminiferal fauna of the Maritimes Basin to the North American Realm.

In the faunal list of Mamet (1970), the occurrence of *Plectogyranopsis* ex gr. *P. hirosei* (Okimura, 1965) and *Haplophragmella* Rauzer-Chernousova and Reitlinger in Rauzer-Chernousova et al., 1936 need to be highlighted. The latter is a Paleotethyan taxon, and it is likely that specimens recorded in the Windsor Group might be included in the genus *Mstinia* Dain in Dain and Grozdilova, 1953. Only *Mstinia irregularis* (Rauzer-Chernousova, 1938) has been documented in the North American craton by Rich (1980). True *Haplophragmella* seems to be restricted to the former Soviet Union basins, and most specimens (if not all) recorded in western Europe need to be referred to *Mstinia/Nevillea* Conil and Lys in Conil et al., 1980 (Pille, 2008; Vachard et al., 2010). *Plectogyranopsis hirosei* is only known from the Paleotethys Realm (eastern and western), except in the Arctic (Mamet et al., 1993). *Endothyranella* sp. is reinterpreted here as *Mikhailovella gracilis* (Rauzer-Chernousova, 1948 [Rauzer-Chernousova, 1948a]), a typical Paleotethyan taxon, and *Mikhailovella* sp. of Mamet (1970) is rather similar to the *Mikhailovella fresnedosensis* Cózar, 2001 recorded at Sierra Morena (Cózar, 2001). In addition, the Maritimes Basin assemblages also contain *Omphalotis*, *Pseudoendothyra* Mikhailov, 1939, and *Pseudolituotuba* Vdovenko, 1971, genera typically represented in the Paleotethyan and Boreal realms.

Koktjubina Marfenkova, 1991 was originally described from Kazakhstan by Marfenkova (1991), and she also included a previously described species from Kazakhstan by Vdovenko (1962), *Spiroplectammina exotica* Vdovenko, 1962, and a species described from the Windsor Group by Mamet (1970), *Biseriammina? windsorensis* Mamet, 1970. The genus is predominantly of Paleotethyan affinities, although some rare exceptions are known from the Midcontinent. Rich (1980, pl. 5, fig. 1, non fig. 4) determined *Biseriella? exotica* (Vdovenko, 1962) in the southern Appalachians, and the specimens identified as *Biseriella parva* (Chernysheva, 1948) (pl. 5, figs. 2, 3, 6, 7, 10) are also attributable to *Koktjubina*. Later, Rich (1986, pl. 1, figs. 14–15) identified similar specimens of *Biseriella parva* as *Biseriella exotica*. This species, now *Koktjubina exotica* (Vdovenko, 1962), might be also present in the Peratrovich Formation of southern Alaska (Mamet et al., 1993, pl. 13, fig. 7 only).

Three species of *Koktjubina* are recorded in Ireland, i.e., *Koktjubina? atlantica* Cózar and Somerville, 2012, *Koktjubina windsorensis* (Mamet, 1970), and *Koktjubina exotica*. The most evolved species, described as *Koktjubina? atlantica* by Cózar and Somerville (2012), is widespread in Ireland and recorded in the Brigantian of SE Ireland. This species occurs in the Windsor Group (Mamet, 1970, pl. 1, fig. 5, as undetermined Biseriamminidae) and in the Canadian Cordillera (Mamet, 1976, pl. 81, figs. 12, 13, as *Biseriella* sp.). *Koktjubina windsorensis* is recorded only in the Benburb area of Northern

Ireland (see location, Mitchell and Mitchell, 1983), where it occurs in the latest Asbian and Brigantian (Cózar and Somerville, 2012). As mentioned above, *Koktjubina windsorensis* is known throughout the Windsor Group in the Maritimes Basin, where it was identified as a species of *Biseriammina* Chernysheva, 1941 by Mamet (1970). Its first appearance in the Maritimes Basin in lower Windsor Group strata differs from its most commonly reported occurrences in the late Viséan and Serpukhovian (e.g., von Bitter et al., 2007). The third species recorded in Ireland is *Koktjubina exotica*, which occurs in the Benburb area and in NW Ireland, but as mentioned above, also in the Midcontinent. These three species clearly suggest a faunal interchange between the Maritimes Basin and Ireland, and *Koktjubina windsorensis* seems to be endemic to the Maritimes Basin and Northern Ireland.

Jansa et al. (1978) and Brisebois (1979) documented, in widely separated portions of the Maritimes Basin, the occurrence of *Polysphaerina bulla* Mamet, 1973. Described from Belgium and France (Conil and Lys, 1964; Mamet, 1973), this taxon is a unilocular tuberitid with secondary spheres (see Vachard, 2016). It is otherwise known only from basins in the western Paleotethys, including Ireland and Britain (e.g., Vachard and Tahiri, 1991; Cózar and Rodríguez, 2000; Pille, 2008).

On the other hand, revision of foraminiferal assemblages previously published by other authors in von Bitter et al. (2007) are typically Paleotethyan in origin. Moreover, it can be concluded from the above-discussed data, that the foraminiferal genera from the Maritimes Basin are typically European and north African (see Table 2). Thus, in summary: (1) there is a single foraminiferal taxon (*Eoendothyranopsis*) in the Maritimes Basin assemblages that is considered more common in the North American Realm, although it has not been illustrated; (2) there are three typical Paleotethyan foraminiferal species: *Plectogyranopsis hirosei*, *Mikhailovella gracilis*, and the unilocular *Polysphaerina bulla*, as well as the genera *Haplophragmina* Reitlinger, 1950, *Omphalotis*, *Pseudoendothyra*, and *Pseudolituotuba*; (3) there is one virtually endemic Paleotethyan genus, *Koktjubina*, of which one species (*Koktjubina windsorensis*) is known only from the Maritimes Basin and Northern Ireland; and (4) one other species (*Mikhailovella fresnedosensis*) is only recorded in the Maritimes Basin and SW Spain.

Another interesting feature of the foraminiferal assemblages of the Maritimes Basin is that they occur at similar stratigraphic levels as in western Europe (von Bitter et al., 2007). It is well-known that the majority of North American taxa originated in the Paleotethys realm, and that they migrated westward. This process of migration is characterized by a delay of 2–3 Myr, and even up to 5 Myr, before their first appearances in North America, compared to the Paleotethys realm (Mamet, 1977; Davydov, 2014). The apparent absence of these lags in the Maritimes Basin also suggests Paleotethyan affinities for the fauna of the Maritimes Basin.

Other fossil groups

Conodonts.—The main studies of conodont faunas from the Maritimes Basin are those of Globensky (1967), von Bitter (1976), and von Bitter and Plint-Geberls (1982, 1987), subsequently summarized by von Bitter et al. (2007). Only

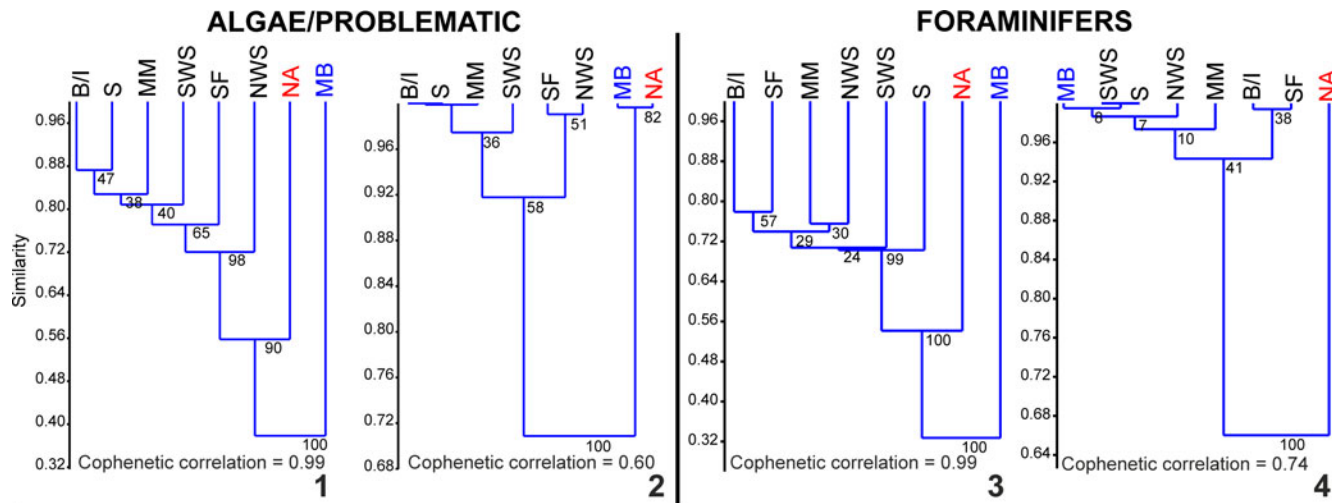


Figure 4. Dendrograms from hierarchical cluster analyses of algae/problematic algae and foraminifers using the Jaccard coefficient (1, 3), and Raup-Crick coefficient (2, 4) by unweighted pair-group average (UPGMA) method (node percentages are bootstrap support with 1,000 iterations). B/I = Britain and Ireland; MB = Maritimes Basin; MM = Moroccan Meseta; NA = North America; NWS = NW Spain; S = Sahara; SF = southern France; SWS = SW Spain.

Globensky (1967) suggested that the conodont assemblages were representative of the North American realm, although following the reinterpretation of some of Globensky's specimens by von Bitter (1976), the assemblage has more recently been considered as Eurasian. This has been corroborated in the biogeographic provinces defined by Higgins (1981), and more recently, it has been recognized that common taxa are shared between the Maritimes Basin and Britain, e.g., *Mestognathus* Bischoff, 1957, *Taphrognathus transatlanticus* von Bitter and Austin, 1984, *Clydagnathus windsorensis* (Globensky, 1967), *Vogelgnathus pesauidi* (Purnell and von Bitter, 1992), *Vogelgnathus campbelli* (Rexroad, 1957), and *Vogelgnathus postcampbelli* (Austin and Husri, 1974) (von Bitter and Austin, 1984; von Bitter et al., 1986; Purnell and von Bitter, 1992).

Rugose corals.—Since the pioneering work of Lewis (1935), rugose corals from the Maritimes Basin have been traditionally considered paleobiogeographically closer to western European assemblages than to American rugose-coral assemblages (Hill, 1973, 1981). Although taxonomic determinations were not conclusively documented, Poty (2002) recently revised those rugose corals and confirmed that most are typically represented in western Europe, notably in basins from northern England, Ireland, and southern France (*Actinocyathus* d'Orbigny, 1849, *Amplexizaphrentis* Vaughan, 1906, *Axophyllum* Milne-Edwards and Haime, 1850, *Koninckophyllum* Thomson and Nicholson, 1876, *Lonsdaleia* McCoy, 1849, *Nemistium* Smith, 1928, *Palastraea* McCoy, 1851, and *Siphonodendron* McCoy, 1849).

Miospores.—Following the study by Clayton (1985), palynologists have widely accepted that Atlantic Canada belongs to the same paleobiogeographic province as Europe. Biostratigraphic zones defined in the Windsor Group and coeval strata (e.g., Utting, 1987; Utting and Giles, 2004) are comparable to those used in western Europe (e.g., Neves et al., 1972, 1973; Clayton et al., 1977). A close comparison

of both spore zonal schemes was documented by Utting and Giles (2004), and the European miospore zonal scheme, as well as European regional substages, are now used in biostratigraphic analyses of the region (e.g., Jutras et al., 2001, 2015; von Bitter et al., 2007; Utting and Giles, 2008).

Brachiopods.—Von Bitter and Legrand-Blain (2007) studied the gigantoproductids from the Windsor Group in Nova Scotia, based on specimens they collected themselves and those illustrated by previous authors. They recognized several taxa denominated as typical 'Old World' brachiopods, especially highlighting the occurrence of *Latiproductus* sp. and *Gigantoproductus* cf. *G. crassiventer* (Prentice, 1949), and the close relationship between Nova Scotia and central England.

Trilobites.—Trilobites have not yet been studied in detail in the region, but Brezinski (2003) recorded *Paladin eichwaldi* (Fischer von Waldheim, 1825) in the Windsor Group, which he interpreted to be a typical European taxon.

Paleobiogeographic results

The dendrograms resulting from hierarchical cluster analyses of algae/problematic algae and foraminifers using the Jaccard coefficient show a low similarity index for the Maritimes Basin (Fig. 4.1, 4.3). The highest similarity indices obtained with algae (0.44) and foraminifers (0.34), although still low values, suggest a closer position for the Maritimes Basin with the North American craton. However, in the case of foraminifers, the similarity index with SW Spain is also 0.34. This is interpreted as the result of 'missing' or under-represented data in the Maritimes Basin, which gives an artificial coincidence with the poorest North American Realm, or is composed of numerous endemic forms. The dendrograms using the Raup-Crick coefficient provide more diverse results. The algal cluster also shows a close position of the Maritimes Basin with North America (Fig. 4.2). In contrast, the foraminiferal cluster shows

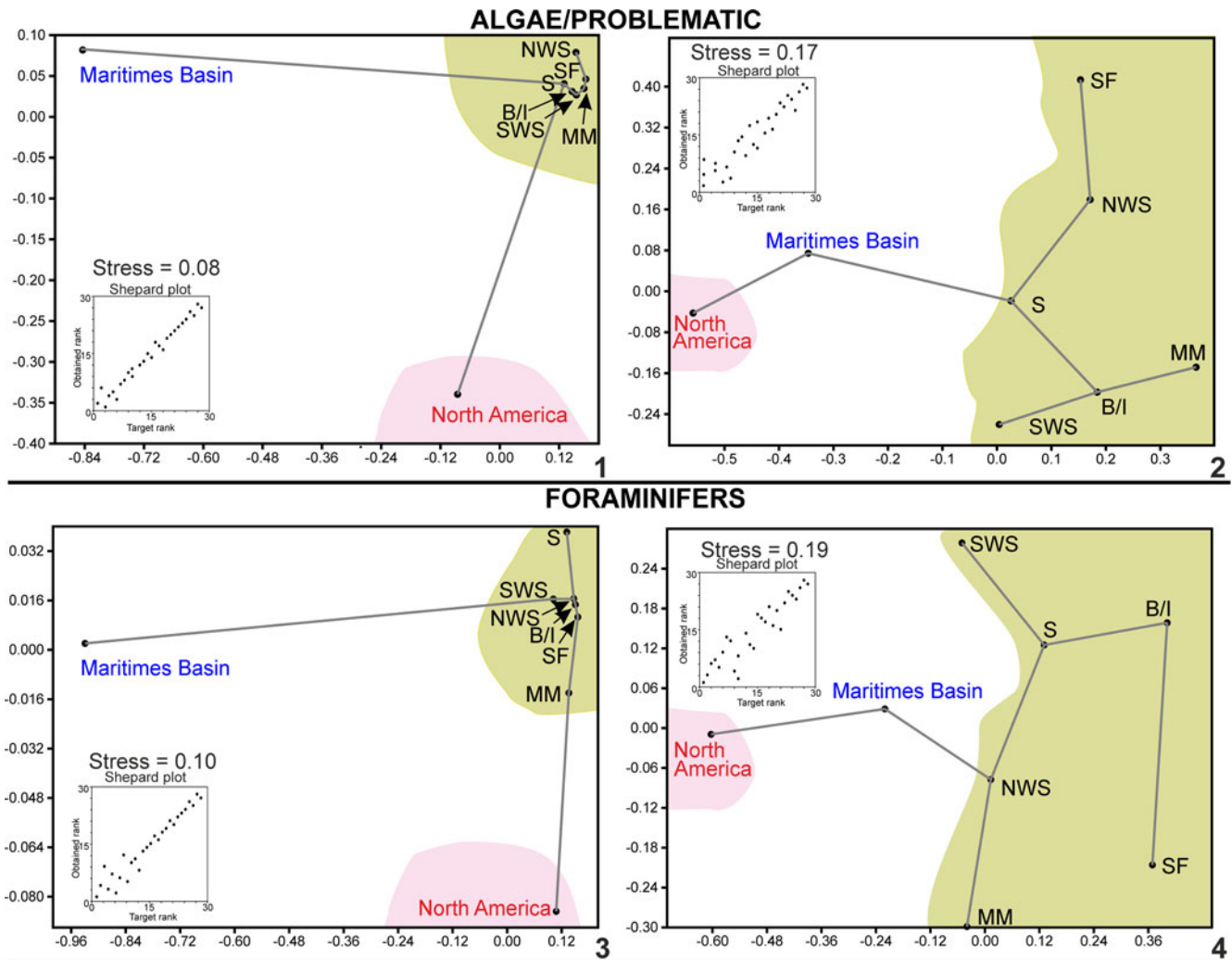


Figure 5. Non-metric Multidimensional Scaling (NMDS) ordination method using the Jaccard coefficient (1, 3) and Raup-Crick coefficient (2, 4) of algae/problematic algae and foraminifers. Abbreviations as in Fig. 4.

higher similarities with terranes in Spain and Gondwana (Fig. 4.4). It might be possible to explain the apparent ‘anomaly’ of the algal data in both the Jaccard and Raup-Crick coefficient methods, in which they show closer affinity to North America, as a result of the fewer number of genera (one-third less) in the database compared to the foraminifers.

The ordination methods (NMDS) using the Jaccard coefficient always suggest widely distant positions between the Maritimes Basin and North American and Paleotethyan realms, slightly closer to the Paleotethys realm, specifically, the Gondwana craton (Sahara) (Fig. 5.1). The foraminifers show closer affinities with the northern Variscan Front (Moroccan Meseta and Sierra Morena, SW Spain) (Fig. 5.3).

These affinities are emphasized using the Raup-Crick coefficient, in which the Maritimes Basin is mostly in an intermediate position between North America and western Europe/northern Africa, which is the most logical presumption. The closer distances, depending on the fossil group, are with the southeastern terranes (NW Spain) and Gondwana (Sahara) (Fig. 5.2, 5.4), but not with Britain/Ireland, as previously authors have proposed.

To minimize this plausible ‘absence of data’ effect in the Maritimes Basin, both groups were analyzed together, and the biota results show a closer proximity to Gondwana or the southern terranes (Fig. 6), at similar distances than with North America. Secondly, it is observed that there is a close relationship between the Maritimes Basin and terranes in the northern Variscan Front, e.g., SW Spain. However, a close relationship with Laurussia was not observed, as some particular taxa of foraminifers, conodonts, brachiopods, and miospores have suggested. It must be noted that the analysis for algae has been run also considering only *Kulikia* and not *Pekiskopora*, and the results were similar. This confirms that the occurrence of a particular taxon did not exert excessive weight in paleobiogeographic comparisons.

A major concern about the lack of diversity of the Maritimes Basin is seen in the dichotomic results using the Jaccard or Raup-Crick coefficients for individual fossil groups (Figs. 4, 5). The Jaccard coefficient is one of the more widely used coefficients for biogeographic models, but owing to missing data, the Raup-Crick coefficient has become more commonly used in paleobiogeographical models, to highlight

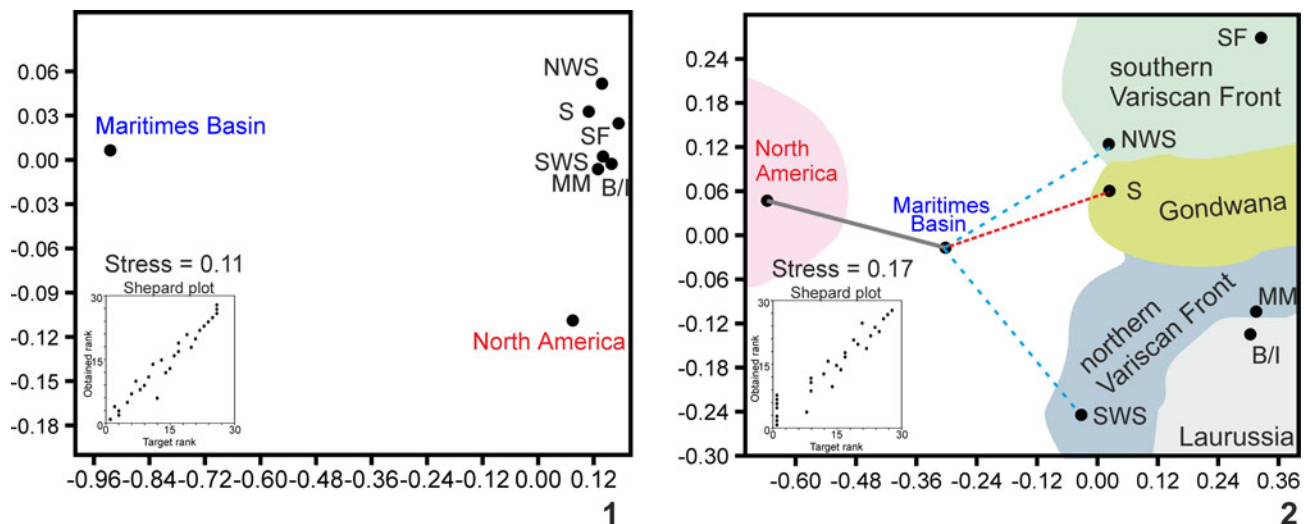


Figure 6. Paleobiogeographical relations of the two fossil groups used in Fig. 5. Non-metric Multidimensional Scaling (NMDS) with the Jaccard coefficient (1) and Raup-Crick coefficient (2). Abbreviations as in Fig. 4.

unusual taxa and not the more widely expanded taxa. This difference between the indices is minimized when the database is larger (Fig. 6), showing similar results.

The lack of diversity is a marked handicap in analysis of the fauna and flora of the Maritimes Basin, because the total number of recorded foraminiferal and algal genera are only one-quarter or one-third as large as those in the Paleotethys Realm (26 vs 107 and 23 vs 70, respectively), and one-half of those in North America (26 vs 53, and 23 vs 42, respectively) (already considered as containing impoverished assemblages; see Tables 1, 2). Thus, although low diversity was considered a characteristic feature of the Maritimes Basin by Jansa and Mamet (1984), it is apparent that further research is necessary to increase its recorded diversity, which currently looks insufficient; owing to this apparent low diversity, the statistical results have to be taken with some caution.

Paleobiogeographic implications

Because the oldest Viséan rocks of the Windsor Group succession are dominated by thick evaporites (Fig. 3), Mamet (1970) and Jansa and Mamet (1984) postulated that the Maritimes Basin was a semiclosed platform. This was invoked for the precipitation of evaporites, because most paleogeographic reconstructions show Ireland/Britain and the Maritimes Basin at approximately the same low latitude, between 10° and 20°S (e.g., Roy, 1973; Smith et al., 1973; but not Ziegler, 1978). Jansa and Mamet (1984) considered that the distance between Ireland and the Maritimes Basin was at least 1,000 km, and separated partly by a graben/rift structure (Rockall-Hatton Bank of Le Pichon, 1977 and Ziegler, 1978) and involved a wide Rheic Ocean. Recent reconstructions suggest that this distance was ~800 km during the Devonian (Waldron et al., 2018). Thus, it can be assumed that the distance during the Mississippian was even less, due to the closing related to the progressing Variscan orogeny.

Despite the faunal, floral, and stratigraphical similarities between the Maritimes Basin and western European/northern African basins, it is certainly apparent that there are also

dissimilarities, which prevent a perfect interconnectedness. On the other hand, the tectonic style in the Maritimes Basin is more typically Appalachian, following the assumed attachment of the terranes of the North American region since the Devonian.

The presence of a land barrier between western Europe and Newfoundland was discussed and dismissed by previous authors (e.g., Jansa and Mamet, 1984). We agree with that conclusion, because the existence of a land barrier would have prevented the marine faunal and floral interchange that is now well known. The occurrence of an ocean that acted as a potential paleobiological barrier, controlled by currents, water depth, and ocean width (Jansa and Mamet, 1984), is the most likely hypothesis. However, the presence of this ocean disagrees with the hypothesis that considered that the closure of the Rheic Ocean occurred during the Devonian or in the earliest Mississippian (e.g., Nance et al., 2012) and only a Rheohercynian Ocean could have been open from the Middle to Late Mississippian (see Fig. 7). The close similarities and clear influence of Paleotethyan late Viséan assemblages suggest a narrower ocean than previously supposed, and also, not very deep, to allow migration of most benthic biota. It is difficult to estimate ocean width, but it was likely to have been <1,000 km, as recent reconstructions have suggested. Whatever the separation, fluid and constant faunal/floral interchange must have been permitted. However, the low diversity of the Maritimes Basin assemblages is a conditioning factor because it might be the result of the few studies in the region, or it might be actual low diversity. In the first case, if the diversity of assemblages (number of genera) could be increased as a result of more studies in the region, that would imply a more constant interchange of fauna, and thus, a narrower oceanic width. In contrast, if, after more studies in the region, the diversity is not significantly increased, this would imply a certain isolation of the Maritimes Basin, either by a wider ocean or by stronger oceanic currents, allowing only sporadic interchange of fauna/flora with the Paleotethys realm (as during major transgressive events). It is also noteworthy that during sedimentation of the basal Windsor

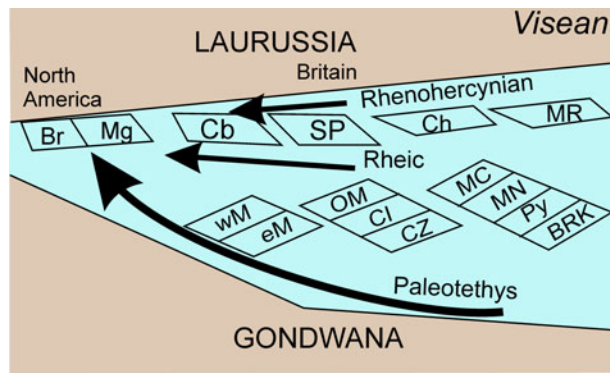


Figure 7. Paleobiogeographical sketch of the Maritimes Basin and basins in western Europe and North Africa during the late Visean-early Serpukhovian. Black arrows are plausible migration routes to the Maritimes Basin. Terranes based on Stampfli et al. (2013). Br = New Brunswick; BRK = Betics-Rif-Kabbilies; Cb = Coastal Block; Ch = Channel; CI = Central Iberian Zone; CZ = Cantabrian and Asturian-Leonese Zone; eM = eastern Moroccan Meseta; MC = Central Massif of France; Mg = Meguma; MN = Montagne Noire; MR = Mid-Germany rise; OM = Ossa-Morena Zone; Py = Pyrenees and Catalonia; SP = South Portuguese Zone; wM = western Moroccan Meseta.

Group (evaporites of cycle 1, but also in cycles 2–5; Fig. 3), the conditions were distinctly different from those in most of western Europe, i.e., in a restricted basin, with poor communication with the ocean that did not allow a fluid faunal interchange. However, episodes of evaporite precipitation are known in the Mississippian of Ireland, England, Scotland, and Belgium (West et al., 1968; Delmer, 1988; Millward et al., 2018). Nevertheless, the evaporite-rich character of the Windsor Group, likely in part, explains the strongest faunal differences in the lower part of the succession, irrespective of whether it is early Visean or middle Visean.

The resulting data are more controversial, perhaps, in part, arising from the paucity of the eastern Canadian assemblages. The most widely supported hypothesis is that direct communication between the Maritimes Basin and Ireland/Britain is not obviously supported by statistical analyses, but rather suggests a stronger similarity and closer geographic proximity with Gondwana and the terranes in the Variscan Front. This implies that although individual species might imply an artificially closer paleobiogeographic relationship between the Maritimes Basin and Ireland/Britain, the whole assemblage is more representative of Gondwana. Certainly, lateral migration through the Rheic Ocean platforms is more easily envisaged, and the migration of *Albertaporella* from the North American Realm to the south of Ireland during the early Visean confirms a still-open Rheic Ocean. During the late Visean-early Serpukhovian, the migration of many similar species of foraminifers, conodonts, rugose corals, and gigantoproductid brachiopods to the Appalachians confirms that that communication still existed.

In some paleogeographic models (e.g., Stampfli et al., 2013), this communication between the Maritimes Basin and Britain could be also possible via the Rheohercynian Ocean, which was open during the Mississippian (Fig. 7). A rather similar position of the terranes and continents can be observed in the reconstructions by Blakey (2008, fig. 10C), with the Sahara and the Reguibat promontory in front of the Maritimes Basin, although in this reconstruction the Rheohercynian Ocean was

not connected. Tectonic and sedimentological models promote comparison of the Maritimes Basin with those in Ireland and Britain (e.g., Waldron et al., 2018), and it is automatically assumed that the biological influence of those northern regions is inherited. However, alternative scenarios might need to be considered in which the benthic biota arrived in the Maritimes Basin by crossing the Paleotethys Ocean from more southerly positions near the Gondwana coast, or from the northwestern terranes across a still-open Rheic Ocean (Fig. 7). This would suggest narrower oceans in this region for the late Visean-early Serpukhovian period. Indirectly, for this communication with the Paleotethys Ocean to occur, it is envisaged that the Moroccan Meseta was not attached to Gondwana during the Visean (Fig. 6), a fact described only for the early to mid-Visean (Cózar et al., 2020), whereas for the late Visean-early Serpukhovian interval, it is not yet clearly defined. However, if the Meseta was attached to Gondwana, this would imply higher similarity indices between the Meseta and the Maritimes Basin than with Gondwana, which is not the case. The occurrence of Saharan assemblages in the Maritimes Basin suggests that the annexation of the Moroccan Meseta to Gondwana had not happened during the late Visean and early Serpukhovian.

Paleobiogeographic models are, in general, in disagreement with the paleogeographic models based on tectonics, magmatism, or paleomagnetism. For the last, there is a predominance of models that suggest that the closure of the Rheic Ocean occurred during the Devonian, with no connection between the Rheic and Paleotethys oceans (e.g., Kroner and von Romer, 2013; Stampfli et al., 2013; Scotese, 2015), whereas another group of authors considered that the gateway between the two oceans existed until the Permian (Vai, 2003; Walsh et al., 2007; Domeier et al., 2012). Rarely, some authors have highlighted the importance of fossil groups for these paleogeographic reconstructions for the Carboniferous (e.g., Cocks and Torsvik, 2011). Related to this aspect, ammonoids, rugose corals, brachiopods, and foraminifers do not show synchronicity in the timing of the closure of the Rheic-Paleotethys gateway, ranging from the mid-Visean, late Visean, early Serpukhovian, and late Serpukhovian, respectively, but clearly, all are later than the Devonian (Korn et al., 2012; Aretz et al., 2013; Quiao and Shen, 2014, 2015; Davydov and Cózar, 2019). The fauna and flora of the upper cycles of the Maritimes Basin (cycles 2–5), with strong similarities with the Paleotethys realm, confirm good communication at least until the early Serpukhovian (or a younger age for the Windsor-Codroy groups; von Bitter et al., 2007). Anomalous impoverished Visean assemblages in the Maritimes Basin suggest at least intermittent communication with the North America Realm during the same period. Species in common between the Paleotethyan and the North American realms during the Visean/Serpukhovian confirm communication through the Maritimes Basin. Marine communication of the Paleotethys and North American realms through the Maritimes Basin ceased very near the beginning of the Serpukhovian with the termination of any open marine deposition that might have supported even impoverished marine faunas. This stratigraphic break is marked by the top of the Windsor and Codroy groups, assigned a latest Visean to earliest Serpukhovian age by von Bitter et al. (2007). In the Maritimes Basin, miospores recorded a major paleoenvironmental crisis in the Arnsbergian

(late Serpukhovian) (Utting, 1987; Utting and Giles, 2008; Jutras et al., 2015), a period associated with glacial episodes, shifts in carbon and oxygen isotopic data, and a global-scale late Paleozoic sea-level fall (Isbell et al., 2003; Grossman et al., 2008; Haq and Schutter, 2008; Mory et al., 2008; Gulbranson et al., 2010; Stephenson et al., 2010; Barham et al., 2012; Giles, 2012; Davydov, 2014). These facts coincide with the ultimate closure of the Rheic-Paleotethys gateway, and thus, the formation of the so-called Alleghenian Isthmus, interpreted to have occurred during the late Serpukhovian (Davydov and C  zar, 2019). Before the early Serpukhovian cessation of marine communication, and well before the onset of severe and extensive glaciations of the Pennsylvanian during the coldest times of the Paleozoic (Giles, 2012), marine connections through the Maritimes Basin were at best intermittent and short-lived (Giles, 2009) and limited to short episodes of glacioeustatic marine transgression. Until marine communication ceased, the biota of the Maritimes Basin reflects multiple sources with intermittent linkages to all of our studied regions.

Conclusions

Analyzing the foraminiferal taxa in the Maritimes Basin, several genera and species typically represented in the Paleotethys realm can be recognized, contrasting with previous studies that the Maritimes Basin lacked typical Paleotethyan genera and species. Typical North American fauna/flora are negligible or absent, and apparent similarities are based on the absence of typical Paleotethyan genera and species. Low diversity has been argued by some as a feature typical of the Maritimes Basin, although it could be simply a result of less-detailed paleontological works or the predominance of hostile facies.

The Maritimes Basin has been compared with basins in Laurussia, in particular Ireland and England. The influence of the Laurussian margin is supported by the occurrence of some species of brachiopods, miospores, and foraminifers, with dispersal via the Rhenohercynian Ocean. However, multivariate analysis of the marine benthic microfossils confirms that although the assemblages are of Paleotethyan affinities, they are closer to assemblages in the Gondwana platform and terranes of the Variscan Front (Moroccan Meseta/SW Spain). Owing to the relative position of the terranes between the Laurussia and Gondwana continents, we suggest that migration of the biota occurred not only via the incipient Paleotethys Ocean, but also by a still-open Rheic Ocean, with additional influence of the Rhenohercynian Ocean. Our assessment indicates multiple sources for the biota of the Maritimes Basin. Paleogeographic models that located the Maritimes Basin opposite the North African coast would fit better in the observed paleobiogeographic relationships.

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