PALEOECOLOGY AND SEDIMENTOLOGY OF THE *PRASOPORA* ZONULE IN THE DUNLEITH FORMATION (ORDOVICIAN), UPPER MISSISSIPPI VALLEY

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ABSTRACT
The dome-shaped bryozoan Prasopora *and its accompanying fauna display distinct distributional patterns in Middle to Late Ordovician epeiric sea deposits of the Galena Group in the Upper Mississippi Valley. These rocks consist of interbedded carbonates and siliciclastics, and* Prasopora *is abundant in some intervals, but absent in others.* Prasopora *is most abundant in the widely recognized* Prasopora *zonule in the Dunleith Formation of the Galena Group.*

We studied the Prasopora *zonule and surrounding beds at an outcrop south of Guttenberg, Iowa. Point counts showed distinct vertical changes in faunal composition and sedimentology. Where* Prasopora *abundance is high, so is that of other bryozoans, but brachiopod abundance is low. Carbonate mud content is lowest where* Prasopora *and other bryozoans dominate and highest where brachiopods dominate. We considered taphonomic, ecological, and environmental explanations for these faunal and sediment distribution patterns. Statistical analyses of fossil-size differences among the units studied did not show evidence of taphonomic sorting due to storm currents. At Guttenberg, brachiopod and bryozoan abundances appear to be associated with the change in carbonate mud content at the onset of the zonule as well as the zonule's position at the transition from a shallowing-upward cycle to the beginnings of a transgressive systems tract.*

INTRODUCTION
Rock layers rich in the bryozoan genus *Prasopora* are found sporadically within the Galena Group (Ordovician, Trentonian Stage) of the upper Midwestern United States, including much of southern and central Wisconsin (fig. 1). *Prasopora* is particularly abundant in one interval in the Dunleith Formation of the Galena Group. Although this "*Prasopora* zonule" has been widely recognized (Kay, 1929; Sloan, 1956; Rose, 1967; Levorson and Gerk, 1972–1973; Willman and Kolata, 1978; Delgado, 1983), controls on the abundance of *Prasopora* in the Galena Group have not been investigated previously. The purpose of our study was to determine controls on *Prasopora* concentration through consideration of sedimentology, paleoecology, and taphonomy.

GEOLOGIC SETTING
Galena Group
Stratigraphic nomenclature for Trentonian Stage deposits varies slightly among states of the Upper Midwest. Herein we employ the group, formation, and member names of Levorson and others (1987) still commonly used in Iowa. According to that system, the Galena Group contains the Spechts Ferry, Guttenberg, Dunleith, Wise Lake, and Dubuque Formations (fig. 1). The Galena Group extends through parts of Iowa, Minnesota, Illinois, and much of southern Wisconsin. Most of the beds in Wisconsin, however, are heavily dolomitized because post-depositional phreatic water influence was greater toward the Wisconsin Arch. Therefore, we have chosen an undolomitized outcrop containing well preserved fossils in northeastern Iowa for the focus of this study. Because of regional horizontal continuity of strata, we assume that conclusions about the *Prasopora* zonule in Iowa hold true for that of Wisconsin.

The sedimentology, biota, and geometry of Galena Group rocks are typical of the storm-swept interior seaway that characterized the upper Midwest during the Middle and Late Ordovician. Episodic storm-event indicators include bioclastic grainstones that pinch and swell laterally; some show graded bed-

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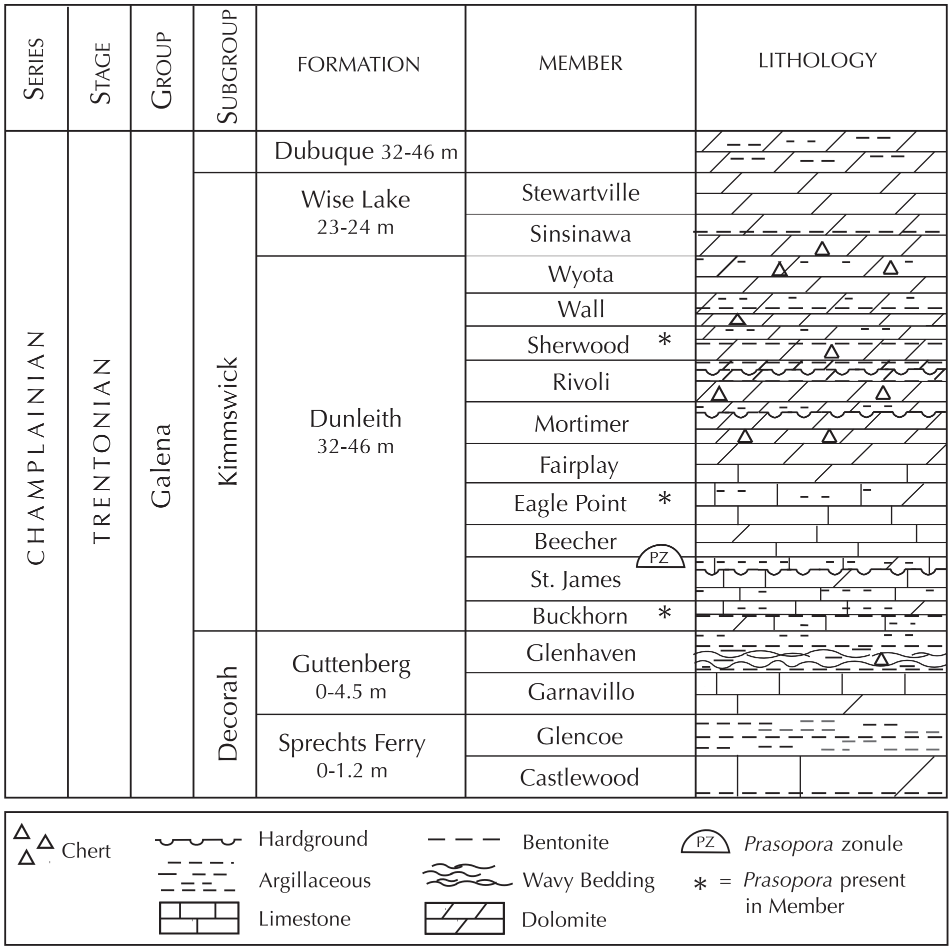

Figure 1. *Stratigraphic column of the Galena Group (after Levorson and others, 1987). The* Prasopora *zonule is at the St. James–Beecher Member contact. Other* Prasopora*-bearing beds are marked. Hardgrounds are common throughout the Galena Group; the most prominent ones are indicated here.*

ding, although it is commonly obscured as a result of bioturbation. Rocks of the Galena Group are made up of partially to completely dolomitized carbonate mud and fossil debris. Small amounts of terrigenous silt are present, probably derived from the Transcontinental Arch to the northwest (Willman and Kolata, 1978). Several bentonite layers derived from volcanoes of the Taconic Uplands have been documented (Kolata and others, 1986). A striking feature of Galena Group stratigraphy is the presence of numerous hardgrounds (previously termed corrosion zones), which represent depositional hiatuses and intervals of submarine cementation (Delgado, 1983). Early diagenetic processes of the Galena Group strata include submarine dissolution of aragonite, submarine cementation forming numerous hardgrounds and nodules, and some submarine dolomitization within filled burrows (Delgado, 1983). Later diagenetic processes include silicification of biotics, formation of chert nodules, dolomite mottling, and regional dolomitization, which is more prevalent in outcrops east of the Mississippi River. The regional post-depositional, mesogenetic dolomitization probably resulted from the mixing of fresh and marine phreatic water during the worldwide eustatic drawdown at the end of the Ordovician Period (Delgado, 1983). The Wisconsin Arch was exposed and receiving freshwater recharge at this time, which explains why the dolomitization is more prevalent eastward toward the arch (Delgado, 1983).

A lack of shoreline or nonmarine sedimentary features, in conjunction with the broad, laterally continuous sedimentary units within the Galena Group, suggests that deposition occurred on an extensive platform or ramp. Indicators of intertidal or supratidal environments are absent; no stromatolites, mudcracks, hummocky cross-bedding, or fenestral porosities have been observed. Modern day analogues for the Galena platform include the cool water Lacepede shelf off Australia (James, 1990) and the Bahama Bank (Kolata, 1975; Arens and Cuffey, 1989).

The fossils of the Galena Group consist mainly of benthic biota, including brachiopods, crinoids, gastropods, and bryozoans.

Prasopora

Prasopora colonies are distinct among Galena Group fossils because of their relatively large, domal form (fig. 2). The hemispheres of the colonies are generally 2 to 4 cm in diameter and contain thin-walled, elongate zooecial tubes with widely spaced diaphragms and intervening special support structures (mesopores and acanthopores; Bassler, 1953; Cuffey, 1997). *Prasopora* belongs to the class Stenolaemata, the dominant bryozoan class of the Ordovician (McKinney and Jackson, 1989). *Prasopora*-bearing strata in eastern North America have been the subject of several previous investigations (Sparling, 1964; Arens and Cuffey, 1989; Cuffey, 1997).

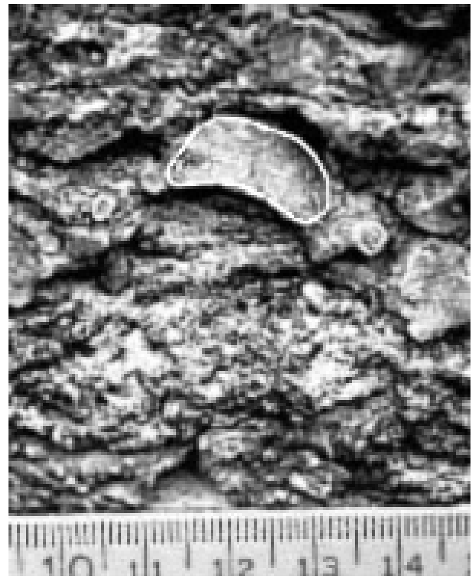

Figure 2. *A colony of the bryozoan* Prasopora *(approximately 2.5 cm wide) is indicated by a white outline in this photograph taken at the outcrop. Scale bars are in millimeters.*

Prasopora zonule

Centimeter-scale concentrations of *Prasopora* have been recognized in the Decorah Subgroup and in the Buckhorn, St. James, Beecher, Eagle Point, and Sherwood Members of the Dunleith Formation (Sloan, 1956, 1987; Delgado, 1983; Kolata, 1987; Levorson and others, 1987). The most impressive concentration of *Prasopora* is a particular zonule around the St. James–Beecher Member boundary (fig. 1). This zonule is visible in outcrops throughout the Upper Mississippi Valley, even in regions where dolomitization is pervasive. The approximately 45 cm thick *Prasopora* zonule is predominantly carbonate with shale partings, similar to that of other Galena Group sediments.

We studied a locality south of Guttenberg, Iowa (fig. 3), where the Galena Group strata are especially well exposed. We divided the lower Beecher and upper St. James Members into six units (A–F) on the basis of lithology and fossil content (figs. 4 and 5; Sanders, 1996). Units A and B lie within the upper St. James Member, below the *Prasopora* zonule. A prominent bedding plane between them marks the change from the less resistant unit A to more resistant unit B. Unit B is distinguished from unit A by having less carbonate mud. The *Prasopora* zonule comprises three distinct units (C, D, and E). Units C and D are within the St. James Member and unit E is in the Beecher Member. A prominent hardground lies at the base of the lowest unit of the zonule, unit C. This 12.5 cm thick unit (and the non-zonule subjacent unit B) consists of a calcareous packstone with grainstone-rudstones pinching and swelling laterally. Unit D above, approximately 9 cm thick, is a thinly bedded, fissile packstone. The top of this fissile unit marks the St. James–Beecher contact. The third and topmost unit of the *Prasopora* zonule (unit E) is a poorly stratified wackestone, approximately 23 cm thick, at the base of the Beecher Member. Above the zonule is unit F, a resistant carbonate separated from the zonule by a distinctive, non-scoured hardground surface.

MATERIALS AND METHODS

We obtained lithologic and faunal composition data by point counting sediment grains and fossils in thin sections and polished slabs (table 1; fig. 6). We measured the sizes of fossil fragments to determine the extent of breakage indicating taphonomic reworking in each layer (table 2; fig. 7). The longest axis of each fossil grain in thin section was measured using a digital image processor. Also, the extent of burrowing, abrasion, and the position relative to life-position of fossil bodies was examined.

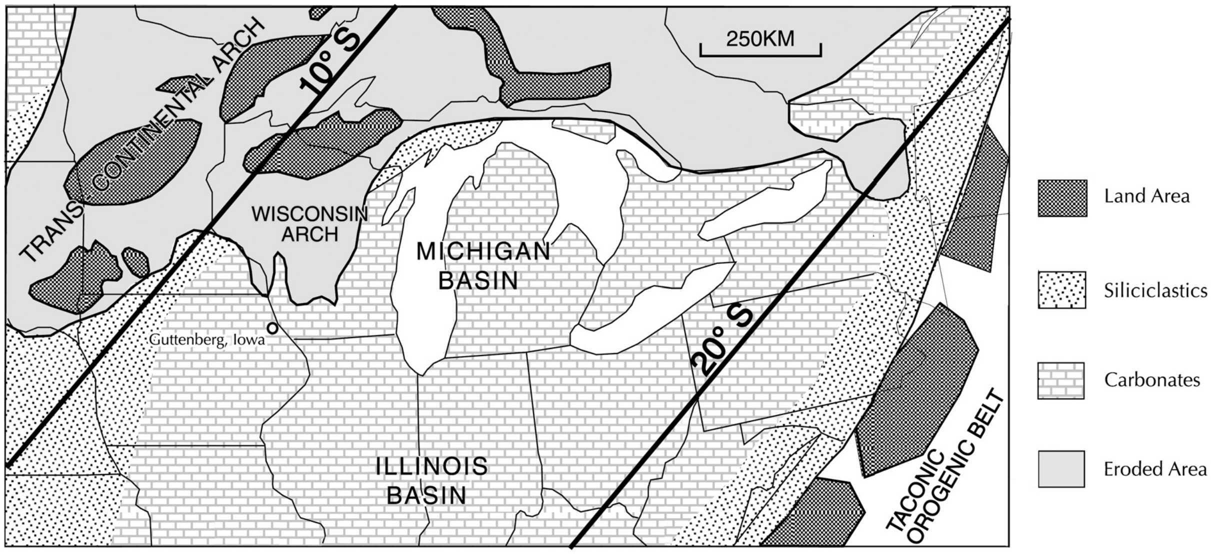

Figure 3. *Map indicating the interpreted paleogeography of the study region (compiled from Witzke, 1980 and Choi, 1995). Structural highs (the Transcontinental and Wisconsin Arches) and basins (Illinois and Michigan) are indicated along with paleolatitudes. Guttenberg, Iowa, is indicated. The outcrop discussed in this paper is a roadcut on the west side of Iowa State Highway 52, 0.5 km south of Guttenberg.*

We took lithologic point counts from thin sections viewed with a petrographic microscope (1.5x) connected to a video screen. Each centimeter on the screen represented 1.0 mm on the thin section. One 2.5 by 5 cm thin section was used for every 5 cm of vertical thickness of outcrop section. A grid divided into 20 points placed 5 cm apart was overlaid on the image. The lithology under each point on the grid was placed into one of these categories: mud (mud-sized particles that appeared to be carbonate in composition), dolomite crystals, fossils, calcite cement crystals, silt, and other. ("Other" refers to trace elements and unidentified grains.)

Faunal frequency measurements come from polished slabs viewed under a dissecting microscope (1.5x). A 4 cm^2 frame was moved across the slab at regular intervals. At each interval, the fossils that fell within the square were classified into the following categories: brachiopod, non-prasoporan bryozoan, *Prasopora,* or other. (The faunal category "other" refers to the fossils that had such low abundances that their counts were insignificant: trilobites, gastropods, crinoids, and bivalves.) If a fossil spanned two squares, it was counted only once. *Prasopora* colonies were considerably larger than other fossils, so their relative frequencies appeared low even where they are highly visible in outcrop.

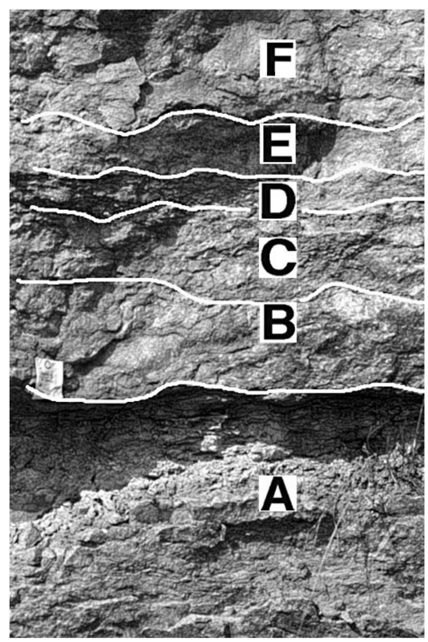

Figure 4. *Photograph of units A–F taken at the Guttenberg outcrop.*

RESULTS

Most of the fossils of units A–F were fragmented and did not appear to be in life position. *Prasopora* colonies were nearly whole and only slightly abraded. They were not in life position and exhibited no preferred orientation. Physical and biological reworking obscured the nature of the attachment surface of *Prasopora* and other invertebrates.

The faunal and lithological distributions in units A–F are shown in table 1 and figure 6. Of the points counted from unit A, 39 percent were carbonate mud. Unit A has the highest proportion of carbonate mud of any unit as well as a large proportion of brachiopods (76%) and a relatively small proportion (17%) of non-prasoporan bryozoans (fig. 6; table 1). Unit B, which lies directly below the zonule, is like unit A in that it is relatively high in the percentage of brachiopods (77%) and low in the percentage (18%) of non-prasoporan bryozoans (fig. 6; table 1). In addition to the presence of a prominent (conformable) bedding plane between the two units (figs. 2 and 3), unit B is distinguished from unit A by having less carbonate mud (fig. 6; table 1). Unit C, the lowermost *Prasopora* zonule unit, marks the shift from brachiopod-dominated to bryozoan-dominated fauna and also shows a drop in mud content. The bar graph in figure 6 demonstrates the large increase in non-prasoporan bryozoans in unit C (up 30% from unit B). At this point there is also a drop in brachiopod percentage (from 77% to 39%). Unit C also has the lowest percentage of carbonate mud (20%) of all units (fig. 6; table 1). A Z-test on the distribution of mud percentages in units A–C shows that unit C's mud content falls outside the 94 percent confidence interval (Z = 1.558). This is the only unit in which mud content is significantly lower. Above this initial unit of the zonule, mud levels rise again (27%, 33%, and 30% in units D, E, and F, respectively). The highest proportion of *Prasopora* (10%) is in unit D, a fissile layer, composed mainly of dolomite and fossils (fig. 6; table 1). Unit E is in the topmost *Prasopora* zonule unit. The carbonate mud content is 6 percent higher than that of unit D. In the Beecher Member above the zonule, unit F has the lowest percentage of fossils (21%) overall, but a high-

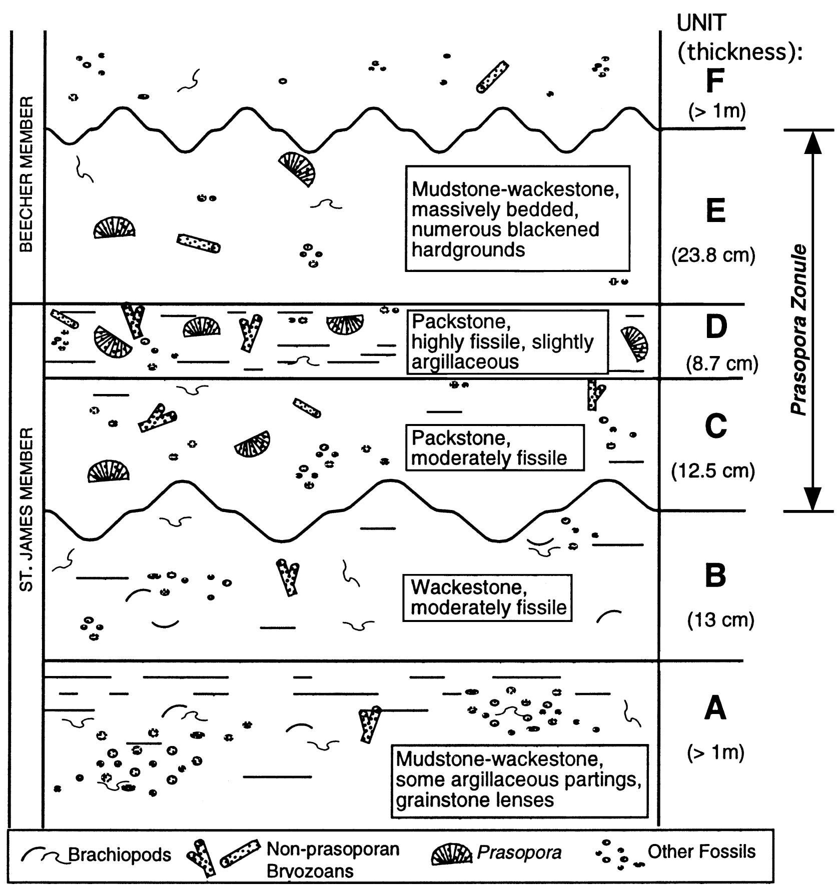

Figure 5. *Cartoon of units A–F, Guttenberg outcrop. Lithologies are indicated in boxes. The zonule is bounded by two prominent hardgrounds, indicated by the wavy contact lines.* Prasopora *fossils are most abundant in unit D, the thin, fissile layer. The other two zonule units are more massively carbonate, similar to the rest of the Beecher Member. Unit C contains grainstone lenses.*

Table 1. Point count data (n = number of points; percent = percent within unit). Refer to figure 6 for graph.

Faunal Distribution

	Brachiopods		Non-prasop. bryoz.		*Prasopora*		Other	
Unit	**n**	**percent**	**n**	**percent**	**n**	**percent**	**n**	**percent**
A	290	76	65	17	1	~0	28	7
B	430	77	102	18	2	~0	25	5
C	130	39	162	48	25	8	18	5
D	67	47	45	32	14	10	15	11
E	135	45	109	37	16	5	37	13
F	90	57	37	23	3	2	28	18

Lithologic Distribution

	Mud		Dolomite		Fossils		Calcite		Silt		Other	
Unit	**n**	**percent**	**n**	**percent**	**n**	**percent**	**n**	**percent**	**n**	**percent**	**n**	**percent**
A	2109	39	1790	33	1175	22	138	3	184	3	4	~0
B	1283	30	1659	38	1112	26	133	3	117	3	4	~0
C	488	20	1002	41	762	32	41	2	124	5	0	~0
D	990	27	1128	31	1131	31	199	6	170	5	8	~0
E	1015	33	251	8	936	30	883	28	25	1	10	~0
F	2500	30	3456	42	1720	21	604	7	27	~0	9	~0

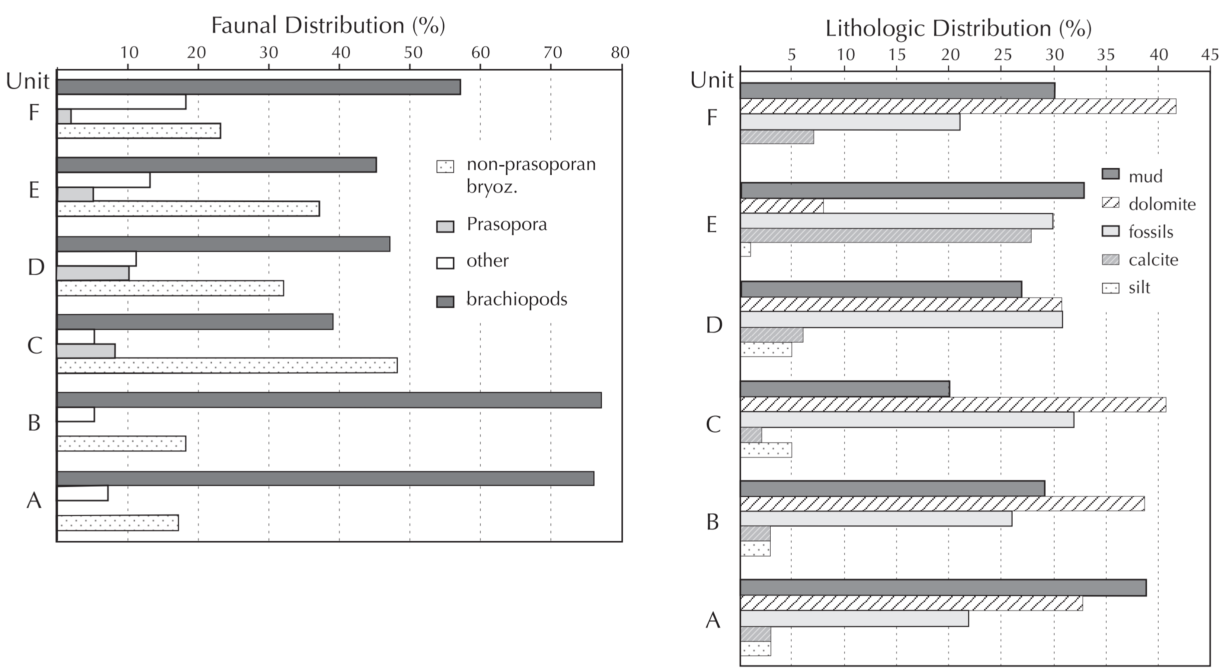

Figure 6. *Percentages of faunal and lithological types within each unit, Guttenberg outcrop. See table 1 for point count data; refer to text for point-counting methods.*

er proportion of other fossils (18%; fig. 6; table 1).

To test for consistent differences among units in the size of fossil fragments, we performed a Kolmogorov–Smirnov test on brachiopod and non-prasoporan bryozoan size data (Sokal and Rohlf, 1981). These analyses indicated that the size of fossils inside versus outside of the zonule is not significantly different (p [the Kolmogorov–Smirnov probability statistic] = 0.730 for brachiopods; p = 0.383 for non-prasoporan bryozoans). For 726 brachiopods, mean sizes were

Table 2. Size of fossils, Guttenberg outcrop, in millimeters. s = standard deviation, n = number of points. Refer to figure 7 for graph.

	Brachiopods			Non-prasoporan bryozoans			*Prasopora*			Other		
Unit	mean	s	n	mean	s	n	mean	s	n	mean	s	n
A	115.0	116.0	193	169.7	89.9	12	—	—	0	66.4	52.7	51
B	144.5	120.3	150	188.7	115.6	13	228.0	0.0	1	95.1	50.2	37
C	91.0	83.0	211	240.2	158.8	58	426.2	121.2	11	104.1	95.0	25
D	157.0	122.9	122	227.1	122.4	31	91.5	31.8	2	66.2	37.8	51
E	189.9	102.1	23	234.6	184.1	13	160.0	84.9	2	113.4	80.3	14
F	66.3	57.3	247	234.6	160.1	9	328.0	0.0	1	58.7	52.2	93

1.41 mm (s [standard deviation] = 1.33) outside the zonule and 1.36 mm (s = 1.20) in the zonule. For 154 non-prasoporan bryozoans, mean sizes were 2.33 mm (s = 1.38) outside the zonule and 2.72 mm (s = 1.68) inside the zonule.

Brachiopod fragment sizes coarsen upward from zonule layer C to zonule layer E and from non-zonule unit A to non-zonule unit B (fig. 7, table 2). Average sizes of non-prasoporan bryozoan fragments exhibit no such trends within or outside of zonule layers, but fluctuate erratically upward (fig. 7; table 2).

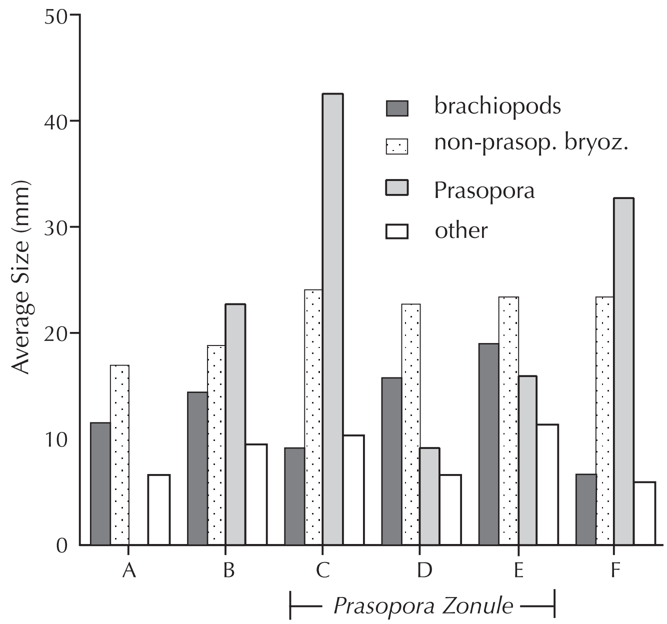

Figure 7. *Size of fossils, Guttenberg outcrop. The longest axis of each fossil grain in thin section was measured using a digital image processor. See table 2 for size measurements.*

DISCUSSION

The most striking feature of the faunal data is the inverse relationship between the abundances of brachiopods and bryozoans (including *Prasopora* and other bryozoans). The most prominent feature of the lithologic data is the decrease in mud content from unit B to unit C at the base of the *Prasopora* zonule. This coincides with a decrease in brachiopods and an increase in bryozoans. To shed light on these observations, we considered a variety of sedimentologic, taphonomic, and paleoecologic factors.

Rock type does not change much from unit to unit. All units are calcareous with small amounts of silt and argillaceous material. Bioturbation obscures other sedimentary structures. Dolomitization is variable (for instance, unit E is mostly undolomitized), but does not appear to be related to the presence or absence of the zonule in the units. Sedimentary texture varies among units (units C and D are packstone and the rest are mudstone–wackestone). Particularly noticeable is the decrease in proportion of finer-grained sediments at the base of the zonule; a shift back to higher proportions of fine sediment is evident upward and out of the zonule. This variation in sedimentary texture likely represents a change in paleoenvironment (substrate or environmental energy).

We considered hydraulic sorting as a taphonomic explanation for the observed faunal patterns. Alternating environmental energies inside and outside the zonule could result in differential breakage of fossil types, ultimately affecting abundances observed from point counts; however, we have no evidence supporting this. Measurements of the fossil groups show no trends in size with respect to position in relation to the zonule. Because sedimentary structures other than burrows are absent, it is difficult to determine the extent of reworking by waves and currents. That the *Prasopora* colonies in the zonule are not in life position, do not exhibit a preferred orientation, and are unfragmented with only slight abrasion suggests that the colonies were swept up, tumbled around, and redeposited near where they had grown. Evidence of long-distance transport or repetitive wave action is lacking.

Repeated scouring of the submarine surface appears to have occurred in the Galena sea, as evidenced by the many hardgrounds. These hardgrounds have been interpreted as cemented submarine erosion surfaces because signs of subaerial exposure, such as mudcracks and evaporites, are absent. Hardgrounds could have served as colonization surfaces for brachiopods and bryozoans. Studies of microhabitat partitioning and colonization of hardgrounds show that shallow, stormy shelf environments can contain series of living communities overlying dead, cemented ones (Palmer and Palmer, 1977; Brett and Liddell, 1978; Arens and Cuffey, 1989; Wilson and others, 1992). However, our examination of thin sections as well as outcrops revealed no evidence of *Prasopora* or other bryozoans cementing themselves to the hardground surface or to brachiopod shells in units A–F.

The alternation of brachiopod and bryozoan abundances around the *Prasopora* zonule may reflect differential tolerances of these organisms to environmental conditions or substrates. Many of the brachiopods that characterize the Galena Group (for example, *Sowerbyella* and *Rafinesquina*) are those that used their broadness and flatness to create a snowshoe effect that allowed them to rest on soft bottoms and keep their shell margins above the sediment-water interface (Rose, 1967; Thayer, 1975; Lehman and Pope, 1989). The Dunleith Formation's branching and fan-shaped bryozoans, such as *Batostoma* and *Hallopora,* could not have remained upright and functional on a mud substrate as easily as the broad, flat brachiopods. At Guttenberg, the non-zonule layers might represent times when an abundance of carbonate mud prevented bryozoans from colonizing as rapidly as brachiopods. Then, perhaps when sediments more suitable for attachment were available, as in unit C, bryozoans could dominate the substrate and remain even as carbonate mud content rose again.

The shift in dominant grain size at the start of the zonule could account for the alternating abundances of brachiopods and non-prasoporan bryozoans, but it does not explain the concentration of *Prasopora* in the zonule. In Dunleith-equivalent rocks elsewhere, *Prasopora* is found in shale. On the eastern edge of the North American craton, where orogenic activity and delta formation occurred, *Prasopora* is found most commonly in siliciclastic shales or carbonate mudstones and shaly mudstones (Sparling, 1964; Ross, 1967; Arens and Cuffey, 1989). To the north of Guttenberg, nearer the Transcontinental Arch, zonule-equivalent outcrops near Decorah, Iowa, and Spring Grove, Minnesota, consist primarily of siliciclastic shale (Levorson and Gerk, 1972–1973). Elsewhere in the Decorah area, *Prasopora* has been collected from fine-grained carbonate and shale layers of the Decorah Subgroup (Delgado, 1983; Sloan, 1987). Thus, the presence of *Prasopora* is not limited to a particular lithologic facies.

The St. James–Beecher transition is an important interval in the Dunleith Formation because not only is the *Prasopora* zonule a prominent feature, but a change in the sedimentology and other biota is also evident. The St. James–Beecher contact is widely recognized in the Upper Mississippi Valley as marking a shift from relatively shaly carbonate in the Buckhorn and St. James Members to relatively pure carbonate sediment above (Templeton and Willman, 1963; Willman and Kolata, 1978). The amount of shale present varies with proximity to the Transcontinental Arch (fig. 3). In southeastern Minnesota, the Buckhorn–St. James interval is sometimes referred to as nearly pure shale, and the overlying Beecher equivalent (Cummingsville Formation) is a shaly limestone (Witzke, 1987; Sloan, 1997). Despite lithostratigraphic name changes, the boundary between the shalier interval (below) and the more carbonate-rich interval (above) is traceable on a regional basis. The *Prasopora* zonule is present at this boundary, regardless of the particular lithofacies present. Witzke and Bunker (1996) placed the entire lower Dunleith in one depositional cycle (number 5A in their terminology) and indicated that it was apparently subdivided into finer-scale cycles (fig. 2 of Witzke and Bunker, 1996). They regarded the presence of shale as a progradational indicator and purer carbonates as showing deepening. The sharpness of the St. James–Beecher boundary and the presence of numerous hardground surfaces in the Beecher suggest an abrupt increase in water depth, which shut off clastic influx and winnowed the seafloor. The *Prasopora* zonule would thus mark the final shoaling stage of the St. James sequence and the initial stage of transgression in the Beecher sequence.

CONCLUSIONS

The most striking features of our data are the alternating abundances of brachiopods and bryozoans in Guttenberg units A–F and the drop in mud content in the first zonule layer. The *Prasopora* zonule, which on a regional scale marks an important lithologic transition, appears to record an environmental or ecologic change. The results of lithologic and faunal counts from the Guttenberg outcrop rule out taphonomy, environmental energy shifts, or sediment composition (meaning mineralogy, not texture) as explanations for the abundance of *Prasopora* in the zonule. The abundance of fine sediment (carbonate mud) is related to the proportion of bryozoans (*Prasopora* and non-prasoporan) in some of the Guttenberg units A–F. Thus, although the exact significance *Prasopora* concentrations in the Dunleith Formation is still unclear, sedimentary texture appears to be a controlling factor in the alternating abundances of brachiopods and bryozoans in the Guttenberg units.

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