parison with other proposed phylogenetic placements of monotremes (Fig. 4).

As noted earlier, a well-developed mandibular trough, indicative of a complete Meckel's cartilage and postdentary jaw bones contacting the dentary in adult individuals, occurs in a number of Mesozoic mammals (or near-mammals) other than *Teinolophos* (*12–16*). However, because of the uncertain phylogenetic positions of these taxa with respect to true mammals (monotremes and theriiforms), none provides unequivocal support for the multiple origin of the definitive mammalian middle ear bones. Nonetheless, they suggest the possibility that the freeing of the mammalian ear bones from the lower jaw may have occurred more often than can be conclusively documented at present. If the postdentary bones were already functioning in hearing in late nonmammalian cynodonts and basal mammaliaforms (*1, 10, 37*), then this final step in the functional separation of the mammalian middle ear system from the feeding apparatus would be expected to occur in all later lineages.

References and Notes

1. E. F. Allin, J. A. Hopson, in *The Evolutionary Biology of Hearing*, D. B. Webster, R. R. Fay, A. N. Popper, Eds. (Springer Verlag, New York, 1992), pp. 587–614.
2. C. Patterson, in *Vicariance Biogeography: A Critique*, G. J. Nelson, D. E. Rosen, Eds. (Columbia Univ. Press, New York, 1980), pp. 446–500.
3. T. S. Kemp, *Zool. J. Linn. Soc. London* **77**, 353 (1983).
4. M. J. Novacek, in *The Skull, v. 2, Patterns of Structural and Systematic Diversity*, J. Hanken, Brian K. Hall, Eds. (Univ. of Chicago Press, Chicago, 1993), pp. 438–545.
5. J. Meng, A. R. Wyss, *Nature* **377**, 141 (1995).
6. Y. Wang, Y. Hu, J. Meng, C. Li, *Science* **294**, 357 (2001).
7. J. Meng, Y. Hu, Y. Wang, C. Li, *Zool. J. Linn. Soc. London* **138**, 431 (2003).
8. J. A. Hopson, *Am. Zool.* **6**, 437 (1966).
9. G. Fleischer, *Säugetierk. Mitt.* **21**, 131 (1973).
10. E. F. Allin, *J. Morphol.* **47**, 403 (1975).
11. R. Presley, *Sympos. Zool. Soc. London* **52**, 127 (1984).
12. D. M. Kermack, K. A. Kermack, F. Mussett, *J. Linn. Soc. (Zool.)* **47**, 312 (1968).
13. M. Chow, T. H. Rich, *Aust. Mammal.* **5**, 127 (1982).
14. F. A. Jenkins Jr., A. W. Crompton, W. R. Downs, *Science* **222**, 1233 (1983).
15. F. A. Jenkins Jr., S. M. Gatesy, N. H. Shubin, W. W. Amaral, *Nature* **385**, 715 (1997).
16. O. W. M. Rauhut, T. Martin, E. Ortiz-Jaureguizar, P. Puerta, *Nature* **416**, 165 (2002).
17. C. Reichert, *Müllers Arch. Anat. Physiol. Wiss. Med.* **1837**, 120 (1837).
18. K. A. Kermack, F. Mussett, H. W. Rigney, *Zool. J. Linn. Soc. London* **53**, 87 (1973).
19. Z.-X. Luo, Z. Kielan-Jaworowska, R. L. Cifelli, *Acta Palaeontol. Pol.* **47**, 1 (2002).
20. M. O. Woodburne, T. H. Rich, M. S. Springer, *Mol. Phylog. Evol.* **28**, 360 (2003).
21. M. O. Woodburne, *J. Mamm. Evol.* **10**, 195 (2003).
22. T. Rich *et al.*, *Rec. Queen Vic. Mus.* **106**, 1 (1999).
23. T. Rich *et al.*, *Acta Palaeontol. Pol.* **46**, 113 (2001).
24. The holotype of *T. trusleri* was identified as a monotreme primarily on the basis of its bilophodont lower molar crown pattern, similar to that of the Early Cretaceous (Albian) monotreme *Steropodon* and the Cenozoic platypus *Obdurodon* (*23*). A much worn but recognizably bilophodont molar (Fig. 2, G and H) was found in close association with the referred specimen, NMV P212933, which preserves broken roots in alveoli three and four that are similar in size to those of the isolated tooth. Both the type and the referred specimen also resemble fossil and living platypuses in the unusually large size of the mandibular (inferior alveolar) foramen and canal, and the referred

specimen (plus a fragmentary juvenile dentary, NMV P212811) resembles them in preserving a postero-internal angle (p.a, Fig. 2E) that may be homologous with the platypus mylohyoid process (*38*). Despite some proportional differences from the holotype of *T. trusleri*, the most complete referred dentary and the four more fragmentary specimens are provisionally attributed to the same species.
25. G. Krusat, *Mem. Serv. Geol. Portugal* **27**, 1 (1980).
26. J. A. Lillegraven, G. Krusat, *Contr. Geol. Univ. Wyoming Spec. Pap.* **28**, 39 (1991).
27. A. S. Romer, *Osteology of the Reptiles* (Univ. of Chicago Press, Chicago, 1956).
28. S. Fourie, *Ann. S. Afr. Mus.* **65**, 337 (1974).
29. The possibility must be considered that the presumed splenial contact surface of *Teinolophos* may instead be a contact surface for a remnant of Meckel's cartilage, as recently described in gobiconodontid triconodonts (*6, 7*). The facet on the dentary of gobiconodontids for the ossified Meckel's cartilage is a prominent longitudinal groove below the mandibular foramen that is continuous anteriorly with the slitlike meckelian groove seen in basal mammaliaforms and many early mammals. Although the anterior part of the presumed splenial facet in *Teinolophos* is in a position similar to the depression for the ossified Meckel's cartilage in gobiconodontids, its posterior part, below the mandibular trough, more closely resembles the splenial facet of nonmammalian cynodonts and docodontids, in which the complete Meckel's cartilage would have lain within the mandibular trough, enclosed by the dermal rod of postdentary bones. Furthermore, in the referred juvenile specimen (NMV P212811) of *T. trusleri*, in which one would expect a more prominent groove supporting a more fully developed Meckel's cartilage than in older individuals, the facet below the mandibular trough is flat and not at all excavated. Therefore, we believe that the contact surface below the mandibular trough in *Teinolophos* was for the splenial bone rather than Meckel's cartilage; the latter, as in *Morganucodon* and docodontids, lying more dorsally, within the mandibular trough.
30. G. G. Simpson, *A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum* [British Museum (Natural History), London, 1928].
31. J. Phillips, D. Penny, *Mol. Phylogenet. Syst.* **28**, 171 (2003).
32. A. M. Musser, *Comp. Biochem. Phys. A* **136**, 927 (2003).
33. T. Rowe, *J. Vertebr. Paleontol.* **8**, 241 (1988).
34. T. Rowe, in *Mammal Phylogeny, v. 1, Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*, F. S. Szalay, M. J. Novacek, M. C. McKenna, Eds. (Springer Verlag, New York, 1993), pp. 129–145.
35. G. W. Rougier, J. R. Wible, J. A. Hopson, *Am. Mus. Novit.* **3183**, 1 (1996).
36. J. A. Hopson, in *Encyclopedia of Paleontology*, R. Singer, Ed. (Fitzroy Dearborn, Chicago, 2000), pp. 691–701.
37. U. Zeller, in *Mammal Phylogeny, v. 1, Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*, F. S. Szalay, M. J. Novacek, M. C. McKenna, Eds. (Springer Verlag, New York, 1993), pp. 95–107.
38. A. M. Musser, M. Archer, *Philos. Trans. R. Soc. London Ser. B* **353**, 1063 (1998).
39. F. R. Parrington, *Philos. Trans. R. Soc. London Ser. B* **261**, 231 (1971).
40. B. Patterson, *Fieldiana Geol.* **13**, 1 (1956).
41. D. R. Prothero, *Bull. Am. Mus. Nat. Hist.* **167**, 277 (1981).
42. J. R. Wible, G. W. Rougier, M. J. Novacek, M. C. McKenna, D. D. Dashzeveg, *Am. Mus. Novit.* **3149**, 1 (1995).
43. Z.-X. Luo, R. L. Cifelli, Z. Kielan-Jaworowska, *Nature* **409**, 53 (2001).
44. A. Forasiepi, G. Rougier, A. Martinelli, *J. Vertebr. Paleontol.* **24** (suppl. 3), 59A (2004).
45. Q. Ji, Z.-X. Luo, S. Ji, *Nature* **398**, 326 (1999).
46. J. R. Wible, J. A. Hopson, in *Mammal Phylogeny, v. 1, Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*, F. S. Szalay, M. J. Novacek, M. C. McKenna, Eds. (Springer Verlag, New York, 1993), pp. 45–62.
47. J. A. Hopson, in *Major Features of Vertebrate Evolution*, D. R. Prothero, R. M. Schoch, Eds. (Paleontological Society, Knoxville, TN, 1994), pp. 190–219.
48. Z. Kielan-Jaworowska, A. W. Crompton, F. A. Jenkins Jr., *Nature* **326**, 871 (1987).
49. A. Janke, X. Xu, U. Arnason, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 1276 (1997).
50. D. Penny, M. Hasegawa, *Nature* **387**, 549 (1997).
51. Supported jointly by the Committee for Research and Exploration of the National Geographic Society, grant 7370-02, and the Australian Research Council, project DP0209280. The manuscript was critiqued by W. A. Clemens, L. L. Jacobs, M. C. McKenna, J. Meng, P. F. Murray, G. W. Rougier, M. S. Springer, and M. O. Woodburne.

Shell Composition Has No Net Impact on Large-Scale Evolutionary Patterns in Mollusks

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A major suspected bias in the fossil record of skeletonized groups is variation in preservability owing to differences in shell composition. However, despite extensive changes in shell composition over the 500-million-year history of marine bivalves, genus duration and shell composition show few significant relationships, and of those, virtually all are contrary to bias from preferential loss of highly reactive shell types. Distortion of large-scale temporal patterns in marine bivalves owing to preservability is thus apparently weak or randomly distributed, which increases the likelihood that observed patterns in this and other shelled groups carry a strong biological signal.

In the sedimentary record, biological hard parts, inorganic grains, and cements originally composed of calcite are typically better preserved than their aragonitic counterparts (*1, 2*). This calcite bias, along with experimental evidence that skeletal microstructure can also strongly influence preservation (*3–6*), is of concern because of the potential to distort paleoecological patterns among shelled invertebrates, which constitute the bulk of the marine metazoan

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Fig. 1. Trends over Phanerozoic time in the raw number and proportions of marine bivalve genera categorized by shell mineralogy (**A** and **B**), organic content (**C** and **D**), and SAV of first-order crystallites (**E** and **F**), as shown by 20-million-year binning of genus range data.
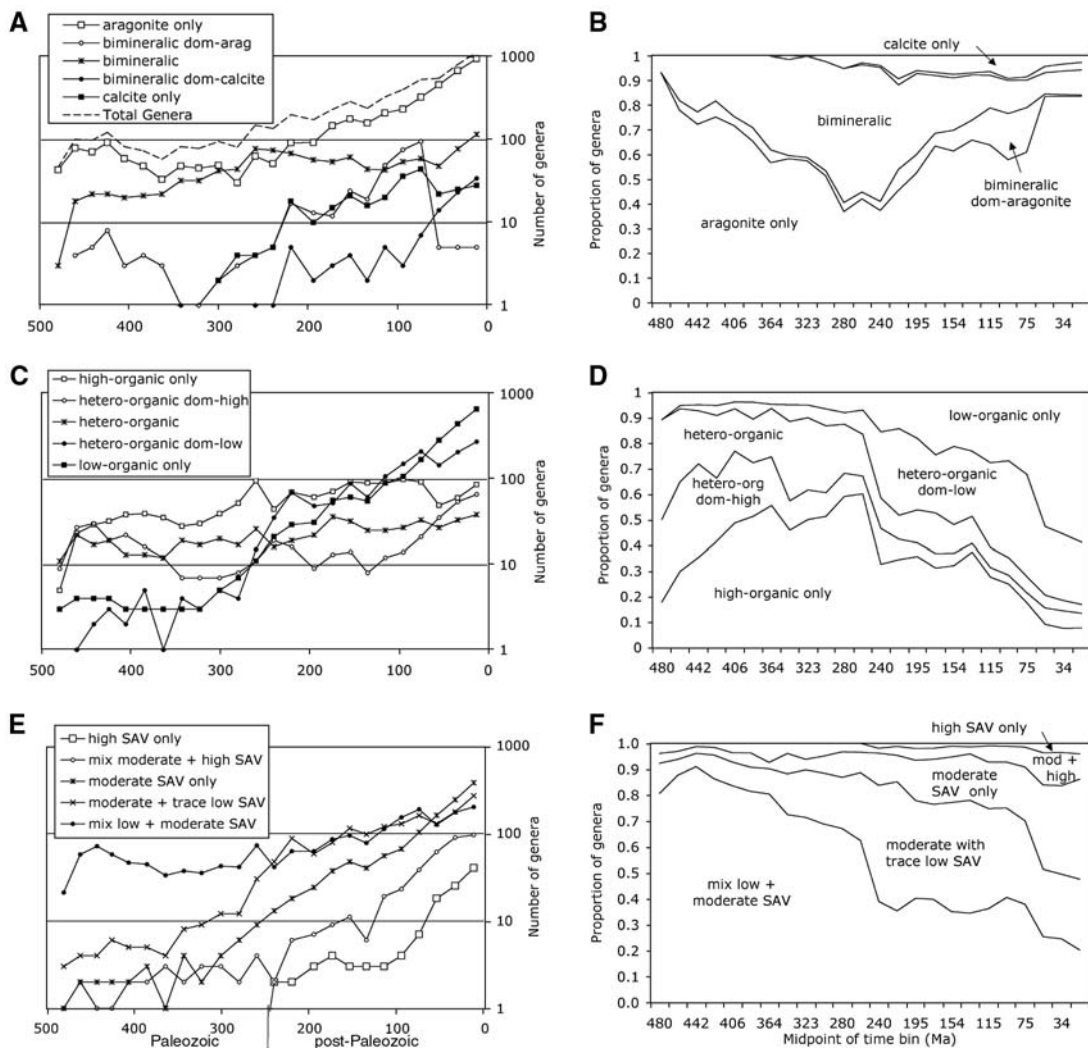
fossil record (7–10). Differential preservation of taxa is also a likely source of bias in large-scale evolutionary patterns and is expected to truncate observed geologic durations, damp diversity patterns, and compromise taxonomic identifications (6, 11–17). However, its quantitative impact on large-scale evolutionary patterns remains largely unexplored (6, 18).

Preservational biases are evaluated here with the use of bivalve mollusks, an excellent test case because of their compositionally diverse shells. I test (i) whether observed changes in shell composition through the Phanerozoic are consistent with cumulative loss of highly reactive shell types, (ii) whether singleton taxa [confined to a single chronostratigraphic interval and often attributed to sampling deficiencies; reviewed in (19)] tend to have more reactive shells than nonsingleton taxa, and (iii) whether median durations of genera having highly reactive shells are shorter than those of genera with less reactive shells.

Information on shell composition compiled from the literature (for 475 genera, 156 families or subfamilies) was quantified by scoring the shell of each genus on a set of

3-point scales for its overall mineralogy, organic content, and crystallite surface area to volume ratio (SAV) (6) (figs. S1 and S2; tables S1 and S2); the results were merged with an existing database of the known stratigraphic ranges of all marine bivalve genera having fossil records [(20), as updated by (21)]. Because shell composition tends to be highly conserved both among species within a genus and among genera within a family (22), it is possible to extrapolate from these 475 genera to 89% of the 2983 genera in the stratigraphic-range database, using published familial assignments and using a consensus method when confamilial genera have conflicting shell compositions (6).

A literal reading of the fossil record indicates that genus-level diversity for the class Bivalvia (dashed line in Fig. 1A) is fairly steady from its initial diversification until the late Paleozoic, when it begins a steep rise that continues through the post-Paleozoic to a present-day diversity of ~1300 living genera, of which ~1000 have a known fossil record (21, 23). If diversity trends were determined largely by the intrinsic preservability of shell

types—which is a worst-case scenario—then, working backward in time from the present day, groups with low preservation potential (shells composed entirely or largely of aragonite, high-organic, or high surface area microstructures) should be missing more of their early members than groups with high preservation potential. This would steepen their diversity trajectories, diminishing their proportional diversity when tracked back in time, and, if the bias were sufficiently severe, shifting their first occurrences to younger dates relative to groups with high preservation potential.

Instead, observed changes in the generic diversity and proportional representation of preservational groups are largely inconsistent with broad-scale preservational bias. Preservational groups exhibit a variety of discordant and even anastomosing trajectories in raw diversity (Fig. 1, A, C, and E). Moreover, proportional data (which are less subject to bias from temporal variation in sampling intensity; Fig. 1, B, D, and F) show that compositional differences between younger and older faunas are largely contrary to taphonomic expectations. For example, the early and mid-

Paleozoic are dominated by genera with entirely aragonitic shells and with exclusively to dominantly high-organic microstructures (Fig. 1, B and D). The presumably most durable calcite-bearing taxa have their highest proportional richness in the late Paleozoic and early Mesozoic, whereas genera with low-organic shells only rise to dominance in Cenozoic rocks. In contrast, trends in crystallite SAVs are consistent with preservational bias, although they could also reflect phylogeny. Early Paleozoic bivalve faunas are dominated by genera with significant proportions of low-SAV crystallites in their shells, whereas the Mesozoic [250 to 65 million years ago (Ma)] is dominated by shells composed largely or entirely of moderate-SAV microstructures, and the Cenozoic (since 65 Ma) sees a continued increase in the proportions of moderate- and high-SAV microstructures (Fig. 1F).

A complex ad hoc history of changing environmental and diagenetic conditions would be required to generate this set of patterns artifactually: Changes in bivalve shell mineralogy do not match postulated alternations of aragonite and calcite seawaters [as noted by (24)], and, although trends in the proportional diversity of high-organic genera are in crude agreement with numbers of silicified benthic faunas [numbers from (25)], no other shell characters nor any raw diversity trends agree. Trends are thus more likely biological in origin, with shell composition evolving under selection to provide biomechanical advantage against increasing durophagous predation (26, 27) and/or as an aspect of increasing metabolic efficiency (28), given that organic matrix is more costly to deposit than the mineral phase (29). Whatever the drivers of the trends, Fig. 1 reveals that the Permian-Triassic boundary (250 Ma) was a watershed in shell composition: Through the Paleozoic (>250 Ma), bivalves show declining proportions of entirely aragonitic taxa, increasing proportions of high-organic shells, and high proportions of shells containing relatively low-SAV microstructures; in the post-Paleozoic (<250 Ma), bivalves show increasing proportions of entirely aragonitic taxa, decreasing proportions of high-organic shells, and a relatively even mix of low-, moderate-, and high-SAV microstructures (Fig. 1, B, D, and F). Given these changes, the presence of only 42 genera shared between Paleozoic and post-Paleozoic intervals, and the much higher diversity of post-Paleozoic bivalves (2471 genera versus 554 in the Paleozoic), the database is partitioned into two separate 250-million-year intervals in tests for preservational bias using singleton status and genus durations.

If a highly reactive shell decreases genus-level preservation potential, and if singleton status derives from poor preservation, then singletons should exhibit greater frequencies of highly reactive shells than nonsingleton taxa. However, the frequency of highly reactive shells among singleton genera differs significantly from their frequency among nonsingleton genera for only five of the nine comparisons (Table 1) (fig. S3), and of these five, only two are consistent with taphonomic expectations (singletons have proportionally more high-organic shells than do nonsingletons, both within the post-Paleozoic subset and in the Phanerozoic overall). Three of the significant differences are opposite to expectations: Singletons have proportionally fewer entirely aragonitic shells in the post-Paleozoic and Phanerozoic and fewer dominantly high-SAV shells in the Phanerozoic than do nonsingletons. Rearranging the question to ask "How similar are preservational groups in their proportions of singletons?" yields a similar pattern, with either no significant difference (five tests) or significant differences that, in three of the remaining four tests, are contrary to preservational bias (table S3 and fig. S4).

If a highly reactive shell decreases genus-level preservation potential, then genera having highly reactive shells should have shorter median durations than genera with other shell compositions. However, regardless of (i) the inclusion or exclusion of singleton taxa, (ii) whether genera are considered in toto or partitioned into Paleozoic and post-Paleozoic subsets, or (iii) whether one considers individual compositional aspects of shells or combined scores (24 nested comparisons, of which 20 compare medians for >100 genera and are analyzed here), median stratigraphic durations of genera either do not differ significantly as a function of shell composition or differ significantly but opposite to taphonomic expectations (fall below the diagonal in Fig. 2) (table S4). Of 18 nonsignificant comparisons, 15 also have differences that are opposite to taphonomic expectations.

Finer partitioning of the database, so that mineralogy and organic content can be considered simultaneously (those aspects most reliably estimated from the literature; lack of multivariate normality disallows multiple regression), reinforces the results of the preceding single-factor analyses (table S5). Variation among post-Paleozoic genera is opposite to taphonomic expectation: Genera with resistant shells (i.e., containing some quantity of calcite and composed entirely of low-organic microstructures) have a significantly shorter median duration and higher proportion of singletons than do genera with shells composed exclusively of high-organic aragonite. The implication is that first-order patterns in post-Paleozoic genus ranges are robust to preservational bias imposed by variation in shell composition; these taxa constitute ~85% of Phanerozoic bivalve diversity. In contrast, variation among Paleozoic

Fig. 2. Bivalves having highly reactive shell compositions—that is, composed entirely of aragonite or high-organic microstructures, dominated by high-SAV microstructures, or having shells that combine these attributes—tend to have median genus durations that are longer than other genera (fall below the diagonal line), contrary to the taphonomic expectation that their durations would be significantly shorter. Dashed lines indicate 10% divergence from equivalence in duration.
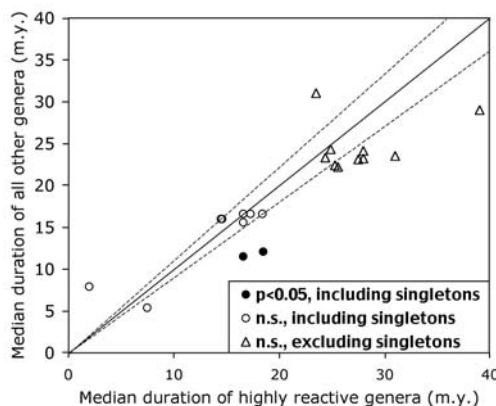
Table 1. Results of *G* tests for differences in the proportions of singletons and nonsingletons that have highly reactive shell compositions [see (6) for operational definitions]. Min, mineralogy; Org, organic content; SAV, surface area:volume ratio; Phan, Phanerozoic; Pz, Paleozoic; post-Pz, post-Paleozoic.

Aspect tested	Time bin	Singleton genera		Nonsingleton genera		Observed P value	Sequential Bonferroni (corrected) P value	Difference consistent with taphonomic expectation?
		N	% with highly reactive shell	N	% with highly reactive shell			
Min	Phan	671	61	2175	73	0.000001	0.000008	No, opposite
Min	Post-Pz	454	58	1952	74	0.000001	0.000007	No, opposite
Org	Post-Pz	454	17	1943	14	0.000001	0.000006	Yes
Org	Phan	646	27	2146	18	0.0001	0.0005	Yes
SAV	Phan	605	6	2056	10	0.002	0.008	No, opposite
Min	Pz	217	67	262	56	0.018	n.s. (0.054)	Yes
SAV	Post-Pz	437	8	1881	11	0.055	n.s.	No, opposite
Org	Pz	192	50	240	52	0.7	n.s.	No, opposite
SAV	Pz	168	2	210	2	0.95	n.s.	No

genera is consistent with preservational bias—low-organic calcitic taxa have a longer median duration and a smaller proportion of singletons—but differences are not statistically significant (table S5). The magnitude of bias among Paleozoic taxa is thus evidently small [single-factor tests indicate that mineralogy is the strongest factor but is always nonsignificant in impact (tables S3 and S4)].

This analysis does not eliminate potential bias generated by other intrinsic (e.g., body size, original abundance, life habit) or extrinsic factors in preservation [e.g., available rock volume, degree of lithification (11–17)]. However, these results indicate that bias in large-scale evolutionary patterns related to shell composition is weak at best among marine bivalves or is so complex as to be effectively random. That is, although all observed durations and diversities may be offset downward from their true (original, biological) values—perhaps more severely in the Paleozoic, given the direction of the nonsignificant difference in durations—there appears to be no systematic distortion in those values among genera as a function of shell composition. Differences in durations among bivalve clades are thus more likely to be biologically real than artifacts of differences in shell composition, even though shell composition tends to follow phylogenetic lines. These results are very encouraging for biological analysis of the fossil record at this scale, including the retention of singleton data in evolutionary analyses. Preservational distortion within this major group is not as large as might be feared from short-term experiments (3–5) or from the striking diversity contrasts that can occur between adjacent beds (7–10). These preservational differences, however real at the level of individual assemblages, apparently do not scale upward to macroevolutionary patterns.

The apparent lack of bias in genus duration data may have several explanations, which are not mutually exclusive. First, there may be considerable redundancy in preservation (10): Although many beds may lack aragonitic taxa entirely, random beds with adequate preservation (composite molds and mineral replacements with high morphologic acuity) might be sufficiently densely spaced for the geologic ranges of taxa with reactive shells to be recognized as accurately as those of less reactive taxa. Second, highly reactive shells might be especially prone to replacement by more stable minerals, actually increasing rather than decreasing their per capita preservation potential [references in (4, 30)]. Third, highly reactive shells commonly have poor preservational quality even when diagenetically replicated (coarse crystalline textures, extraneous coatings) and thus might have lower taxonomic acuity and tend to be assigned to existing named taxa ("lumping"). This would promote artifactual range extension and thereby reduce rather than increase observed percentages of singletons among taxa with highly reactive shells, contrary to the usual algorithm for modeling preservational effects (6).

Many skeletonized macroinvertebrate groups in the fossil record have compositions lying within the range spanned by bivalves, and thus there is reason to suspect that differences in skeletal mineralogy and microstructure might have as little net impact on first-order evolutionary patterns as found here among marine bivalves.

References and Notes
1. D. Sanders, *J. Afr. Earth Sci.* **36**, 99 (2003).
2. J. W. Morse, A. Mucci, F. J. Millero, *Geochim. Cosmochim. Acta* **44**, 85 (1980).
3. L. M. Walter, *SEPM Spec. Publ.* **36**, 3 (1985).
4. C. P. Glover, S. M. Kidwell, *J. Geol.* **101**, 729 (1993).
5. E. M. Harper, *J. Zool.* **251**, 179 (2000).
6. See supporting data on *Science* Online.
7. C. F. Koch, N. F. Sohl, *Paleobiology* **9**, 26 (1983).
8. L. Cherns, V. P. Wright, *Geology* **28**, 791 (2000).
9. V. P. Wright, L. Cherns, P. Hodges, *Geology* **31**, 211 (2003).
10. A. M. Bush, R. K. Bambach, *J. Geol.* **112**, 625 (2004).
11. D. M. Raup, *Bull. Carnegie Mus. Nat. Hist.* **13**, 85 (1979).
12. M. Kowalewski, K. W. Flessa, *Geology* **24**, 977 (1996).
13. S. K. Donovan, C. R. C. Paul, Eds., *The Adequacy of the Fossil Record* (Wiley, Chichester, UK, 1998).
14. A. B. Smith, *Philos. Trans. R. Soc. London Ser. B* **356**, 351 (2001).
15. M. Foote, in *Paleobiology II, a Synthesis*, D. E. G. Briggs, P. R. Crowther, Eds. (Blackwell, Oxford, 2001), pp. 500–504.
16. A. B. Smith, in *Paleobiology II, a Synthesis*, D. E. G. Briggs, P. R. Crowther, Eds. (Blackwell, Oxford, 2001), pp. 504–509.
17. S. M. Kidwell, S. M. Holland, *Annu. Rev. Ecol. Syst.* **33**, 561 (2002).
18. E. M. Harper, in *The Adequacy of the Fossil Record*, S. K. Donovan, C. R. C. Paul, Eds. (Wiley, Chichester, UK, 1998), pp. 243–267.
19. M. E. Foote, *Paleobiology* **26**, 578 (2000).
20. J. J. Sepkoski Jr., *Bull. Am. Paleontol.* **363**, 1 (2002).
21. D. Jablonski, K. Roy, J. W. Valentine, R. M. Price, P. S. Anderson, *Science* **300**, 1133 (2003).
22. J. D. Taylor, W. J. Kennedy, A. Hall, *Bull. Br. Mus. (Nat. Hist.) Zool. Suppl.* **3**, 1 (1969).
23. A. I. Miller, J. J. Sepkoski Jr., *Paleobiology* **14**, 364 (1998).
24. S. M. Stanley, L. A. Hardie, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **144**, 3 (1998).
25. J. K. Schubert, D. L. Kidder, D. H. Erwin, *Geology* **25**, 1031 (1997).
26. S. A. Wainwright, *Nature* **224**, 777 (1969).
27. M. Kowalewski, P. H. Kelley, Eds., *The Fossil Record of Predation* (Paleontological Society Papers 8) (Paleontological Society, Lancaster, PA, 2002).
28. R. K. Bambach, *Paleobiology* **19**, 372 (1993).
29. A. R. Palmer, *Proc. Natl. Acad. Sci. U.S.A.* **89**, 1379 (1992).
30. R. G. Maliva, R. Siever, *J. Geol.* **96**, 387 (1988).
31. I thank T. R. Waller, D. Jablonski, and J. Pojeta for stimulating discussions and D. Jablonski, M. Foote, M. Labarbera, T. A. Rothfus, M. Kowalewski, and two anonymous persons for helpful reviews. Analyses used the bivalve stratigraphic range data of J. J. Sepkoski Jr. as updated by D. Jablonski (version June 2004). Supported by NSF-EAR grant 0345897.

Two Abundant Bioaccumulated Halogenated Compounds Are Natural Products

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Methoxylated polybrominated diphenyl ethers (MeO-PBDEs) have been found bioaccumulated in the tissues of a variety of aquatic animals and at concentrations comparable to those of anthropogenic halogenated organic compounds, including polychlorinated biphenyls (PCBs). The origin of the MeO-PBDEs has been uncertain; circumstantial evidence supports a natural and/or an industrial source. By analyzing the natural abundance radiocarbon content of two MeO-PBDEs isolated from a True's beaked whale (*Mesoplodon mirus*), we show that these compounds were naturally produced.

It has long been known that industrially produced halogenated organic compounds and their metabolites accumulate in human and other animal tissues. One example is polybrominated diphenyl ethers (PBDEs), used as flame retardants, which have emerged as a contaminant of concern because of the detection of increasing levels in human breast milk (1). Structurally related compounds, methoxylated polybrominated diphenyl ethers (MeO-PBDEs), have recently been identified in a variety of fish (2) and marine mammals (3); they form a new class of bioaccumulated compounds. The origin of these MeO-PBDEs is not immediately obvious. Many MeO-PBDEs are known natural products, isolated from sponges (4–9), algae (10), and acorn worms (11). However, their structural similarity to industrial PBDEs cannot be ignored. Industrially produced PBDEs lack a methoxy group, but this group could be introduced by

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