Palaeogeography, Palaeoclimatology, Palaeoecology 383–384 (2013) 79–91

Contents lists available at SciVerse ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Palaeoecology of Devonian sclerobionts and their brachiopod hosts from the Western Canadian Sedimentary Basin

Kristina M. Barclay *, Chris L. Schneider, Lindsey R. Leighton

University of Alberta, Earth and Atmospheric Sciences Department, Edmonton, Alberta T6G 2E3, Canada

ARTICLE INFO

Article history:
Received 26 January 2013
Received in revised form 3 May 2013
Accepted 7 May 2013
Available online 15 May 2013

Keywords:
Devonian
Givetian
Frasnian
Palaeoecology
Brachiopoda
Skeletobionts
Host
Western Canadian Sedimentary Basin
Assemblages

ABSTRACT

The majority of the studies on Devonian epibiosis are limited to those encrusting one, or only a limited number of host taxa. We present not only the first detailed study of sclerobionts and brachiopod hosts from the Devonian of the Western Canadian Sedimentary Basin, but we also examine entire assemblages of potential brachiopod hosts for sclerobionts. Over 1280 brachiopods were collected from the lower Firebag Member of the Waterways Formation (Late Givetian) in northeastern Alberta, and both the lower Hay River and upper Twin Falls Formations (Frasnian) of the southern Northwest Territories. The three units do not represent a continuous sequence, but represent three successive intervals in the history of the basin. Brachiopods were identified to genus level and examined for sclerobionts. Sclerobionts were identified to the lowest taxonomic level possible (usually genus).

Data analyses were subdivided into three categories: (1) comparison of host assemblages, (2) comparison of sclerobiont assemblages, and (3) interactions between host and sclerobiont assemblages. Brachiopod assemblages increased in richness, evenness, and diversity across the three units, which corresponds to a decrease in terrigenous mud observed between the lithology of the lower Firebag and Hay River assemblages, and the younger Twin Falls assemblage. *Desquamatia* was the most abundant brachiopod collected from all three stratigraphic units. Sclerobiont assemblages experienced similar trends to the host assemblages, with an increase in evenness and diversity across each assemblage. Richness remained less varied between sclerobiont assemblages, with only one new taxon appearing in the latest stratigraphic unit (upper Twin Falls Formation). However, because sclerobionts and their hosts operate on such different spatial scales, changes experienced by the hosts may not have affected sclerobionts in the same manner and therefore should not be interpreted as such.

Interactions between host and sclerobionts were examined for: (1) sclerobiont preference for host size, (2) sclerobiont preference for host taxa, and (3) sclerobiont preference for host valve. While there was increased encrustation of larger hosts in all assemblages, the brachiopod, *Desquamatia*, was most encrusted by sclerobionts, regardless of size, in the younger Twin Falls Formation. Preferences by sclerobionts for particular valves differ between the host assemblages, even among the same host taxa. These results suggest that (a) the inclusion of all possible brachiopod hosts from a given assemblage greatly improves the understanding of sclerobiont–host relationships, and (b) encrustation patterns, even on the same host taxa, do not always remain static between assemblages.

1. Introduction

Encrusting organisms that attach to biotic hosts offer unique insights into organism interactions that would otherwise not normally be preserved in the fossil record. This is due to the in situ preservation of encrusting organisms on the hard surfaces of their hosts that may even record detailed interactions such as succession between different encrusting organisms on one host (Alvarez and Taylor, 1987; Taylor and Wilson, 2003; Rodland et al., 2004), synchronous growth of encrusting organisms and their host (Alvarez and Taylor, 1987; Bose et al., 2011), and evidence that the host was alive or dead during the time of encrustation (Schneider, 2003; Taylor and Wilson, 2003; Bose et al., 2011). As well, encrusting organisms will often show apparent "preferences" for a particular substrate, or location on a substrate.

This study focuses on the comparisons of three assemblages of Devonian brachiopods from the Western Canadian Sedimentary Basin and their interactions with encrusting organisms. Encrusting organisms are those that must attach to a hard or firm substrate, whether biotic or abiotic. Therefore, these organisms are found to occur more commonly on biotic hosts when in environments with greater accumulations of soft sediments on which the only hard

* Corresponding author at: 1-26 Earth Science Building, University of Alberta, Edmonton, Alberta T6G 2E3, Canada. Tel.: +1 780 492 3983; fax: +1 780 492 2030.
E-mail address: kbarclay@ualberta.ca (K.M. Barclay).

0031-0182/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.palaeo.2013.05.007

substrate is often the shells of larger organisms such as brachiopods (Taylor and Wilson, 2003; Rodland et al., 2006; Bose et al., 2011; Brett et al., 2011, 2012). In this study, we will follow the terminology proposed by Taylor and Wilson (2002), and shall refer to encrusting organisms that attach to, or bore into, any hard substrate (in this case, brachiopods) as "sclerobionts". Biotic substrates, regardless of whether organisms were alive or dead at the time of encrustation, are referred to herein as "hosts".

Fossil sclerobiont–host relationships provide information on palaeoecological phenomena, such as sclerobiont preference of hosts, sclerobiont preference for location on a host, sclerobiont competition, and even anti-predatory benefits of sclerobionts to the host organism (Kesling et al., 1980; Alvarez and Taylor, 1987; Bordeaux and Brett, 1990; Lescinsky, 1996; Taylor and Wilson, 2003; Rodland et al., 2004, 2006; Bose et al., 2011). One of the most well studied sclerobiont–host systems is that between brachiopod hosts and their sclerobionts (e.g. Alvarez and Taylor, 1987; Bose et al., 2011). Most studies that examine sclerobiont communities involve either a single host taxon or single sclerobiont taxon (e.g. Alvarez and Taylor, 1987; Rodland et al., 2006; Bose et al., 2011; Zatoń and Krawczyński, 2011), yet examining an entire assemblage of hosts *and* sclerobionts may provide a more complete representation of the original fossil community (e.g. Rodland et al., 2004). By examining three entire assemblages of brachiopod hosts and their sclerobionts, we aim not only to provide a more accurate, quantitative representation of the patterns present in these original fossil communities, but also to compare these patterns between assemblages across the Late Givetian to Early Frasnian of the Western Canadian Sedimentary Basin (a region whose sclerobiont communities have never been examined thoroughly). Comparison of three entire assemblages of brachiopods will illuminate any changes in encrustation habits through time and also will test for the generality of encrustation patterns within one extensive basin.

Sclerobionts on Devonian brachiopod hosts have been extensively studied, mostly due to the high rates of encrustation during this time period compared to the rest of the Palaeozoic Era (Alvarez and Taylor, 1987; Taylor and Wilson, 2003; Brett et al., 2012). Despite this large amount of literature on Devonian host–sclerobiont interactions, encrusting communities from the Devonian of the Western Canadian Sedimentary Basin have received little attention. The only previous works on sclerobionts from Western Canada are fossil lists that include the encrusting taxa *Aulopora* and *Microconchus* (listed as *Spirorbis*) from Givetian and Frasnian brachiopods from northeastern Alberta (Crickmay, 1957; Norris, 1963), and a pilot study of sclerobionts on brachiopod hosts (Schneider and Leighton, 2010). In contrast, brachiopods from the Givetian and Frasnian of Western Canada have been well documented (Norris, 1965; Johnson, 1974, 1975; Day, 1998; Day and Copper, 1998; Ma and Day, 2000). This study not only provides further documentation of sclerobiont–brachiopod assemblages from the Devonian of the Western Canadian Sedimentary Basin, but is also one of the few Devonian studies to examine complete assemblages of both hosts *and* sclerobionts.

2. Geology

During the Late Givetian and Early Frasnian, Western Canada was part of a passive margin covered by a shallow sea, although an offshore, active island arc has been suggested (Moore, 1988). During the time interval studied, the Western Canadian Sedimentary Basin lay in the tropics (Witzke and Heckel, 1988) (Fig. 1). The climate was humid (Loranger, 1965; Witzke and Heckel, 1988), and the resulting rainfall, combined with the uplift and erosion of an orogen to the present-day northeast, most likely from the Ellesmerian Fold Belt (Stoakes et al., 1992; Wendte, 1992), or the Caledonian or Franklinian orogenic belts (Moore, 1988; Wendte and Uyeno, 2005), led to a significant amount of terrigenous sediment in the basin (Wendte and Uyeno, 2005). The influx of terrigenous mud into the basin from this erosion of orogens to the northeast was sufficient to overprint the general rise in sea-level with the regressive, argillaceous sequences of the Waterways Formation (Schneider et al., in press). By the time of deposition of the youngest unit in this study, the Twin Falls Formation (Frasnian) (Fig. 2), the Western Canadian Sedimentary Basin had separated into distinct carbonate shelves with argillaceous infill of the deeper, central basin (Switzer et al., 1994).

The oldest unit of interest in this study is the Firebag Member from the base of the Waterways Formation (Fig. 2), corresponding with transgressive–regressive (T–R) cycle IIb and the *Skeletognathus norrisi* conodont zone (Johnson et al., 1985; Day, 1998). The Firebag Member contains a lower shale and an upper shale separated by a middle argillaceous limestone. The middle limestone is an argillaceous mudstone to wackestone with few fossils. Both shales are generally not fossiliferous except for distinct horizons of fossils. Brachiopod samples for this study were collected from an approximately 20 cm-thick fossiliferous interval at the increasingly calcareous transition between the top of the lower shale and the base of the middle argillaceous limestone. Fossils were collected loose from a weathered surface.

A second brachiopod assemblage was collected from member B of the Hay River Formation (Montagne Noire conodont zone 6) (Fig. 2), which marks the beginning of T–R cycle IIc (Day, 1998). Nomenclature and stratigraphic correlation of the Hay River Formation varies among authors (Jamieson, 1967; Hadley and Jones, 1990; MacNeil and Jones, 2006; Energy Resources Conservation Board, 2009). The present study follows the nomenclature and stratigraphy recognised in the Energy Resources Conservation Board (2009) Table of Formations for the Hay River Formation, and the members established by Jamieson (1967), and used in Day (1998), which splits the Hay River Formation into informal members A through F (Fig. 2). The Hay River Formation consists of approximately 400 m of shale with thin, laterally traceable limestone units (Williams, 1977). Fossils are usually associated with the limestone units. Some of the limestone beds, notably in a limestone in member C, are biostromal and contain corals and stromatoporoids. Member B is mostly shale that contains an argillaceous limestone bed, locally a floatstone to rudstone. Fossils were collected loose from a shale horizon immediately below the base of this member B limestone.

The third brachiopod sample was collected from the upper member of the Twin Falls Formation (Fig. 2), which corresponds with T–R cycle IId-1 and the Montagne Noire conodont zone 9 (Day, 1998). T–R cycle IId marks a sea-level high for the Devonian (Johnson et al., 1985; Day, 1998). Nomenclature also varies between authors, with MacNeil and Jones (2006) splitting the lower Alexandra Member into a distinct formation. The present study uses the nomenclature of the Energy Resources Conservation Board (2009) Table of Formations for the Twin Falls Formation with the higher-resolution stratigraphy suggested by Day (1998), which separates the Twin Falls Formation into two members: the Alexandra Member in the lower portion and an informal upper member. The upper member is an open marine, non-argillaceous limestone. The fossils collected for this study had weathered loose from the surrounding gravel of spill piles (less than one metre thick).

Near the Alberta–Northwest Territories border, the Waterways Formation is contiguous and thus, stratigraphically equivalent to the lower Hay River Formation, the latter extending further north into the Northwest Territories. In Alberta, the Waterways Formation is an argillaceous limestone and shale with occasional, non-argillaceous biostromal and carbonate sand facies (Loranger, 1965; Buschkuehle, 2003). The Hay River Formation in northern Alberta and the southern Northwest Territories is mostly shale, with a few laterally extensive limestone beds. Although the members of the Waterways and Hay River formations have not been correlated, the Hay River Formation contains equivalents of the Waterways through Ireton Formations (Fig. 2). Reefs from the Alexandra Member of the Twin Falls Formation of the southern Northwest Territories are equivalent to the reefs of the Grosmont Formation