



A NEW PALEOECOLOGICAL LOOK AT THE DINWOODY FORMATION (LOWER TRIASSIC, WESTERN USA): INTRINSIC VERSUS EXTRINSIC CONTROLS ON ECOSYSTEM RECOVERY AFTER THE END-PERMIAN MASS EXTINCTION

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ABSTRACT—The Dinwoody Formation of the western United States represents an important archive of Early Triassic ecosystems in the immediate aftermath of the end-Permian mass extinction. We present a systematic description and a quantitative paleoecological analysis of its benthic faunas in order to reconstruct benthic associations and to explore the temporal and spatial variations of diversity, ecological structure and taxonomic composition throughout the earliest Triassic of the western United States. A total of 15 bivalve species, two gastropod species, and two brachiopod species are recognized in the study area. The paleoecological analysis shows that the oldest Dinwoody communities are characterized by low diversity, low ecological complexity and high dominance of few species. We suggest that this low diversity most likely reflects the consequences of the mass extinction in the first place and not necessarily the persistence of environmental stress. Whereas this diversity pattern persists into younger strata of the Dinwoody Formation in outer shelf environments, an increase in richness, evenness and guild diversity occurred around the Griesbachian–Dienerian boundary in more shallow marine habitats. This incipient recovery towards the end of the Griesbachian is in accordance with observations from other regions and thus probably represents an interregional signal. In contrast to increasing richness within communities (alpha-diversity), beta-diversity remained low during the Griesbachian and Dienerian in the study area. This low beta-diversity reflects a wide environmental and geographical range of taxa during the earliest Triassic, indicating that the increase of within-habitat diversity has not yet led to significant competitive exclusion. We hypothesize that the well-known prevalence of generalized taxa in post-extinction faunas is primarily an effect of reduced competition that allows species to exist through the full range of their fundamental niches, rather than being caused by unusual and uniform environmental stress.

INTRODUCTION

THE END-PERMIAN mass extinction represents the most profound crisis in the history of metazoan life, with an estimated species loss of up to 96 percent in the marine realm (Raup, 1979). Starting with Hallam (1991), the ensuing recovery period received increasing attention. Studies of the post-extinction interval are important in order to understand how biota and ecosystems respond to massive environmental perturbations (Clapham and Payne, 2011), how rapidly ecosystems are able to recover and how evolutionary processes proceed in vacated ecospace (e.g., Erwin, 2001; Brayard et al., 2009; Hofmann et al., 2013). Widely held assumptions on the Early Triassic recovery interval emphasize that ecosystem restoration was considerably delayed as a result of ongoing environmental stress (e.g., Wignall and Hallam, 1992) or of the intensity of species loss (Schubert and Bottjer, 1995). Recently, however, evidence emerged that the recovery was a more volatile process, with notable ecologic recovery taking place in benthic ecosystems on a much wider geographic scale (e.g., Krystyn et al., 2003; Beatty et al., 2008; Shigeta et al., 2009; Kaim et al., 2010; Hautmann et al., 2011; Hofmann et al., 2011) in the course of the Griesbachian and early Dienerian, i.e., considerably earlier than generally assumed. Paleoecological studies of the immediate post-extinction phase are, thus, of primary importance to resolve the questions if environmental stress was persistent in the early aftermath of the extinction and whether previously reported indications of early recovery were of local or of global significance. The Dinwoody Formation of

the western U.S. records this critical time interval but with the exception of four quantitative samples presented by Schubert and Bottjer (1995), its faunal content has not yet been comprehensively studied with respect to paleoecology. Moreover, no modern taxonomic description of the fauna has been provided since the monograph of Ciriacks (1963) on Permian and Early Triassic bivalves from the western U.S. Here we present a quantitative paleoecological survey involving 40 sampled levels from nine sections spanning the full geographic and environmental range of the Dinwoody Formation. We aim to resolve recovery patterns of benthic ecosystems throughout the Griesbachian and lower Dienerian and across environmental gradients within the Dinwoody Formation and to integrate these results with recent advances in the understanding earliest recovery phase after the end-Permian mass extinction.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The Dinwoody Formation, which is recorded in Idaho, southwestern Montana, western Wyoming, and northern Utah (Fig. 1.2; Paull and Paull, 1994), represents a marine tongue deposited during a rapid Early Triassic transgression over a low-relief, terrestrial area that mainly exposed marine strata of Middle Permian age (Newell and Kummel, 1942; Paull and Paull, 1994). The Dinwoody Sea was an epicontinental embayment with connection to the Panthalassa Ocean to the west (Fig. 1.1). During Permian and Early Triassic times, the area remained tectonically quiescent (Paull and Paull, 1994). The maximum thickness of the Dinwoody Formation is about

750 meters in the depot center, located today in southeastern Idaho (Kummel, 1954). It pinches out towards the east in Wyoming and to the south in Utah (Fig. 1.2) (Newell and Kummel, 1942; Clark and Carr, 1984). General lithofacies patterns (e.g., Kummel, 1957; Clark and Carr, 1984; Paull and Paull, 1994) suggest that the Dinwoody Formation was deposited in a ramp-like configuration including inner shelf, outer shelf and deeper shelf environments.

The biostratigraphy of the Dinwoody Formation is not well constrained and of rather low resolution. Ammonites are very rare throughout the study area. Three conodont zones covering a time interval from the early Griesbachian to the Dienerian have been recognized in the Dinwoody Formation (Clark and Carr, 1984). Except for a general scheme as given in Clark and Carr (1984, fig. 1), a precise zonation with respect to lithostratigraphic relationships has never been worked out for the Dinwoody Formation. In terms of lithostratigraphy, the Dinwoody Formation is informally subdivided into three units in Wyoming (Newell and Kummel, 1942). These are the “Basal siltstone”, the “*Lingula* zone”, and the “*Claraia* zone”. Kummel (1954) noted that this subdivision is not well developed in southeastern Idaho. During our field work, this zonation was difficult to recognize and practically of no value in localities other than in western Wyoming (Gros Ventre Canyon). Siltstones that would fit the descriptions of the “Basal siltstone” of Newell and Kummel (1942) are widespread throughout the Formation. Although there is a certain temporal dominance of *Lingula* in the lower part of the Formation, the occurrence of *Lingula* is generally related to local facies effects, which diminishes the stratigraphic utility of the “*Lingula* zone” of Newell and Kummel (1942). *Claraia mulleri* and *Claraia stachei* are closely related species which have been reported to co-occur in the same stratigraphic levels within the Dinwoody Formation (Newell and Kummel, 1942; Ciriacks, 1963). Although a precise biostratigraphic scheme has not been established, data from more offshore sections (e.g., Candelaria Formation, western Nevada), that facilitate a correlation with ammonoid data (Ware et al., 2011), suggest that these two species are abundant around the Griesbachian–Dienerian boundary interval.

We see some potential to establish a more reliable stratigraphic scheme by integrating sedimentological data (e.g., tracking relative sea level changes throughout the study area) with new conodont collections, but this is not within the scope of this study.

FIELD LOCALITIES AND METHODS

Fieldwork was conducted in August 2010 (by RH) in southwestern Montana and southeastern Idaho and in June 2011 (RH and MH) in western Wyoming, Montana, and northeastern Utah. Bed-by-bed logging and fossil sampling was performed at nine sections of the Dinwoody Formation. Detailed locality information can be found in Figure 1.2 and Table 1. Fossil collections were derived from discrete limestone and calcareous sandstone and siltstone beds, which were representatively sampled and mechanically decomposed for fossil extraction. Standard macro-invertebrate preparation techniques were performed to reveal morphologic details for taxonomic determination. Each collection was performed either until it yielded more than 100 specimens or until further sampling revealed no new finds of taxa. Occasionally, sampling was limited by poor exposures. Beds showing evidence of strong reworking, as for instance size-sorting, pronounced gradation or abundant abrasion of fossils, were not included in the quantitative analysis. Sampled intervals are suggested to

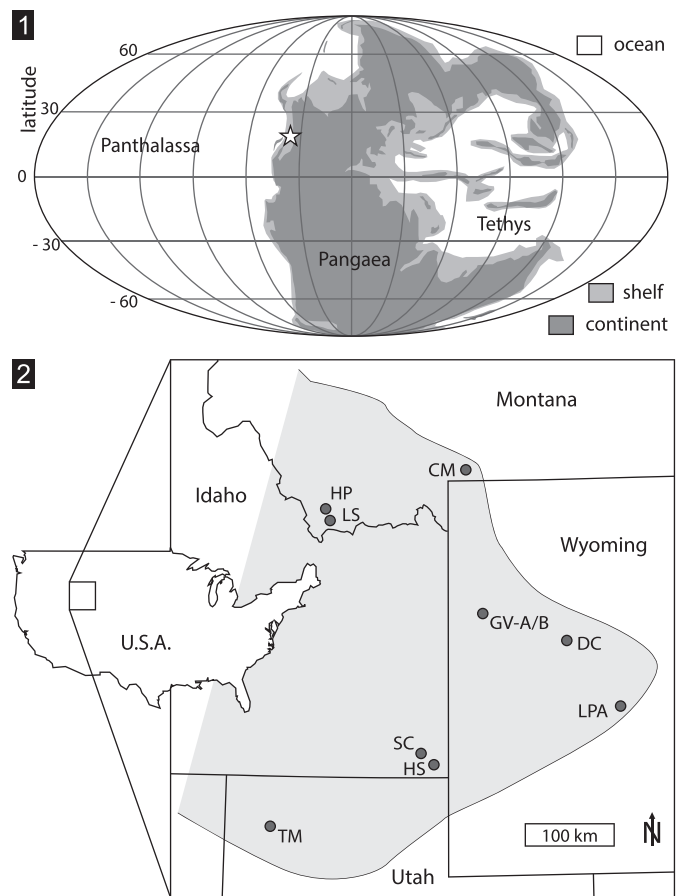


FIGURE 1—1, global paleogeographic reconstruction for the Early Triassic after Blakey (2012); white star indicates the position of the Dinwoody Basin at the eastern Panthalassa margin; 2, geographic positions of the measured sections and the extent of the Dinwoody Basin (grey shaded area) during the Griesbachian. After Paull and Paull (1994) referring to Maughan (1979).

represent autochthonous and para-autochthonous communities as bivalves are frequently observed in life position and are generally recorded as complete unabraded valves or molds of complete specimens. Identification of the sedimentological facies is based on field observations. Taxa recognized in this study include bivalves, gastropods, and brachiopods. The quantitative faunal list with absolute abundances is given in an Excel spread sheet available as an online Supplemental file.

Faunal abundance data were analysed with the software package PAST (Hammer et al., 2001). Cluster analysis followed the procedure applied in Hofmann et al. (2013), which also yielded the most reasonable groupings in the present data set, using the unweighted paired group method (UPGMA) as implanted in PAST in combination with the Morisita index of similarity (Morisita, 1959). The Q-mode cluster analysis groups samples into sets that are similar with respect to presence and abundance of taxa. This procedure is used to detect recurrent assemblages and to emphasize differences among distant groups. The dominance index D, as obtained from PAST (Hammer et al., 2001), was used as an inverse measure of ecological evenness.

Beta-diversity measures the degree of habitat partitioning along environmental gradients. A simple measure of beta-diversity is dividing the bulk number of taxa recorded in a set of adjacent communities (gamma diversity sensu Whittaker, 1972, 1975) by the average alpha-diversity of these communities

TABLE 1—Geographic information for the sections of the Dinwoody Formation visited during this study.

Code	Section	Geographic information	GPS coordinates (WGS 84)	Reference
LPA	Little Popo Agie Canyon	Wind River Range, Wyoming	N 42°40'27.90", W 108°40'52.40"	Ciriacks (1963)
DC	Dinwoody Canyon	Wind River Range, Wyoming	N 43°21'31.70", W 109°24'15.90"	Newell and Kummel (1942)
GV-A	Gros Ventre Canyon A	Gros Ventre Range, Wyoming	N 43°38'21.50", W 110°34'27.90"	Newell and Kummel (1942)
GV-B	Gros Ventre Canyon B	Gros Ventre Range, Wyoming	N 43°38'10.30", W 110°33'59.00"	Newell and Kummel (1942)
CM	Cinnabar Mountain	Gallatin Range, Montana	N 45°05'34.00", W 110°47'28.50"	Ciriacks (1963)
LS	Little Sheep Creek	Tendoy Range, Montana	N 44°33'41.01", W 112°42'43.41"	Scholten (1955)
HP	Hidden Pasture	Tendoy Range, Montana	N 44°40'38.00", W 112°47'24.78"	Scholten (1955)
HS	Hot Springs Canyon	Bear Lake Area, Idaho	N 42°06'48.70", W 111°15'16.90"	Kummel (1954)
SC	Sleight Canyon	Bear Lake Area, Idaho	N 42°14'03.29", W 111°25'40.38"	Kummel (1954)
TM	Terrace Mountains	Box Elder County, Utah	N 41°27'51.10", W 113°28'09.10"	Clark et al. (1977)

(Whittaker, 1975). However, because this approach is highly sensitive to the number of habitats in each set (everything else being equal, the larger set of habitats will have a higher beta-diversity), it is not very practical if it is aimed at comparing beta-diversity of different sets of communities at different stages of recovery. Another measure of beta-diversity is the coefficient of community or Jaccard Coefficient (Jaccard, 1901), as used by Sepkoski (1988). However, application of the Jaccard-coefficient for measuring beta-diversity requires an a priori recognition of neighboring habitats, which remains subjective in typical paleontological samples. These are generally scattered with respect to geography and time. In practice, paleocommunities occur variably within stratigraphic sections, and two communities recorded in strata, even in direct succession, may never represent two communities that lived adjacent to each other in the past.

In order to avoid these uncertainties, we introduce a new approach to calculate beta-diversity from paleontological data, based on mean minimum beta-diversity. In a first step, all samples that have been identified by the cluster analysis as belonging to the same association are pooled, resulting in a full list of species occurring in this association (this step corresponds to the standard reconstruction of species composition in paleocommunities; e.g., Aberhan 1992). Then, similarity coefficients between the different associations are calculated. We herein use the well-established Jaccard coefficient, although alternative similarity coefficients might be applicable as well. The resulting similarity matrix forms the basis for arranging associations according to the smallest differences in their taxonomic composition, which is used as an approximation of the former geographic arrangement. In a final step, the average values of beta-diversity between pairs of adjoining associations are calculated, giving a measure of habitat differentiation of the system as a whole.

The principal advantages of this procedure are 1) that it provides a standardized scheme of data treatment independent of subjective identification of neighbored habitats and 2) that beta-diversity values between different, stratigraphically separated sets of communities can be compared, regardless of the number of habitats recorded, because a higher number of habitats per se will not alter average beta-diversity between habitats, at least as long as the habitat gradient is more or less linear.

However, there are also problems with this method that have to be considered when interpreting mean minimum beta-diversity values. First, it should be noted that arranging associations according to minimum beta-diversity is just an approximation to former geographic relationships of these associations. However, this is also the case for any reconstruction based on sedimentary facies, and we think that the advantage of applying a standardized procedure outbalances

this disadvantage in studies that primarily aim to compare beta-diversity between different sets of paleocommunities in time.

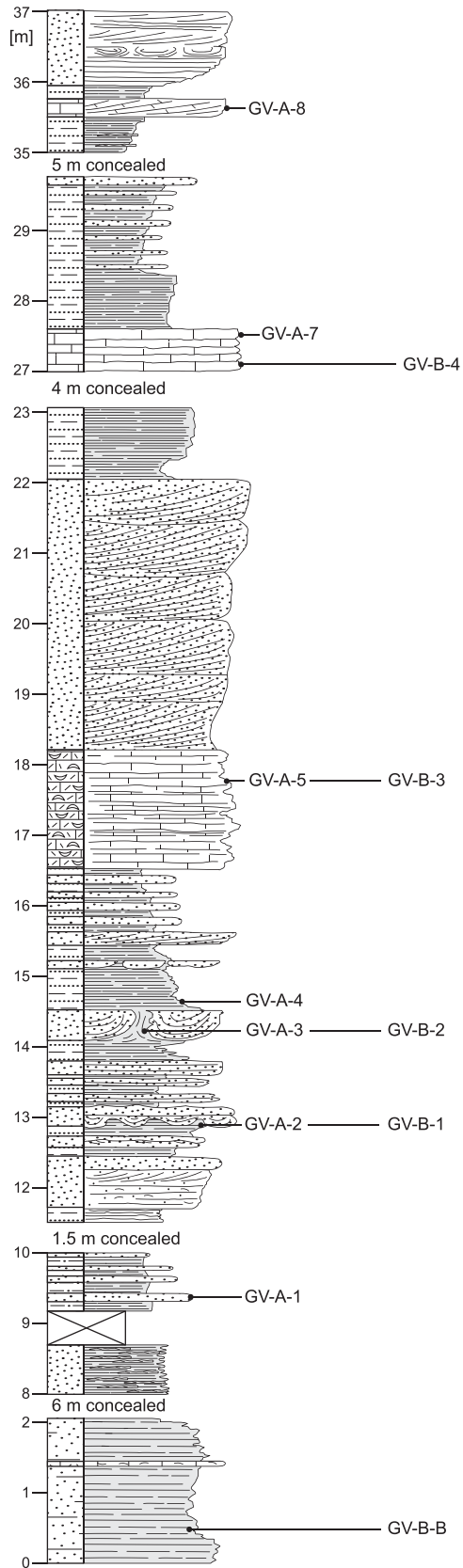
A more fundamental problem is that this method cannot measure progressing habitat contraction in a given set of paleoenvironments. If increasing competition leads to wedging new communities in-between the boundaries of existing paleocommunities, this will increase beta-diversity of the system as a whole but not necessarily average beta-diversity between adjacent habitats, as measured by the mean minimum beta-diversity approach. This limits the application of the method to relatively early stages of recovery, when the number of competing species was relatively low and habitat contraction has not yet started. For the Early Triassic of the western U.S., it has recently been demonstrated that taxonomic differentiation between habitats was still low in the Spathian Virgin Formation (Hofmann et al., 2013), which represents a much more advanced recovery stage than the fauna of the Dinwoody Formation considered herein, according to overall diversity, number of guilds, and time elapsed since the mass extinction. In conclusion, the minimum beta-diversity approach is considered as the most appropriate method for comparing beta-diversity of the Dinwoody benthic faunas with those from the Virgin Formation, which is aimed herein.

SEDIMENTARY ENVIRONMENTS OF THE STUDIED SECTIONS

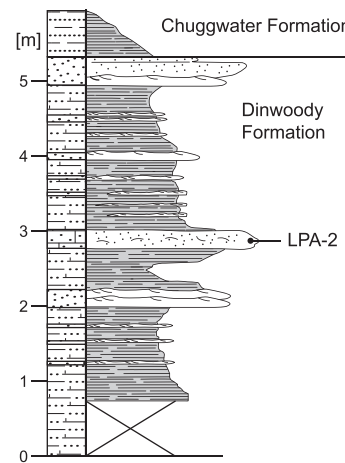
Gros Ventre Canyon (GV-A, GV-B).—Due to the spatial proximity, the two sections at the Gros Ventre Canyon are very similar in terms of their lithological succession (Fig. 2.1, 2.2). Where exposed, the lower interval is composed of laminated siltstones (Fig. 3.3) and claystones. The major part of the section is composed of laminated siltstones, silty sandstones, and sandstones that were most likely deposited under quiet water conditions. Some discrete, massive bioclastic limestone beds are intercalated. In the siliclastic intervals, ripple cross-lamination and trough cross bedding are frequently observed. Some massive sandstone beds show ball and pillow structures. All of these features indicate bedload deposition under the influence of waves and storms and, thus, argue for an inner shelf setting.

Wind River Range (LPA, DC).—The Dinwoody Formation in the Wind River Range of western Wyoming forms a mainly siliclastic wedge of shallow marine sediments thickening towards the northwest. The contact to underlying strata of Permian age is represented by a gap of unknown duration. The contact to the overlying continental red beds of the Chugwater Formation seems conformable. At the Little Popo Agie Canyon locality sampled by us, the Dinwoody Formation (Fig. 2.3) is represented by a 5-m thick alternation of siltstone, sandstone, and marly limestone. Evidence for deposition in a shallow water environment is provided by the presence of abundant ripple cross-lamination and synaeresis cracks in the middle part of the section (Fig. 2.2). The section at Dinwoody Canyon is exclusively siliclastic and was found to be virtually unfossiliferous except for some poorly preserved internal molds and is therefore not included in the analysis.

1 Gros Ventre Canyon A, B (GV-A, GV-B)



2 Little Popo Agie Canyon (LPA)



Legend

Lithology	Sedimentary features
claystone/shale	parallel lamination/bedding
siltstone	wavy parallel lamination/bedding
sandy siltstone	cross bedding
muddy sandstone	ripple-cross lamination
sandstone	ball and pillow
conglomeratic sandstone	
calcareous sandstone	Miscellaneous
marlstone	[m] meter
calcareous siltstone	covered section
silty limestone	
shale/mudstone interbedding	
limestone	
sandy limestone	
clastic limestone	
bioclastic limestone	
dolostone	

FIGURE 2—Sections of the Dinwoody Formation of western Wyoming and southern Montana. 1, Gros Ventre Canyon; 2, Little Popo Agie Canyon.

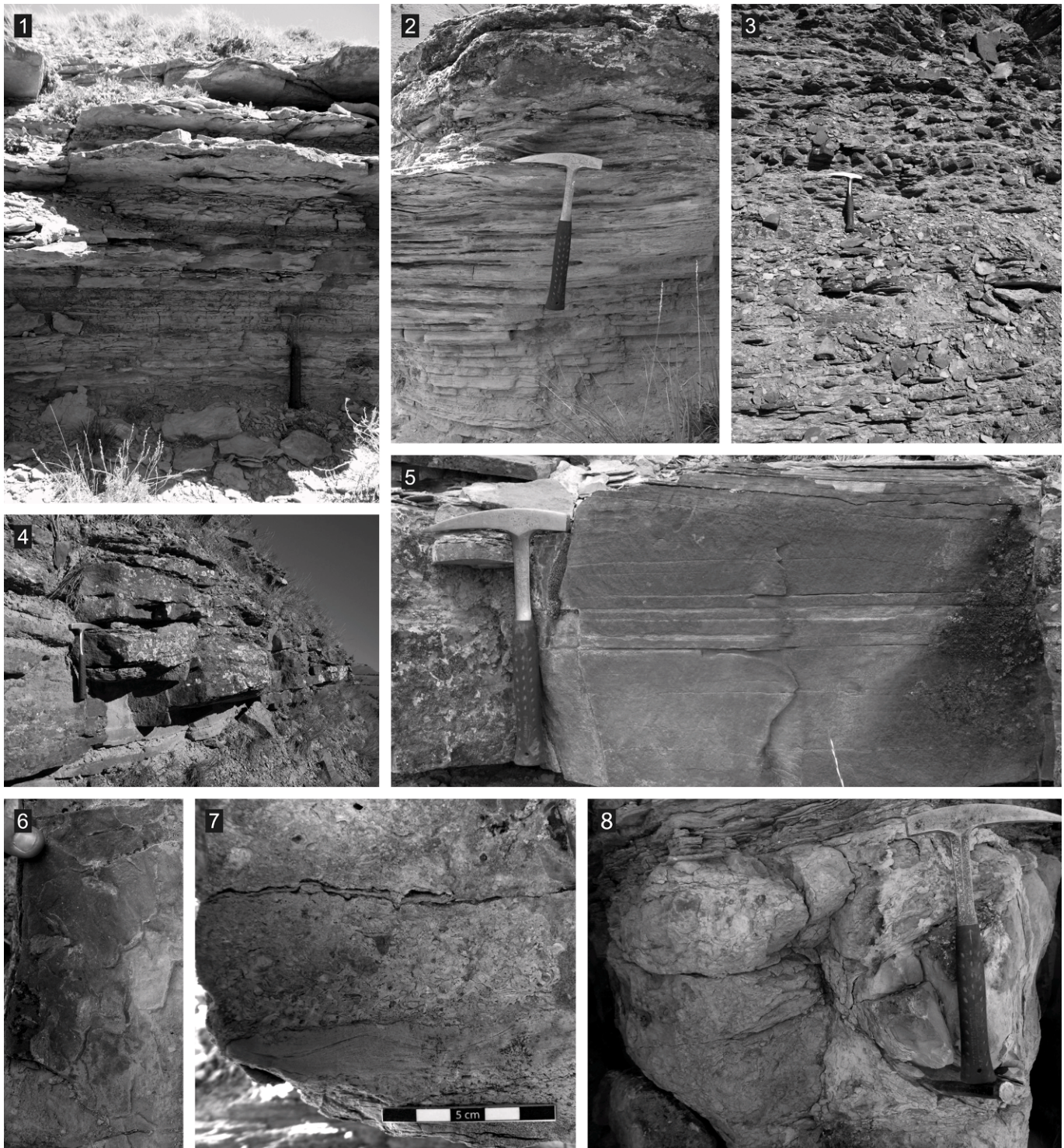


FIGURE 3—Sedimentary features and facies of the Dinwoody Formation of the Wind River Range, Gros Ventre Range, and the Tendoy Range. 1, lower portion of the section LPA showing interbeddings of laminated calcareous siltstones and ripple cross-laminated sandstones of a lower shoreface facies; 2, laminated siltstones topped by massive grainstones of the lower shoreface facies in section LS; 3, rhythmic interbeddings of siltstones and fine-grained limestones of the lower part of section HP suggested to represent outer shelf deposits; 4, massive grainstones of the inner shelf typical for the middle part of section HP; 5, very fine-grained sandstones of the upper plane bed regime giving rise to cross-beds and waning of current energy, seen at section LS; 6, synaeresis cracks diagnostic for salinity fluctuations, section LS; 7, ripple cross-laminated calcareous sandstone giving rise to graded tempestitic bioclastic rudstone, top of section GV-A; 8, ball and pillow-type deformation within sandstones typically recorded in the lower part of section GV-A. Hammer for scale=32 cm in height.

Cinnabar Mountain (CM).—At Cinnabar Mountain, 18 m of strata (Fig. 4.1) recognized as Dinwoody Formation (e.g., Ciriacks, 1963) are exposed between the strata of the Permian Shedhorn Sandstone Formation and red beds of presumably

Triassic age. The contact to the underlying unit appears non-conformable. The section is dominated by laminated siltstones as well as bituminous and sandy packstones and grainstones. The comparably low thickness and the paleogeographic position of the

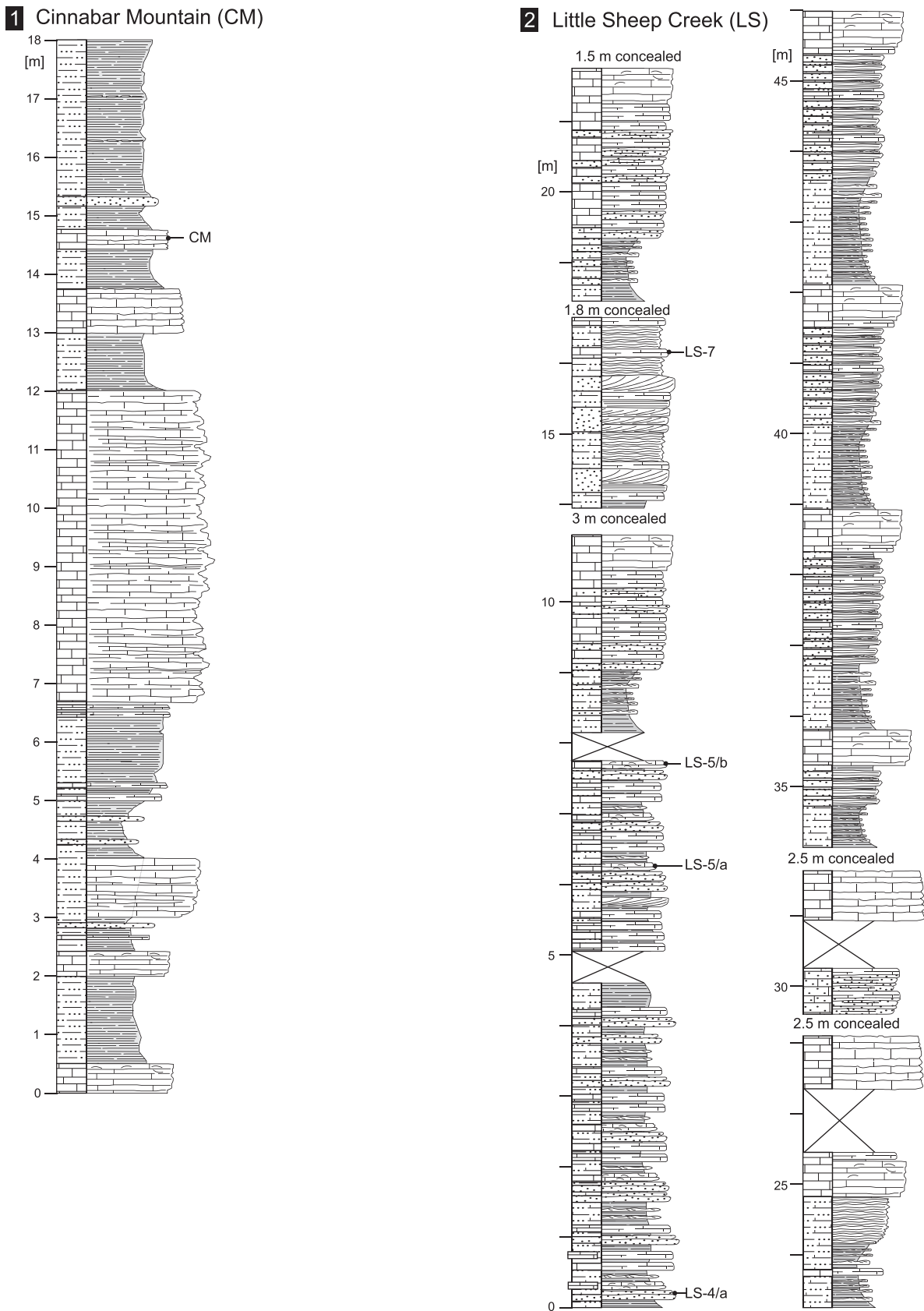


FIGURE 4—Sections of the Dinwoody Formation in southern Montana. 1, Cinnabar Mountain Pasture; 2, Little Sheep Creek.

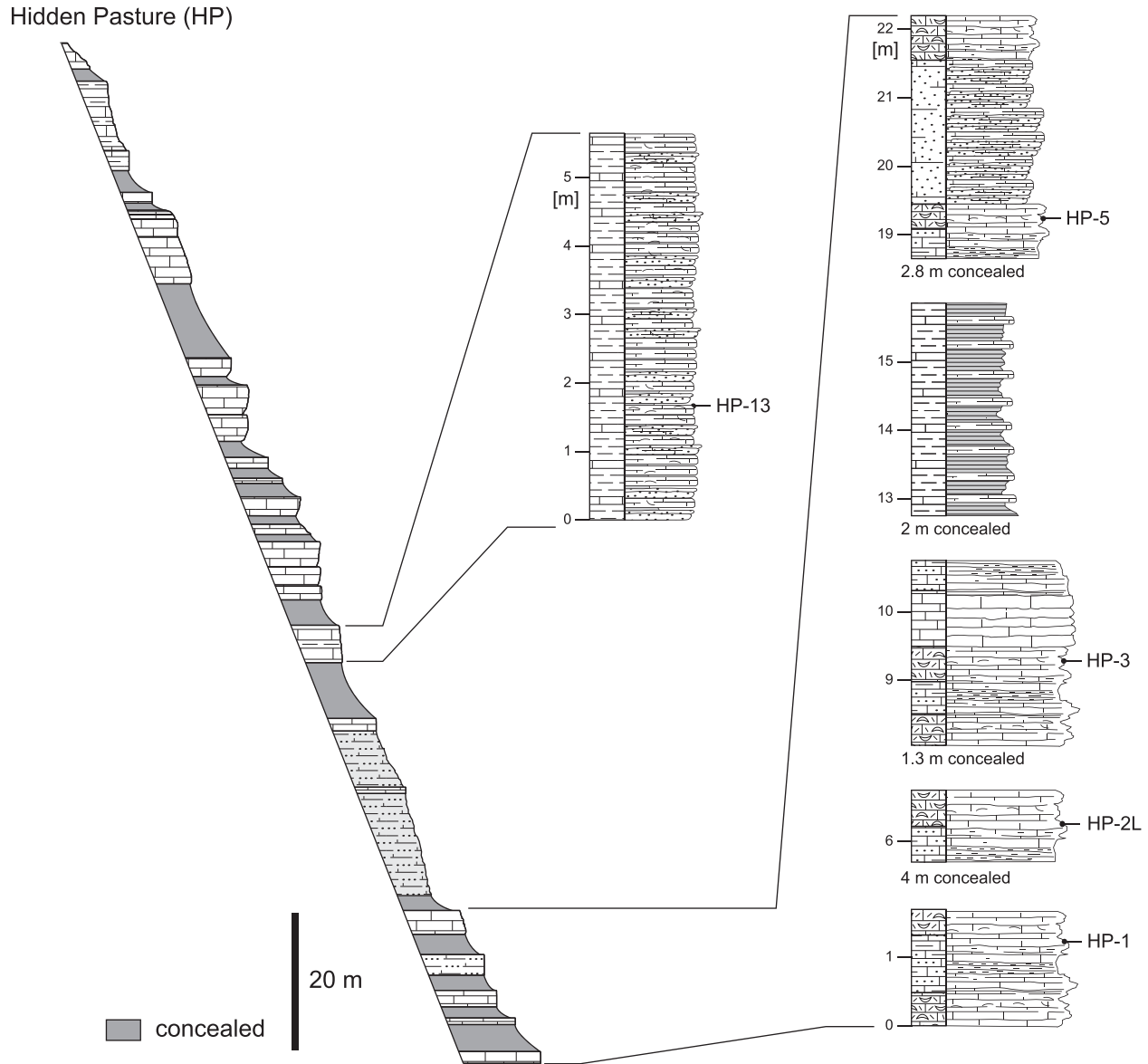


FIGURE 5—Section of the Dinwoody Formation at the Hidden Pasture locality of southern Montana.

section indicate that these strata were deposited in a rather proximal setting of the Dinwoody basin. The lack of criteria to recognize shallow and marginal marine deposition (e.g., cross bedding, ripple lamination, mud cracks) and the dominance of laminated siltstone as well as the high content of bitumina in the limestones suggests that this part of the basin was rather restricted with predominating quiet water conditions.

Tendoy Range (LS, HP).—In the Tendoy Range of southwestern Montana, the Dinwoody Formation attains a thickness of about 190 meters but pinches out towards the east and the north (Scholten et al., 1955). The Permian–Triassic transition has not been observed. The transition to the overlying red beds (Woodside Formation) appears to be gradual. In both the Little Sheep Creek (LS) (Fig. 4.2) and Hidden Pasture (HP) section (Fig. 5) visited during this study, the sedimentary record starts within Lower Triassic strata. These are composed of calcareous siltstones, fine-grained sandstones and limestones. Most siltstone intervals are poorly exposed. In the sandstone-dominated units, sedimentary structures including synaeresis cracks, wave and current ripple-lamination, trough cross-beds indicate shallow marine deposition in a wave-agitated environment. Most

limestones are composed of massive bioclastic grainstone and rudstone and are intercalated within shallow marine sandstone beds. All sampled fossiliferous levels represent a shallow marine facies.

Bear Lake Area (HS, SC).—The section at Sleight Canyon (Fig. 6.1) is dominated by a monotonous succession of finely laminated siltstones. In the lower part, thin beds of very fine-grained sandstones are intercalated and levels with convolute bedding occur (Fig. 6.1). Some sets of siltstone beds show distinct lenticular lower boundaries (Fig. 7.5). Thin horizons with climbing ripples occur rarely within these beds. Despite the overall fine-grained nature of the deposits, these sedimentary signatures argue for fast deposition. Hence, this part of the section is interpreted to record sedimentary bypass of silt-size particles at the outer slope of the Dinwoody basin. The upper third of the section comprises slightly calcareous siltstones, which have a more massive appearance presumably due to increased bioturbation (Fig. 7.2) and wave activity as indicated by some ripple cross-laminated horizons. The section is topped by large-scale trough cross-bedded sandstones and capped by a distinct conglomerate bed.

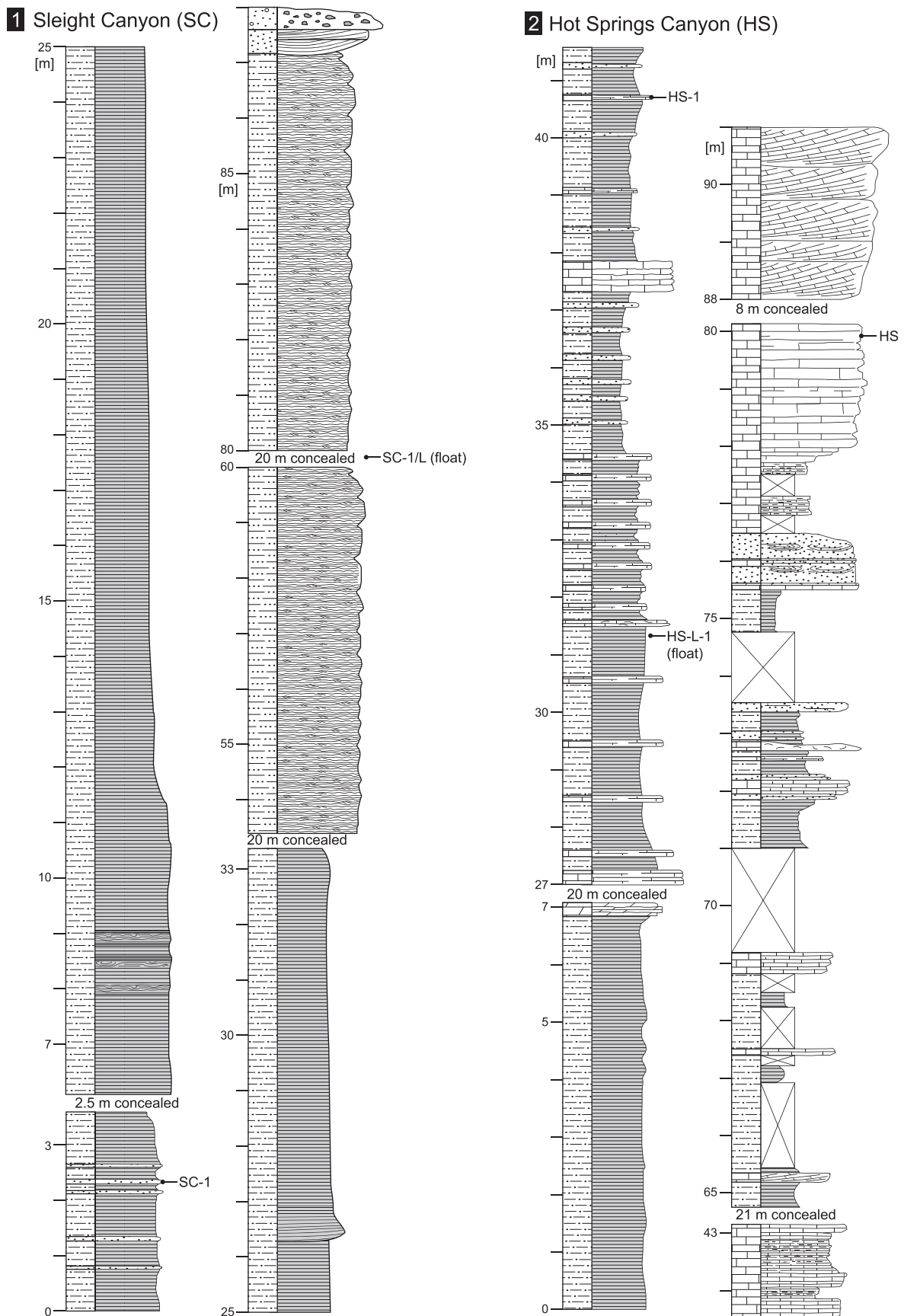


FIGURE 6—Sections of the Dinwoody Formation of southeastern Idaho. 1, Sleight Canyon; 2, Hot Springs Canyon.



FIGURE 7—Sedimentary features and facies of the Dinwoody Formation in the southwestern Idaho. 1, laminated siltstone of the outer shelf, section SC; 2, bioturbated siltstone intervals at the top of section SC; 3, laminated shales and siltstones of the outer shelf/basinal facies, head of hammer pointing up-section, section HS; 4, large scale trough cross-bedded sandstones interbedded with bioturbated siltstones indicating shallowing upward trend in section SC; 5, incised wide-angle channels of siltstone in the middle part of section SC.

At Hot Springs Canyon (Fig. 6.2), the lower part is similarly developed with thin sandstone beds being more frequently intercalated. Discrete carbonate beds, mainly massive mudstone and floatstone, are intercalated towards the top of the section, which is capped by massive, indistinctly trough cross-bedded recrystallized limestone. The following interval is poorly exposed but reddish scree is indicative of the Woodside Formation. Both sections are largely unfossiliferous and all sampled levels are interpreted to have been deposited in outer shelf environments as suggested by the absence of sedimentary structures indicative of wave activity. This agrees well with paleogeographic reconstructions, which place the Bear Lake area within the offshore basin of the Dinwoody Basin (e.g., Paull and Paull, 1994).

Terrace Mountain (TM).—In this area, the Dinwoody is about 500 meter thick (Stifel, 1964). Because virtually the whole section is covered by vegetation or float, a reliable reconstruction of the sedimentary environment and logging of a continuous section at the Terrace Mountain locality was not possible. Rarely exposed massive limestone beds were sampled in an east–west transect perpendicular to the strike of the Terrace Mountain syncline. According to the description of Stifel (1964) and McCarthy and Miller (2002), the dominant lithotype is laminated siltstone. Based on the relatively large thickness and the overall

dominance of fine-grained sediments, we infer that rocks of the Dinwoody Formation in this area were deposited in an outer shelf setting.

SYSTEMATIC PALEONTOLOGY

The taxonomy of the Dinwoody macroinvertebrate fauna is comparatively well known and identification of species is rather unproblematic using the studies of Girty (1927), Newell and Kummel (1942), Ciriacks (1963), and Newell and Boyd (1995) as a guideline for principle species identification. A most up-to-date monograph on a similar fauna from Far-Eastern Russia has been provided by Shigeta et al. (2009). All figured (Fig. 8) specimens are housed in the collection of the Paleontological Institute and Museum, Zurich University (abbreviation PIMUZ).

- Class BIVALVIA Linnaeus, 1758
- Infraclass AUTOLAMELLIBRANCHIATA Grobden, 1894
- Subclass PTERIOMORPHA Beurlen, 1944
- Order PTERIOIDA Newell, 1965
- Suborder PTERIINA Newell, 1965
- Superfamily AMBONYCHIOIDEA Miller, 1877
- Family MYALINIDAE Frech, 1891
- Genus MYALINELLA Newell, 1942

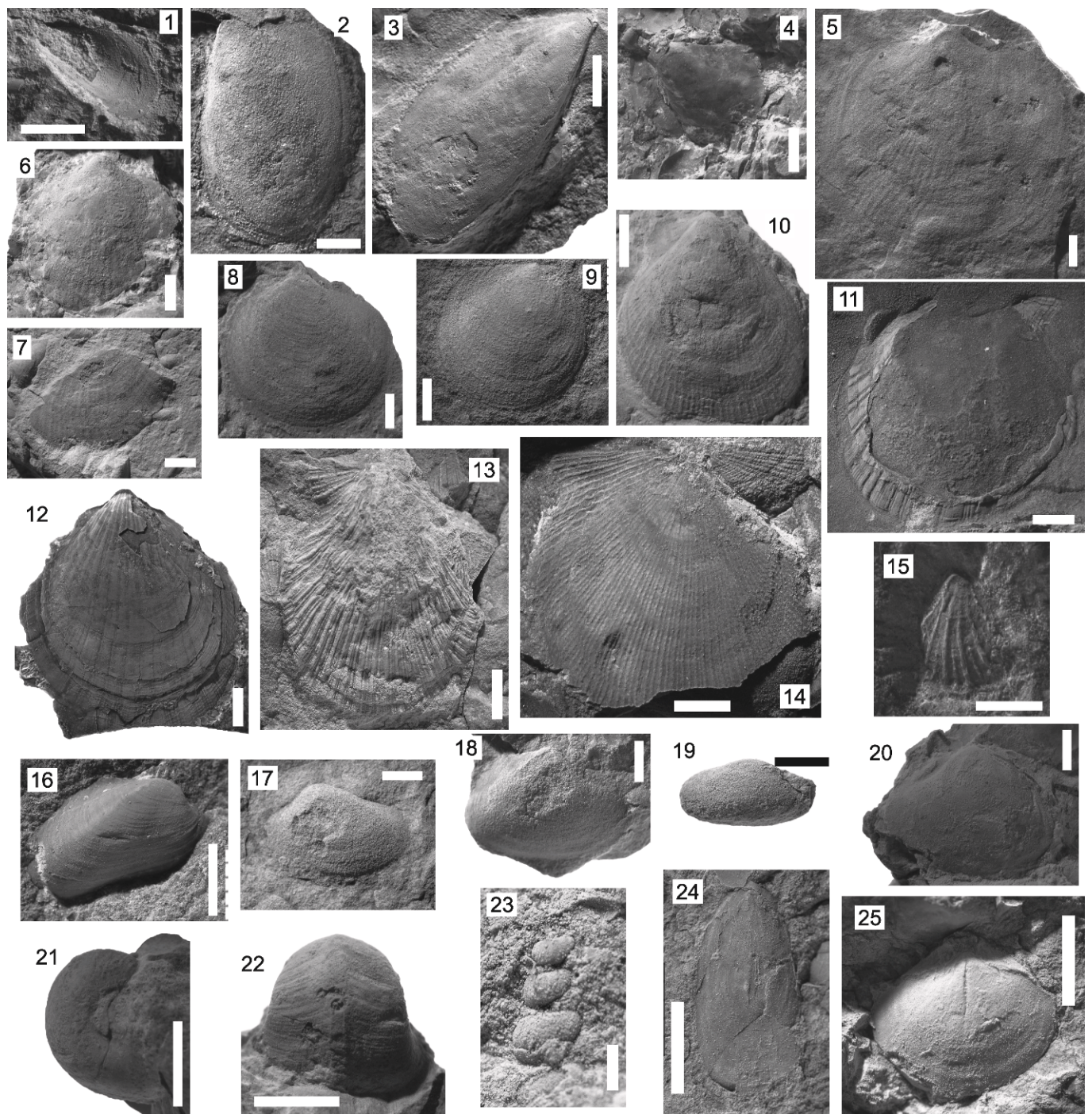


FIGURE 8—Body fossils of the Dinwoody Formation recognized in this study. 1, *Myalinella postcarbonica*, right valve, HS, PIMUZ 30523; 2, *Promyalina spathi*, left valve, GV-A-4, PIMUZ 30538; 3, *Promyalina putiatinensis*, right valve, LPA-2, PIMUZ 30528; 4, *Pteria? ussurica*, left valve, GV-A-8, PIMUZ 30540; 5, *Claraia mulleri*, left valve, float at section GV-A, PIMUZ 30539; 6, *Claraia mulleri*, left valve, GV-A-5, PIMUZ 30541; 7, *Claraia cf. stachei*, left valve, LPA-A, PIMUZ 30529; 8, *Claraia aurita*, left valve, CM, PIMUZ 30531; 9, *Claraia aurita*, right valve, CM, PIMUZ 30532; 10, *Leptochondria occidentana*, left valve, LPA-2, PIMUZ 30527; 11, *Eumorphotis amplicostata*, left valve, HP-2L, PIMUZ 30537; 12, *Eumorphotis amplicostata*, left valve, LS-5/b, PIMUZ 30536; 13, *Eumorphotis multiformis*, left valve, LS-7, PIMUZ 30533; 14, *Eumorphotis multiformis*, right valve, LS-7, PIMUZ 30534; 15, *Eumorphotis cf. ericius*, left valve, LS-7, PIMUZ 30535; 16, *Permophorus bregeri*, right valve, HS, PIMUZ 30524; 17, *Unionites fassaensis*, left valve, GV-A-3, PIMUZ 30542; 18, *Unionites fassaensis*, right valve, GV-B-1, PIMUZ 30543; 19, *Unionites canalensis*, left valve, GV-B-2, PIMUZ 30544; 20, *Neoschizodus laevigatus*, right valve, GV-A-5, PIMUZ 30545; 21, *Dicellonema abrekensis* LPA-2, lateral view, PIMUZ 30526; 22, *Dicellonema abrekensis*, LPA-2, dorsal view, PIMUZ 30526; 23, *Coelostylina* sp. A, HS, PIMUZ 30525; 24, *Lingula borealis*, ventral valve, GV-B-B, PIMUZ 30546; 25, *Periallus woodsidensis*, dorsal valve, TM-4, PIMUZ 30530. If not otherwise indicated, all scale bars=5 mm.

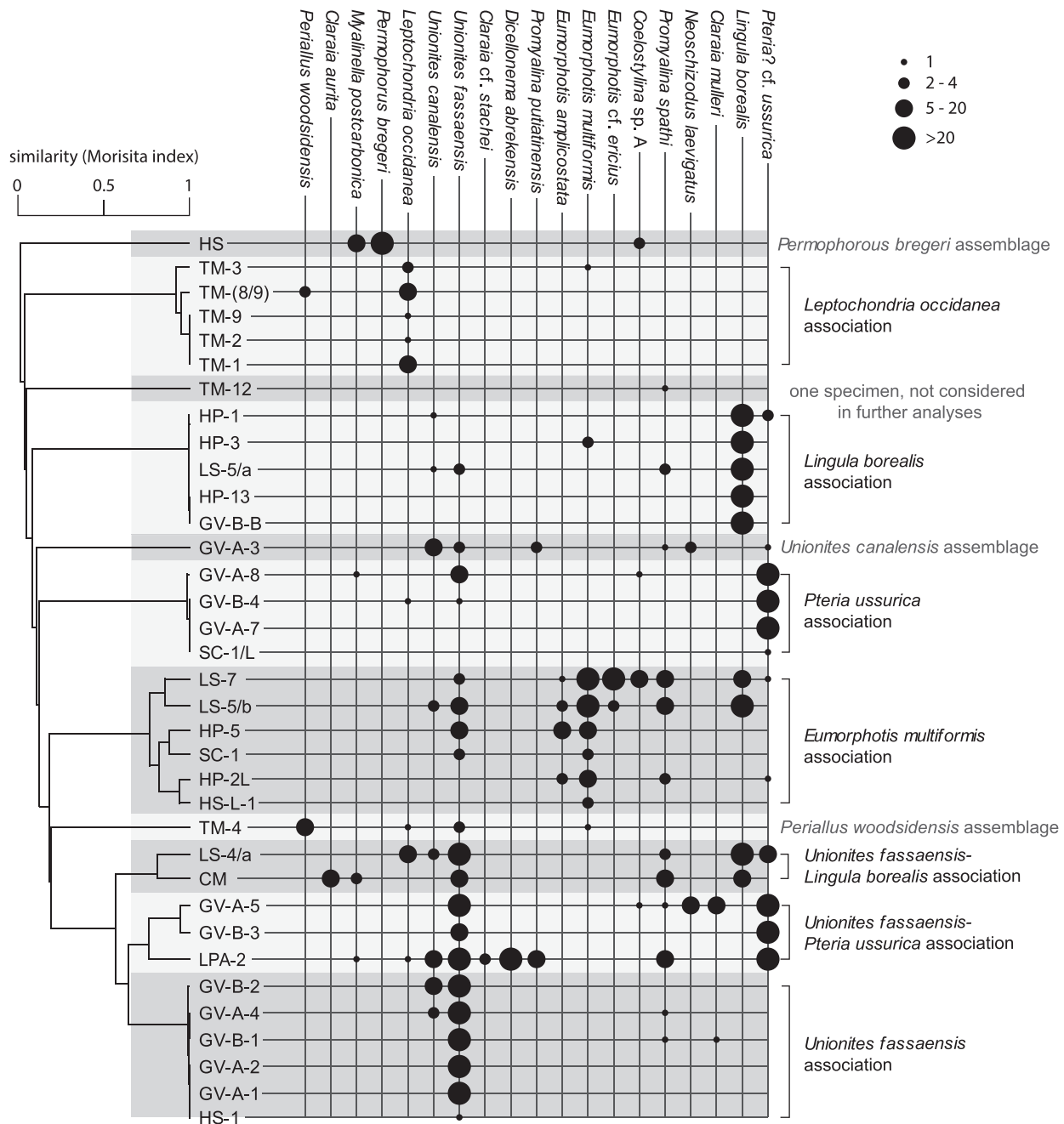


FIGURE 9—Results of the Q-Mode (samples) cluster analysis using the unweighted paired group algorithm and Morisita index of similarity. Classes of abundances (circle size) represent the quartiles of absolute-abundance frequencies.

ranges from 0.26 to 1 (mean average=0.51). However, two samples (SC-1, HS-L-1) with very low number of specimen cause underestimation of diversity and overestimation of dominance of the average values. Ecological guilds present in this association include epifaunal- (five species), shallow infaunal (three species), and endobysate (one species) suspension feeders as well epifaunal detritivores (one species). However, in terms of numerical abundance, epifaunal and shallow infaunal forms clearly dominate.

The relatively high overall diversity, low dominance, and ecological heterogeneity of this assemblage suggest that no pronounced environmental stress was present during deposition. Samples that constitute this assemblage are mainly derived from

limestones of the sections of the Tendoy Range (LS, HP), where they are present over long lithostratigraphic ranges.

Pteria ussurica association.—The *Pteria ussurica* association (Fig. 10.5) is represented by the samples SC-1L, GV-A-7, GV-A-8, and GV-B-4 and is overwhelmingly dominated by this species. Other species include *Unionites fassaensis*, *Myalinella postcarbonica*, and *Coelostylina* sp. A, which are recorded infrequently. Individual sample diversity ranges from 1 to 4 (mean average=2.3). Dominance ranges from 0.79 to 1 (mean average=0.94). Ecological guilds present in this association include epifaunal suspension feeders (two species) as well as shallow infaunal-, endobysate suspension feeders and epifaunal detritivores represented by one species each. However, endobysate suspension feeders completely dominate in numerical

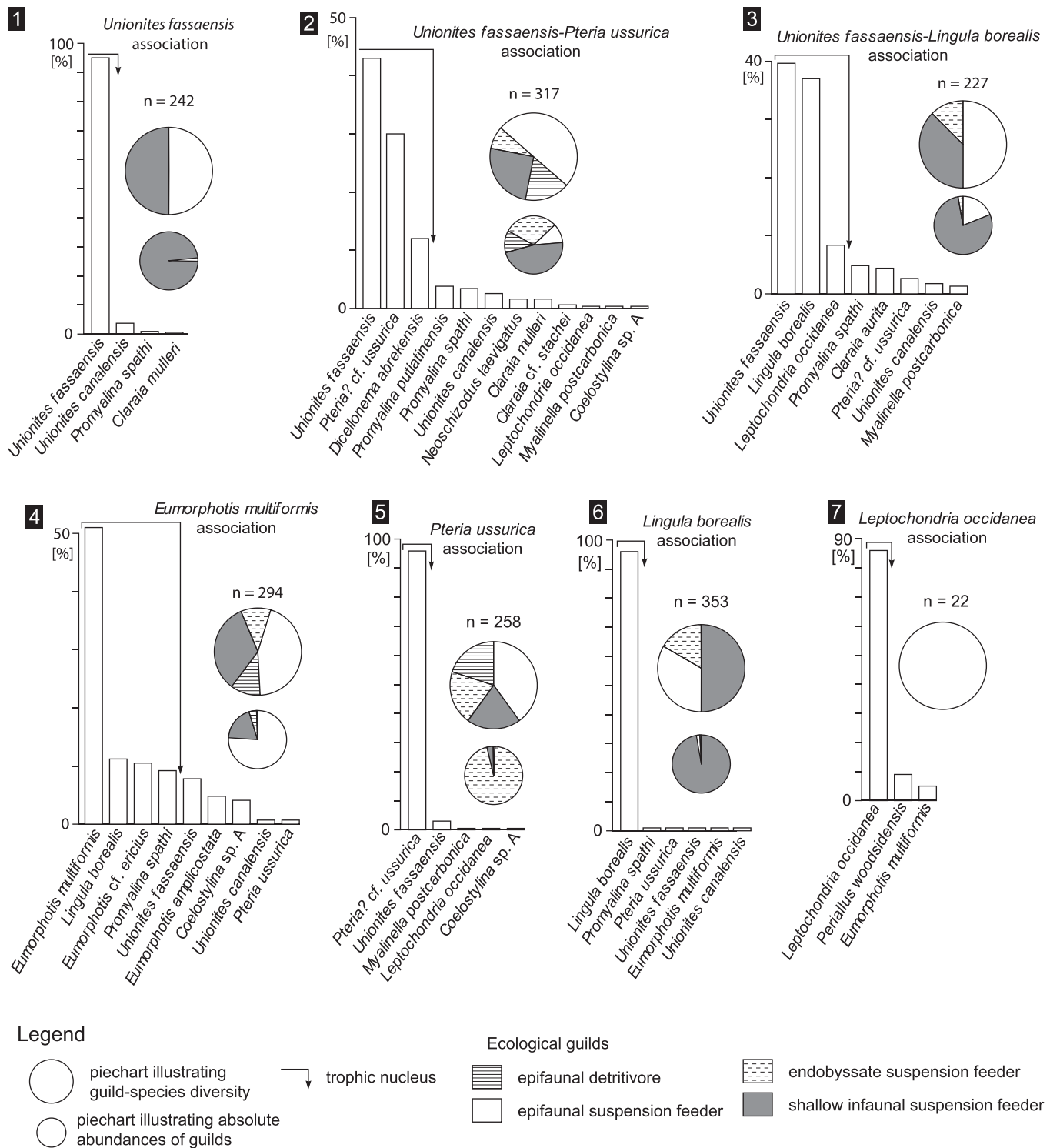


FIGURE 10—Benthic associations recognized in the Dinwoody data set showing frequencies of identified fossils, the trophic nucleus, guild species diversity based on the number of species representing benthic guilds (large pie charts) as well as absolute abundance of guilds (small piecharts). These diagrams are based on merged samples that were grouped into one association in the cluster algorithm. 1, *Unionites fassaensis* association; 2, *Unionites fassaensis-Pteria ussurica* association; 3, *Unionites fassaensis-Lingula borealis* association; 4, *Eumorphotis multiformis* association; 5, *Pteria ussurica* association; 6, *Lingula borealis* association; 7, *Leptochondria occidentanea* association.

abundance. It seems that this association is a strongly depleted *Unionites fassaensis-Pteria ussurica* association and with its high dominance values and low diversities, it may indicate harsh or unstable environmental conditions. It could represent a decline in ecosystem stability after relatively balanced conditions recorded

in the samples in the middle part of the Formation at the same localities.

Lingula borealis association.—This association (Fig. 10.6) is recorded by the samples GV-B-B, HP-13, HP-3, HP-1, and LS-5/a. It is dominated by *Lingula borealis*. Other species in this

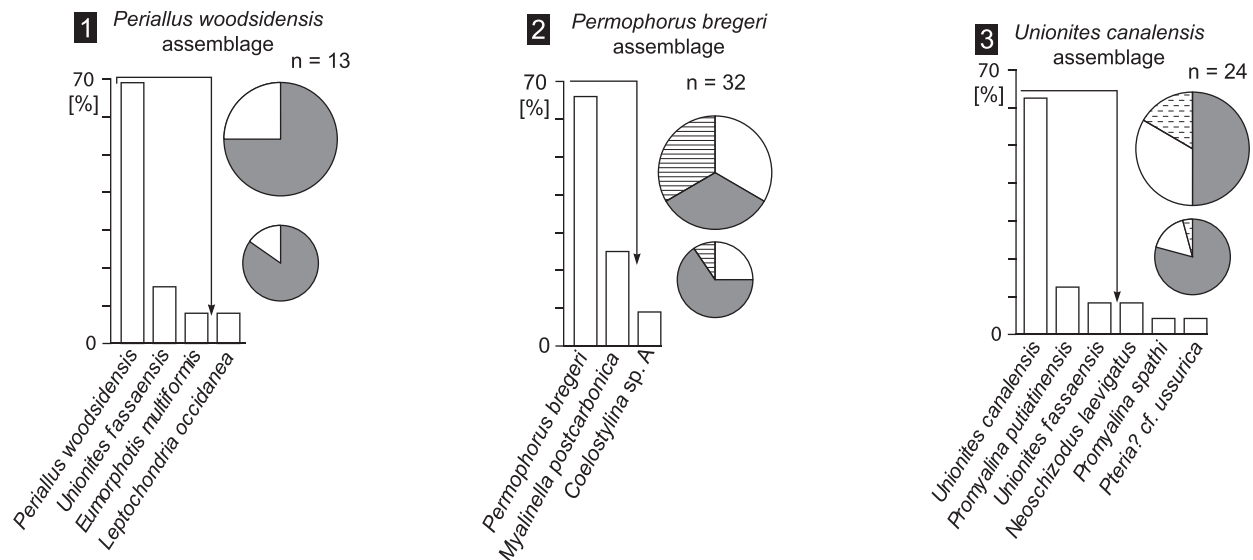


FIGURE 11—Benthic assemblages that were not assigned to associations in the cluster algorithm. See Figure 10 for legend and explanations. 1, *Periallus woodsidensis* assemblage; 2, *Permophorus bregeri* assemblage; 3, *Unionites canalensis* assemblage.

association are *Eumorphotis multiformis*, *Pteria ussurica*, *Unionites fassaensis*, *Unionites canalensis*, *Promyalina spathi* but these are numerically of minor importance. Individual sample diversity ranges from 1 to 4 (mean average=2.2). Dominance ranges from 0.87 to 1 (mean average=0.93). Ecological guilds include shallow infaunal (three species), epifaunal (two species) and endobysate (one species) suspension feeders. In terms of absolute abundance, shallow infaunal suspension feeders are overwhelmingly dominant. The high dominance values, low diversities, and the ecological structure, which is dominated by infaunal suspension feeders, is suggestive of stressed conditions, which may characterize the siliclastic siltstone to very fine-grained sandstone facies in which *Lingula borealis* commonly occurs.

Alternatively, the ecological parameters and low diversity may be related to the stratigraphical proximity to the mass extinction level, because this association is preferentially recorded in the lower parts of the sections GV-B, HP and LS.

Leptochondria occidentanea association.—The *Leptochondria occidentanea* association (Fig. 10.7) is exclusively recorded by the samples from the section TM and dominated by this species, which forms its trophic nucleus. Accessory species are *Eumorphotis multiformis* and *Periallus woodsidensis*. Due to poor preservation and very little sample material, the number of specimens is not very high and ecological indices are probably not very significant. Sample diversity is 1 or 2 (mean average=1.4) and dominance values range from 0.63 to 1 (mean average=0.86). The group of epifaunal suspension feeders is the only ecologic guild present in this association. The high dominance values, low diversities, and the impoverished ecological structure indicate unstable conditions but, as already noted, the low number of sampled specimens in this section makes any interpretation tentative only.

Periallus woodsidensis assemblage.—Sample TM-4 constitutes

this assemblage (Fig. 11.1) and contains *Periallus woodsidensis*, *Unionites fassaensis*, *Eumorphotis multiformis*, and *Leptochondria occidentanea*. Species richness is four and dominance is 0.51. The allocation of this assemblage within the cluster analysis appears surprising since this sample is not fundamentally different from samples that clustered in the *Leptochondria occidentanea* association. Accordingly, this assemblage is very similar to the ecological characteristics outlined in the paragraph above.

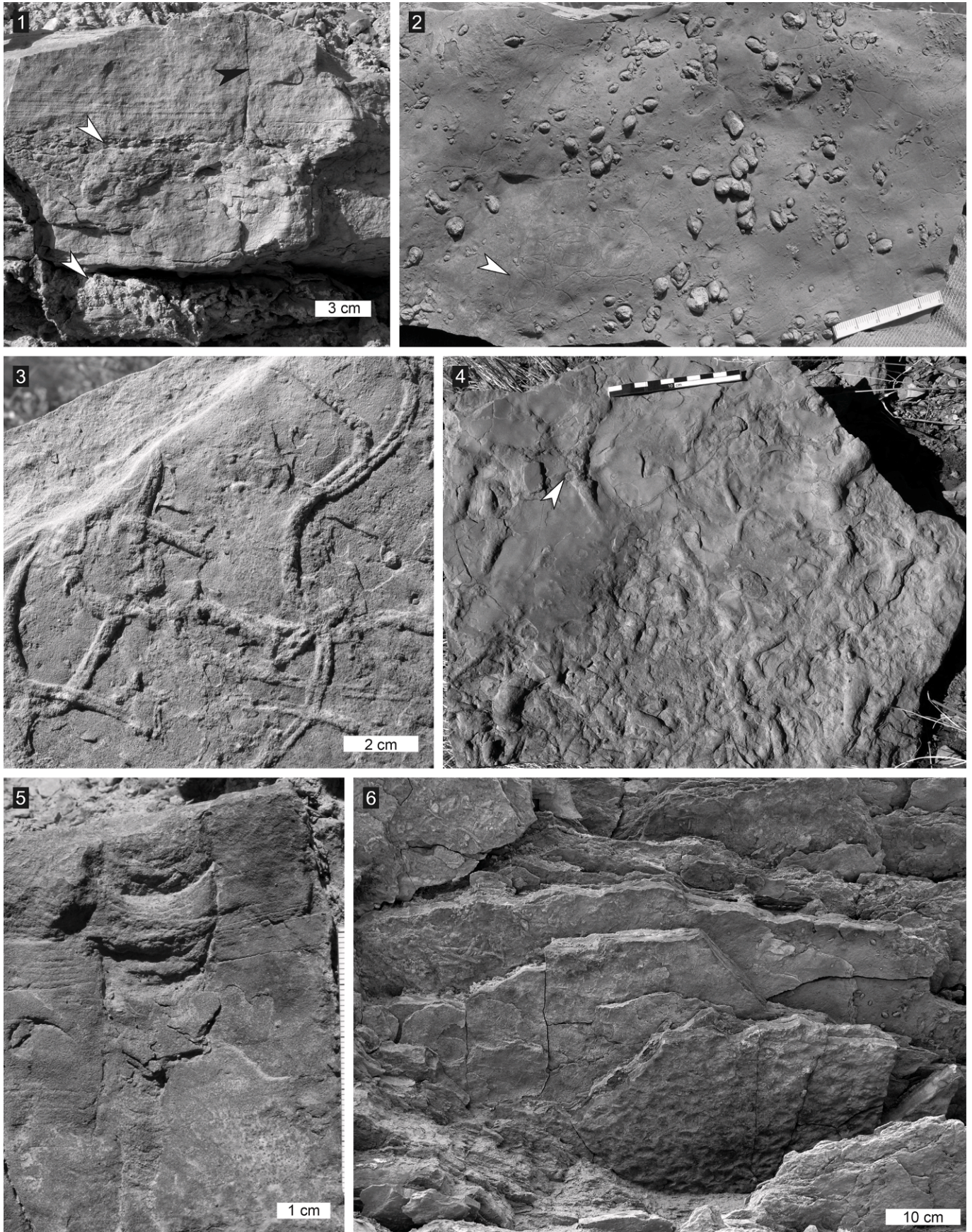
Permophorus bregeri assemblage.—The trophic nucleus of this assemblage (sample HS; Fig. 11.2) is represented by *Permophorus bregeri* and *Myalinella postcarbonica*. *Coelostylinia* sp. A is a minor component of this assemblage. The dominance is 0.50. *Myalinella postcarbonica* is an epifaunal- and *Permophorus bregeri* a shallow infaunal suspension feeder. *Coelostylinia* sp. A is an epifaunal detritivor. All three ecologic guilds are represented by one species each. The absolute abundance numbers indicate the dominance of shallow infaunal suspension feeders. As noted in the discussion on *Permophorus bregeri*, this species appears to be unique to sections in southeastern Idaho and, thus, the isolated position in the cluster analysis could reflect a paleogeographic signal.

Unionites canalensis assemblage.—The *Unionites canalensis* assemblage (Fig. 11.3) is represented by the sample GV-A-3 and its trophic nucleus is composed of *Unionites canalensis*, *Promyalina putiatinensis*, and *Unionites fassaensis*. Additional occurrences include *Promyalina spathi*, *Pteria ussurica*, and *Neoschizodus laevigatus*. Species richness is six and dominance is 0.42. This sample is very similar to the *Unionites fassaensis*–*Pteria ussurica* association, and all ecological characteristics outlined in the corresponding paragraph apply to this association, too.

Ichnology.—Trace fossils (Fig. 12) were not systematically sampled and a lengthy discussion is beyond the scope of this

Figure 12—Trace fossils of the Dinwoody Formation. 1, *Skolithos linearis* (black arrow) in laminated sandstones with truncated top; note the pervasively bioturbated intervals (white arrows); 2, *Lockeia* isp. (positive hyporelief) and *Gordia marina* (negative hyporelief, white arrow), a typical ichnoassemblage of the middle Dinwoody Formation as recorded in section HP; 3, *Gyrochorte* cf. *comosa* as positive epirelief in fine-grained sandstones of the upper Dinwoody Formation at section HP; 4, pervasive horizontal bioturbation in lower bedding plane view dominated by *Palaeophycus tubularis* and questionably *Thalassinoides* isp. (wide arrow); 5, retrusive *Diplocraterion* isp. seen in full relief in siltstone in the lower part of section HS; 6, exposed lower bedding planes revealing abundant horizontal bioturbation, middle section HP.

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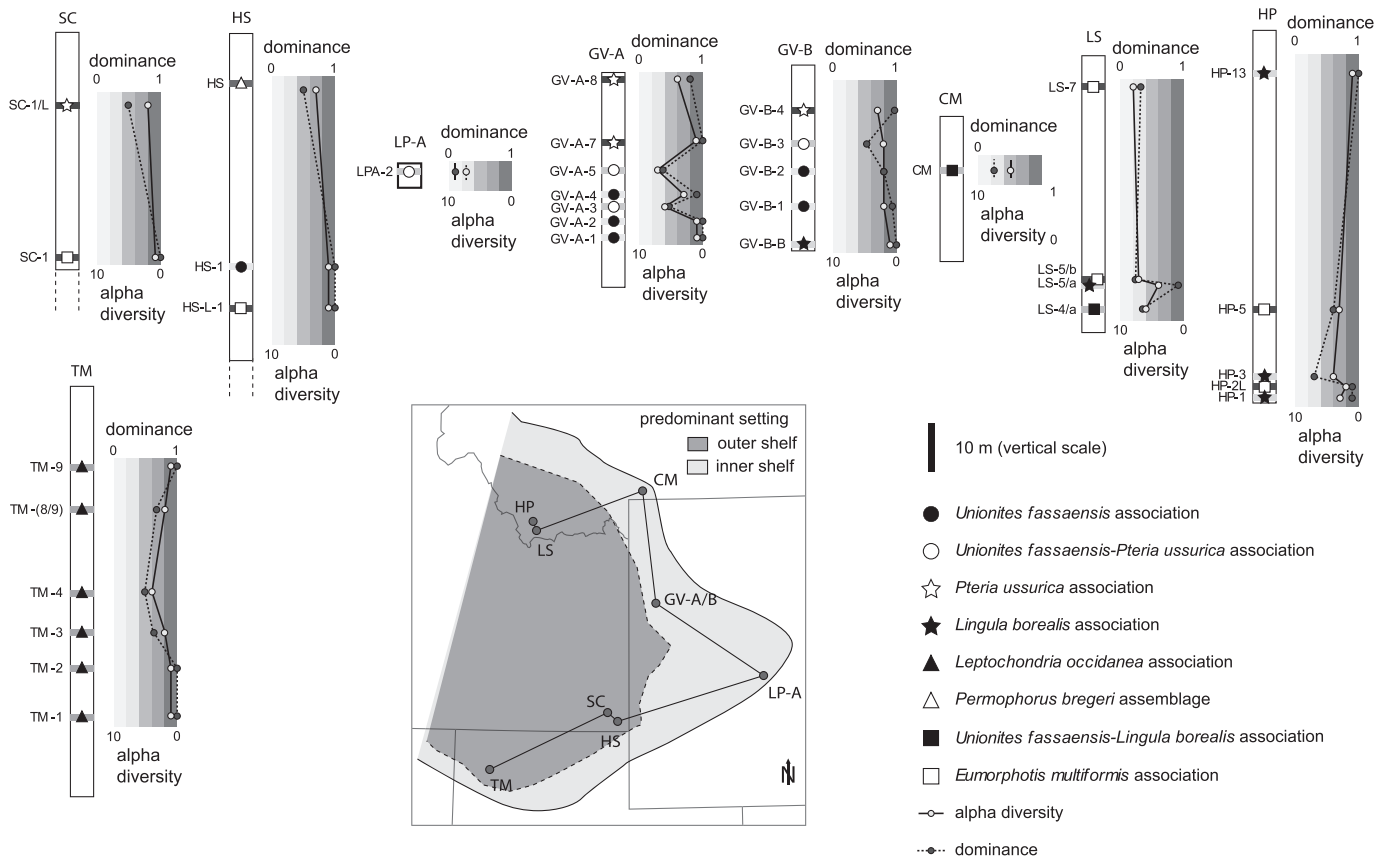


FIGURE 13—Comprehensive compilation of diversity, dominance and associations to depict spatial and temporal trends within the Dinwoody Formation. Columns height represents scaled stratigraphic thicknesses. Dashed lines below the columns indicate that unsampled parts of the sections are excluded to maintain graphic lucidity. For lithological information and precise sample levels see Figures 2, 4, and 5. Arrangement of sections follows the transect indicated on the locality map.

paper, but some general observations are worth being added here. Intensive bioturbation (Fig. 12.1) is rarely observed and in most parts of the sections and even scarce biogenic sediment reworking is rare. However, exposed bedding planes (Fig. 12.4, 12.6) of virtually unbioturbated strata revealed that horizontal epifaunal and shallow tier trace fossils such as *Asteriacites*, *Gordia* (Fig. 12.2), *Gyrochorte* (Fig. 12.3), *Lockeia* (Fig. 12.2), *Palaeophycus*, and *Planolites* may be abundant. Vertical bioturbation is represented by *Arenicolites*, *Diplocraterion* (Fig. 12.5), and *Skolithos* (Fig. 12.1), which are more frequently observed in the middle part of the Hot Springs, Slight Canyon, Little Sheep Creek, and Hidden Pasture sections. The trace fossils indicate a very simple tiering structure which is dominated by epifaunal and shallow infaunal detritus feeders (*Planolites*, *Gyrochorte*, *Gordia*) and epifaunal to infaunal suspension feeders (*Arenicolites*, *Diplocraterion*, *Lockeia*, *Palaeophycus* and *Skolithos*). Additionally, *Asteriacites* and *Palaeophycus* indicate the presence of epifaunal to shallow infaunal carnivores or scavengers.

Summary.—In general, the ecological structure of the Dinwoody fauna is very simple. In the shelly fauna, epibyssally attached, endobyssate, and shallow infaunal suspension feeders as well as epifaunal detritus feeders are recognized, which sums up to four out of 13 typically Mesozoic benthic guilds (cf. Aberhan, 1994). In most samples, epifaunal and shallow infaunal bivalves form the main constituents. *Lingula* or *Pteria* are locally dominant. The trace fossils add three more benthic guilds (shallow infaunal detritus feeders, infaunal suspension feeders, and epifaunal or shallow infaunal carnivores) to the list. With bivalves, gastropods, and inarticulate brachiopods, only three

marine invertebrate classes are recorded. Apart from a single specimen of the ophiurid resting trace *Asteriacites* observed in section LPA, echinoderms are absent. Trace fossil/trace maker relationships of remaining trace fossils mentioned above are too equivocal to reliably conclude on the presence of particular soft-bodied marine invertebrates in the Dinwoody Formation.

SPATIAL AND TEMPORAL TRENDS

Apart from ecological conditions, the diversity, taxonomic composition, and ecological structure of paleocommunities is, to a varying extent, also controlled by age (stratigraphic level) and paleogeography. Although trends are not very distinct in the Dinwoody data set and a poor age control hampers precise correlation of samples, detailed analyses reveal some insight into recovery dynamics of the Early Triassic marine ecosystems in the western U.S. Trends of alpha-diversity, dominance of samples and the spatial distribution of the benthic associations are summarized in Figure 13.

Ecology structure and diversity through time and space.— There is a considerable stratigraphical gap between Permian and Triassic rocks. Accordingly, the actual extinction horizon is not recorded in the study area. Strata of the basalmost Dinwoody Formation (Fig. 13) contain paucispecific associations such as the *Unionites fassaensis* and the *Lingula borealis* association, which both are characterized by very few numerically dominant taxa and a very simple ecology with one guild being highly dominant. In these beds, the *Eumorphotis multiformis* association (Fig. 14.1) is also represented by low-diverse samples.

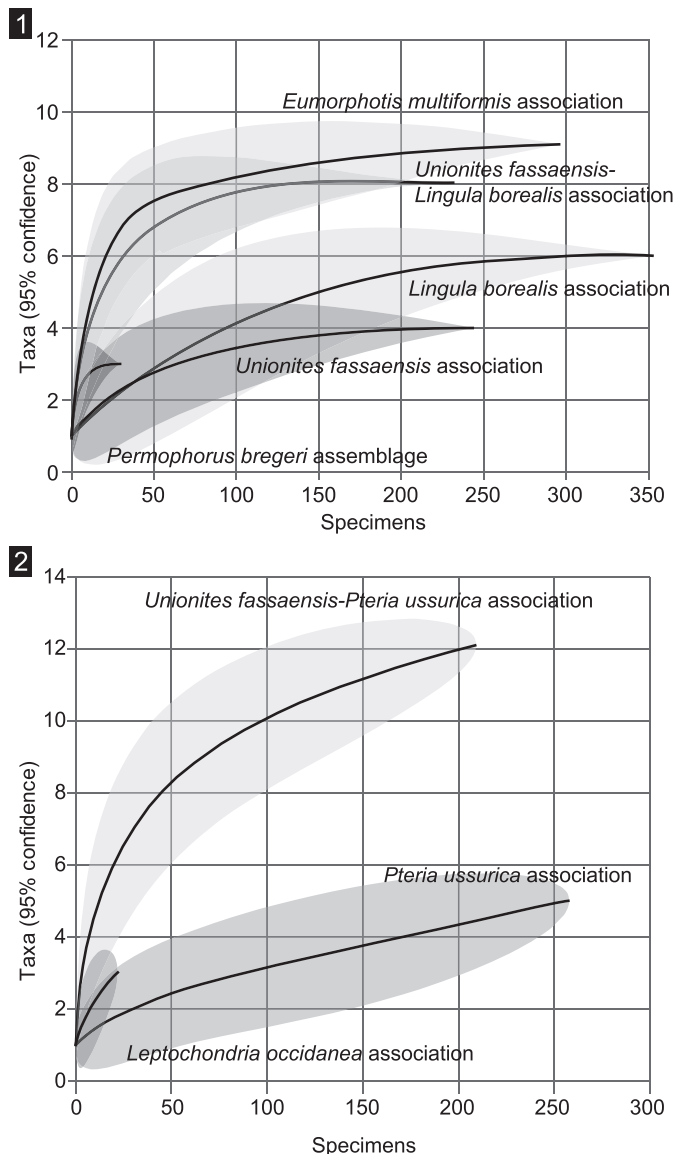


FIGURE 14—Rarefied alpha diversities for the associations identified in the data set. 1, associations which level off, indicating that further sampling effort would have had no significant impact on alpha diversities; 2, associations with more open rarefaction curves indicating that further sampling would have added more species and thus indicates that alpha-diversity values for these associations are tentative.

In the middle part of the sections LPA, GV-A/B, HP and LS, faunas considerably increase in diversity with up to nine species recorded in single samples and up to 12 species present in the fairly diverse *Unionites fassaensis*–*Pteria ussurica* and the *Eumorphotis multiformis* associations. Both associations and constituting samples also exhibit the lowest dominance values ($D=0.25$) of the whole dataset. Furthermore, these communities indicate balanced ecological conditions with several ecological guilds occurring in similar abundances (see Fig. 10). The *Pteria ussurica* association of the sections GV-A/B documents a huge decline to very low diversities and high dominance values higher in the sections. The sections of outer shelf settings, i.e., HS, SC, and TM, show no marked differences in diversity and dominance through time and all samples are characterized by low diversity–high dominance communities. This could indicate that water depth and paleogeography have had an effect on the ecological

structure and diversity. However, samples from these intervals are low in specimen number, and the rarefaction curves of corresponding associations (Fig. 14.2) suggest that diversity values may suffer from undersampling. Accordingly, any interpretation needs to be substantiated by more data.

Rarefaction analyses of the associations reveal sufficient sampling effort in most other cases (Fig. 14.1), with exception of the *Unionites fassaensis*–*Pteria ussurica* association (Fig. 14.2). This, however, would only corroborate its status as the most diverse association. Also the rarefaction curves of the *Leptochondria occidanea* and *Pteria ussurica* associations indicate that additional sampling would have added significantly more taxa (Fig. 14.2). The samples constituting the *Leptochondria occidanea* association are in fact characterized by a very low specimen number and it cannot be excluded that this low-diversity signal from the section TM is mainly due to poor sampling density and preservation. The *Pteria ussurica* association is comparatively well sampled and we do not expect that increased sampling would have increased alpha-diversity to a level comparable to more diverse association.

Ichnological data more or less mirror the trend seen in diversity data. Most of the trace fossils mentioned above represent domichnia and thus indicate normal marine, oxygenated conditions (e.g., Savrda and Bottjer, 1986; Ekdale and Mason, 1988). Trace fossils are particularly abundant in the middle part of the sections HP, LS and LPA.

In summary, the Dinwoody Formation is dominated by typical post extinction faunas, which are characterized by low diversity, low ecological guild diversity, and high dominance. Relatively diverse communities (for Early Triassic standards; cf. Schubert and Bottjer, 1995) are present in inner shelf deposits and restricted to the middle part of the Dinwoody Formation. Based on the occurrence of the species *Claria* cf. *stachei* and *Claraia mulleri* in the corresponding associations, this signal seems to occur around the Griesbachian–Dienerian boundary interval.

Paleogeographic variations.—It has been suggested that Early Triassic faunas had vast spatial ranges and that the portion of wide-ranging taxa on a basinal and interregional scale was generally high, at least on the genus level (Schubert and Bottjer, 1995; but see Wasmer et al., 2012). However, the portion of taxa that are unique to few associations is quite high in the Dinwoody Formation (Fig. 15), indicating some partitioning with respect to stratigraphic level or paleogeography. Figures 9 and 13 show that this partitioning mirrors spatial differences rather than stratigraphic signals, possibly due to a combination of facies effects and geographically restricted occurrences of taxa, e.g., communities which are dominated by *Unionites* are more typically recorded in deposits with a high portion of siliclastic material. As already pointed out in the discussion on the corresponding associations, this could express the tendency of this genus to tolerate salinity fluctuations (Fürsich, 1993; Geyer et al., 2005), which might have accompanied the deposition of terrigenous material. However, some associations also tend to be restricted to geographic regions. Wyoming sections mainly host the *Unionites fassaensis*–*Pteria ussurica* and the *Pteria ussurica* associations. The *Eumorphotis multiformis* association is well developed in the section of Montana and Idaho. The *Leptochondria occidanea* association is unique to northwestern Utah. However, especially the latter association probably suffers from low sampling density and low outcrop area as well as generally bad preservation at this locality. Such secondary effects may account for this pattern. A comparison with the fauna of Virgin Formation, which exhibits a low beta-diversity (Hofmann et al., 2013), furthermore shows that beta-diversity is still comparably low in Dinwoody Formation (see online Supplemental file, Excel sheet “diversity” and discussion below).

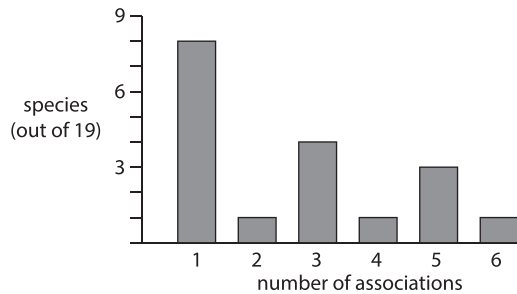


FIGURE 15—Graph illustrating the endemism of the fauna. The height of the bars indicates how many species occur in how many associations. The more the spectrum is shifted towards the left, the higher is the rate of taxa that are unique to few associations.

DISCUSSION

The Griesbachian and Dienerian substages represent the immediate aftermath of the end-Permian mass extinction. The established geochronological framework for the Early Triassic (Mundil et al., 2004; Ovtcharova et al., 2006; Galfetti et al., 2007) suggests that these two substages span a time interval of less than 1.5 million years. Faunas of this time interval, and generally of the entire Early Triassic, were suggested to be of low ecological complexity, low diversity, high dominance, and a high proportion of so-called disaster species and cosmopolitan taxa (Schubert and Bottjer, 1995; Hallam and Wignall, 1997). Recent analyses (e.g., Krystyn et al., 2003; Hautmann et al., 2011; Hofmann et al., 2011) show that faunas with comparatively high diversities and low dominance values occurred at least locally, suggesting that benthic recovery was either diachronous in different paleogeographic regions (e.g., Twitchett and Barras, 2004; Twitchett et al., 2004), or that the restoration was well under way on an interregional scale significantly earlier than generally assumed (Hautmann et al., 2011; Hofmann et al., 2011). Accordingly, a continuous documentation of recovery throughout this time interval is important for testing each of these two scenarios. The Lower Triassic of the western United States represents a key area because it holds the most continuous record of a low-latitude setting from eastern Panthalassa of that time interval.

The benthic paleoecology of the Dinwoody Formation has been studied rather peripherally in Schubert and Bottjer (1995), who focused on a much broader stratigraphic and spatial scale. Schubert and Bottjer (1995) suggested that the Dinwoody communities are “characterized by very high dominance, low diversity assemblages consisting primarily of potential disaster forms, *Lingula* and *Claraia*”. In contrast, Schubert and Bottjer (1995, appendix 3) indicated nine genera of benthic organisms in the ecologically quite even samples “D3” and “D4”, which in terms of diversity and evenness overlap with more advanced faunas from the Sinbad and Virgin Formation presented in the same study. Nevertheless, the survey of Schubert and Bottjer (1995) together with some later studies (e.g., Twitchett and Wignall, 1996; Pruss and Bottjer, 2004) consolidated the view that deleterious environmental conditions persisted well into the Early Triassic (Wignall and Hallam, 1992) and, hence, were most likely responsible for a delayed recovery. The analysis presented herein allows us to reconstruct recovery patterns of Griesbachian and Dienerian benthic faunas of the western U.S. in more detail and to evaluate the recovery status and the influence of environmental stress.

Recovery patterns.—Ecological guild diversity, alpha-diversity and dominance of taxa are parameters that are generally used to define recovery stages (e.g., Schubert and Bottjer, 1995;

Twitchett et al., 2004; Twitchett, 2006; Hofmann et al., 2011). According to the criteria of Twitchett (2006, fig. 3), incipient recovery occurred at least in inner shelf habitats of the Dinwoody basin around the Griesbachian–Dienerian boundary interval. This is indicated by sample diversities of up to nine taxa (and more in associations), comparatively large diameters of burrows (more than 2 cm) and large-sized shelly fossils (up to 6 cm sized bivalves) as well as locally abundant vertical bioturbation. Benthic communities thus reached a recovery stage that was previously not expected for equatorial regions of eastern Panthalassa during this time interval (Twitchett and Barras, 2004). Moreover, the Dinwoody fauna supports the hypothesis of an interregional recovery signal around the upper Griesbachian and lower Dienerian time interval (Hautmann et al., 2011; Hofmann et al., 2011) in benthic communities.

In contrast to late Griesbachian/early Dienerian faunas of inner shelf settings, most samples from outer shelf settings and from the basal part of the Dinwoody Formation show a significant lower diversity. Wignall and Hallam (1992) suggested that outer shelf deposits of the Dinwoody Formation were accumulated under anoxic and dysoxic conditions and hypothesized that oxygen deficiency was one of the main factors to delay the recovery from the end-Permian mass extinction. The spatial trends outlined herein do not contradict this idea at least for the deeper part of the basin, but they are also in accordance with alternative explanations. The low diversity could reflect locally insufficient sample density and low specimen numbers. As outlined earlier, the *Leptochondria occidanea* association (Fig. 14.2) might have been insufficiently sampled and, thus, its true diversity has been underestimated. However, rarefaction curves of all other low diverse associations (Fig. 14.1) indicate sufficient sampling, which suggests that the general pattern outlined above is real.

Apart from oxygen deficiency, other local stress factors such as salinity fluctuations and continental run-off could have had influenced diversity, dominance, body size, bioturbation, and tiering, which were previously used as parameters for characterizing recovery stages (Twitchett, 2006, fig. 3). The low diverse *Unionites fassaensis* and *Lingula borealis* associations are exclusively recorded in siliclastic units. The former is typically associated with beds indicating high sedimentation rates. The genus *Unionites* is known to occur in brackish water settings (Fürsich, 1993; Geyer et al., 2005). *Lingula* forms mass occurrences in massive fine-grained sandstones and shales, which both testify a high input of terrestrial material. Accordingly, both associations could correspond to periods of high siliclastic input, which were likely associated with fluctuations in salinity. The rarity of stenohaline taxa such as echinoderms and ammonoids in the Dinwoody basin lends some support for this hypothesis. Similarly, Schulbert and Nützel (2005) suggested that the stressed communities of the Dienerian Gastropod Oolite Member of the Werfen Formation (Dolomites, Italy) likely reflect local fluctuations in salinity. However, freshwater input from continental sources would result in a gradient of increasing salinity from the margin of the basin towards its center, a trend that is not in accordance with the diversity increase in the opposite direction (from the center to the margin) observed in the later interval of the Dinwoody Formation. This limits the application of a reduced salinity scenario to the basal part of the Dinwoody Formation.

Another possible explanation of the low diversity of outer shelf communities is that this pattern is simply not unusual. Miller (1988) demonstrated that bivalves have shown a comparable onshore–offshore diversity trend throughout the Phanerozoic of northern America. If this diversity pattern is continuously observed throughout time intervals with no marked extinctions, the same trend cannot be considered as diagnostic for extinction

aftermaths and moreover, is not a robust indicator of unusual environmental stress. Furthermore, it is well established that near shore environments typically host first order evolutionary innovations in benthic faunas before they expand offshore (Jablonski et al., 1983; Bottjer et al., 1996). Accordingly, the relevance of low-diverse offshore faunas in the Early Triassic might have been greatly overestimated in the discussion of tempo and affecting factors of recovery processes.

Returning to the prevalence of depauperated associations recorded in the lowermost Dinwoody Formation (i.e., the *Lingula borealis* and the *Unionites fassaensis* association, Fig. 13), the most straightforward explanation is that these simply reflect the immediate outcome of the extinction event itself, rather than the persistence of unusual conditions. Eurytopic genera such as *Lingula* (Rodland and Bottjer, 2001) and *Unionites* can quickly proliferate when ecospace is vacant and no specialized taxa compete. Conversely, the diversity rise in the younger interval of the Dinwoody Formation is most likely caused by the establishment of more specialized species, which outcompete pioneering generalists as they successively reappeared after the extinction (e.g., “preadapted survivors” of Kauffman and Harries, 1996). In the Dinwoody Formation, possible candidates are taxa such as *Promyalina putiatinensis*, *Eumorphotis amplicostata*, or *Leptochondria occidanea*. These species are rare in sum but contribute to higher diversities in some samples. All of them are attached epifaunal suspension feeders. The competitive advantage of these species in comparison to the two infaunal species *Lingula borealis* and *Unionites fassaensis* could be a more efficient filter feeding (Cranford and Grant, 1990; McRoberts and Newton, 1995). These, or closely related species became also widely established in the Spathian Virgin Formation, which records normal marine conditions (Hofmann et al., 2013). Accordingly, their appearance in the Dinwoody Formation makes persistent environmental stress rather unlikely.

Summarized, the low diversity of post-extinction faunas does not necessarily require unusual environmental conditions or ubiquitous stress (Hallam, 1991; Wignall and Hallam, 1992). Alternative explanations include 1) sampling bias, 2) local facies effects, 3) normal onshore-offshore trends, and 4) the immediate outcome of the extinction event itself. For the Dinwoody Formation, particularly the scenarios 3 and 4 challenge previous models of oxygen deficiency as the major driver of diversity pattern.

Trends in alpha- and beta-diversity.—Hofmann et al. (2013) proposed that trends in alpha-diversity (within-habitat diversity) and beta-diversity (between-habitat) provide a potential tool for discriminating between two recovery stages, the first ending with habitat saturation and the second ending with completion of ecosystem differentiation. “Undersaturated” ecosystems that prevail in the first recovery phase are characterized by a low degree of competitive exclusion simply because the number of competing species was low. In this situation, the need for resource partitioning, e.g., by separation along environmental gradients, is lower than in background times, and species may be able to exist through the full range of their fundamental niches. Accordingly, a relatively low beta-diversity is predicted as being indicative for undersaturated ecosystems. The scenario of ecosystem undersaturation offers an intrinsic explanation for the wide environmental range of taxa in the aftermath of the end-Permian mass extinction as an alternative to previous models that hypothesized the persistence of harsh environmental conditions (Pruss and Bottjer, 2004; Boyer et al., 2004; Mata and Bottjer, 2011). The stage of ecosystem undersaturation ends when diversity has increased by origination and/or immigration of new taxa to a level where competition urges species into their ecological optimum, thereby increasing beta-diversity.

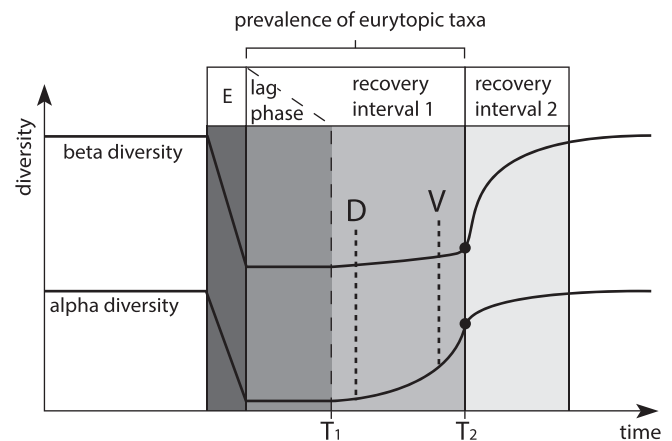


FIGURE 16—Generalized model (Hofmann et al., 2013) illustrating the role of habitat saturation in recovery processes. The drop of alpha-diversity in course of an extinction (E) leads to a corresponding loss of beta-diversity and a highly reduced competition among species. A lag phase marks a time interval in which no significant radiation and increase in alpha-diversity is observed (Erwin 2001). After initial diversification (T1, start of recovery interval 1), competition within habitats increases following recovering alpha-diversity. Beta-diversity remains low throughout this interval because adding new species does not result in significant competition for resources. Eventually, alpha-diversity reaches a threshold value where a critical number of species competes for same, limited resources. The time when this habitat saturation is reached is herein referred to as T2. From this time onward (recovery interval 2), species are increasingly restricted to particular niches because of competitive exclusion from neighbouring habitats. Recovery interval 2 ends when all curves level off. Logistic growth of alpha-diversity is adopted from Erwin (2001). The data from the Dinwoody Formation suggest that alpha-diversity is lower than in the Virgin Formation (Hofmann et al., 2013) whereas beta-diversity is low in both units.

The Dinwoody fauna offers a first opportunity for a comparison of alpha- and beta-diversity between Griesbachian to early Dienerian (this study) and Spathian (Hofmann et al., 2013) ecosystems of the western United States. Calculations of beta diversities for both Formations is provided in the online Supplemental file (Excel sheet “Diversity”). Mean alpha-diversity is lower in the Dinwoody Formation (6.7 species) than in Virgin Formation (13 species). Using the mean minimum beta-diversity approach outlined in the methods section, we find that beta-diversity of the Dinwoody fauna (mean maximum Jaccard coefficient of similarity=0.44) is similar to that of the Virgin fauna (mean maximum Jaccard coefficient of similarity =0.48), based on the data of Hofmann et al. (2013). The slightly higher beta-diversity (lower Jaccard coefficient) for the Dinwoody fauna is probably due to the much larger geographical extent of the sampled area and to the longer stratigraphical interval covered by the samples. These new data are therefore in accordance with the hypothesis that beta-diversity was generally low in Early Triassic ecosystems and that alpha-diversity increase precedes beta-diversity increase (Fig. 16). Between-habitat differentiation (recovery interval 2 in Fig. 16) is, thus, a Middle to Late Triassic affair, possibly fostered by increased competition.

In summary, the data of the Dinwoody Formation is in accordance with the model of Hofmann et al. (2013), which suggests that the wide environmental and geographic range of taxa is an intrinsic effect of post-extinction faunas and thus does not necessarily reflect deleterious environmental conditions.

CONCLUSIONS

Our quantitative paleoecological analysis of the benthic fauna of the Dinwoody Formation reveals that outer shelf environments and the basal part of inner shelf environments were

dominated by low diverse/high dominance associations. In contrast, inner shelf environments of the middle part of the Dinwoody Formation record comparably diverse communities with low species dominance. We infer that moderate recovery was possible at the tropical eastern margin of Panthalassa. This observation supports recent evidence for a first interregional recovery pulse around the Griesbachian–Dienerian boundary interval. The low diversity recorded in outer shelf settings is possibly not fundamentally different from comparable onshore-offshore trends in background times. The low diversity in inner shelf settings at the base of the formation most likely results from the intensity of the mass extinction itself, possibly added by local environmental stress such as reduced salinity. The Dinwoody fauna is characterized by low beta-diversity and, hence, little faunistic differentiation between habitats. This finding supports the scenario of ecologically undersaturated Early Triassic ecosystems (Hofmann et al., 2013), which temporarily allowed species to exploit unusual wide environmental and geographic ranges. Important features of post-extinction faunas such as the wide environmental range of surviving taxa and the dominance of “disaster” species may thus express intrinsic traits of ecosystems that have been affected by a mass extinction event.

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ACCESSIBILITY OF SUPPLEMENTAL DATA

Supplemental data deposited in Dryad repository: <http://dx.doi.org/10.5061/dryad.5mg73>.

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