Late Cambrian hard substrate communities from Montana/ Wyoming: the oldest known hardground encrusters

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Hardground surfaces from the Late Cambrian Snowy Range Formation in Montana/Wyoming are the oldest known non-reefal hard substrates exhibiting encrusting fossils. These surfaces range in age from Early Franconian to early Trempealeauan. Hardgrounds were developed on slightly hummocky to planar, truncated surfaces of glauconite-rich, carbonate, flat pebble conglomerates, which were deposited during episodes of storm scouring in shallow subtidal environments of the Montana/Wyoming shelf. Snowy Range hardgrounds are encrusted by a low diversity assemblage of fossils dominated by simple discoidal holdfasts of pelmatozoans, probably crinoids, and including small conical spongiomorph algae? and probable stromatolites. Macroborings (e.g. *Trypanites*) are notably absent from all hardground surfaces, although sharp-walled, vertical, cylindrical holes (borings?) occur in micrite clasts imbedded in certain flat pebble conglomerates. No evidence of faunal succession or microecologic partitioning of irregular surfaces was observed on these Cambrian hardgrounds. □ *Hardgrounds, epibionts, macroborings, pelmatozoan echinoderms, paleoecology, Cambrian, Montana/Wyoming.*

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Hardgrounds afford a unique opportunity for paleoecological studies. Because of their predominantly encrusting and endolithic life modes, hard substrate faunas are frequently preserved *in situ* on hardgrounds, thereby permitting accurate reconstruction of the density, diversity, spatial patterns, and, occasionally, competitive interactions of epifaunal organisms in ancient marine communities (Palmer & Fürsich 1974; Palmer & Palmer 1977; Brett & Liddell 1978; Fürsich 1979; Palmer 1982). Although encrusting cavity-dwelling faunas (coelobites) have recently been described from cryptic environments in Lower Cambrian archaeocyathid reefs (James *et al.* 1977; Kobluk & James 1979), the oldest hardground-encrusting communities described to date are from the Middle Ordovician (Palmer & Palmer 1977; Brett & Liddell 1978). Recently, several hardgrounds in intraclastic limestones have been identified from the Snowy Range Formation (Upper Cambrian) of the western Montana/Wyoming border area (also recorded by Palmer 1982). Sedimentologic features indicate that these hardground surfaces were formed by submarine lithification in nearshore shoal areas.

Snowy Range hardgrounds lack macroborings but are encrusted by stromatolites, spongiomorph algae? and pelmatozoan echinoderm holdfasts. The latter provide examples of some of the earliest known attached echinoderms.

Stratigraphic and geographic setting

The Upper Cambrian Snowy Range Formation comprises 20 to over 100 m of interbedded silty shales, thin sandstones and carbonates (Dorf & Lochman 1940; Lochman 1957; Grant 1965; Lochman-Balk 1972). This formation, the youngest Cambrian unit in the northern Rocky Mountains, crops out in the Horseshoe Hills, Bridger, Beartooth and Snowy ranges of south central Montana and northwestern Wyoming. Eastward in Montana, Wyoming and the Dakotas the Snowy Range passes into undifferentiated silty shales, sandstones and thin carbonate pebble conglomerates of the Upper Cambrian Deadwood Formation. In northwestern Montana, the stratigraphically equivalent Red Lion Formation consists predominantly of carbonates, with an abundance of limestone pebble conglomerates. Thus, the Snowy Range represents a transitional facies, intermediate between nearshore clastics and outer-shelf carbonates (Lochman-Balk

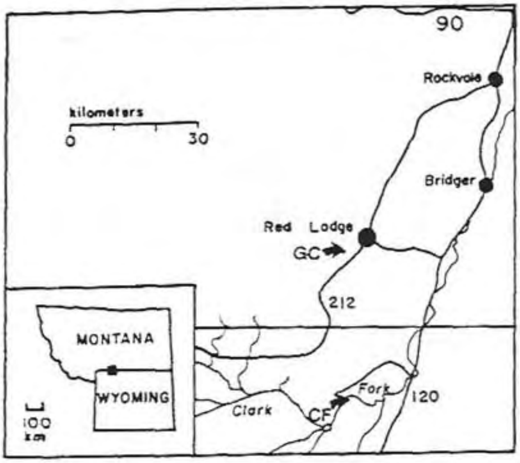

Fig. 1. Location map of Grove Creek (GC) and Clark Fork (CF) sections in the Beartooth Mountains, Montana and Wyoming.

1972). West of Yellowstone Park in Montana and Idaho equivalent age strata (Dresbachian–Trempealeauan) have been eroded prior to the Late Devonian (Lochman 1957; Grant 1965).

Snowy Range strata have been subdivided into three persistent members (Grant 1965). A lower Dry Creek Shale consists of about 15 m of blackish-green to purplish silty shales with thin siltstones, sandstones and arenaceous carbonates. The middle Sage Member consists of a thick sequence (36–67 m) of greenish-gray, soft shale with abundant interbedded greenish carbonate, flat pebble conglomerates (intrasparrudites), calcarenites (biosparites), calcisiltites (biopelmicrites and biopelsparites) and columnar to tabular algal limestones (Grant 1965). The upper Grove Creek Member, which is locally partially or completely truncated by Ordovician through Devonian erosion, is a variable unit of 0–12 m thickness, comprising silty dolostones, greenish, dolomitic shales, and, near the base, thick-bedded, pebble-cobble conglomerates (Grant 1965).

Biostratigraphic studies of Snowy Range trilobites (Grant 1965) indicate that the age of this formation is medial to upper Late Cambrian (uppermost Dresbachian to lower Trempealeauan). In the Bridger Range, the stratigraphic contact between the Sage and Grove Creek Members coincides with the Franconian/Trempealeauan Stage boundary, but at localities farther east, up to 30 m of the upper Sage beds may also be included in the basal Trempealeauan *Illaenurus* Zone (Grant 1965).

The Snowy Range Formation is exposed beneath cliffs of the resistant Bighorn Dolomite (Lower Ordovician) on the southern periphery of the Beartooth Range along the Montana/Wyoming border, from just east of Yellowstone Park to near Red Lodge, Montana. Lower portions of the formation are typically covered with talus but the Sage and Grove Creek members are well exposed at several localities. In the present study, two sections of the Snowy Range Formation were measured and studied in detail as follows (Fig. 1): (1) Exposures above the steep northwest-facing south bank of the north fork of Grove Creek, about 8 km (5 mi) south of Red Lodge, Carbon County, Montana (N 1/2, NW 1/4 sec. 26, T 8S, R 20E; Red Lodge 15' Quadrangle; see Dorf & Lochman 1940; Grant 1965). (2) Outcrops above a tributary gully along the northern side of the canyon of Clark Fork of the Yellowstone River, 10 km west of highway 120, and approximately 5 km south of the Montana–Wyoming border and about 15 km south of Cooke City, Montana; Park County, Wyoming (secs. 6,7, T 56N, R 103W; Deep Lake 15' Quadrangle).

Sections, measured downward from the base of the Bighorn Dolomite, comprise the entire Grove Creek and the upper quarter to third of the Sage Member. Both localities expose a 3 to 4 m upper interval of yellowish-weathering silty dolostones, dolomitic shales and flat pebble conglomerates (upper submember of the Grove Creek), underlain by 7 to 10 m of yellowish-green shale, dolomitic calcisiltites and yellow-weathering, rounded pebble-cobble conglomerates (lower Grove Creek submember). Following the usage of Dorf & Lochman (1940:544) and Grant (1965:14–16), the basal contact of the lower Grove Creek submember is placed at the lowest bed of orange-stained conglomerate with well-rounded, red- to greenish-stained, perforated (bored?) carbonate pebbles. In both sections this unit is followed by a long covered slope, presumably shale. Lowest measured intervals were a series of greenish-gray flat pebble conglomerates, calcisiltites and green shales (Fig. 2) of the upper Sage Member.

Encrusted hardgrounds, described herein, occur primarily in the upper Sage Member at both sites. Rounded, pebble conglomerates with perforated (bored?) carbonate clasts occur in the overlying Grove Creek Member, but no encrusting fossils were observed on the upper surfaces of these beds. Both sequences belong to the lower Trempealeauan Stage.

A single example of a pebble conglomerate with encrusting crinoid(?) holdfasts was also obtained from about 13 m above the base of the Snowy Range Formation at the Clark Fork locality. This unit occurs about a meter above a columnar algal limestone ledge (*Collenia magna*) marking the base of the Sage Member, but below brachiopod coquinoid limestones (*Eoorthis–Ceratreta* subzone; Grant 1965). This portion of the Snowy Range Formation belongs to the *Elvinia* trilobite zone of the lower Franconian Stage. This unit is the lowest observed Snowy Range hardground and the holdfasts on it appear to represent the oldest known hardground encrusting fauna.

Hardground lithologies

The Snowy Range hardgrounds are developed on the upper surfaces of carbonate flat pebble conglomerates (intrasparrudites). They are typically overlain by a thin layer of green shale. The conglomerates consist of tabular laminated micritic pebbles up to 15 cm across which are typically stained green with glauconite and which in some cases show reticulate pitting (submarine corrosion?; Fig. 3A). Pebbles are rounded to subangular and in many cases show imbrication (Fig. 3B). The matrix surrounding the carbonate pebbles consists of fine skeletal debris, particularly trilobite and echinoderm fragments, minor quartz silt and sparry calcite. The flat pebble conglomerates form lenticular to continuous bands up to 30 cm in thickness which generally exhibit sharp basal contacts and may truncate bedding in the underlying shales and siltstones. Upper surfaces of the conglomerate bands vary from planar to irregular and hummocky.

Approximately one-third of the flat pebble conglomerates examined in the upper portion of the Sage Member exhibit evidence of early lithification. A total of 10 hardground horizons were identified and studied in detail in the two outcrops. Evidence for early lithification of these carbonates include the following criteria: truncation of intraclasts, pitting and etching of the upper surfaces of clasts, and the presence of encrusting fossils on the surfaces.

Several hardgrounds observed in the Snowy Range Formation developed on planar abrasion

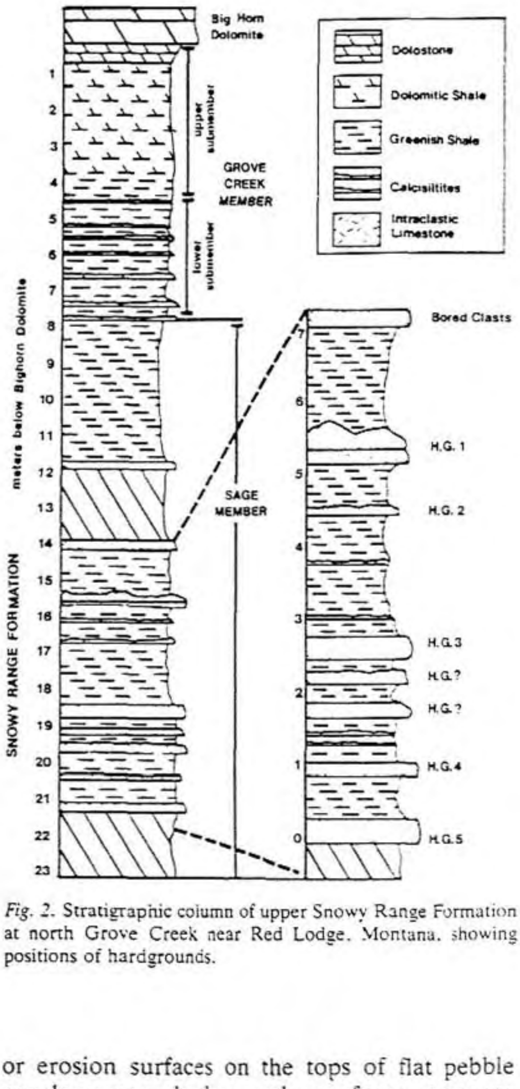

Fig. 2. Stratigraphic column of upper Snowy Range Formation at north Grove Creek near Red Lodge, Montana, showing positions of hardgrounds.

or erosion surfaces on the tops of flat pebble conglomerate beds; such surfaces truncate edgewise-imbricated flat pebbles (Fig. 3B). Other hardgrounds occur on the non-truncated upper sides of flat pebble conglomerates which may be undulatory with pebbles standing out in relief on the surfaces. In certain instances the flat pebbles have been undercut and exhibit overhanging surfaces (Fig. 3C) which have been encrusted by pelmatozoan holdfasts. Burrowing does not appear to have been an important factor in shaping any of the Cambrian hardgrounds observed, although Frykman (1980) reports irregular hardgrounds from the Middle Cambrian of Greenland associated with burrowing.

Finally, certain hardgrounds were developed on hummocky, mound-like masses of micritic

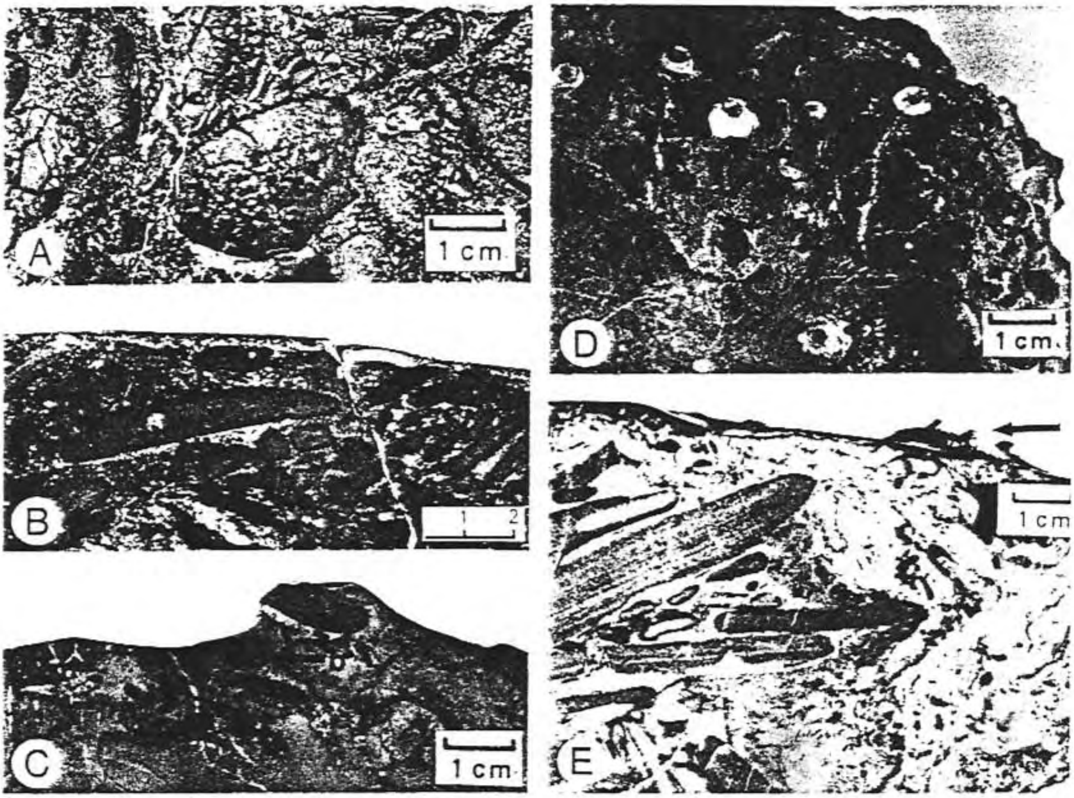

Fig. 3. Features of hardgrounds from the Cambrian Snowy Range Formation; all specimens from north Grove Creek, Red Lodge, Montana. □A. Upper surface of carbonate pebble conglomerate bed showing rounded calcisiltite pebbles with septaria-like cracks and finely-pitted surfaces. □B. Cross-section of flat pebble conglomerate (intrasparite) hardground; note nearly planar upper surface which truncates flat limestone pebbles. Scale in cm. □C. Cross-section of hummocky hardground developed on intramicrite (algal?) mound; note elevated and slightly undercut knob; also note infilling of crevices by skeletal debris (arrow-a) and stromatolitic? lamination of carbonate silt infilling slight depression (arrow-b). □D. Upper surface of hummocky hardground and an intramicrite mound, showing abundant encrusting pelmatozoan holdfasts. □E. Cross-section of hummock shown in D, showing micritic sediment with small, round intraclasts (on right) juxtaposed (algally bound?) onto mound of imbricated flat pebble conglomerate (left); note pelmatozoan holdfasts attached to hardground on upper surface of intramicrite (arrow).

sediment containing scattered small, rounded, glauconite-coated flat pebbles (Fig. 3C, D). These mounds or hummocks, which range up to 30 cm in height and approximately 50 cm across, rest on hummocky to planar beds of flat pebble conglomerate. They may represent non-laminated algal boundstones, or synsedimentary lithified carbonate mud mounds (lithoherms). However, these masses of sediment were evidently lithified on the sea floor as they show features such as undercutting of crevices and abundant encrusting pelmatozoan holdfasts indicative of firm to hard substrates (Fig. 3E).

Hardground biotas

All of the recognizable Snowy Range hardgrounds exhibit encrusting epibionts. The most abundant form consists of discoidal holdfasts of pelmatozoans. These are conical expansions of stereom ranging in diameter from 1 to 7 mm and with circular column facets 0.5–2.0 mm in diameter (Fig. 4A, B). Three categories of holdfasts were observed, including simple rounded disks with circular outlines (Fig. 4A, B), conical 'volcano shaped' holdfasts (Fig. 4C), and low, discoidal forms with slightly lobate margins (Fig. 4D).

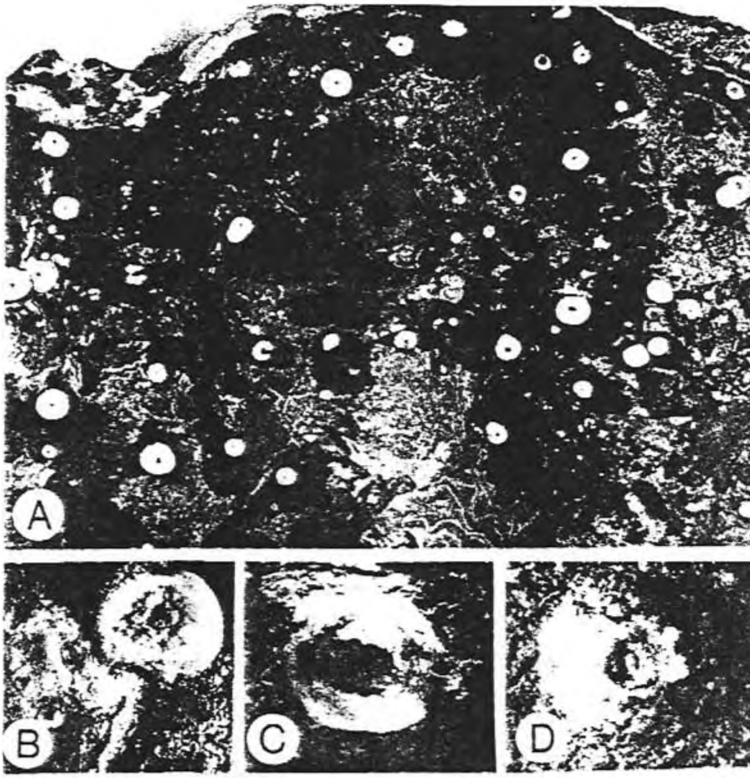

Fig. 4. Pelmatozoan holdfasts on Snowy Range hardgrounds. □ A. Upper surface of typical hardground from the upper Sage Member at Clark Fork Canyon, showing density and size distribution of discoidal holdfasts; note overlapping pairs of holdfasts (arrow a) and low, conical spongiomorph algal? mound (arrow b, center); × 0.65. □ B. Overlapping, discoidal holdfast morphotype; from slab shown in A; × 2.5. □ C. Conical holdfast morphotype; × 2.5. □ D. Low discoidal morphotype with slightly lobate margins; × 2.0. C and D from hummocky hardground in upper Sage Member at north fork of Grove Creek.

None of the morphotypes exhibits any trace of a many-plated integument. Holdfasts occur in aggregates of up to 20 individuals per 100 cm^2, with an average density for over 6300 cm^2 of sampled hardground surface of about 10 per 100 cm^2. Many holdfasts were attached to the surfaces of carbonate intraclasts; however, others were fixed directly to the intervening matrix of the pebble conglomerates, further indicating that this material was lithified at the time of colonization by pelmatozoans. Holdfasts occur on the upper, lateral, and undercut crevice surfaces of the hardground hummocks.

The identity of these pelmatozoan holdfasts could not be definitely established, although a reasonable guess can be made. Unusual stem morphology and rarity of the associated eocrinoid *Trachelocrinus resseri* (Sprinkle 1973) eliminate it as the major encruster. Other associated pelmatozoan plates include those of epispire-bearing and macrocystellid eocrinoids, a ?blastozoan with small radially-braced plates, a cheirocrinid cystoid and a form (?hybocrinoid) with thick, smooth-surfaced plates. This smooth-plated form was common and it may have been the dominant encruster. The simple discoidal holdfasts closely resemble those of later Ordovician hybocrinoids. However, to date, no hybocrinoids have been reported from rocks as old as the Trempealeauan.

A second fossil found encrusting on the Cambrian hardground surfaces consists of small (1 to 2 cm diameter) conical mounds, typically with depressed centers (Fig. 5). Cross-sections of such mounds reveal a reticulate, fibrous appearing internal structure resembling that of the calcified Cambrian spongiomorph alga *Renalcis* (Kobluk & James 1979; J. K. Rigby, pers. comm. 1981).

Other biotic elements found in calcarenites associated with the hardgrounds include plates of a large edrioasteroid, a phyllocystid stylophoran carpoid and at least two other echinoderms of unknown affinity. These organisms may have lived on the hardgrounds or on nearby muddy sea floors. Orthid brachiopods, abundant in some parts of the upper Sage Member, may have been attached by pedicles to hardground surfaces.

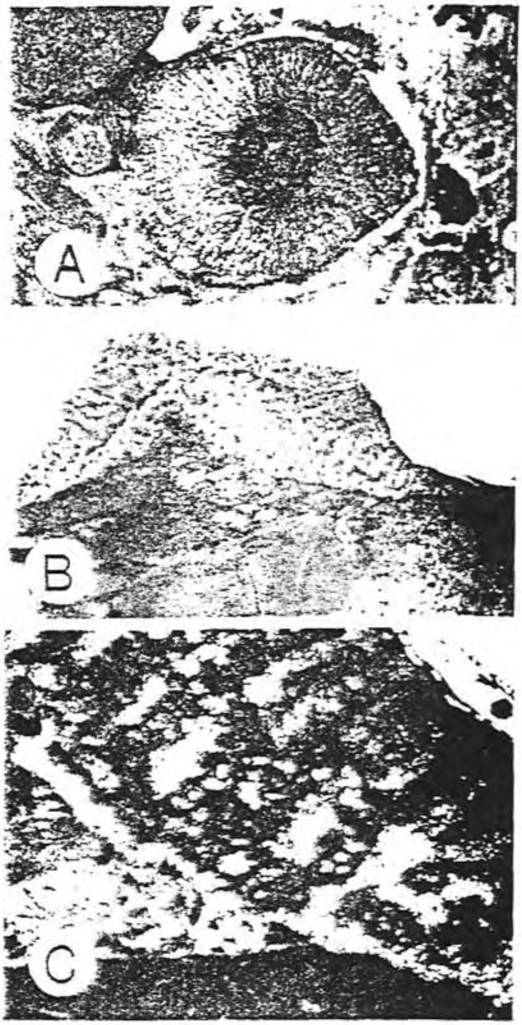

Fig. 5. Spongiomorph [illegible] ands on Snowy Range hardgrounds. All specimens [illegible] Upper Sage Member at Clark Fork Canyon, Wyoming. □A. Enlargement of specimen shown in Fig. 4A [illegible] conical form and radial 'canals'; × [illegible]. □B. [illegible] another specimen showing contact with hardground [illegible] note internal canals; ×4.3. □C. Photomicrograph [illegible] shown in B, showing enlargement of sediment [illegible] canals and contact surface; ×32.

No remains of [illegible] encrusting organisms such as bryozoans, [illegible] or craniid brachiopods were found [illegible] the hardground surfaces. Also, macroborings [illegible] as *Trypanites*, which are abundant even [illegible] Early Ordovician hardgrounds (Jaanusson [illegible] Lindström 1963), were notably absent from [illegible] Cambrian hardground surfaces. The only large trace fossils found associated with these surfaces were cylindrical, slightly irregular, straight-sided borings? from 2 mm to 3 mm in diameter which penetrate micritic intraclasts, but not the matrix (Fig. 6).

Depositional environment and paleoecology

Depositional environments of the Middle–Upper Cambrian in Montana and Wyoming have previously been studied in detail (Lochman 1957; Lochman–Balk 1972). Late Cambrian Snowy Range sediments accumulated in the western portion of a stable, inner shelf sea, which extended eastward to the upper Mississippi Valley. The Montana/Wyoming shelf was bordered to the west by an actively subsiding outer carbonate shelf, and on the east and southeast by the Canadian Shield and the Transcontinental Arch, both emergent areas of exposed Pre-Cambrian rock. Upper Cambrian sections exhibit a northeastward increase in terrigenous clastic sediments, presumably reflecting proximity to a major river or rivers draining the Canadian Shield (Lochman-Balk 1972). Slight diastrophic upwarp of this source region during the Dresbachian and Franconian ages resulted in an increase in detrital sedimentation, reflected in the shales of the Dry Creek and Sage members. Lochman-Balk (1972:138) visualizes a very broad 'tidal flat' (800 km^2) extending from the eastern shoreline into central Montana and Wyoming during the late Franconian, with an inner littoral sand flat and an outer mud flat (Deadwood facies), bordered seaward by a subtidal muddy shelf, or shelf lagoon in which limestone pebble conglomerates and shales accumulated (Snowy Range facies).

Montana/Wyoming shelf seas were shallow (probably less than 30 m) as evidenced by abundant storm deposits (flat pebble conglomerates), oolites, primary dolomites, and algal structures (Lochman 1957). Limonitic oxidation rinds on carbonate clasts within fresh samples of certain flat pebble conglomerates in the Snowy Range Formation probably developed by submarine weathering; such rinds are common in totally marine hardgrounds of Mesozoic age (F. Fürsich, pers. comm.). Conglomerates, including several on which hardgrounds were developed, yield no evidence of emergence.

An abundance of carbonate pebble conglomerates characterizes several Middle–Upper Cambrian facies in the Rocky Mountains (Sepkoski

1982). In part, this may be due to the broad expanse of the very shallow subtidal to intertidal environments conducive to partial lithification of fine-grained carbonate sediments and subsequent scouring by storm waves.

Discontinuous (nodular) early lithification of the carbonate pebble sediments is indicated by their evident erodability as large coherent clasts, often with sharp edges, and the presence of sharply-defined trace fossils (borings?) within the clasts. Sepkoski & Bambach (1979) and Sepkoski (1982) reasoned that extensive bioturbation inhibits early lithification by inmixing of fine clays and attributed the abundance of flat pebble conglomerates in the Cambrian to a scarcity of deep-burrowing organisms at that time. The preservation of primary lamination in most Snowy Range limestone clasts appears to support this contention.

Formation of flat pebble conglomerates implies episodic scouring of the sea floor, presumably during intense storms. Random to slightly imbricated orientation of flat pebbles and their packing in a matrix of coarse fossil debris with sparry calcite cement indicate high energy conditions which resulted in the winnowing of fine-grained sediments.

A variety of evidence suggests that such episodes of disturbance punctuated a background of typically slow sedimentation rates. Glauconite, which occurs both as grains and as coatings on many pebbles and hardground surfaces, is an excellent indicator of low rates of deposition in quiet water, slightly reducing environments (McRae 1972). The generally disarticulated and fragmental nature of fossils as well as certain beds of well-rounded limestone pebbles suggest periodic reworking of sediments on the sea floor. Finally, evidence of synsedimentary lithification both in the carbonate clasts and in hardgrounds on the upper surfaces of Snowy Range pebble conglomerate bands indicates periods of nondeposition, permitting cements to precipitate in grain interstices (cf. Bathurst 1976:398–406).

Following the deposition of lags of limestone pebbles and fossil debris this material was indurated by the formation of early cements. This lithification probably occurred slightly below the sediment–water interface. In certain instances, the initial binding of local hummocks of pebbles and debris also may have been aided by algal encrustation. Cross-sections of some hummocks show local clumps of edgewise pebbles surrounded by irregular masses of micrite with vague

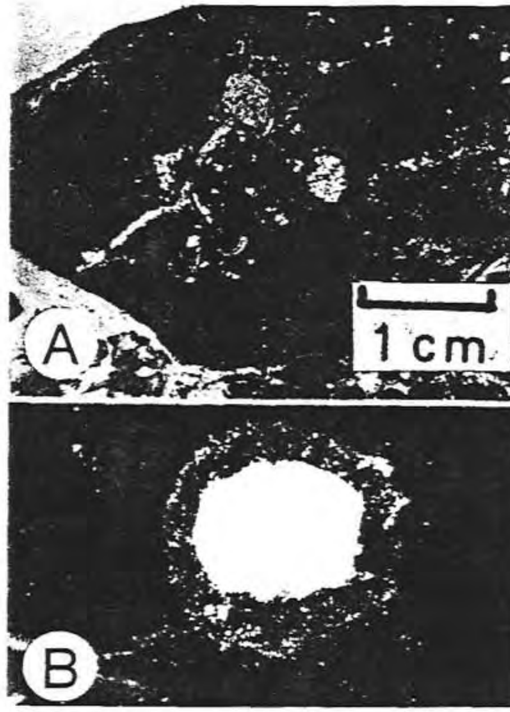

Fig. 6. □A. Perforated flat, micritic pebble from intrasparite bed near base of Grove Creek Member, Snowy Range Formation, at North Grove Creek, Montana; note large size of borings? and circular outline. □B. Photomicrograph of another boring? from the same locality; note spar infilling and light (oxidation?) halo around the hole; × 35.0.

patchy or mottled textures, suggestive of algal boundstones (cf. Pratt 1982). Evidently, there was little or no burrowing of the pebbly sediments prior to lithification, since original imbricate fabrics are preserved in most cases. This contrasts with most Ordovician and later hardgrounds and, again, supports the hypothesis of Sepkoski & Bambach (1979). However, hardground surfaces were typically shaped by submarine erosion after lithification. Many surfaces were undercut somewhat and others were erosionally 'planed' to nearly flat surfaces which truncate clasts.

Although holdfasts on Snowy Range hardgrounds are generally well preserved, none show articulated columns or thecal remains. In all cases the pelmatozoans died and were disarticulated prior to the final burial of the hardgrounds. Furthermore, relatively little disarticulated skeletal material was found on the surfaces of the hardgrounds indicating that these surfaces were swept clear of debris by currents. Columnals and plates are an important component of certain flat pebble conglomerates and calcarenites which are associated with the hardgrounds. A few holdfasts and several of the algal? mounds also exhibit slight abrasion and/or corrosion, but most specimens do not.

No evidence of faunal succession/progression was observed on the surfaces, but the frequent overgrowth of the articular facets of holdfasts by other holdfasts indicates encrustation of the surface by more than one generation of pelmatozoans.

Discussion

The Upper Cambrian (Franconian to Trempealeauan) discontinuity surfaces described herein are among the oldest known hardgrounds and are the oldest known surfaces to preserve encrusting faunas. Sepkoski (1977) made a detailed study of the stratigraphy and paleontology of slightly older Dresbachian rocks in Montana and Wyoming, but found no evidence of borings or encrusting fossils on hardgrounds (J. J. Sepkoski, pers. comm. 1978). We surveyed flat pebble conglomerates in the Middle Cambrian Upper Gros Ventre Shale (= Park Shale) of northern Wyoming, including some beds with truncated upper surfaces suggesting synsedimentary lithification, but also found no evidence for encrusting faunas.

Snowy Range hardgrounds show a low diversity of skeletonized encrusting biotas largely dominated by one or two species of small attached pelmatozoans. The occurrence of such holdfasts in the lower Sage Member (Franconian) could represent the oldest record of hybocrinoids and the oldest indirect evidence of crinoids, aside from the questionable Middle Cambrian *Echmatocrinus* (Sprinkle 1973). These hardground encrusting pelmatozoans, whatever their identity, possessed simple discoidal holdfasts, which are solid masses of stereom with a well-developed articular facet for true columnals (such columnals are also known from biosparite beds of the Snowy Range Formation).

The presence of probable algal structures on hardground surfaces contrasts with most later Paleozoic hardground biotas which lack algal crusts. Possibly, this is associated with an absence of grazing organisms in the Cambrian. Gastropods are associated with hardgrounds from at least the Middle Ordovician onward (Brookfield & Brett in prep.).

The absence of macroborings on all types of Late Cambrian hardgrounds is both surprising and probably significant since borings are common on Lower Ordovician discontinuity surfaces (Jaanusson 1961) and are the most ubiquitous and abundant fossil on later hardgrounds (Brett & Liddell 1978:346). This observation is also enigmatic in view of the recent discovery of macroborings (*Trypanites*) in Lower Cambrian archaeocyathid reefs from Labrador (Kobluk *et al.* 1978; Kobluk & James 1979). However, this observation is consistent with the hypothesis of Kobluk *et al.* (1978) that *Trypanites*-type boreholes were produced by separate groups of organisms: one which evolved in the Early Cambrian, specialized in boring into archaeocyathid reefs and presumably became extinct with the extinction of archaeocyathids, and later forms which appeared in earliest Ordovician time and continued throughout much of the Phanerozoic.

Finally, it may be significant that cylindrical, slightly tapering holes occur in certain of the micrite clasts within hardgrounds and other types of flat pebble conglomerates in the Snowy Range Formation. These holes (see above), which are similar in size and shape to *Trypanites*, were evidently produced in fine-grained, micritic sediments prior to their deposition as clasts based on their orientation in the conglomerates. Because these pebbles are entirely composed of fine-grained sediments, it is not possible to determine whether or not the holes are true borings (i.e. cut grains). We suggest that they are burrows or borings formed in semilithified micrites. However, the organisms responsible for such ichnofossils evidently did not bore into the cemented surfaces of the hardgrounds; no macroborings of similar type were found cutting grains or cements in the pebble conglomerates. Perhaps, these were the dwelling burrows of organisms which excavated firm but not entirely lithified fine-grained sediments. The producers of these holes may represent precursors of organisms which were capable of excavating truly indurated sediment.

Upper Cambrian hardground biotas predate the appearance of most skeletonized colonial organisms (e.g. bryozoans) which commonly occupy or even dominate space in later hard substrate communities (cf. Jackson 1977; Palmer 1982). Therefore, greater spatial dominance by solitary organisms (e.g. echinoderms) might be predicted. Based on our admittedly small samples, this appears to be the case. Observed densities of echinoderm holdfasts (4–15/100 cm^2, for four hardgrounds sampled) on several Snowy Range hardground slabs greatly exceed maximal densities of similar-sized holdfasts on later hard substrate assemblages known to us.

In two cases, hummocky Snowy Range hardgrounds exhibit irregular topographies including flattened upper, steep lateral and slightly undercut or overhanging surfaces. In both instances, we noted that the distribution of a single morphotype of pelmatozoan holdfasts was essentially random with respect to hardground topography. The holdfasts were about equally abundant on gently-sloped upper surfaces and steep lateral faces. Recent studies provide evidence for weak differentiation of exposed vs. cryptic biotas in Middle Ordovician hardgrounds (Brett & Liddell 1978), and somewhat more pronounced polarization in the Silurian (Spjeldnaes 1974) and Devonian (Koch & Strimple 1968). It would appear that faunal partitioning of microenvironments by different organisms has increased considerably since the Cambrian.

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