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The geological completeness of paleontological sampling in North America

Shanan E. Peters and Noel A. Heim

Abstract.—A growing body of work has quantitatively linked many macroevolutionary patterns, including short- and long-term changes in biodiversity, rates of taxonomic extinction and origination, and patterns of extinction selectivity, to temporal variability in the sedimentary rock record. Here we establish a new framework for more rigorously testing alternative hypotheses for these and many other results by documenting the large-scale spatiotemporal intersection of the North American sedimentary rock and fossil records. To do this, we combined 30,387 fossil collections in the spatially explicit Paleobiology Database with a comprehensive macrostratigraphic database consisting of 18,815 sedimentary lithostratigraphic units compiled from 814 geographic regions distributed across the United States and Canada. The geological completeness of paleontological sampling, here defined as the proportion of the available sedimentary rock record that has been documented to have at least one fossil occurrence, irrespective of taxonomy or environment, is measured at four different levels of stratigraphic resolution: (1) lithostratigraphic rock units, (2) hiatus-bound rock packages, (3) regional stratigraphic columns, and (4) sediment coverage area (km^2). Mean completeness estimates for 86 Phanerozoic time intervals (approximately stages; median duration 5.3 Myr) range from 0.18 per interval in the case of lithostratigraphic rock units to 0.23 per interval for stratigraphic columns and sediment coverage area. Completeness estimates at all four levels of stratigraphic resolution exhibit similar temporal variation, including a significant long-term increase during the Phanerozoic that is accentuated by an abrupt Campanian–Maastrichtian peak. This Late Cretaceous peak in completeness is approximately five times greater than the least complete Phanerozoic time intervals (Early Cambrian, Early Devonian, late Permian, and Early Cretaceous). Geological completeness in the Cenozoic is, on average, approximately 40% greater than in the Paleozoic. Temporal patterns of geological completeness do not appear to be controlled exclusively by variation in the frequency of subsurface rock units or an increase over time in the proportion of terrestrial rock, but instead may be general features of both the marine and terrestrial fossil records.

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Introduction

In 1976, David Raup (Raup 1976) convincingly demonstrated that long-term diversity patterns derived from a compilation of fossil marine animal species were similar to long-term patterns in the area and volume of preserved sedimentary rock. On the basis of this striking result, Raup hypothesized that the observed trajectory of species diversity since the Ordovician may be more apparent than real, thereby igniting an intense debate over the strength of biological signals in fossil diversity data and the magnitude of the Phanerozoic increase in marine animal diversity, if any (see Miller 2000 for an excellent summary).

Although the true long-term biodiversity trajectory remains an area of active research and considerable debate (e.g., Alroy et al. 2001, 2008; Smith 2007; Stanley 2007; McGowan and Smith 2008), a growing body of work not only has affirmed Raup's initial rock-diversity comparisons, but it has gone further to show that many other macroevolutionary patterns, including short-term changes in diversity (e.g., Smith 2001; Peters and Foote 2001; Peters 2005; Smith and McGowan 2007), rates of genus extinction and origination (Smith et al. 2001; Peters and Foote 2002; Peters 2005; Peters and Ausich 2008), and differential rates of extinction among Sepkoski's (1981) Paleozoic and Modern Evolutionary Faunas (Peters 2008a), are quantitatively reproduced by the sedimentary rock record. Thus, it is becoming increasingly apparent that a detailed understanding of both the rock and fossil records is requisite for testing the strength of biological signals in many macro-

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evolutionary patterns and, more importantly, for determining their underlying causes.

Despite the empirical value of those studies to date that have compared macroevolutionary patterns with temporal variation in the rock record, all have used the same general and somewhat limited methodology, wherein a direct measure of spatiotemporal variability in the sedimentary record, such as the number of gap-bound rock packages (Peters 2005, 2006a) or geologic map area (Raup 1976; Smith and McGowan 2008; McGowan and Smith 2008; Wall et al. 2009), is compared to temporal variability in macroevolutionary patterns that derive from summary paleontological data, such as the number of genera in Sepkoski's global compendium of marine animals (Sepkoski 2002). Because these types of macroevolutionary patterns are several times removed from the field occurrences that constitute the actual fossil record, it has been impossible to determine the full extent to which spatiotemporal variation in the rock record relates to variation in paleontological data.

Here we seek to overcome this limitation by combining field-based fossil collection data in the spatially explicit Paleobiology Database (http://paleodb.org) with a comprehensive macrostratigraphic database for the United States and Canada. This exercise permits the first quantitative examinations of the large-scale spatiotemporal intersection of the rock and fossil records. Our objectives in this study are twofold: (1) to determine where in time and space the sedimentary rock record overlaps with our knowledge of the metazoan body fossil record and where it does not, and (2) to measure the large-scale geological completeness of paleontological sampling in one of the best-studied continents in the world (Kiessling 2005). In so doing, we hope to establish an analytical framework that can be used to rigorously overcome geologically controlled sampling biases and to more rigorously interrogate the common cause hypothesis, which posits that similar temporal patterns in the rock and fossil records reflect a shared set of forcing mechanisms, such as environmental changes related to the expansions and contractions of epicontinental seas (Newell 1952; Peters 2005, 2006a, 2008a).

Data and Methods

Stratigraphic Data.—Using the principles of macrostratigraphy (Peters 2006b, 2008b), we compiled the temporal ranges of 18,815 sedimentary and volcaniclastic lithostratigraphic rock units comprising 4938 hiatus-bound sedimentary rock packages from stratigraphic successions at 814 geographic locations in the United States and Canada (Fig. 1A). Charts from the Correlation of Stratigraphic Units of North America (COSUNA), published by the American Association of Petroleum Geologists (Childs 1985; Salvador 1985), were the principal sources of data for the United States. A similar set of charts, published by the Geological Survey of Canada (Douglas 1970), served as the primary source of geological information for Canada. Both the Canadian and U.S. compilations provide comprehensive summaries of the known rock records, including stratigraphic names (if named) and temporal ranges for all rock units (igneous, metamorphic, and sedimentary) in the regions represented by each of the 814 column locations used here (Fig. 1A). Rocks from both the surface and subsurface are included. Because the original COSUNA compilation specified the regions for two stratigraphic columns in the upper Mississippi embayment that did not actually appear in the final published version of the charts, we used Grohskopf (1955) and Dockery (2008) to add COSUNA-style stratigraphic columns to these regions.

Geological ages for the top and bottom of each rock unit were referenced to time bins (primarily stages) in the Phanerozoic, ranging from the Early Cambrian to Holocene. The numerical ages for these discrete time bins were derived from estimates posted by the International Commission on Stratigraphy at http://www.stratigraphy.org/geowhen/geolist.html and from the TimeScale Creator (http://tscreator.org). Because so many informal and unnamed Pleistocene alluvial and glacial sedimentary units are included in the macrostratigraphic compilation, we analyzed only 86 time intervals from the Early Cambrian

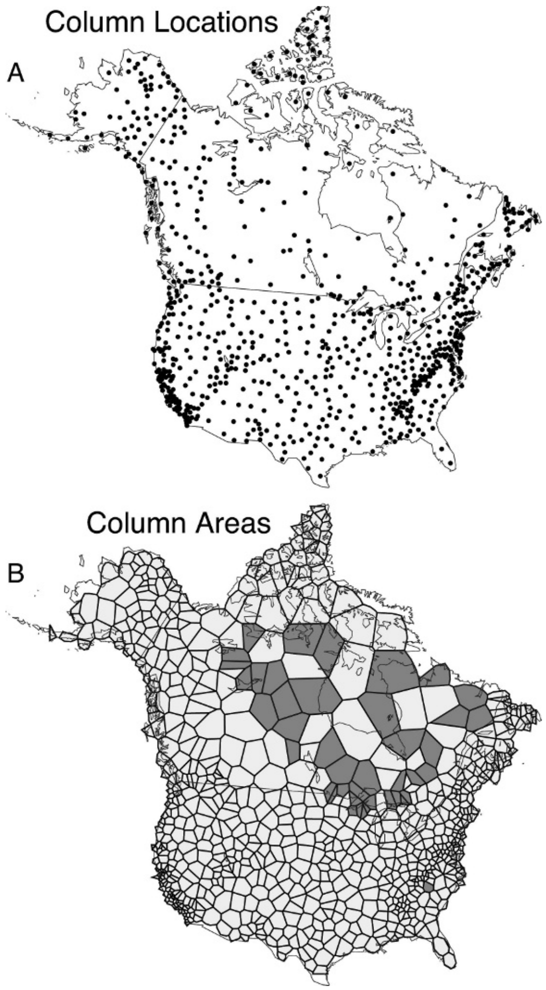

FIGURE 1. Geographic distribution of macrostratigraphic data. A, Location of columns, which represent composite stratigraphic sections that include the entire known rock record for the region around each point. B, Approximate column areas calculated by Delaunay triangulation (see ''Data and Methods''). Columns that have no pre-Pleistocene Phanerozoic sediment are shaded dark gray. Note that the areas shown in B were algorithmically computed and that the actual geographic coverage of some of the rock units may range outside of the boundaries of their respective column polygons.

to the Piacenzian (Pliocene). See the online supplemental material (http://dx.doi.org/10.1666/09003.s1) for a complete listing of the time intervals, numerical ages, and data used in this study.

To estimate the areal extents of the sedimentary rock units present in each stratigraphic column, we calculated a Dirichlet tessellation (Fig. 1B) around each of the 814 column locations (Fig. 1A) using the Delaunay triangulation function in the deldir package for R (R Development Core Team 2008). The nature of this division is such that all points within each polygon are closer to the reference column for that polygon than to any other column. The spacing of columns and the resultant areas of their surrounding polygons generally reflect the complexity of the geological record of that region, with continental margins having, on average, a closer packing of columns and the Canadian Shield having more diffuse packing of columns than the sediment-covered continental interior. Mean column area for all of North America, including the sparsely sampled Canadian Shield (Fig. 1) and the remote western regions of Canada, is approximately 24,300 km^2, or about the size of West Virginia. In the United States, mean column area is ~39% smaller, at 15,200 km^2.

In the absence of data to the contrary, we presume that the areal extent of rock units that occur in one column but not in an adjacent column extends, on average, halfway between the two. To the extent that this assumption is valid, sediment coverage area for each lithostratigraphic unit is best represented by summing the Dirichlet tessellation areas for all of the columns containing that unit.

Paleontologic Data.—We used the official mirror of the Paleobiology Database (PaleoDB) located at the University of Wisconsin-Madison (http://paleodb.geology.wisc.edu) to estimate the spatial and temporal distribution of paleontological sampling (mirror is synced daily with primary archive at http://paleodb.org). At the time of the final analysis for this paper (19 April 2009), the PaleoDB contained 33,474 fossil collections in the United States and Canada that had at least one potentially informative text string entered in the stratigraphic group, formation, or member fields (3961 collections had no entries in any of these fields). Because biodiversity estimates were not the focus of this study, all PaleoDB collections with at least one fossil occurrence were included as valid fossil collections, regardless of the taxonomic resolution or identity of that occurrence. Because the PaleoDB consists almost entirely of body fossil occurrences, with only minimal trace fossil representation, our results must be interpreted entirely within the context of the metazoan body fossil record.

Fossil-Rock Matching Procedure.—In order to measure the intersection of the rock and fossil records, it was necessary to match each PaleoDB fossil collection to a specific lithostratigraphic rock unit in the macrostratigraphic database (Macrostrat). This was done by using algorithms that could take advantage of the underlying table structures in both Macrostrat and the PaleoDB. For each fossil collection, all of the rock units with a stratigraphic name matching the collection's stratigraphic name(s) were retrieved. If more than one rock unit in Macrostrat was identified as a potential match for that collection (units with the same stratigraphic name can appear in many stratigraphic columns), the rock unit belonging to the column (Fig. 1A) with the minimum great circle distance from the PaleoDB collection coordinates was assigned as a tentative match. To reduce the frequency of spurious matches and to prevent fossil collections with greatly errant geographic coordinates from being included, no matches exceeding 300 km were permitted.

Match results from this algorithmic procedure were stored as key pairs in a separate database table and no modification was made to either the PaleoDB or Macrostrat entries. All matches were assumed to apply throughout the entire temporal range of the matched rock unit. A schematic representation of the matching procedure and the results for stratigraphic columns in Wisconsin are shown in Figure 2.

After the automatic matching procedure was executed for (in sequential order) the

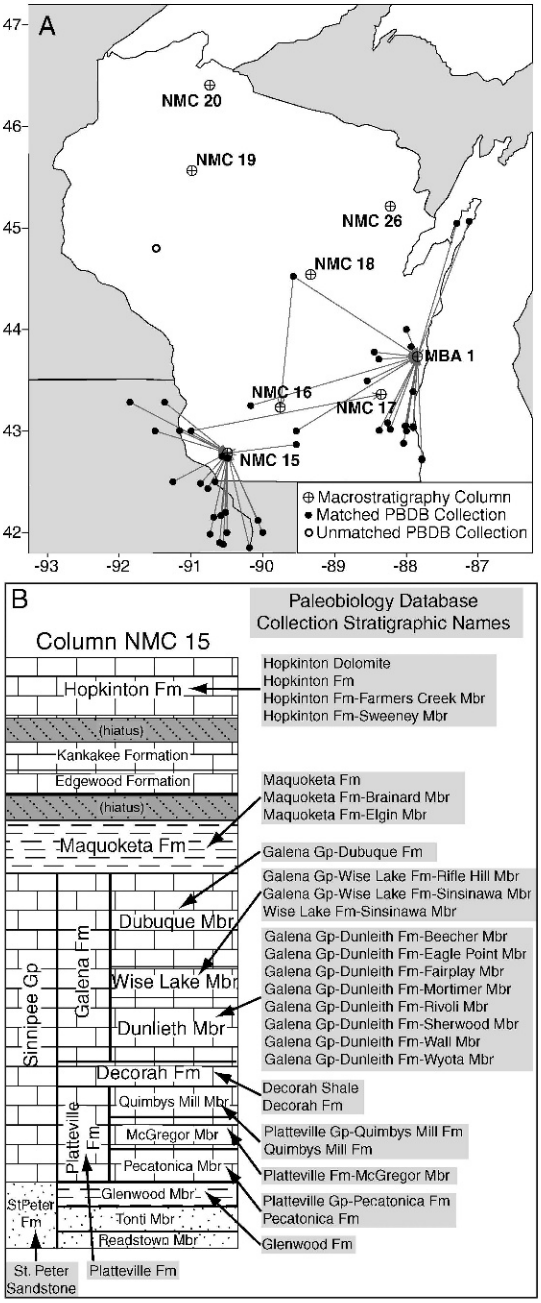

FIGURE 2. Example of fossil-collection matching procedure. A, Map of the region around Wisconsin showing location of PaleoDB collections and geologic columns. Lines attached to collections show column matches. Note that some fossil-collection coordinates are incorrect in the PaleoDB. For example, the collections with coordinates located near NMC 18 are on Cambrian and Precambrian aged rock, but the collections are Ordovician in age. These collections were assigned generic coordinates for the geographic center of Wisconsin when they were entered in the PaleoDB. Here, they have been matched to the nearest columns that contain the appropriate rock unit. B, Example portion of column NMC 15. Lithostratigraphic units are labeled by their name in Macrostrat. Distinct stratigraphic name combinations for matched PaleoDB fossil collections are shown in gray boxes. The units to which name combinations have been matched are indicated by arrows. Note variation in unit hierarchy (Gp, Fm). In this example, 1/1 columns, 2/3 packages, and 12/14 lithostratigraphic units have been matched. See text for discussion and explanation.

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formations, groups, and members specified for each PaleoDB fossil collection, all of the matches were manually checked for accuracy. Any spurious matches resulting from, for example, incorrect partial string congruence were deleted. All collections were matched to the finest possible stratigraphic resolution given the stratigraphic information in Macrostrat and the PaleoDB. For example, a fossil collection containing both a member and a formation designation was matched to the appropriate member in Macrostrat. If no members were present for that formation in Macrostrat, then the collection was matched at the formation level. Similarly, PaleoDB fossil collections assigned to a formation that contained member-level subdivisions in Macrostrat were assumed to apply to all of the members of that formation (e.g., Fig. 2B). Although such inconsistencies in the precision of stratigraphic nomenclatural hierarchy are undesirable, most of the completeness measures used here (hiatus-bound packages, columns, and coverage area) are not overly sensitive to the vagaries of lithostratigraphic subdivision or to the details of the unit-collection matching procedure.

Despite the inevitable complications arising from inconsistent stratigraphic hierarchy in any analysis of this scale, more than 75% of the fossil collections in the PaleoDB could be algorithmically and correctly matched to a specific rock unit in Macrostrat, indicating a high degree of consistency in the stratigraphic nomenclature used in these two independent compilations. Nevertheless, approximately 25% of the PaleoDB collections with at least some potentially informative text in the stratigraphic name fields could not be matched to rock units. In many cases, misspellings, typos, incongruent stratigraphic nomenclature and/or hierarchy (e.g., use of old or new stratigraphic nomenclature that does not appear in Macrostrat), or wildly incorrect geographic coordinates in the PaleoDB collection fields prevented a match. Manual matches were made for all such discrepancies that could be recognized and overcome. The U.S. National Geologic Map Database (http://ngmdb.usgs.gov/Geolex/geolex.html) and the Lexicon of Canadian Geological names (http://cgkn1.cgkn.net/weblex/weblex_e.pl) were particularly useful for identifying stratigraphic nomenclatural synonymies and for penetrating opaque stratigraphic hierarchy on a case-by-case basis.

At the time of the final analysis for this paper, 90.8% (30,387) of the 33,474 PaleoDB fossil collections in the United States and Canada that contain potentially informative stratigraphic names had been successfully matched to a rock unit. Collections that could not be matched because of incorrect coordinates and/or ambiguous stratigraphic nomenclature were left as stratigraphic orphans and were not included in this study. Matched PaleoDB fossil collections provide rather complete coverage of the sediment-covered portion of North America (Fig. 3), and, with the possible exception of the remote Canadian Cordillera, there does not appear to be any strong systematic geographic distribution among the 9.2% of fossil collections that could not be matched to a rock unit (Fig. 3; Spearman rank-order correlation between the number of matched and unmatched fossil collections per equal-area grid cell is 0.385).

Measuring Completeness.—Geological completeness of paleontological sampling is here defined as the proportion of the total available sedimentary rock record that has thus far yielded at least one documented fossil collection in the Paleobiology Database. This proportion was measured at four different levels of stratigraphic resolution: (1) lithostratigraphic units, (2) gap-bound rock packages, (3) stratigraphic columns, and (4) sediment coverage area (see Fig. 2B for examples of the first three; see Fig. 1 for coverage area). Because it is possible for a time interval with little preserved sediment and few fossil collections to have 100% geological completeness if those collections derive from the entire rock record, neither the total number of fossil collections nor the total amount of sedimentary rock in each time interval need determine geological completeness (Fig. 4). Geological completeness is, therefore, similar to other macrostratigraphic quantities (Peters 2006, 2008b) in that it is inherently spatiotemporal in meaning. Whether or not the available geological record

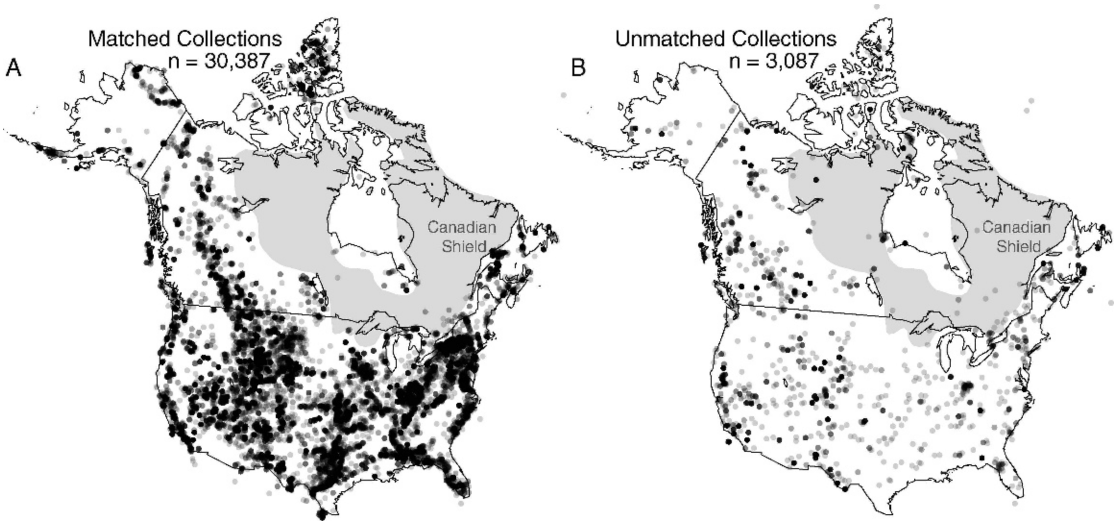

FIGURE 3. Geographic distribution of PaleoDB collections. A, Collections matched to a lithostratigraphic rock unit. B, Collections that have not been matched to a rock unit. Points are transparent so that dark areas indicate many stacked collections. The Canadian Shield, which is largely devoid of Phanerozoic sediment, is indicated by gray areas. Collections plotting within the shield are mostly from Paleozoic sediment outliers, many of which are represented in Macrostrat. Because fossil collection coordinates are manually entered into the PaleoDB, there are inevitable errors and some unmatched collections are incorrectly located in the oceans. Incorrect collection coordinates account for many of the unmatched PaleoDB collections.

provides a complete or consistent sample of true biological diversity pertains to another level of completeness (absolute completeness) and is a different question.

Because Macrostrat provides a comprehensive summary of the rock record and because the spatial framework (Fig. 1) for this study is constant for all time intervals, it is unlikely that the spatial distribution of geological control points (Fig. 1A) has substantially affected temporal variation in these completeness estimates. Nevertheless, the absolute values for completeness must, to some extent, be sensitive to the spatial distribution of geological control points and should, therefore, be interpreted accordingly.

Results

Previous macrostratigraphic analyses (Peters 2005, 2006a,b, 2008a) have included only the United States and have focused on gap-bound rock packages. Here, gap-bound sediment packages, the number of recognized lithostratigraphic rock units, and absolute sediment coverage areas (km^2) are estimated for the combined rock records of the United States and Canada (Fig. 5). Not surprisingly, results for gap-bound packages in this study are similar to previously published macrostratigraphic analyses for the United States, primarily because the COSUNA compilation is common to all (though separately compiled for this study) and because the Canadian Shield, which is largely devoid of Phanerozoic sedimentary cover, constitutes a substantial fraction of Canada's continental area (Fig. 3). Patterns of sedimentation in both the United States and Canada are also positively correlated due to the globally synchronous influence of eustatic sea level change and to the general tectonic continuity of much of the region.

Temporal trends in all four of the macrostratigraphic time series evaluated here (lithostratigraphic rock units, gap-bound rock packages, composite stratigraphic columns, and sediment coverage area) relate to the total amount of preserved sedimentary rock (Peters 2006a, 2008b) and are broadly similar to one another in terms of short-term variability and long-term trends (Table 1, Fig. 5). This similarity supports previous assertions (e.g., Peters 2005, 2008b) that the most basic macrostratigraphic quantity, the total number

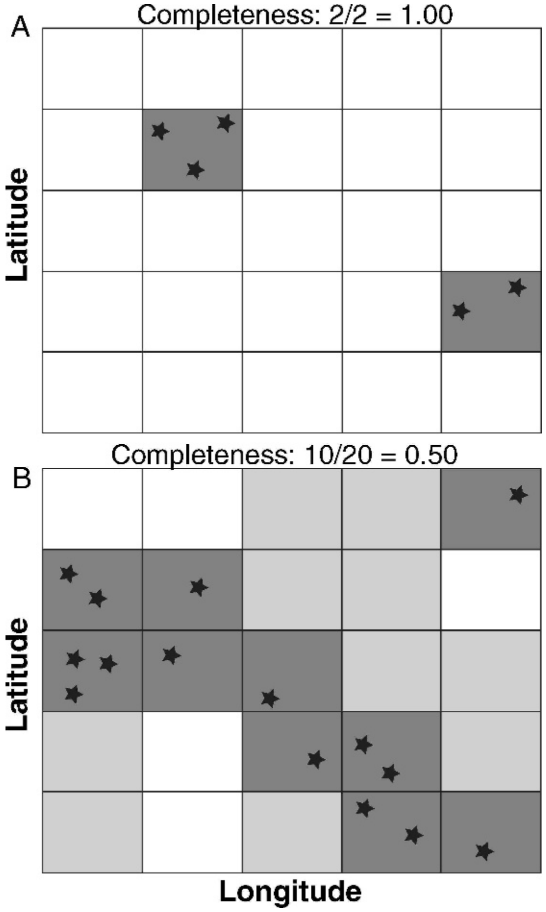

FIGURE 4. Schematic illustration of the meaning of geological completeness for two hypothetical time intervals. A, Only two areas have sediment (shaded grids), but both have one or more fossil collections (stars) and adding more collections will not increase geological completeness. B, Although there are more collections (stars) and more cells filled with rock (shaded grids), only half of the available rock has a fossil collection (dark gray). If collections are added in a targeted fashion, geological completeness could increase.

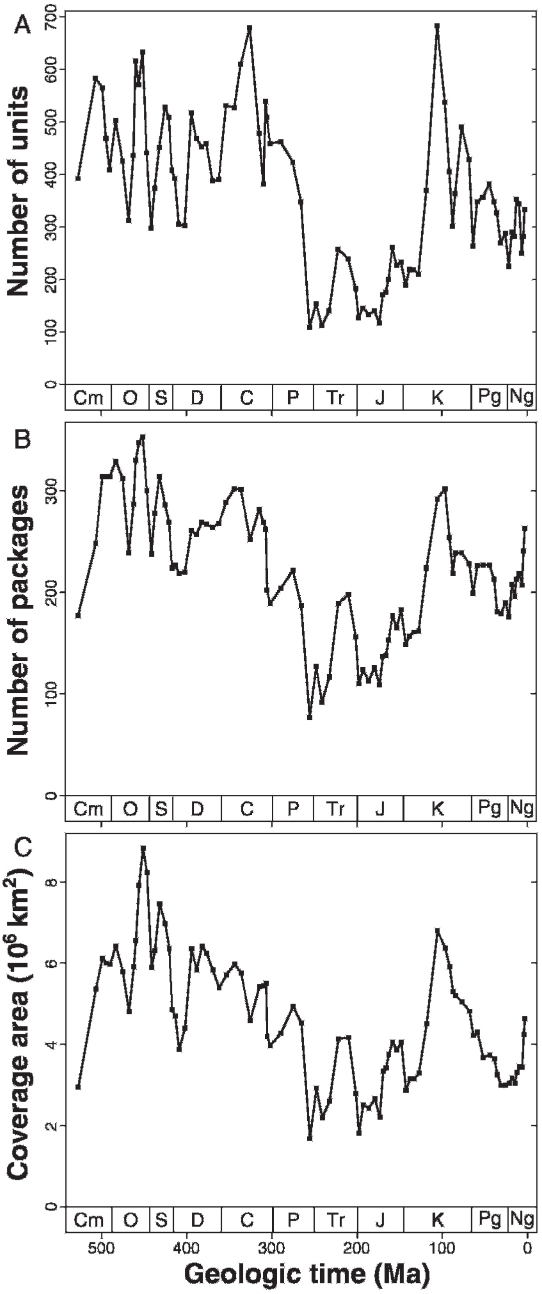

FIGURE 5. Macrostratigraphic quantities for the sedimentary rock record of the United States and Canada. A, Total number of lithostratigraphic units (see Fig. 2B). B, Total number of gap-bound sediment packages. C, Total sediment coverage area measured in millions of km^2. Data are plotted at age of interval midpoint from the Early Cambrian through Pliocene.

of rock packages, is an area-weighted measure of total rock quantity. Because most columns (Fig. 1A) contain just one sediment package in each time interval (5.3 Myr median duration), time series for the total number of columns and the total number of sediment packages are highly congruent (Table 1); results for columns will, therefore, not be presented graphically here (see Tables for result summaries and online supplemental file for data).

Time series for the total number of units (Fig. 5A) and the total area of sediment coverage (Fig. 5C) constitute new geological results that have many interesting implications for temporal variations in sedimentation and large-scale sequence stratigraphy in

TABLE 1. Linear product-moment correlation coefficients for sedimentary macrostratigraphic quantities (data from Fig. 4). Bold values show coefficients for time series that have been detrended by taking first differences, thereby emphasizing short-term variability; other values are coefficients for raw time series, which reflect long-term trends.

	Units	Packages	Columns	Area
Units	—	.863	.850	.806
Packages	**.682**	—	.995	.916
Columns	**.642**	**.972**	—	.903
Area	**.677**	**.891**	**.902**	—

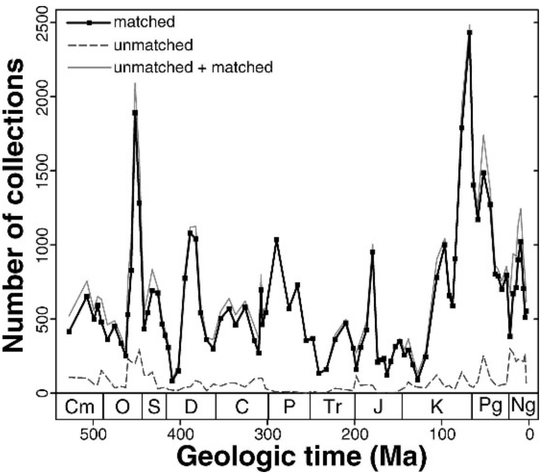

FIGURE 6. Total number of PaleoDB fossil collections, inclusive of all taxa and all environments. Dark line with points shows number of collections that have been matched to a rock unit; dashed line shows the number of collections that remain to be matched. Sum total of all collections, matched and unmatched, indicated by gray line. Data are plotted at age of interval midpoint from the Early Cambrian through Pliocene.

North America (sensu Sloss 1963, 1976). The total number of units, for example, reflects lithologic variability within macrostratigraphic packages and, to some degree, the extent to which geologists have subdivided different parts of the rock record. Both of these factors vary prominently in time and space, reflecting a combination of evolving paleoenvironments in North America and the geographic distribution and surface exposure of sedimentary rocks. For example, the peak in the number of lithostratigraphic units that occurs in the late Carboniferous reflects the fact that stratigraphers have finely subdivided the well-known and lithologically heterogeneous cyclothems of the Pennsylvanian (Fig. 5). The goal of this study, however, is not to address the geological implications of the Macrostrat results, but to estimate the extent to which our knowledge of the fossil record overlaps with that of the sedimentary rock record.

The total number of PaleoDB fossil collections, inclusive of all taxa and all environments, that have been matched to a sedimentary rock unit at the time of this study increases towards the Recent (Fig. 6), but only modestly so (slope = 0.53 collections/Myr; $r = 0.204$). This increase in the number of matched collections is not a procedural artifact of being able to more consistently match young fossil collections to young rocks. More than half of the unmatched fossil collections (total of 3967) are Jurassic or younger (Fig. 6) and, if anything, there is a weak long-term temporal increase in the number of unmatched collections ($r = 0.117$).

Time series for the total number of sedimentary rock units (Fig. 7A), the total number of gap-bound sediment packages (Fig. 7B), and total sediment coverage area (Fig. 7C) matched to at least one fossil collection in the PaleoDB are all broadly similar to one another (Table 2, Fig. 7). This is notable because lithostratigraphic units (Figs. 5A, 7A) represent, at least to some extent, arbitrary subdivisions of sediment packages. Intervals and regions with finely subdivided stratigraphic columns should, all else being equal, have fewer units matched to a fossil collection than intervals or regions with coarse lithostratigraphic subdivisions. Nevertheless, the overall similarity of the time series for matched units to the time series for those attributes of the rock record that are independent of the number and hierarchy of lithostratigraphic units (i.e., gap-bound packages, columns, and coverage area, any of which may be represented by one or many lithostratigraphic units in each time interval), suggests that there is little systematic temporal variability in stratigraphic nomenclatural practice and that the way in which collections have been assigned to lithostratigraphic units does not vary systematically with age.

Unlike the total number of matched fossil collections (Fig. 6), none of the time series for

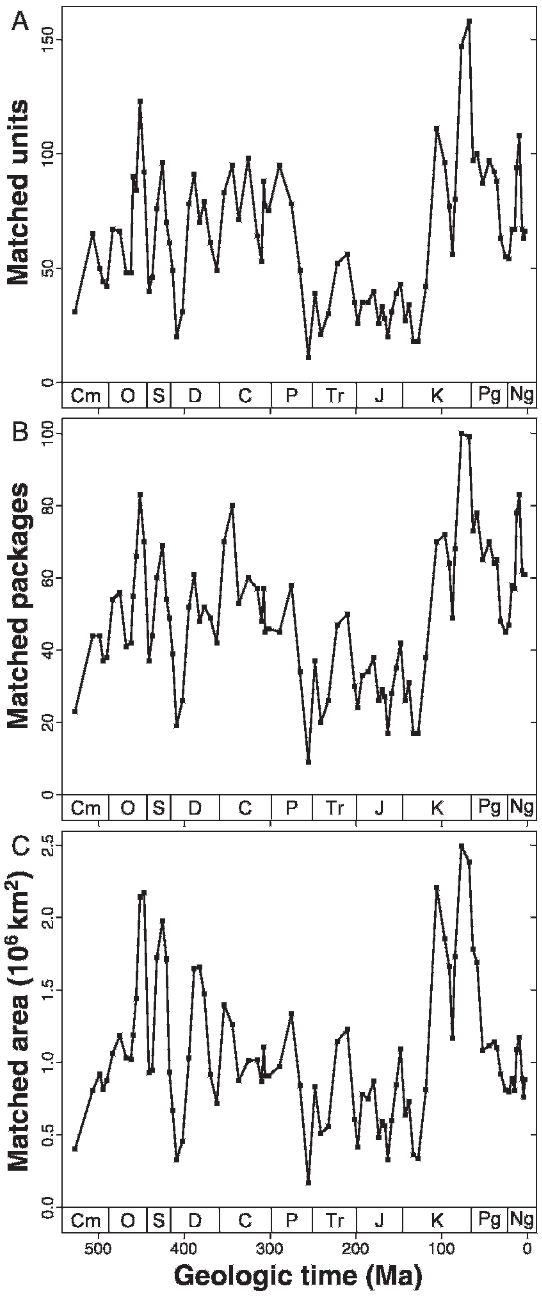

FIGURE 7. Number of geological units matched to at least one PaleoDB fossil collection. A, Number of lithostratigraphic units matched to at least one collection. B, Number of gap-bound packages matched to at least one collection. C, Total sediment coverage area matched to at least one collection. Data are plotted at age of interval midpoint from the Early Cambrian through Pliocene.

TABLE 2. Linear product-moment correlation coefficients for sedimentary rock units that have been matched to at least one fossil collection in the PaleoDB (data from Fig. 7). Bold values show coefficients for time series that have been detrended by taking first differences, thereby emphasizing short-term variability; other values are coefficients for raw time series, which reflect long-term trends.

	Units	Packages	Columns	Area
Units	—	.949	.942	.849
Packages	**.901**	—	.997	.844
Columns	**.888**	**.994**	—	.833
Area	**.821**	**.877**	**.875**	—

matched rock units (Fig. 7) exhibit a strong long-term trend during the Phanerozoic. This discrepancy occurs because it is possible for many fossil collections to be matched to the same rock unit. Indeed, the average number of PaleoDB collections per lithostratigraphic unit (Fig. 8) varies considerably over time and exhibits a weak long-term increase ($r = 0.141$). Late Cretaceous and Cenozoic time intervals have, on average, more collections per rock unit than the Phanerozoic mean of 9.4 collections per rock unit per time interval. An unusually high average number of collections per unit occurs in the late Permian (Fig. 8), indicating that a disproportionate number of matched fossil collections are concentrated in just a few lithostratigraphic units, in this case in the well-sampled Glass and Guadalupe Mountains of west Texas.

Geological completeness of paleontological sampling is here operationally defined as the proportion of the available sedimentary rock

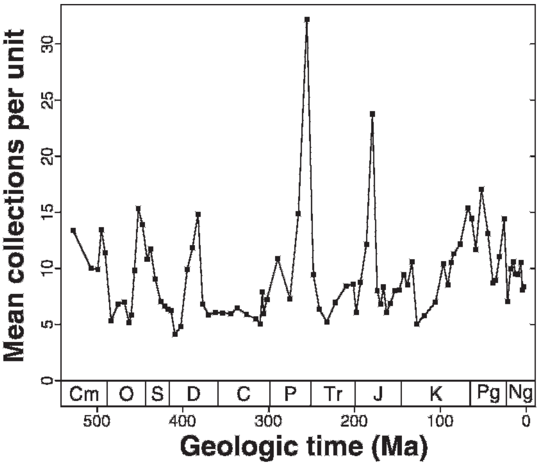

FIGURE 8. Average number of PaleoDB fossil collections per matched lithostratigraphic rock unit. Phanerozoic average is 9.3 collections per matched unit. Data are plotted at age of interval midpoint from the Early Cambrian through Pliocene.

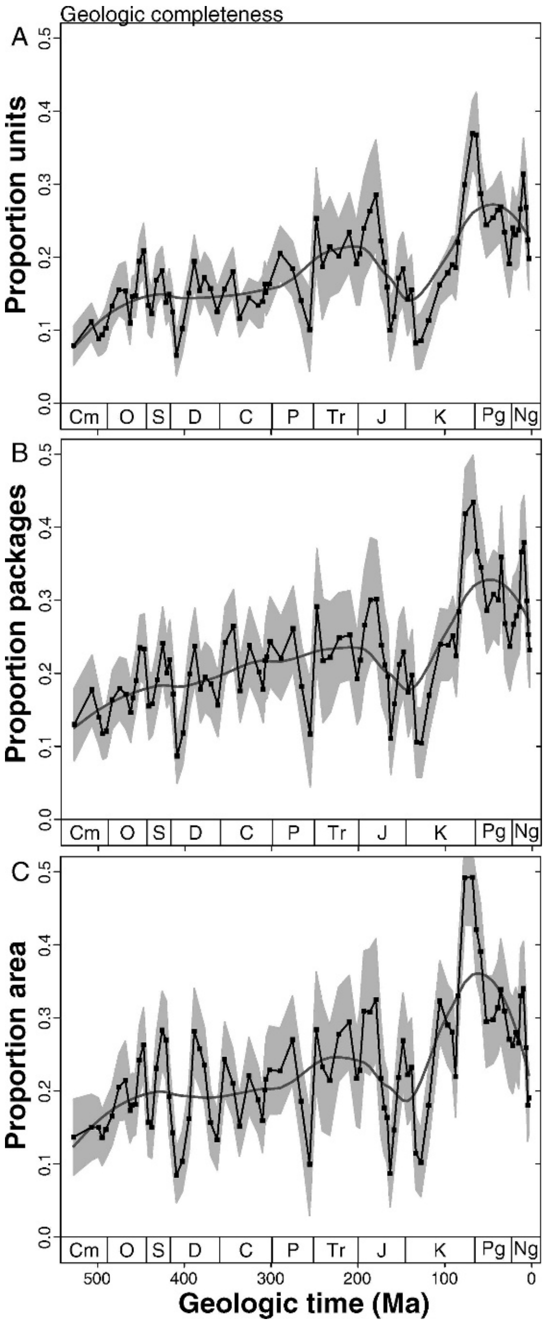

FIGURE 9. Geological completeness of paleontological sampling. Completeness is measured as the proportion of the available geologic record (Fig. 5) that has been matched to at least one PaleoDB fossil collection (Fig. 7). A, Proportion of lithostratigraphic units matched to at least one fossil collection. B, Proportion of gap-bound packages matched to at least one collection. C, Proportion of total coverage area matched to at least one collection. Gray shaded areas enclose the 95% confidence limits about the estimated proportion (black lines, points); confidence limits in C use total number of column control points. Solid gray lines represent loess regressions, a distance-weighted local regression technique, with an alpha (smoothing parameter) of 0.4. Note that the absolute values of the completeness estimates increase from A to C as stratigraphic inclusivity increases. Data are plotted at age of interval midpoint from the Early Cambrian through Pliocene. See text for discussion.

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TABLE 3. Linear product-moment correlation coefficients for estimates of the geological completeness of paleontological sampling (data from Fig. 9) and the total number of fossil collections (data from Fig. 6). Bold values show coefficients for time series that have been detrended by taking first differences, thereby emphasizing short-term variability; other values are coefficients for raw time series, which reflect long-term trends. Note that the total number of collections is positively correlated with geological completeness, but relatively weakly so. Results are broadly similar when the data are limited to Paleozoic and post-Paleozoic subsets.

	Units	Packages	Columns	Area	Collections
Units	—	.944	.937	.884	.615
Packages	**.858**	—	.997	.921	.661
Columns	**.854**	**.992**	—	.923	.667
Area	**.755**	**.875**	**.872**	—	.703
Collections	**.495**	**.486**	**.497**	**.525**	—

record (Fig. 5) that has at least one fossil collection in the PaleoDB (Fig. 7). A total of 18,815 Phanerozoic sedimentary lithostratigraphic units are present in Macrostrat and, of these, 3282 (17%) have at least one fossil collection. Gap-bound sedimentary packages, which may have one or many units, number 4938 in the Phanerozoic and, of these, 1422 (29%) contain at least one unit that has been matched to a fossil collection. For the analyses that follow, gap-bound rock packages with collection-bearing rock units spanning only a portion(s) of their total temporal range were counted as matched only over the time span of the matched unit(s). Measured in this way, mean Phanerozoic completeness at the package level is 0.22 per time interval.

Time series for all completeness estimates (lithostratigraphic units, gap-bound sedimentary packages, and sediment coverage area) exhibit similar short-term variability and comparable long-term trajectories (Table 3, Fig. 9). Some of the most notable features in all of the completeness estimates are (1) an increase from the Early Cambrian to the Late Ordovician, (2) a long Paleozoic plateau with superimposed short-term variability, (3) a low

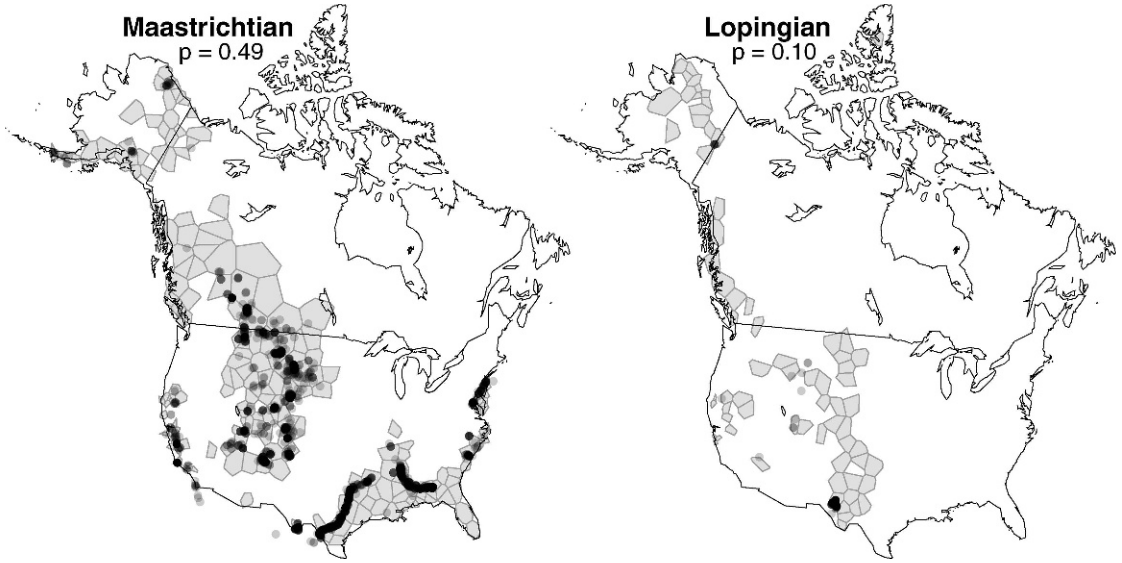

FIGURE 10. Preserved sediment coverage area and matched PaleoDB collections for two time intervals. Completeness estimates (p) are calculated as the total area (in km^2) matched to at least one fossil collection (points) divided by the total area of sediment coverage (gray polygons). Collection points are transparent so that dark areas indicate many stacked collections. Note that some matched collections are expected to fall outside of the polygons, owing to the approximate nature of the algorithmically generated polygons (see Fig. 1) and collection coordinate errors in the PaleoDB. Fossil collections matched to lithostratigraphic units that range into the Lopingian and Maastrichtian in the current version of Macrostrat are shown, regardless of the ages of the specific horizons of those collections.

in the mid-Jurassic through Early Cretaceous, and (4) a large Campanian–Maastrichtian peak followed by a sustained high in the Cenozoic. On average, post-Campanian completeness estimates are approximately 50% greater than pre-Campanian estimates, and completeness estimates during the well-sampled Maastrichtian are approximately two times greater than the Paleozoic average (Fig. 9). Note that the total number of fossil collections, which is commonly assumed to be a good proxy for the intensity of paleontological sampling, is positively correlated with all of the geologically based completeness estimates tabulated here, but that the correlations are comparatively weak, especially for first differences (Table 3).

To provide a visual representation of the meaning of the completeness estimates shown in Figure 9, maps of sediment coverage area and matched fossil collections were generated for two end-member time intervals, the Maastrichtian, which has high completeness, and the comparatively poorly sampled Lopingian (late Permian; Fig. 10). It is clear from the Maastrichtian map that completeness is high during this time because fossil collections are spread out over nearly half of the total area that is covered by Maastrichtian-aged sediment, including nearly the entire length of the Gulf and Atlantic Coastal Plains. Fossil collections assigned to units that range into the Lopingian, by contrast, are heavily concentrated in west Texas, with only a few collections outside of this region (the high concentration of collections in Texas is also responsible for the high average number of collections per unit shown in Figure 8).

Although there is significant short-term variation in all of the geological completeness estimates calculated here, one the most important features common to all is a significant long-term increase (Fig. 9), and this would not be apparent in strictly paleontologically based measures of sampling effort. For example, on average, Paleozoic fossil collections are distributed over an area that is comparable in size to the area over which Cenozoic fossil collections are distributed, but total sediment coverage in the Paleozoic is considerably greater than it is in the Cenozoic, even though the total number of sedimentary

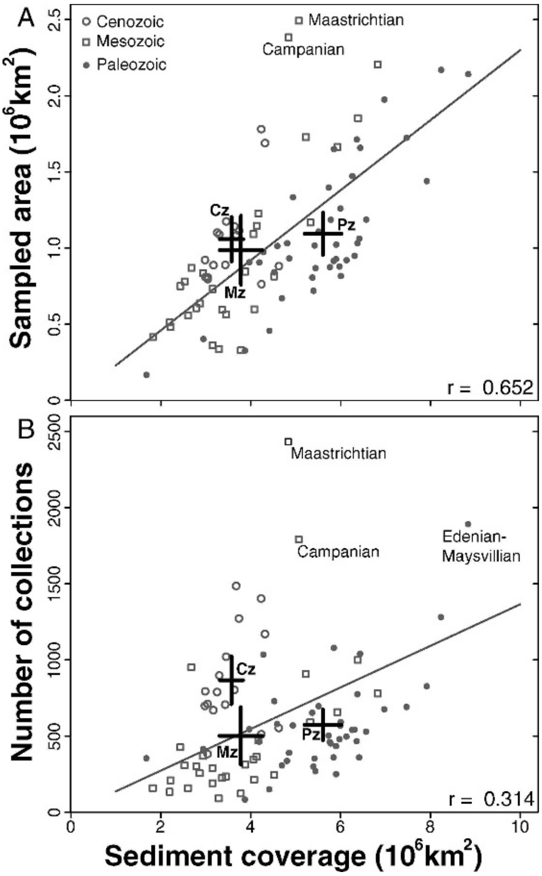

FIGURE 11. Scatterplots of paleontological sampling versus total sediment coverage area. A, Total area sampled (from Fig. 7C) versus total sediment coverage area (from Fig. 5C). Gray line shows the Phanerozoic average proportion of sampled sediment coverage area. B, Total number of matched collections (from Fig. 6) versus total sediment coverage area (from Fig. 5C). Gray line shows the Phanerozoic average number of collections per km^2 sediment coverage area. Black crosses show mean values ± two standard errors of the mean for the Paleozoic (Pz), Mesozoic (Mz), and Cenozoic (Cz). Note the tendency for the Paleozoic to be below, the Mesozoic to be near, and the Cenozoic to be above the Phanerozoic average level of sampling relative to the preserved rock record. Linear product-moment correlation coefficients (r) shown.

units in the Cenozoic is inflated by the presence of many volcanic units with volcaniclastic intervals (Peters 2006b). Thus, the Cenozoic sedimentary rock record is much more completely sampled relative to total sediment coverage area than is the Paleozoic (Fig. 11A). Similarly, the Paleozoic and Mesozoic have, on average, similar numbers of fossil collections, but those collections are spread out over a significantly smaller area of preserved sediment in the Mesozoic than they are in the Paleozoic (Fig. 11B), resulting in higher geological completeness of paleontological sampling in the Mesozoic.

Discussion

Estimating variability in paleontological sampling intensity and then quantitatively overcoming this variability using sampling standardization techniques (e.g., Raup 1975; Alroy 2000) has become a powerful de facto analytical tool for calibrating many macroevolutionary patterns in the fossil record. In the majority of cases (e.g., Miller and Foote 1996; Alroy et al. 2001, 2008; Krug and Patzkowsky 2007; Kiessling 2008; Powell 2008), estimates of sampling intensity derive exclusively from fossil data (e.g., the number of fossil specimens, occurrences, and collections), making it possible to rigorously control for many different aspects of sampling effort, but not to evaluate the completeness or uniformity of that effort relative to the rock record that might yet produce fossils. Macrostratigraphy provides a quantitative framework that is independent of the fossil record and that can, therefore, be leveraged as a new tool for fully evaluating and then correcting for the effects of geologically controlled variability in paleontological sampling.

Despite these advantages, there remain several prominent uncertainties with respect to the actual meaning of the geological completeness estimates summarized here. In particular, the absence of a fossil collection in a rock unit could be due to several different factors (beyond procedural and book-keeping errors related to the rock-collection matching process; see ''Data and Methods''): (1) the rock unit might have fossils, but those fossils might not yet be described in the literature (publication failure); (2) the rock unit might have fossils that are described in the literature, but that reference might not yet be in the PaleoDB (data entry failure); (3) the rock unit might have fossils, but it might also be poorly exposed or restricted to the subsurface (outcrop failure); or (4) the unit might actually be barren of body fossils (real absence). All four of these factors have undoubtedly contributed to the (in)completeness of geological sampling. Some of these factors are likely to be random effects that have little or no influence on temporal patterns of geological completeness or our knowledge of the fossil record. Others might vary significantly with geologic age and could, therefore, substantively affect temporal patterns of completeness and/or our understanding of biological evolution. Below we discuss each of the possible explanations for geological (in)completeness.

Publication and Data Entry Failures.—Every publication that provides occurrence-based fossil data in North America has not yet been entered into the PaleoDB, just as every fossil-bearing rock unit has not yet been studied and its fossil content adequately described in the literature. It is, therefore, inevitable that some (possibly even most) of the incompleteness of paleontological sampling can be attributed to the fact that the work of paleontologists, both compilation- and field-oriented, is far from finished. Is there a systematic tendency for paleontologists to concentrate on some time intervals and neglect others, as, for example, initially suggested by Sheehan (1977)? Global socio-economic discrepancies notwithstanding (Kiessling 2005), we side with Raup, who argued that paleontologists have gone about sampling the rock record that is available to them and that publication/data entry errors and omissions represent random effects that, by themselves, impart no significant temporal structure to the data. Nevertheless, some aspects of these results, such as the dramatic peak in completeness that occurs in the Campanian–Maastrichtian (Fig. 9), likely reflect differential levels of interest and effort among paleontologists.

One of the practical benefits of matching PaleoDB fossil collections to an independent measure of the rock record is that it provides the necessary framework for rigorously measuring the effects of publication and data entry failures and for then overcoming them. For example, rather than continuing to gather new fossil data more or less haphazardly from the field and literature, Macrostrat enables most of the sedimentary rock units in North America that have not yet been matched to a fossil collection in the PaleoDB to be identified by name, located geographically, aged geologically, and described in terms of their general lithological attributes and contact relationships. If no paleontological information can be found in the literature for these unmatched rock units, then purposeful, directed fieldwork might be in order. The combination of literature searches and targeted new fieldwork for these currently unmatched units will facilitate a rapid increase in the geological completeness of paleontological sampling in the PaleoDB and a more complete picture of the large-scale evolutionary history of life in North America.

Outcrop Failure.—Baring geographic remoteness, there are two reasons why a rock unit might be difficult to access and to sample paleontologically: (1) the unit might be isolated from the surface by deep burial beneath younger sediments and/or tectonic overthrusting, and (2) the unit might be in a region that has few surface exposures, owing to the effects of continental weathering and/or the lack of tectonic uplift. Although both of these causes of outcrop failure contribute to geological incompleteness, neither is an absolute determinant of incompleteness. Subsurface units do in fact yield many taxonomically informative fossils, including large macroscopic invertebrates, such as those Silurian faunas that have been recovered from cores in the deep subsurface of central Florida (Pojeta 1976). Nevertheless, it is reasonable to suspect that older rocks might, on average, be more prone to outcrop failure due to burial and that long-term trends in geological completeness (Fig. 9) might reflect this fact. The COSUNA compilation permits a cursory evaluation of this hypothesis.

Of the 4679 lithostratigraphic units that are currently identified as occurring only in the subsurface and that have not yet been matched to any fossil collection, there is a long-term, if irregular, decline in their frequency toward the Recent ($r = -0.418$; Fig. 12A). In some time intervals, such as the Late Pennsylvanian and early Permian, as many as 40% of the total number of lithostratigraphic units are located in the subsurface. By subtracting the number of subsurface units (Fig. 12A) from the total number of

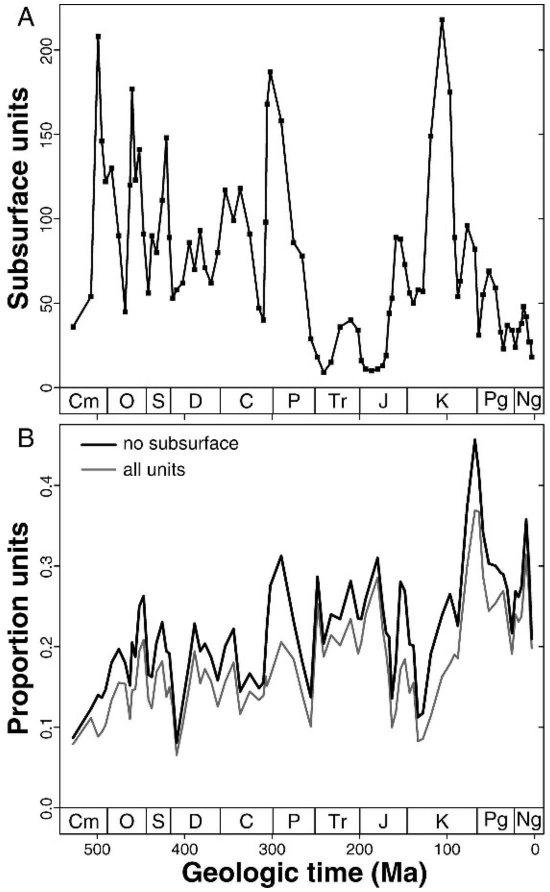

FIGURE 12. Subsurface rock units. A, Total number of rock units that are identified as being exclusively subsurface in the COSUNA database. B, Proportion of total lithostratigraphic units that have been matched to at least one fossil collection (geological completeness). Gray line shows results for all units, as in Figure 7A; dark line excludes from the tabulation all subsurface units. Data are plotted at age of interval midpoint from the Early Cambrian through Pliocene. See text for discussion.

units in each time interval (Fig. 5A), geological completeness can be reevaluated independent of subsurface effects, at least as currently estimated on the basis of Macrostrat.

Excluding all subsurface units from the completeness tabulation results in a higher mean proportion of matched units (22% as opposed to 18%), but the overall temporal trajectory remains little changed (Fig. 12B). This suggests that completeness estimates are in fact quantitatively influenced by subsurface rocks, but that the long-term temporal increase in geological completeness (Figs. 9, 12B) is unlikely to be driven by this factor alone.

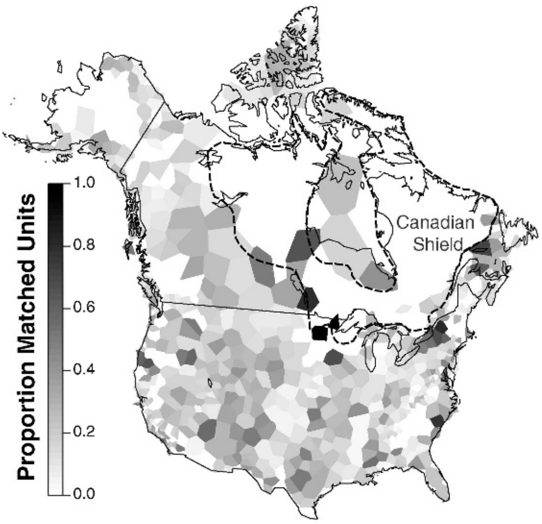

FIGURE 13. Geographic variation in geological completeness of paleontological sampling measured as the proportion of lithostratigraphic units at each location that have been matched to at least one fossil collection. Approximate boundary of the Precambrian Canadian Shield is enclosed by the dashed line. Note the prevalence of regions with high completeness near the margins of the shield, and the prevalence of low completeness in much of the American Great Plains. See text for discussion.

Unfortunately, it is impossible to determine at this time the extent to which surface exposure characteristics have contributed to outcrop failure and, therefore, to geological incompleteness. Geologic maps can help to identify those units that might be located at the surface, but they do not help to identify those units that might not be exposed in paleontologically useful outcrops. Nevertheless, the geographic distribution of completeness does provide some indication that both types of outcrop failure (burial and geomorphic characteristics) are important. For example, in regions where Phanerozoic sedimentary cover is thin and there are few subsurface units, such as along the margin of the Canadian Shield, completeness is generally high (Fig. 13). In regions where there is a greater thickness of sedimentary cover, but also few surface exposures, such as in the Great Plains of the central United States (Fig. 13), completeness is lower than average. Concentrations of fossil collections in strike-parallel outcrop belts, and the gaps between them (e.g., Maastrichtian, Fig. 10), also suggest that both geomorphic characteristics and the thickness of sedimentary cover contribute significantly to completeness estimates.

Although we cannot fully determine the relative importance of subsurface units and surface expression at this time, it is important to note that we are not attempting to document a correlation between rock availability and sampled biodiversity, as Raup (1976), Peters and Foote (2001), McGowan and Smith (2008), and others have done. Instead, we are estimating the extent to which the entire sedimentary record, exposed or not, has contributed to paleontological knowledge. Our results indicate that outcrop failure, which is controlled by both subsurface units and geomorphologic characteristics, is a significant, but not exclusive, determinant of the geological completeness of paleontological sampling.

Real Absence.—Some rock units that are geographically accessible and exposed at the surface may lack a fossil collection in the PaleoDB simply because they are actually barren of all taxonomically informative body fossils. The possibility that the frequency of unfossiliferous sediment has changed over geological time has been addressed by two recent studies (Peters 2007; Smith and McGowan 2008). Both found evidence for similar long-term declines in the frequency of unfossiliferous sediment during the Phanerozoic, but they disagreed over the underlying cause. Peters (2007) argued for unique environments within epicontinental seas and changes in their prevalence over time as the most important control on unfossiliferous sediment (as first suggested by Bambach 1977), whereas Smith and McGowan (2008) argued for a biological cause and linked the decline in fossiliferous sediment to Phanerozoic biodiversity and biological saturation of the physical landscape (see discussion below). Regardless of what might be responsible for the pattern, if there is any significant change over time in the frequency of unfossiliferous sediment, then it is possible that the patterns of geological completeness measured here (Figs. 9, 12B) could reflect this fact.

The possibility that geological completeness estimates (Fig. 9) might reflect a secular decrease in the frequency of unfossiliferous sediment is intriguing because it raises the possibility of biological (sensu Smith and McGowan 2008) and/or environmental (sensu Bambach 1977; Peters 2007) signals in these results. There are, however, other possible explanations. For example, diagenetic alteration of sediments and the chemical dissolution of their enclosed fossils is commonplace (e.g., Wright et al. 2003). If older rocks are more likely than younger rocks to have lost all taxonomically informative fossils to diagenesis, then this could contribute to a long-term increase in geologic completeness (Fig. 9). Younger rocks may also simply yield their fossils more readily owing, for example, to a lesser degree of lithification (Kowalewski et al. 2006; Hendy 2009; Sessa et al. 2009). Some depositional environments may also have taphonomic and diagenetic characteristics that do not favor fossil preservation, and the prevalence of these environments might change over time, possibly in ways that could affect both short- and long-term patterns of completeness. For example, the late Permian terrestrial red beds that blanket much of the midsection of the United States (Fig. 10B) are virtually devoid of body fossils, probably for environmental as well as taphonomic and diagenetic reasons (trace fossils are more common than body fossils, though rare vertebrate and plant fossils have been found), and this likely contributes to the low geological completeness of this time interval in North America.

In summary, it is likely that real absences, controlled by environmental characteristics as well as diagenetic and taphonomic factors, have contributed significantly to geological incompleteness. Similar to the publication and data entry failures described above, the framework provided by macrostratigraphy will serve as a useful template for rigorously determining the relative contributions of these two factors and for measuring spatiotemporal variation in unfossiliferous sediment.

Changing Biological Landscape.—We have chosen to focus on the geological completeness of paleontological sampling for the entire metazoan fossil record, irrespective of taxonomic affinities or environments. Our rational for doing so is twofold: (1) any uncertainties with respect to environmental interpretations and taxonomic identifications are rendered irrelevant, and (2) we are actually interested in knowing the inclusive completeness of the fossil record relative to the entire sedimentary rock record. It is conceivable, however, that the dominant signal in our geological completeness estimates (Fig. 9) is an expanding biological landscape toward the Recent. That is, if the actual abundance and environmental distribution of life were increasing over time, such as unquestionably occurred during the initial evolution of multicellular organisms and again during their subsequent invasion of land, then the proportion of rock units that yield fossils (i.e., geological completeness) must similarly increase. In particular, it could be argued that biological diversification during the Phanerozoic, especially on land, is responsible for the increase in geological completeness documented here (for further discussion, see the explanation for temporal trends in unfossiliferous sediments in Smith and McGowan 2008).

We believe that there are several reasons to discount the possibility of such biological signals in these data. First, and most importantly, in order to be counted as fossil-bearing, a rock unit need only produce one specimen of one fossil species. Thus, the geological completeness estimates derived here are completely divorced from any measure of diversity or ecological packing within local communities (sensu Bush and Bambach 2004), provided that metazoans have already expanded to the point where the full range of habitable environments support at least one readily preserved species. We maintain that the physical landscape was ''saturated'' in this respect by the end of the Devonian (certainly by the end of the Triassic), regardless of whether or not global or local diversity has increased since that time. The fact that the bulk of the increase in geological completeness appears to occur in the Late Cretaceous (Fig. 9) provides, we believe, prima facie evidence for discounting a ''biological saturation'' hypothesis for an increase in geological completeness.

Nevertheless, it is worth considering the possibility that evolution within terrestrial environments has contributed in some way to the temporal trends in completeness documented here. To this end, we parsed all of the matched rock units into marine, marginal marine, mixed marine-terrestrial, and terrestrial environments on the basis of environmental data contained in Macrostrat and the PaleoDB. There is a significant increase in the mean proportion of matched terrestrial rock units from the Paleozoic to the Mesozoic, but there is no long-term trend in this proportion after the Triassic (Fig. 14). More importantly, there is no significant correlation between the proportion of matched units that are terrestrial (Fig. 14B) and geological completeness estimates (Fig. 9A), even when the data are restricted to the post-Paleozoic (for first differences, $r = -0.123$, $p = 0.427$, raw time-series $r = 0.220$). Although this does not disprove the possibility that changes in the biological saturation of the terrestrial landscape have contributed to the completeness of geological sampling, we find that the weight of evidence available at this time suggests that other factors, such as those discussed above, are likely to be much more important.

Implications for Macroevolutionary Patterns.—Irrespective of the long-recognized similarities between the quantity of exposed sedimentary rock and estimates of fossil biodiversity (e.g., Raup 1976; Smith 2001; Peters and Foote 2001), the results of this study suggest that our knowledge of the fossil record, normalized for temporal variation in the quantity of preserved rock, may change significantly over geologic time, probably as a result of multiple different and interacting factors (see discussion above). It is, therefore, possible that some macroevolutionary patterns, including short- and long-term trends in biodiversity, have been overprinted by both changes in the absolute quantity of preserved sedimentary rock (sensu Raup 1976) and changes in the extent to which that preserved rock has actually been sampled for fossils.

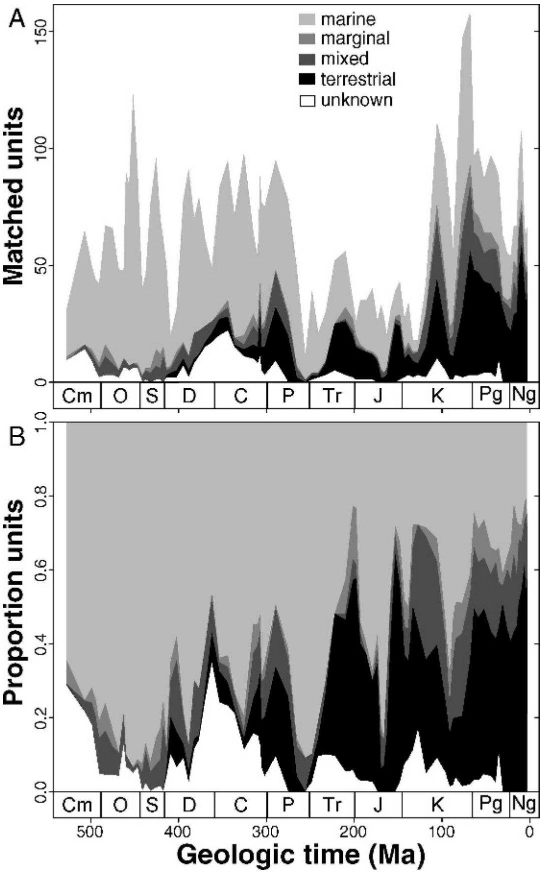

FIGURE 14. Lithostratigraphic units subdivided by paleoenvironment. A, Total number of matched lithostratigraphic units. B, Percentage of matched lithostratigraphic units. Units with an unknown environment are those that could not be reliably identified as marine or terrestrial given current information in Macrostrat and the PaleoDB. Mixed units include both marine and terrestrial environments. Data are plotted at age of interval midpoint from the Early Cambrian through Pliocene. See text for discussion.

In principle, sampling-standardization approaches, such as rarefaction and more advanced techniques (e.g., Alroy et al. 2008), could reduce or eliminate entirely the effects of variable geological completeness. If, however, geological completeness is positively correlated with the overall completeness of paleontological sampling relative to environmental heterogeneity, then systematic changes over time in the extent to which available environments are sampled could dominate most sampling-standardized diversity estimates. This possibility deserves careful consideration because it implies that a long-term trend in standardized diversity might, at least in part, be influenced by geologically controlled changes in the underlying heterogeneity of the paleontological samples that are used to estimate that trajectory and not by true changes in biodiversity. Testing this hypothesis will be possible by simultaneously controlling for traditional measures of paleontological sampling intensity (e.g., specimens, occurrences, collections) and geologically controlled variation in the distribution of those samples relative to the environmental mosaic that is so richly preserved in the sedimentary rock record.

Conclusions

1. Macrostratigraphy provides a robust framework for evaluating paleontological data that is independent of the fossil record, thereby permitting tests of the meaning of absences in fossil data compilations such as the Paleobiology Database (PaleoDB). A macrostratigraphic database (Macrostrat) consisting of 18,815 sedimentary rock units, their stratigraphic names, the ages of their top and bottom contacts, and general lithologies at 814 locations in the United States and Canada provides this framework.
2. At the time of this study, 90.8% (30,387) of the 33,474 PaleoDB fossil collections in the United States and Canada with potentially informative stratigraphic data had been successfully matched to a rock unit in the macrostratigraphic database. Most matching was accomplished by using algorithms that compared geographic coordinates and stratigraphic unit names (subsequently manually verified), indicating a high-degree of consistency in stratigraphic nomenclature between the two compilations.
3. A total of 3282 out of 18,815 (17%) sedimentary rock units and 1422 out of 4938 (29%) gap-bound sedimentary rock packages had been matched to at least one fossil collection as of 19 April 2009. Measured on a per-interval basis from the Lower Cambrian to Pliocene (median interval duration 5.3 Myr), mean geolog-

ical completeness of paleontological sampling is 0.18 for lithostratigraphic units, 0.22 for packages, 0.23 for columns, and 0.23 for sediment coverage area (km^2). These completeness estimates will only increase as new fossil collections are entered into the PaleoDB.

4. The geological completeness of paleontological sampling varies on short time scales and increases significantly during the Phanerozoic; on average, Cenozoic time intervals have a geological completeness that is approximately 40% greater than mean Paleozoic completeness. Estimates for two of the most completely sampled intervals, the Campanian and Maastrichtian, are as much as five times greater than the Cambrian and other time intervals with low geological completeness (Early Devonian, late Permian, Early Cretaceous). It is unlikely that these long-term temporal patterns will change substantially as more collections are added to the PaleoDB.
5. The irregular Phanerozoic increase in completeness does not appear to be driven entirely by the tendency for old sediments to be buried by younger sediments; cursory exclusion of all units known to occur only in the subsurface increases overall completeness, but does not dramatically affect temporal patterns. Terrestrial units are also unlikely to be the only cause of the temporal trajectory unless the completeness of paleontological sampling among terrestrial units is considerably higher than it is among marine units and unless the completeness of terrestrial sampling among terrestrial units changed abruptly in the Late Cretaceous.

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