

## The influence of lithification on Cenozoic marine biodiversity trends

Austin J. W. Hendy

**Abstract.**—Recent research has corroborated the long-held view that the diversity of genera within benthic marine communities has increased from the Paleozoic to the Cenozoic as much as three- to fourfold, after mitigating for such biasing influences as secular variation in time-averaging and environmental coverage. However, these efforts have not accounted for the considerable increase in the availability of unlithified fossiliferous sediments in strata of late Mesozoic and Cenozoic age. Analyses presented here on the Cenozoic fossil record of New Zealand demonstrate that unlithified sediments not only increase the amount of fossil material and hence the observed diversity therein, but they also preserve a pool of taxa that is compositionally distinct from lithified sediments. The implication is that a large component of the difference in estimates of within-community diversity between Paleozoic and Cenozoic assemblages may relate to the increased availability of unlithified sediments in the Cenozoic.

Austin J. W. Hendy.\* *Department of Geology, University of Cincinnati, Cincinnati, Ohio 45221.*  
E-mail: [austin.hendy@yale.edu](mailto:austin.hendy@yale.edu)

\*Present address: *Department of Geology and Geophysics, Yale University, Post Office Box 208109, New Haven, Connecticut 06520-8109*

Accepted: 8 August 2008

### Introduction

The fossil record is inherently biased by factors that distort apparent secular patterns of past biodiversity and ecological change (Newell 1959; Raup 1972; Signor et al. 1982; Paul 1998; Alroy 2000; Alroy et al. 2001), including variations in available rock volume (Raup 1972, 1976; Miller 2000; Peters and Foote 2001; Smith 2001; Crampton et al. 2003) and patchiness in the preservation of soft-bodied animals (Allison and Briggs 1991; Briggs 2003). Recent interest has focused in particular on temporal variations in the quality of sampling of the global Phanerozoic fossil record by paleontologists (Miller and Foote 1996; Alroy et al. 2001), a bias that may be associated with the actual availability of fossil-bearing rocks of particular age. Sampling-standardization techniques have been developed with the expressed intent to overcome this bias, but subsampling methods can impose their own unique distortions (Bush et al. 2004).

Rather than attempting to census global biodiversity in aggregate, some paleontologists have instead adopted the approach of monitoring secular trends in the average or median diversity of individual communities through time, commonly referred to as alpha

diversity (Bambach 1977; Sepkoski 1988; Powell and Kowalewski 2002; Bush and Bambach 2004). Although the relationship between alpha and global diversity may be more complex than once thought (e.g., Sepkoski 1988), interval to interval variations in alpha diversity may provide a meaningful yardstick for biodiversity change at broader scales, while avoiding some of the biases and problems that operate on an aggregate scale (Bambach 1977). Just as with the measurement of global diversity, it is considered a prerequisite to standardize for sampling effort when measuring alpha diversity by using techniques such as rarefaction. This and related methods allow numerical estimates of diversity at sample sizes (occurrences or specimens) smaller than those of the original collection, and hence permit a more meaningful comparison among multiple samples of varying size (e.g., Miller and Foote 1996).

Earlier efforts at monitoring variation in global biodiversity through the Phanerozoic (e.g., Sepkoski et al. 1981; Sepkoski 1984, 1997; Benton 1995) have suggested that diversity at the family level and below rose exponentially through the Mesozoic–Cenozoic, resulting in a three- to fourfold increase relative to the Pa-

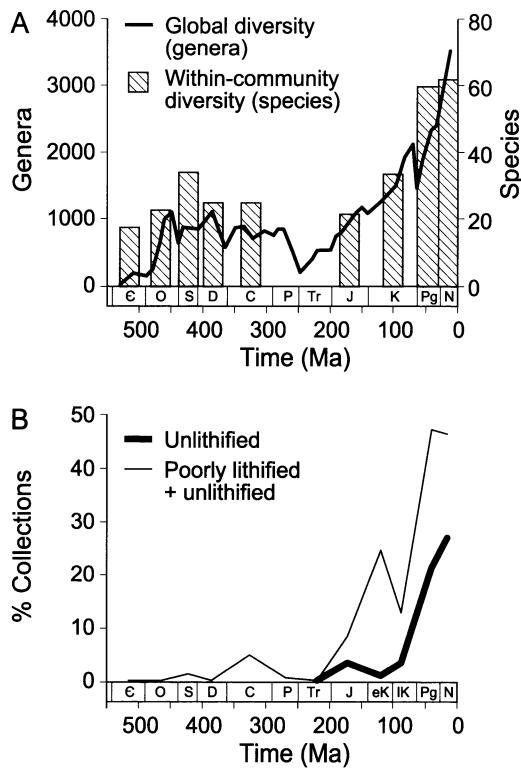


FIGURE 1. A, Variation in global Phanerozoic marine invertebrate biodiversity as perceived from analysis of a synoptic database (redrawn from Sepkoski 1997), with within-community diversity from open marine environments of Bambach (1977) superimposed. B, Variation in proportion of collections derived from unlithified and non-lithified (combined unlithified and poorly lithified) sediments through the Phanerozoic (data from Paleobiology Database, [www.paleodb.org](http://www.paleodb.org)). Note that the Cretaceous and Cenozoic intervals are subdivided into early and late Cretaceous epochs, and Paleogene and Neogene subperiods.

leozoic (Fig. 1A). A similar pattern has been demonstrated for the diversity of individual benthic marine communities (Bambach 1977; Sepkoski 1988), which are inferred to have shown an increase from the Paleozoic to the Cenozoic of as much as two- to threefold (Fig. 1A). A recent investigation (Bush and Bambach 2004) has not only confirmed this long-held view, but also suggested that the increase could be even higher after adjusting for such biasing influences as secular variation in aragonite dissolution, environmental coverage, and latitudinal variation through the Phanerozoic.

That said, previous assessments of alpha diversity did not account for the considerable increase in the availability of unlithified fossil-

iferous sediments in strata of late Mesozoic and Cenozoic age (Fig. 1B). Given this important transition in preservation state, its potential effects must be studied more rigorously. Although an increase in observed local diversity of younger rocks may reflect the ease of extracting large numbers of specimens, preservational biases that enhance the recovery of species from unlithified sediments may also be responsible. Alternatively, changes in local diversity may represent sampling heterogeneities (different environments or communities sampled at different times) or real (biological) increases in regional biodiversity. Therefore, any investigation into the consequences of lithification should be sufficiently constrained geographically and with respect to environmental setting to avoid the confounding effects of other factors, such as depositional environment, latitudinal position, time-averaging, and temporal variations in biodiversity itself (Kowalewski et al. 2006). The assembly of a new data set from bulk-sampled marine invertebrate fossil assemblages in the late Miocene–Pleistocene of New Zealand provides just such an opportunity to estimate the loss of taxonomic information associated with lithification bias in the Phanerozoic fossil record. Here, I present comparisons of the diversity of mollusc- and brachiopod-dominated fossil assemblages at a range of spatial scales and with environmental constraints to demonstrate not only the effect of lithification on the availability of fossil material, but also its effect on taxonomic composition, a bias not mitigated through sampling-standardization techniques. A recent independent study by Sessa et al. (2009) addresses similar issues affecting Paleocene–Eocene age skeletal assemblages of the Gulf Coastal Plain, North America.

## Methods

**Samples and Preparation.**—The primary data set for this investigation is composed of 169 fossil samples, ranging in age from late Miocene to Pleistocene, collected from a narrow range of sedimentary facies in two sedimentary basins (Wanganui and East Coast) of New Zealand. The extensive and continuous late Neogene succession in these basins exhibits a strong lithification gradient between its oldest

and youngest sedimentary components. A concerted effort was made to maintain consistent methods of collection (stratigraphic and spatial integrity of samples), preparation, counting, and identification, although sample treatment varied from assemblage to assemblage because of the nature of enclosing sediments (e.g., weathered or fresh outcrops, lithified or unlithified bedding planes). Nevertheless, where possible sufficient sampling effort was made to obtain 200–300 specimens per collection, amalgamated from multiple replicates collected adjacently along single horizons. In contrast to more exhaustive collection methodologies aimed at retrieving maximum diversities (e.g., Cooper et al. 2006), this approach is more suitable for making comparisons at equivalent sample size between lithified and unlithified assemblages. Sampling was restricted to mollusc- or brachiopod-dominated transgressive shell bed facies (Hendy et al. 2006) to control as much as possible for between-sample variation in time-averaging and to allow the comparison of relatively consistent environments through the time series. All sampled skeletal assemblages were contained within a matrix of sandy silt, silty sand, or pebbly sand and the relative composition of sampled lithologies remains similar in each time interval studied. These samples represented lower shoreface to midshelf bathymetric settings, from sandy or sandy silty substrates, and exhibited characteristics consistent with within-habitat time-averaging. This approach has the advantage of minimizing the potential effects of environment and taphonomy on temporal signals (Peters 2004; Kowalewski et al. 2006), but does limit interpretations to the chosen environment.

In addition, a set of analyses was carried out with a subset of these samples that were dominated by a single ubiquitous infaunal bivalve, *Tawera*, which is present throughout late Neogene fossiliferous deposits in New Zealand (Beu and Maxwell 1990). This data set comprises 53 bulk samples representing the *Tawera* association of late Miocene–early Pleistocene age, including 11 unlithified, 10 poorly lithified, and 21 lithified fossil assemblages. This subset of samples is therefore thought to represent a single paleocommunity from the shel-

fal transgressive environmental gradient through the time series (Hendy and Kamp 2004, 2007; Hendy et al. 2006).

Samples were assigned to one of three lithification grades: *unlithified*, whereby samples may be easily sieved and individual specimens are entirely free of matrix; *poorly lithified*, whereby samples can be sieved or disaggregated following considerable preparation and individual specimens cannot be parted entirely from matrix; and *lithified*, whereby samples cannot be sieved and are best observed as slabs or broken rock fragments, and individual specimens remain embedded in matrix.

*Occurrence Data.*—An additional data set was extracted from the New Zealand Fossil Record File database (FRF) to provide a baseline against which to compare the influence of lithification state on occurrence data, with the abundance data obtained from the 169 bulk samples. The FRF is a historic archive that records faunal records for individual fossil localities around New Zealand in addition to the sedimentary characteristic of localities (for further description see Crampton et al. 2003, 2006). This data set included all faunal lists that possessed semiquantitative data on lithification (expressed as hardness values, from cemented to soft) from Wanganui Basin, North Island, New Zealand. These faunal lists (presence-absence data) encompass the same temporal interval and similar geographic coverage as the bulk-sampled (abundance data) data set described above. Because these represent historical accounts (sometimes composed through repeated collection effort) and were often intended to be exhaustive in their inventory of observed or collected fossils (rather than standardized sampling efforts), they should therefore show an uncorrected bias with respect to any lithification effect.

*Diversity Analyses.*—I compared several arrangements of the bulk-sampled data set: all samples, late Miocene, early Pliocene, late Pliocene, and Pleistocene samples, and samples containing *Tawera*-dominated assemblages. Although all skeletonized invertebrate taxa were counted, analyses include only molluscs and brachiopods (see Appendix). Of particular interest are early Pliocene and late Pliocene samples, which provide the only two time in-

tervals in which direct comparison can be made between contemporaneous unlithified and lithified samples. I estimated genus richness at sampling quotas of 100 and 200 specimens for each sample, using classical rarefaction (Miller and Foote 1996), and determined mean richness values for samples assigned to each of the lithification grades, time intervals, or combination of lithification and time. Mean richness of FRF data, however, does not include any standardization of sample size, because information on individual taxon abundance within faunal lists is not available. For all comparisons I calculated an "increase factor" representing the ratio of difference in mean diversity between lithified and unlithified comparisons. The nonparametric Kolmogorov-Smirnov test and parametric *t*-test (for comparison) were carried out to provide statistical confidence on differences between mean richness of unlithified and lithified data sets. The Kolmogorov-Smirnov test could not be carried out on the comparisons between unlithified and lithified early Pliocene mean richness because the number of samples was insufficient.

*Mineralogy and Size Data.*—I also investigated the mineralogy and body size characteristic of the fauna to determine factors responsible for changing the composition of lithified and unlithified assemblages. Data for the analysis of body size composition of samples were collected from the literature on Cenozoic and extant New Zealand Mollusca (primarily Powell 1979; Fleming 1966; Beu and Maxwell 1990; Cooper et al. unpublished data) and are summarized in the Appendix. Body size is indicated by maximum skeletal dimension of an average adult, and all fossil genera were binned into three classes: <15 mm, 15 to 65 mm, and >65 mm. The somewhat arbitrary boundaries for these size classes were chosen to allow taxa to be spread among only three (small, medium, and large) size groupings. These differ from groupings in other published analyses of size distribution (e.g., Bouchet et al. 2002; Cooper et al. 2006) that focused on a broader range of molluscan taxa, including micro-molluscs (typically <5 mm). Results are presented as the percentage of the genus roster belonging to each of these three

size classes, according to lithification grade; the pattern remains comparable if the percentage of specimens within samples is assessed rather than the percentage of genus diversity.

Analysis of mineralogical composition was also presented as the percentage of the genus roster belonging to categories of either dominantly calcitic or aragonitic shell mineralogy. Data supporting this analysis were derived from the general literature (primarily Moore 1969; Coan et al. 2000); mineralogy was assumed to be consistent within families. Taxa with mixed aragonitic and calcitic shells (e.g., Anomiidae) were regarded as having a calcitic mineralogy; it has been observed that the calcitic portion of these shells remains even after considerable dissolution. These data are also summarized in the Appendix.

## Results and Discussion

*Influence of Lithification on Occurrence Data.*—All else being equal, it is intuitive that preservation in loose, unconsolidated sediments should enhance the collection of larger quantities of fossil material, and this factor often encourages repeat sampling of the same assemblages over time. Analysis of the data assembled from the FRF (Fig. 2) illustrates the effect of lithification on the richness of individual localities in a single sedimentary basin, without standardization for variable sample size. The lists from individual localities represent a variety of collection techniques, ranging from exhaustive to exploratory surveys, and may represent composite lists, amended as a result of successive collecting through time. Hence, although longer faunal lists might reflect greater diversity they might also reflect increased sampling effort, ease of sampling, or repeated collecting. As illustrated in Figure 2A, the mean genus richness of these lists increases fourfold through the late Neogene. Although this may be interpreted as a meaningful biodiversity trend, the observed increase occurs concurrently with a decrease in the lithification of collections included in the analysis. In aggregate, mean and maximum genus richness are about four times greater for collections from unlithified sedi-



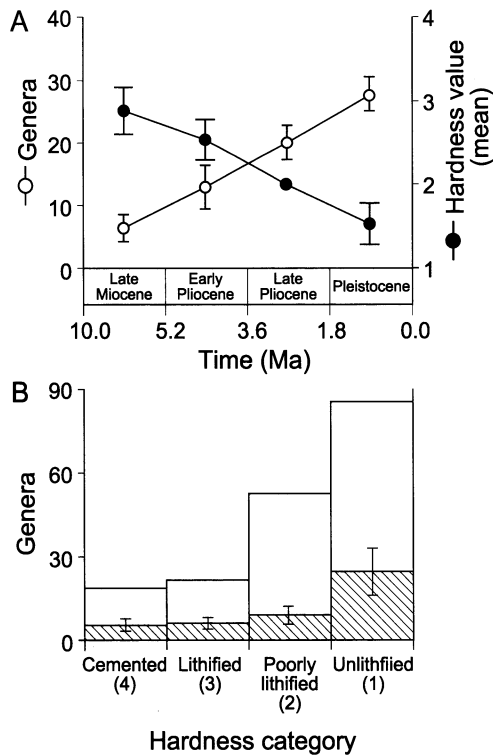


FIGURE 2. Effect of lithification on an occurrence-based data set (FRF). A, Variations in mean richness (total number of genera) and mean degree of lithification of collections from late Miocene–Pleistocene sediments, Wanganui Basin, New Zealand. B, Mean (cross-hatch) and maximum genus richness (white) for collections assigned to lithification categories. Data from New Zealand Fossil Record File (<http://data.gns.cri.nz/fred/>); hardness values range from 4 (cemented = lithified) to 1 (soft = unlithified); error bars indicate 95% confidence intervals.

ments than for collections from cemented or lithified sediments (Table 1, Fig. 2B).

*Influence of Lithification on Abundance Data.*—If this pattern were related simply to the size of the sample collected from individual local-

ities, then techniques that standardize for variations in sampling intensity, such as rarefaction, should mitigate this bias. Figure 3A shows rarefaction curves for the 169 field-collected bulk samples of late Miocene–early Pleistocene age, representing 37 unlithified and 66 lithified fossil assemblages. At comparable levels of sampling, most unlithified samples show considerably higher richness than those from lithified sediments, a pattern that is further amplified by the mean curves for each lithification category (Fig. 3B). At a quota of 100 specimens, unlithified sediments yielded on average close to 20 genera, whereas lithified sediments produced slightly fewer than ten genera for the same sampling intensity. Table 2 indicates that poorly lithified assemblages yield an intermediate mean richness and that the disparity in richness between lithified and unlithified samples was even greater at larger quotas.

Although efforts were made to sample the same range of environments through the study interval, a more effective approach might be to focus on a single biofacies, which makes it easier to maintain consistency in comparison among lithification categories through time. Rarefaction (Fig. 4) of 32 samples dominated by *Tawera* indicates again that at comparable levels of sampling most unlithified samples show considerably higher richness than those from lithified sediments, with poorly lithified assemblages showing an intermediate position (Table 2). Mean curves for each lithification category confirm this pattern. At a quota of 100 specimens richness in unlithified sediments was approximately two and a half times that of lithified sediments (Ta-

TABLE 1. Genus richness in lithified, poorly lithified, and unlithified sediments of the late Neogene New Zealand from the Fossil Record File (FRF) and from field-collected bulk samples. Mean genus richness for FRF data is unstandardized; genus richness for field samples and *Tawera* samples rarefied to 100 specimens (and to 200 specimens, in parentheses).

Data set	Subset	Unlithified	Poorly lithified	Lithified
NZ Fossil	Mean	25.1	9.6	6.0
Record File	Max	88	54	19
Field samples	All	19.7 (25.1)	15.9 (20.5)	9.9 (10.4)
	Pleistocene	20.6	19.6	—
	Late Pliocene	17.4	14.8	12.6
	Early Pliocene	20.9	16.0	8.8
	Late Miocene	—	—	8.6
<i>Tawera</i> association		17.5 (22.5)	13.4 (14.0)	7.8 (8.7)

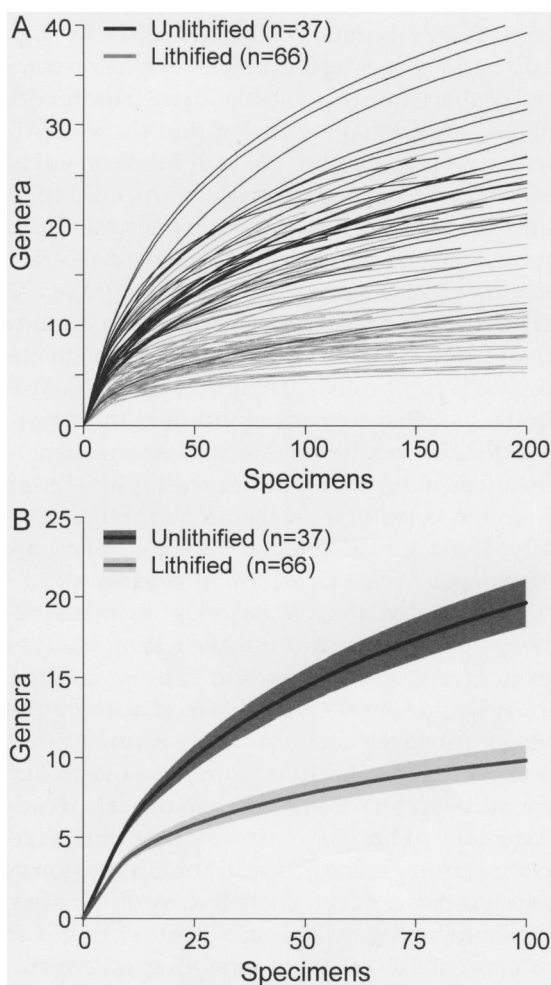


FIGURE 3. Rarefaction of census counts from bulk samples of varying lithification from late Miocene-Pleistocene sediments of Wanganui Basin, New Zealand. A, Rarefaction curves for individual samples coded by lithification category (poorly lithified samples excluded for clarity). B, Means of individual curves in A within each lithification categories with shaded 95% confidence intervals.

ble 2). Unlithified sediments yielded on average close to 19 genera, whereas lithified sediments produced slightly fewer than eight genera for the same sampling intensity.

One further analysis restricted comparisons to individual time intervals, to minimize the possibility that temporal variation in composition of faunas affected the patterns illustrated in Figures 3 and 4. Although unlithified and lithified sediments were lacking from late Miocene and Pleistocene successions, respectively, the pattern of increasing diversity with

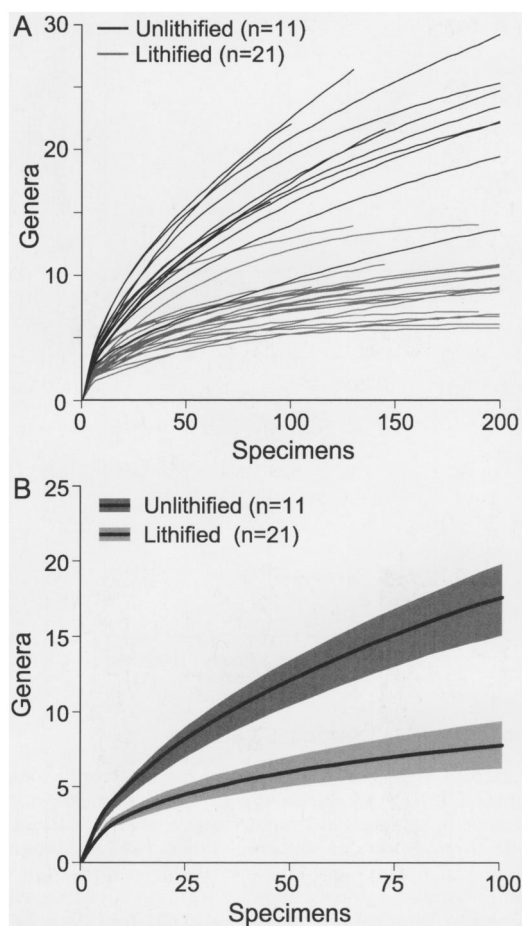


FIGURE 4. Rarefaction of census counts from bulk samples dominated by *Tawera* of varying lithification from late Miocene-Pleistocene sediments of Wanganui Basin, New Zealand. A, Rarefaction curves for individual samples coded by lithification category (poorly lithified samples excluded for clarity). B, Means of individual curves in A within each lithification categories with shaded 95% confidence intervals.

decreasing degree of lithification is evident for each time interval analyzed independently (Table 1), but not through time within any single lithification category. These analyses demonstrate that sampling-standardization techniques alone cannot reconcile the high diversities yielded from the easier recovery of fossils from unlithified samples with the lower diversities of lithified samples, suggesting a fundamental difference in the recoverable faunal composition of lithified and unlithified samples. Sessa et al. (2009) found a similar discrepancy in the sampling-standardized

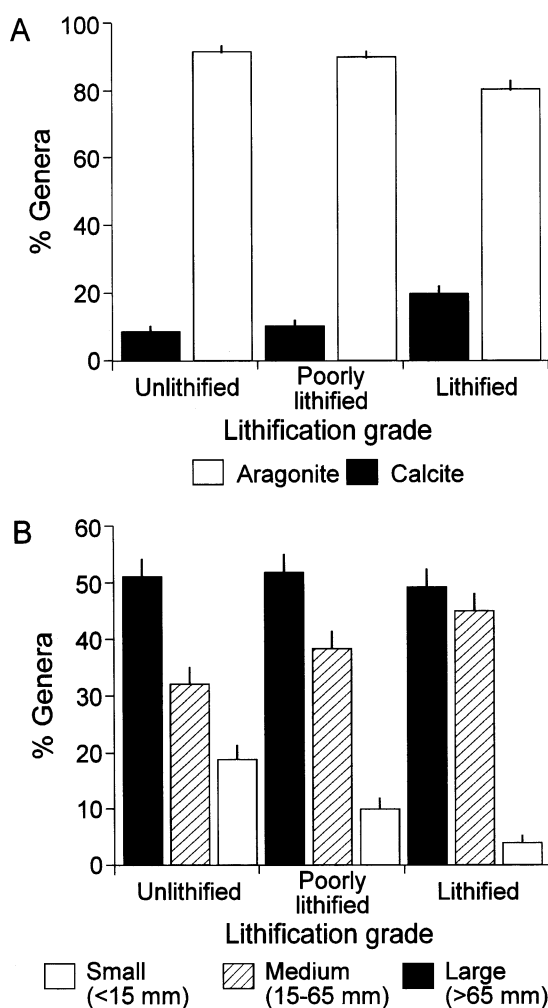


FIGURE 5. Influence of lithification on taphonomic features of skeletal assemblages. A, Relative composition of aragonitic and calcitic skeletal types. B, Relative composition of various size classes. Error bars indicate 95% confidence intervals.

richness between lithified and unlithified assemblages of early Paleogene age.

A recent independent study by Sessa et al. (2009) addresses similar issues effecting Paleocene-Eocene age skeletal assemblages of the Gulf Coastal Plain, North America.

Because the process of lithification commonly involves the cementation of matrix by carbonate sediment, a likely candidate for the genus richness decline in lithified sediments is the preferential destruction of aragonitic skeletal hardparts. Aragonite is commonly dissolved during carbonate diagenesis (Kidwell and Flessa 1995; Jablonski and Sepkoski 1996;

Paul 1998; Cherns and Wright 2000), although dissolution does not necessarily result in complete fossil destruction (Bush and Bambach 2004). Additionally, small or thin-shelled skeletons might be more vulnerable to damage by sediment compaction and carbonate dissolution (Cooper et al. 2006; Kidwell and Flessa 1995; Jablonski and Sepkoski 1996), and small fossils might also be more readily overlooked by collectors in the field because of difficulty in extracting them from lithified sediments (Cooper et al. 2006). The process of fossil extraction from lithified fossil assemblages from the field, or preparation in the lab, inherently involves the splitting of hardened slabs or the fragmentation of larger blocks, processes during which small and fragile specimens are more likely to be damaged or destroyed.

The results presented in Figure 5 suggest that skeletal size and mineralogy indeed account for at least part of the difference in taxonomic content between lithified and unlithified sediment. There is an observable, albeit small, decrease in the proportion of taxa (and occurrences) with predominantly aragonitic skeletons in lithified sediment (Fig. 5A). Likewise there is an increase in the proportion of observed diversity contributed by the smallest and medium size classes of invertebrates in poorly lithified and unlithified sediments (Fig. 5B). The difference, while slight, corroborates independent analyses of the removal of small size classes on sample-level diversity (Kowalewski et al. 2006; Sessa et al. (2009). A comparison of taxonomic composition of lithified and unlithified samples used in this study (see Appendix) indicates that the majority of taxa that are unrepresented in lithified samples tend to be rare (21 of 24 genera constitute less than 3% of mean sample abundance) and are aragonitic (22 of 24 genera).

## Conclusions

In light of existing assumptions about the influence of lithification the three- to fourfold diversity increase observed in unlithified samples in the FRF data set is not an entirely surprising result. Importantly, however, this disparity is not a simple reflection of increased sample size in unlithified sediments. Rarefaction analysis of relative abundance

TABLE 2. Comparison of mean sample-level diversity estimates among faunal lists and samples derived from lithified and unlithified matrix of the late Neogene of New Zealand. The "increase factor" is computed as a ratio of the mean unlithified to lithified diversity. Mean values and statistical comparisons, with the exception of data from the NZ Fossil Record File (FRF), which cannot be standardized, are based on rarefied diversity at sample sizes of 100 specimens; means and increase factors at sample sizes of 200 specimens are shown in parentheses. Abbreviations: samples, all bulk samples; E. Plio., early Pliocene bulk samples; L. Plio., late Pliocene bulk samples; *Tawera*, bulk samples of the *Tawera* association.

Data set	Parameter	FRF	Samples	E. Plio.	L. Plio.	<i>Tawera</i>
Unlithified	mean	25.1	19.7 (25.1)	20.9 (25.3)	17.4 (22.7)	17.5 (22.5)
	<i>n</i>	26	37 (10)	6 (4)	12 (10)	11 (8)
Lithified	mean	6.0	9.9 (10.4)	8.8 (8.6)	12.6 (16.5)	7.8 (8.7)
	<i>n</i>	26	66 (28)	35 (16)	19 (4)	21 (13)
Increase factor		4.1	2.0 (2.4)	2.4 (2.9)	1.4 (1.4)	2.3 (2.6)
<i>t</i> -test	<i>t</i>	4.13	11.20	7.81	3.10	9.64
	<i>p</i>	<0.0001	<0.0001	<0.0001	<0.0041	<0.001
Kolmogorov-Smirnov	<i>D</i>	0.54	0.79	—	0.71	0.91
	<i>p</i>	<0.001	<0.001	—	<0.001	<0.0001

data from bulk samples demonstrated that lithified assemblages will generally not yield the diversity of unlithified assemblages at comparable or even significantly larger sample sizes; instead, there are fundamental differences in the composition and abundance structure from assemblages of unlithified versus lithified sediments, which likely relate to variation in preservation potential within an assemblage. Variations in the size, robustness, and mineralogy of skeletal hardparts could lead to their preferential removal or masking in lithified samples during diagenesis, collection, or preparation. This bias imposed by lithification appears to be as great as, if not greater than, that related to variations in aragonite dissolution, latitudinal distribution, or environmental factors through the Phanerozoic (Bush and Bambach 2004).

Analyses incorporating sampling-standardization of genus occurrences (Alroy et al. 2008) suggest that global Phanerozoic diversity has not shown the trajectory of dramatic increase toward the Recent suggested in earlier synoptic analyses (Sepkoski et al. 1981; Sepkoski 1984); the Cenozoic increase was more muted than that suggested by the raw data. However, other sampling-standardized analyses have claimed to show a tripling or even quadrupling of within-community diversity (Bush and Bambach 2004). The results of this study suggest that a significant part of the increase, perhaps as much as half of it, may be attributable to the increasing availability of

unlithified sediments through the Cenozoic Era. Macroevolutionary trends in the structure of marine communities (e.g., increased ecospace utilization and evolutionary escalation) are likely explanations for any remaining observed increase in within-community diversity through the Phanerozoic, after consideration of lithification, diagenetic, environmental, and latitudinal biases.

### Acknowledgments

This project was funded in part from a NASA Exobiology Grant to Arnold I. Miller (NAG5-13426), and from a University Dean's Distinguished Dissertation Fellowship and Graduate Student Summer Research Grants from the University of Cincinnati to the author. Additional funding was by the American Museum of Natural History Lerner-Gray Fund, Geological Society of America, Paleontological Society, and the American Association of Petroleum Geologists. I thank the members of the Marine Invertebrate Working Group of the Paleobiology Database (<http://paleodb.org>), particularly J. Alroy, for encouraging this research and for helpful discussions. Thanks also to the University of Waikato, and in particular to P. Kamp, K. Bland, and A. Vonk for assistance with fieldwork and laboratory facilities. I also would like to acknowledge discussions and feedback from A. Miller, C. Brett, D. Buick, K. Bulinski, C. Ferguson, and J. Sessa, and constructive reviews



from B. Bennington and A. Smith. This is Paleobiology Database publication no. 87.

### Literature Cited

- Allison, P. A., and D. E. G. Briggs. 1991. The taphonomy of soft-bodied animals. Pp. 120–140 in S. K. Donovan, ed. *The processes of fossilization*. Columbia University Press, New York.
- Alroy, J. 2000. Successive approximations of diversity curves: ten more years in the library. *Geology* 28:1023–1026.
- Alroy, J., C. R. Marshall, R. K. Bambach, K. Bezusko, M. Foote, F. T. Fürsich, T. A. Hansen, S. M. Holland, L. C. Ivany, D. Jablonski, D. K. Jacobs, D. C. Jones, M. A. Kosnik, S. Lidgard, S. Low, A. I. Miller, P. M. Novack-Gottshall, T. D. Olszewski, M. E. Patzkowsky, D. M. Raup, K. Roy, J. J. Sepkoski Jr., M. G. Sommers, P. J. Wagner, and A. Webber. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences USA* 98:6261–6266.
- Alroy, J., M. Aberhan, D. J. Bottjer, M. Foote, F. T. Fürsich, P. J. Harries, A. J. W. Hendy, S. M. Holland, L. C. Ivany, W. Kiessling, M. A. Kosnik, C. R. Marshall, A. J. McGowan, A. I. Miller, T. D. Olszewski, M. E. Patzkowsky, S. E. Peters, L. Villier, P. J. Wagner, N. Bonuso, P. S. Borkow, B. Brenneis, M. E. Clapham, L. M. Fall, C. A. Ferguson, V. L. Hanson, A. Z. Krug, K. M. Layou, E. H. Leckey, S. Nürnberg, C. M. Powers, J. A. Sessa, C. Simpson, A. Tomašových, C. C. Visaggi. 2008. Phanerozoic trends in the global diversity of marine invertebrates. *Science* 321:97–100.
- Bambach, R. K. 1977. Species richness in marine benthic habitats through the Phanerozoic. *Paleobiology* 3:152–167.
- Benton, M. J. 1995. Diversification and extinction in the history of life. *Science* 268:52–58.
- Beu, A. G., and P. A. Maxwell. 1990. Cenozoic Mollusca of New Zealand. New Zealand Geological Survey Paleontological Bulletin 58.
- Bouchet, P., P. Lozouet, P. Maestrati, and V. Heros. 2002. Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society* 75:421–436.
- Briggs, D. E. G. 2003. The role of decay and mineralization in the preservation of soft-bodied fossils. *Annual Review of Earth and Planetary Sciences* 31:275–301.
- Bush, A. M., and R. K. Bambach. 2004. Did alpha diversity increase through the Phanerozoic? Lifting the veils of taphonomic, latitudinal, and environmental biases. *Journal of Geology* 112:625–642.
- Bush, A. M., M. J. Markey, and C. R. Marshall. 2004. Removing bias from diversity curves: the effects of spatially organized biodiversity on sampling-standardization. *Paleobiology* 30:666–686.
- Cherns, L., and V. P. Wright. 2000. Missing molluscs as evidence of large-scale, early skeletal aragonite dissolution in a Silurian sea. *Geology* 28:791–794.
- Coan, E. V., P. V. Scott, and F. R. Bernard. 2000. Bivalve seashells of western North America. Santa Barbara Museum of Natural History, Santa Barbara, Calif.
- Cooper, R. A., A. G. Beu, J. S. Cooper, C. M. Jones, B. Marshall, P. A. Maxwell. 2006. Completeness of the fossil record: estimating losses due to small body size. *Geology* 34:241–244.
- Crampton, J. S., A. G. Beu, R. A. Cooper, C. M. Jones, B. Marshall, P. A. Maxwell. 2003. Estimating the rock volume bias in paleobiodiversity studies. *Science* 301:358–361.
- Crampton, J. S., A. G. Beu, R. A. Cooper, J. S. Cooper, M. Foote, C. M. Jones, B. Marshall, I. Matcham, and P. A. Maxwell. 2006. The ark was full! Constant to declining Cenozoic shallow marine biodiversity on an isolated midlatitude continent. *Paleobiology* 32:509–532.
- Fleming, C. A. 1966. Marwick's illustrations of New Zealand shells, with a checklist of New Zealand Cenozoic Mollusca. Department of Scientific and Industrial Research Bulletin 173.
- Hendy, A. J. W., and P. J. J. Kamp. 2004. Late Miocene-Early Pliocene biofacies of Wanganui and Taranaki Basins, New Zealand. *New Zealand Journal of Geology and Geophysics* 47:769–785.
- . 2007. Paleocology of Late Miocene-Early Pliocene sixth-order glacioeustatic sequences in the Manutahi-1 core, Wanganui-Taranaki Basin, New Zealand. *Palaios* 22:325–337.
- Hendy, A. J. W., P. J. J. Kamp, and A. J. Vonk. 2006. Cool-water shell bed taphofacies from Miocene-Pliocene shelf sequences: utility in sequence stratigraphic analyses. *Geological Society of London Special Publication* 255:285–307.
- Jablonski, D., and J. J. Sepkoski Jr. 1996. Paleobiology, community ecology, and scales of ecological pattern. *Ecology* 77:1367–1378.
- Kidwell, S. M., and F. W. Flessa. 1995. The quality of the fossil record: populations, species, and communities. *Annual Review of Earth and Planetary Sciences* 24:433–464.
- Kowalewski, M., W. Kiessling, M. Aberhan, F. T. Fürsich, D. Scarponi, S. L. Barbour Wood, and A. P. Hoffmeister. 2006. Ecological, taxonomic, and taphonomic components of the post-Paleozoic increase in sample-level species diversity of marine benthos. *Paleobiology* 32:533–561.
- Miller, A. I. 2000. Conversations about Phanerozoic global diversity. In D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):53–73.
- Miller, A. I., and M. Foote. 1996. Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends. *Paleobiology* 22:304–309.
- Moore, R. C. 1969. Treatise on invertebrate paleontology. Part N, Mollusca 6, Bivalvia. Geological Society of America, New York, and University of Kansas, Lawrence.
- Newell, N. D. 1959. Adequacy of the fossil record. *Journal of Paleontology* 33:488–499.
- Paul, C. R. C. 1998. An overview of the completeness of the fossil record. Pp. 1–22 in S. K. Donovan and C. R. C. Paul, eds. *The adequacy of the fossil record*. Wiley, Chichester, U.K.
- Peters, S. E. 2004. Evenness of Cambrian-Ordovician benthic marine communities in North America. *Paleobiology* 30:325–346.
- Peters, S. E., and M. Foote. 2001. Biodiversity in the Phanerozoic: a reinterpretation. *Paleobiology* 27:583–601.
- Powell, A. W. B. 1979. New Zealand Mollusca: marine, land and freshwater shells. Collins, Auckland, New Zealand.
- Powell, M. G., and M. Kowalewski. 2002. Increase in evenness and sampled alpha diversity through the Phanerozoic: comparison of early Paleozoic and Cenozoic marine fossil assemblages. *Geology* 30:331–334.
- Raup, D. M. 1972. Taxonomic diversity during the Phanerozoic. *Science* 177:1065–1071.
- . 1976. Species diversity in the Phanerozoic: an interpretation. *Paleobiology* 2:289–297.
- Sepkoski, J. J., Jr. 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10:246–267.
- . 1988. Alpha, beta, or gamma; where does all the diversity go? *Paleobiology* 14:221–234.
- . 1997. Biodiversity: past, present, and future. *Journal of Paleontology* 71:533–539.
- Sepkoski, J. J., Jr., R. K. Bambach, D. M. Raup, and J. W. Valentine. 1981. Phanerozoic marine diversity and the fossil record. *Nature* 293:435–437.
- Sessa, J. A., M. E. Patzkowsky, and T. J. Bralower. 2009. The impact of lithification on the diversity, size distribution, and re-

- covery dynamics of marine invertebrate assemblages. *Geology* (in press).
- Signor, P. W., J. H. Lipps, and P. H. Schultz. 1982. Sampling bias, gradual extinction patterns, and catastrophes in the fossil record. In I. Silver and P. Silver, eds. *Geologic implications of impacts of large asteroids and comets on the earth*. Geological Society of America Special Paper 190:291–296.
- Smith, A. B. 2001. Large-scale heterogeneity of the fossil record: implications for Phanerozoic biodiversity studies. *Philosophical Transactions of the Royal Society of London B* 356:351–367.

### Appendix

A list of molluscan and brachiopod genera, and abundance data, pooled across all samples included in this study. Genera are listed alphabetically. Abbreviations: Polyplac., Polyplacophora; C, calcite; C/A, mixed calcite (dominant) and aragonite; A/C mixed aragonite (dominant) and calcite; U, unlithified; L, lithified; A, aragonite; *n*, number of samples. Size classes: 1, <15 mm; 2, 15–65 mm; 3, >65 mm. Percentages are derived from the mean percentage composition of each taxon in all unlithified or lithified samples (where at least *n* is >2 in both lithification states).

Class	Genus	Min.	Size	Total		Mean percent			
				U	L	U %	U <i>n</i>	L %	L <i>n</i>
Polyplac.	<i>Acanthochitona</i>	A	1	3					
Gastropoda	<i>Aeneator</i>	A	3	19		4.3	6		
Gastropoda	<i>Alcithoe</i>	A	3	19		1.5	7		
Gastropoda	<i>Alocospira</i>	A	2		26			4.6	4 *
Gastropoda	<i>Amphibola</i>	A	2	1					†
Bivalvia	<i>Amygdalum</i>	A/C	3	5	7	0.6	4	1.3	3
Bivalvia	<i>Anchomasa</i>	A	3	554	47	5.5	64	4.0	8
Bivalvia	<i>Anomia</i>	C/A	3	23	13	1.2	10	1.7	8
Scaphopoda	<i>Antalis</i>	A	2	3		0.3	3		
Gastropoda	<i>Antimelatoma</i>	A	2	2					
Gastropoda	<i>Antisolarium</i>	A	1	3	2				
Bivalvia	<i>Arca</i>	A	2	1					
Bivalvia	<i>Asa</i>	A	2	72	83	3.1	17	2.5	12
Gastropoda	<i>Astraea</i>	A	3	5	2				
Bivalvia	<i>Atamarcia</i>	A	3	4	509				*
Gastropoda	<i>Ataxocerithium</i>	A	1	18		0.7	6		
Bivalvia	<i>Atrina</i>	A/C	3	119	518	2.4	26	18.6	18
Bivalvia	<i>Aulacomya</i>	A/C	3	13	4				
Bivalvia	<i>Austrodozinia</i>	A	3	54	16	13.0	6	1.5	6
Gastropoda	<i>Austrofus</i>	A	2	252	40	2.8	47	2.0	13
Gastropoda	<i>Austrotoma</i>	A	2		2				*
Bivalvia	<i>Austrovenus</i>	A	3	296		8.9	25		
Bivalvia	<i>Barbatia</i>	A	3	71	14	1.6	32	3.3	3
Gastropoda	<i>Baryspira</i>	A	3	299	54	3.5	56	3.0	11
Bivalvia	<i>Barytellina</i>	A	2	4		1.1	4		
Bivalvia	<i>Bassina</i>	A	3	7	6	1.4	3	1.3	3
Bivalvia	<i>Borehamia</i>	C	3	1	36				*
Gastropoda	<i>Buccinulum</i>	A	3	46		2.0	13		
Gastropoda	<i>Cabestana</i>	A	3		2				
Gastropoda	<i>Calliostoma</i>	A	1	81	45	1.5	32	1.6	19
Brachiopoda	<i>Calloria</i>	C	2	203	33	3.5	33	2.7	7
Gastropoda	<i>Callusaria</i>	A	3		10				*
Bivalvia	<i>Cardita</i>	A	1	57		1.4	21		
Bivalvia	<i>Caryocorbula</i>	A	1	87	5	1.3	30	0.5	5
Gastropoda	<i>Cirsotrema</i>	C	2	13		1.2	6		
Gastropoda	<i>Coelotrochus</i>	A	1	50	16	1.6	14	1.2	5
Gastropoda	<i>Cominella</i>	A	2	6	2				
Bivalvia	<i>Cosa</i>	A	1		1				
Bivalvia	<i>Crassostrea</i>	C	3	30	523	2.3	6	32.7	15 *
Bivalvia	<i>Crassula</i>	A	3		10				
Gastropoda	<i>Crepidula</i>	A	2	1692	1357	9.0	86	13.4	54
Bivalvia	<i>Cuspidaria</i>	A	1	2					
Bivalvia	<i>Cyclomactra</i>	A	3	425	35	5.3	57	4.3	4
Gastropoda	<i>Diloma</i>	A	1	7		1.0	4		†
Bivalvia	<i>Divalucina</i>	A	2	3	18				
Bivalvia	<i>Dosina</i>	A	3	36	17	1.3	12	4.0	3
Gastropoda	<i>Ellicea</i>	A	2		2				*

Appendix. Continued.

Class	Genus	Min.	Size	Total		Mean percent				
				U	L	U %	U n	L %	L n	
Gastropoda	<i>Emarginula</i>	A	1	5	14	0.5	3	1.5	5	
Gastropoda	<i>Eucominia</i>	A	2	72		1.7	18			
Bivalvia	<i>Eucrassatella</i>	A	3		1					*
Bivalvia	<i>Eumarcia</i>	A	3	29	237	2.1	14	18.9	14	*
Scaphopoda	<i>Fissidentalium</i>	A	3	55	15	4.0	6	2.0	8	
Gastropoda	<i>Friginatica</i>	A	1	1	4					*
Gastropoda	<i>Galeocorys</i>	A	3	2	14					
Bivalvia	<i>Gari</i>	A	2	147	16	2.7	30	3.4	6	
Gastropoda	<i>Gemmula</i>	A	1		2					
Gastropoda	<i>Glaphyrina</i>	A	3	36		1.4	8			
Bivalvia	<i>Glycymeris</i>	A	3	21	108	4.5	7	6.6	10	*
Bivalvia	<i>Glycymerula</i>	A	2	194	12	2.1	54	0.8	6	
Bivalvia	<i>Gobreaus</i>	A	2	50	7	2.5	19	0.7	6	
Bivalvia	<i>Goniomyrtea</i>	A	1	2						
Gastropoda	<i>Gracilispira</i>	A	2	19		2.4	8			
Bivalvia	<i>Hiatella</i>	A	1	1						
Bivalvia	<i>Hiatula</i>	A	2	19		1.2	8			
Bivalvia	<i>Hunkydora</i>	A	1	3	1					
Gastropoda	<i>Iredalula</i>	A	2	6						
Gastropoda	<i>Josepha</i>	A	2	40		2.9	14			
Bivalvia	<i>Kereia</i>	A	2	6	78					
Gastropoda	<i>Lamprodominea</i>	A	2	1	10					*
Gastropoda	<i>Leporemax</i>	A	3	26		2.0	13			
Gastropoda	<i>Lepsiella</i>	A	1	1						
Bivalvia	<i>Leptomya</i>	A	1	112		3.7	16			
Bivalvia	<i>Lima</i>	A/C	3	2	29					
Bivalvia	<i>Limaria</i>	A/C	2	12	3					
Bivalvia	<i>Limatula</i>	A/C	1	17	33	0.9	7	1.1	14	
Gastropoda	<i>Liratilia</i>	A	1	2						†
Bivalvia	<i>Lutraria</i>	A	3		5					*
Bivalvia	<i>Macomona</i>	A	2	3						
Bivalvia	<i>Mactra</i>	A	3	4		1.5	3			
Bivalvia	<i>Manaia</i>	A	3		104			13.2	11	*
Bivalvia	<i>Maoricardium</i>	A	3	10	30					*
Gastropoda	<i>Maoricolpus</i>	A	3	241	160	3.4	46	12.8	8	
Bivalvia	<i>Maorimactra</i>	A	1	126	47	3.1	31	5.6	13	
Bivalvia	<i>Marama</i>	A	3	30	25	2.3	5	1.8	9	*
Brachiopoda	<i>Margasella</i>	C	2	32		1.9	13			
Bivalvia	<i>Mesopeplum</i>	C	3	5	12	0.5	3	1.3	6	
Gastropoda	<i>Micrelenchus</i>	A	1	11	10					
Bivalvia	<i>Miltha</i>	A	3	6						*
Gastropoda	<i>Modelia</i>	A	1	2						
Bivalvia	<i>Modiolarca</i>	A/C	2	13	5	0.9	4	0.5	5	
Bivalvia	<i>Modiolus</i>	A/C	3	150	63	2.3	23	4.2	12	
Bivalvia	<i>Moerella</i>	A	1	4						
Bivalvia	<i>Monia</i>	C/A	3	4	1					
Bivalvia	<i>Myadora</i>	A	1	70	3					
Bivalvia	<i>Myllitella</i>	A	1	16	1					
Gastropoda	<i>Nassicola</i>	A	2	2						
Bivalvia	<i>Neilo</i>	A	2	5	8					
Bivalvia	<i>Neolepton</i>	A	1	1						
Brachiopoda	<i>Neothyris</i>	C	2	61	525	4.8	5	21.4	14	
Bivalvia	<i>Notirus</i>	A	2	1						
Gastropoda	<i>Notoacmaea</i>	A	1	2						
Bivalvia	<i>Nucula</i>	A	1	346	2					
Gastropoda	<i>Odostomia</i>	A	1	2						
Bivalvia	<i>Ostrea</i>	C	3	1232	891	6.7	113	9.8	80	
Bivalvia	<i>Ovicardium</i>	A	3		2					*
Bivalvia	<i>Panis</i>	C/A	3	6	1					*
Bivalvia	<i>Panopea</i>	A	3	4	28					
Bivalvia	<i>Paphies</i>	A	3	1028	9	8.9	87	1.1	4	

## Appendix. Continued.

Class	Genus	Min.	Size	Total		Mean percent				
				U	L	U %	U n	L %	L n	
Gastropoda	<i>Paracomitas</i>	A	1	2						
Gastropoda	<i>Patelloida</i>	A	1	2						†
Bivalvia	<i>Patro</i>	C/A	3	122	342	2.8	27	9.3	25	*
Bivalvia	<i>Pecten</i>	C	3	7		0.6	6			†
Gastropoda	<i>Pellicaria</i>	A	3	72	6	2.0	17	1.5	3	
Gastropoda	<i>Penion</i>	A	3	34	10	3.3	12	1.8	3	
Bivalvia	<i>Perna</i>	A/C	3	96	123	1.4	42	7.8	13	
Gastropoda	<i>Pervicacia</i>	A	2	8		1.5	5			
Bivalvia	<i>Phacosoma</i>	A	2	68	3					
Gastropoda	<i>Phenatoma</i>	A	2	4						
Bivalvia	<i>Phialopecten</i>	C	3	16	741	1.4	5	14.1	40	*
Bivalvia	<i>Pholadidea</i>	A	2	3						
Bivalvia	<i>Pleuromeris</i>	A	2	96	53	1.6	29	2.0	15	
Gastropoda	<i>Poirieria</i>	A	2	12		1.0	7			
Gastropoda	<i>Polinices</i>	A	2	12	8	1.7	3	1.7	3	*
Bivalvia	<i>Poroleda</i>	A	1	4						
Bivalvia	<i>Pratulium</i>	A	1	62	8	1.5	26	1.4	4	
Bivalvia	<i>Protothaca</i>	A	2		1					
Gastropoda	<i>Proxiuber</i>	A	1	20	2					
Bivalvia	<i>Pseudoxyperas</i>	A	3	8	96	1.6	4	9.8	9	
Bivalvia	<i>Pteromyrtea</i>	A	2	2	5					*
Gastropoda	<i>Pterynotus</i>	A	2	6						
Gastropoda	<i>Puncturella</i>	A	1	26		2.8	3			
Bivalvia	<i>Purpurocardia</i>	A	2	227	249	2.1	70	5.4	34	
Bivalvia	<i>Raina</i>	A	3	7	263	1.2	3	25.6	5	*
Bivalvia	<i>Resania</i>	A	3	5						
Bivalvia	<i>Rexithaerus</i>	A	2	6						
Bivalvia	<i>Ruditapes</i>	A	3	38	222	16.4	4	9.9	9	
Bivalvia	<i>Saccula</i>	A	1	2	2					
Bivalvia	<i>Scalpomactra</i>	A	2	260	65	9.4	22	5.7	5	
Bivalvia	<i>Sectipecten</i>	C	3		57			6.1	7	*
Gastropoda	<i>Semicassis</i>	A	3	1	2					
Gastropoda	<i>Serpulorbis</i>	A	2		2					
Bivalvia	<i>Serratina</i>	A	2	45	19	1.8	19	5.7	3	
Gastropoda	<i>Sigapatella</i>	A	2	971	329	4.5	67	4.4	47	
Bivalvia	<i>Spissatella</i>	A	2		2					*
Gastropoda	<i>Stiracolpus</i>	A	2	201	74	2.3	39	5.1	11	
Bivalvia	<i>Striacallista</i>	A	2	106	1					
Gastropoda	<i>Struthiolaria</i>	A	3	1	122					
Bivalvia	<i>Talabrica</i>	A	1	20						*
Gastropoda	<i>Tanea</i>	A	2	24	4					
Gastropoda	<i>Taniella</i>	A	1	12	4					
Bivalvia	<i>Tawera</i>	A	2	2960	5670	15.1	115	42.5	54	
Gastropoda	<i>Taxonina</i>	A	1	2						
Bivalvia	<i>Tellinota</i>	A	2		1					
Gastropoda	<i>Tenuiacteon</i>	A	2	10	2					
Bivalvia	<i>Tucetona</i>	A	3	2	166					
Gastropoda	<i>Tugali</i>	A	1	7		1.4	4			
Bivalvia	<i>Xenostrobus</i>	A	3	2	234					
Gastropoda	<i>Xymene</i>	A	1	354	22	2.4	62	1.5	7	
Gastropoda	<i>Zeacolpus</i>	A	3	83	912	2.6	17	13.7	22	
Gastropoda	<i>Zeacumantus</i>	A	2	16		1.6	7			
Gastropoda	<i>Zegalerus</i>	A	1	129	54	3.8	26	3.2	11	
Gastropoda	<i>Zemitrella</i>	A	1	9		1.0	4			
Bivalvia	<i>Zemysia</i>	A	1	44	16	2.0	17	1.6	6	
Bivalvia	<i>Zemysina</i>	A	1	2						
Bivalvia	<i>Zenatia</i>	A	3	49	340	1.9	16	12.7	15	
Gastropoda	<i>Zethalia</i>	A	1	893	348	7.3	56	21.0	8	
Bivalvia	<i>Zygochlamys</i>	C	3		3					

\* Regionally extinct prior to Pleistocene (likely to be undersampled in unlithified samples).

† Regional appearance in late Pliocene–Pleistocene (likely to be undersampled in lithified samples).