

# Testing the marine and continental fossil records

M. J. Benton Department of Geology, University of Bristol, Bristol BS8 1RJ, United Kingdom

M. J. Simms Department of Geography and Geology, Cheltenham and Gloucester College of Higher Education, Francis Close Hall, Cheltenham GL50 4AZ, United Kingdom

## ABSTRACT

**The fossil record of continental vertebrates is as good as that of echinoderms at the family level, as shown by tests of the match of cladistic and stratigraphic data and of relative completeness. If echinoderms and vertebrates are typical of their environments, the continental fossil record is not worse than the marine, despite the fact that, at a local level, fossils are usually more abundant in marine sequences than in continental successions. The explanation of this paradox may be that vertebrates have attracted more intensive study than echinoderms, and thus the level of knowledge of their fossil record is some decades ahead of that of echinoderms. This finding validates the use of different kinds of fossil data in broad-scale phylogenetic studies.**

## INTRODUCTION

It has often been asserted that the fossil record of marine shelf benthic organisms is better than that of continental organisms (Benton, 1985; Flessa, 1990; Jablonski, 1991; Raup, 1979; Valentine, 1969). This assumption has been made by scaling up field observations on Phanerozoic rocks. Typically, limestones and clastic rocks laid down on the shallow continental shelf yield abundant fossils of skeletonized invertebrates, such as brachiopods, molluscs, corals, arthropods, bryozoans, and echinoderms (Fürsich, 1990; Kidwell, 1986). Continental sedimentary sequences generally yield less abundant faunas of freshwater fishes and molluscs, terrestrial insects, and vertebrates (Behrensmeyer and Hill, 1980; Retallack, 1984). This differentiation may largely be an effect of the nature of the sediments: sedimentation in river systems and lakes is highly episodic compared to the more continuous deposition on marine shelves and particularly in abyssal areas of oceans (Sadler, 1981).

We test here the idea that groups of organisms known from a rich supply of fossils in the field necessarily have a fuller and better-documented picture of large-scale phylogeny than groups represented by sparse fossil materials. The test groups were echinoderms (marine invertebrates) and tetrapods (continental vertebrates). These groups were selected for comparison because there is a sufficient number of cladograms available for each and because both groups consist of multielement taxa, the skeletons of which may be preserved completely or may break up before burial.

## TESTING THE QUALITY OF THE FOSSIL RECORD

The quality of the long-term global-scale fossil record may be tested by comparison of (1) the order of origin of groups from the stratigraphic record with the order of

branching as indicated by phylogenetic data, and (2) the relative completeness of fossil records based on independent evidence for the size of gaps.

The test of stratigraphic (age) and phylogenetic (clade) evidence about the origins of groups (Norell, 1992, 1993; Norell and Novacek, 1992a, 1992b) consists of comparing the rank order of nodes on a published cladogram (Fig. 1, A and B) with the rank order of group appearances as documented in the paleontological literature (Fig. 1C). The match of clade and age data is assessed by the Spearman rank correlation (SRC) test.

This approach depends upon the observation that there are three essentially independent methods of disentangling the sequence of events in the history of life: (1) the order of fossils in the rocks (stratigraphic data); (2) cladograms, based generally on assessments of the sequence of acquisition of morphological characters; and (3) molecular phylogenies, founded on sequencing of nucleic acids or proteins, or on DNA-DNA hybridization. If it is accepted that these three approaches, stratigraphic, cladistic, and molecular, are essentially independent, then mutual cross testing should be possible. The comparison tests do not assume that any one technique is better than another: they merely compare the matching and assume that, if a large enough sample is used, the results will have statistical validity. Equivalent tests are available (Huelsenbeck, 1994) to test the quality of cladograms against stratigraphic data.

Comparative studies (Benton, 1994, 1995; Benton and Storrs, 1994, 1995; Gauthier et al., 1988; Norell, 1992, 1993; Norell and Novacek, 1992a, 1992b) have shown a good match between cladistic branching order and the order of first fossil representatives for 55%–73% of cladograms of vertebrates. A first attempt is made here to extend the tests to cladograms of nonvertebrates.

A sample of 63 cladograms and molecular

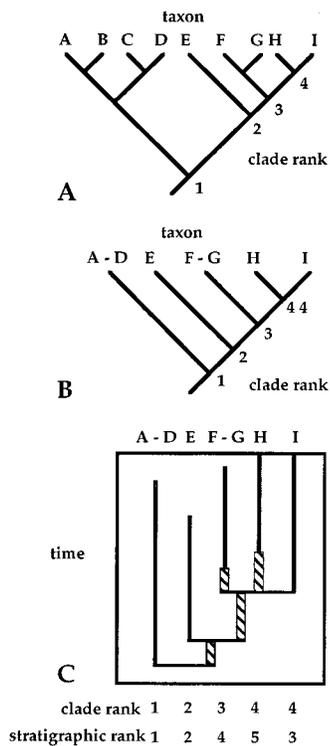
phylogenies of echinoderms was tested for fossil-record quality (Table 1). Data for 72 listed cladograms of vertebrates have been published (Benton and Storrs, 1994, 1995). For purposes of comparison, the nine cladograms of marine taxa (Actinopterygii, Gnathostomata, Sarcopterygii, Sauropterygia, Teleostei) were excluded, leaving 63 trees of continental vertebrates.

If skeletonized marine shelf invertebrates have a markedly better fossil record than continental animals, then the echinoderm test cases should show more examples of statistically significant rank order correlation than the vertebrates. The results of SRC tests (Fig. 2, A and B) apparently show the opposite. Fewer echinoderm cladograms (38%) showed significant ( $P < 0.05$ ) matching of clade order and age order than did the continental vertebrate cladograms (63%). The same is true for highly significant correlations ( $P < 0.01$ ), found in 26% of cases for echinoderms but in 41% of cases for continental vertebrates.

The low pass rate for echinoderm cladograms was surprising, especially in comparison with cladograms of continental vertebrates. This result is almost certainly an artifact of the small size of many of the echinoderm cladograms, 13 (21%) of which include only 4 taxa. Such a small sample size cannot yield critical values for the SRC coefficient (Sprent, 1989). When the small ( $n = 4$ ) echinoderm cladograms are excluded, the SRC scores match more closely those discovered for continental vertebrates (Fig. 2A), but still show a poorer pass rate than do the cladograms of continental vertebrates.

The SRC test of matching between clade and age order considers only one aspect of the quality of the fossil record. Another crucial feature is the relative completeness of particular examples, and this may be assessed by comparing the proportion of known fossil records to gaps, the relative completeness index (RCI) of Benton and Storrs (1994) (Fig. 1).

If marine invertebrates have a better fossil record than continental vertebrates, the RCI values for the former should be markedly higher than those for the latter. This does not appear to be the case. The RCI values for echinoderms and vertebrates range from -5% to 100%, but continental vertebrates have more complete fossil records than do echinoderms (Fig. 2, C



**Figure 1. Methods for assessing quality of fossil record by comparing branching order in cladograms (A-C) with stratigraphic data and by comparing relative amount of gap and known record (C). Cladistic rank is determined by counting sequence of primary nodes in cladogram (A). In many cases, published cladograms do not conform to simple pectinate pattern in which all terminal taxa are simple side branches of single main stem. Frequently, there are more complex topologies in which some branches subdivide further (A), or some nodes may be partially unresolved, and give rise to more than one branch. In these cases, cladogram is reduced to pectinate form (B), and groups of taxa that meet main axis at same point are combined and treated as single unit. Stratigraphic sequence of clade appearance is assessed from earliest known fossil representative of sister groups, and clade rank and stratigraphic rank may then be compared (C). Minimum implied gap (MIG, diagonal rule) is difference between age of first representative of lineage and that of its sister, because oldest known fossils of sister groups are rarely of same age. MIG is minimum estimate of stratigraphic gap, as true age of lineage divergence may lie well before oldest known fossil. Relative completeness of fossil record may be assessed by comparing proportion of known range (standard range length, SRL) to ghost range, in form of relative completeness index (RCI), defined as:**

$$RCI = \left[ 1 - \frac{\sum(MIG)}{\sum(SRL)} \right] \times 100\%.$$

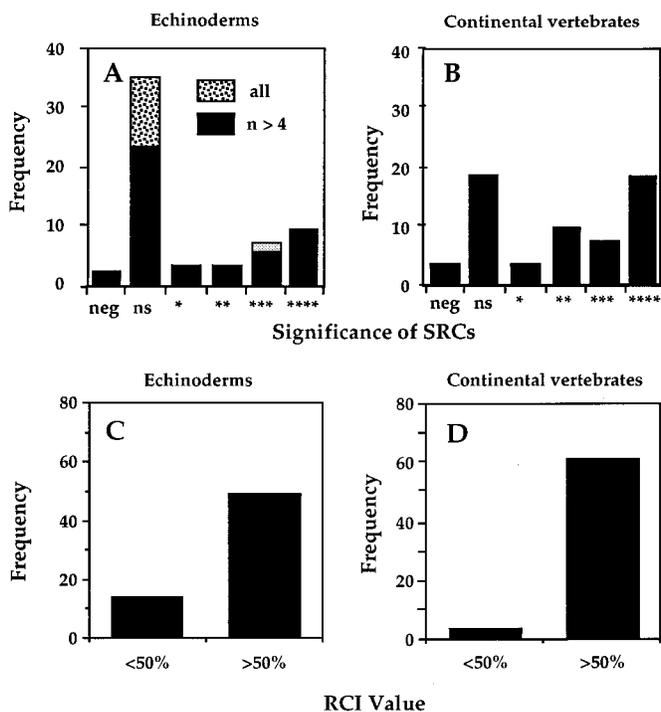
Values of RCI range from 0% (MIG = SRL) to 100% (MIG = 0). Negative values also occur when MIG > SRL. Single standard source of stratigraphic information (Benton, 1993) has been used throughout our work.

**TABLE 1. DATA ON THE GOODNESS OF FIT OF CLADOGAMS AND MOLECULAR PHYLOGENIES OF ECHINODERMS WITH STRATIGRAPHIC DATA**

TAXON	RCI	SRC	Sample size	Source
Echinodermata 1 (M)	96.6	0.833	4	Matsumura et al. (1979)
Echinodermata 2 (M)	93.8	0.833	4	Matsumura et al. (1979)
Echinodermata	100	--	5	Paul and Smith (1984)
Echinodermata 1	89.1	0.817**	11	Smith (1984a)
Echinodermata 2	82.8	0.931**	8	Smith (1984a)
Echinodermata (M)	95.7	0.947*	5	Raff et al. (1988)
Echinodermata	92.9	-0.132	5	Smiley (1988)
Echinodermata	90.2	0.817**	9	Smith (1988a)
Cystoidea	94.7	0.816	4	Paul (1988, fig. 16.1)
Cystoidea	65.8	0.902**	9	Paul (1988, fig. 16.3)
Cystoidea: Cryptocrinida	46.8	-0.344	5	Paul (1988, fig. 16.4)
Cystoidea: Paracrinoidea	87.1	0.120	9	Smith (1984a)
Cystoidea: Paracrinoidea	90.2	0.725	5	Paul (1988, fig. 16.5)
Cystoidea: Rhombifera	71.0	0.833	4	Paul (1988, fig. 16.2)
Crinoidea	8.4	0.664	6	Simms (1994)
Crinoidea: Inadunata	94.5	0.363	5	Donovan (1988)
Crinoidea: Camerata	94.5	0.860	5	Simms (1994)
Crinoidea: Articulata	86.4	0.915**	9	Simms (1988)
Crinoidea: Articulata (I)	65.4	0.940**	12	Simms and Sevastopulo (1993)
Crinoidea: Articulata	33.0	0.844**	9	Milson et al. (1994)
Eleutherozoa	90.2	0.626	8	Smith (1984b)
Eleutherozoa	63.3	0.820*	8	Smith (1988a)
Edrioasteroidea	80.7	0.924*	6	Smith (1985)
Edrioasteroidea	55.4	0.949**	9	Smith and Arbizu (1987)
Asteroidea 1	64.3	0.971**	6	Blake (1987)
Asteroidea 2	24.7	0.755*	7	Blake (1987)
Asteroidea	55.3	0.727*	9	Gale (1987)
Asteroidea: Neoasteroidea	85.1	0.454	8	Gale (1987)
Asteroidea: Paxillosida	45.0	0.316	4	Blake (1987)
Asteroidea: Valvatida	38.0	0.549	10	Blake (1987)
Asteroidea: Velatida	-93.0	0.236	4	Blake (1987)
Echinoidea	79.6	0.745*	7	Smith (1984b, fig. 1.5)
Echinoidea	61.6	0.949	4	Smith (1984b, fig. 7.1)
Echinoidea (M)	60.6	0.738	4	Raff et al. (1988)
Echinoidea	69.2	1.000*	4	Smith and Hollingworth (1990)
Echinoidea (M)	49.9	0.667	5	Feral and Derelle (1990)
Echinoidea	63.9	0.949	4	Smith (1992)
Echinoidea (M)	59.5	0.616	5	Smith et al. (1992)
Echinoidea: Palaeozoic	81.8	0.794	6	Smith (1984b)
Echinoidea: Diadematacea	62.2	0.154	5	Jensen (1981)
Echinoidea: Diadematacea	62.2	0.564	5	Emlet (1988)
Echinoidea: Cidaroida (I)	91.3	0.912**	9	Smith (1990)
Ech.: Psychocidaridae (I)	39.0	0.955**	6	Smith and Wright (1989)
Ech.: Stereocidarini (I)	65.6	0.500	4	Smith and Wright (1989)
Echinoidea: Stirodonta	92.3	0.516	5	Smith (1984b)
Echinoidea: Stirodonta	76.2	0.928*	6	Smith and Wright (1993)
Echinoidea: Salenioida (I)	71.3	0.588*	11	Smith and Wright (1990)
Echinoidea: Saleniinae (I)	72.6	0.649*	5	Smith and Wright (1990)
Ech.: Hyposaleniinae (I)	84.6	0.918**	8	Smith and Wright (1990)
Echinoidea: Camarodonta	68.1	0.821	5	Smith (1984b)
Echinoidea: Camarodonta	41.8	0.000	6	Smith (1988b)
Ech.: Eognathostomata	49.5	0.618	6	Smith (1984b)
Ech.: Neognathostomata	64.6	0.299	6	Mooi (1990)
Echinoidea: Cassiduloida	83.4	0.982**	8	Smith (1984b)
Echinoidea: Clypeasteroida	64.6	0.696	6	Durham (1966)
Ech.: Clypeasteroida	158.3	0.667	5	Seilacher (1979)
Ech.: Clypeasteroida	275.0	-0.132	5	Seilacher (1979)
Echinoidea: Clypeasteroida	90.1	0.572	7	Smith (1984b)
Echinoidea: Holasteroida	38.4	0.971**	6	Smith (1984b)
Echinoidea: Holasteroida	16.3	0.316	4	David (1988, fig. 25.7)
Echinoidea: Holasteroida	14.1	0.316	4	David (1988, fig. 25.9)
Echinoidea: Spatangoida 1	81.3	1.000**	6	Smith (1984b)
Echinoidea: Spatangoida 2	84.2	0.359	5	Smith (1984b)

Note: Cladograms based on morphological data and molecular phylogenies (M) are taken from cited sources, and stratigraphic data on the origins of taxa are from The fossil record 2 (Simms, 1993), except where internal data, from the phylogenetic paper itself, is employed. In some cases, more than one cladogram is cited to a particular source, the result of alternative collapse patterns of the original cladogram. The match of cladistic node order and stratigraphic position was measured by using the Spearman rank correlation (SRC) statistic, and the significance of this statistic is indicated as \* (P < 0.05), \*\* (P < 0.01). The quality of the fossil records implied by each phylogeny was calculated as the relative completeness index (RCI) which is the proportion of the cladistic minimum implied gaps (MIGs) to the known simple range lengths (SRLs) for all taxa in the phylogeny.

**Figure 2.** Comparison of measures of completeness of fossil record of echinoderms and continental vertebrates. **A** and **B:** Assessments of statistical significance of Spearman rank correlation (SRC) tests, recorded as negatively correlated (neg), not significantly correlated (ns), or significantly correlated at  $P < 0.05$  \*,  $P < 0.025$  \*\*,  $P < 0.01$  \*\*\*, and  $P < 0.005$  \*\*\*\*. Many more cladograms of continental vertebrates (**B**), 40 out of 63 (63%), show statistically significant ( $P < 0.05$ ) matches of clade and age order than do cladograms of echinoderms (**A**) (24 out of 63; 38%). Figures for highly significant correlations ( $P < 0.01$ ) show only 16 cases (25%) for echinoderms (**A**), but 26 cases (41%) for continental vertebrates (**B**). When smallest echinoderm cladograms are excluded, those with four terminal taxa (**A**), figures are more comparable: 46% of cladograms show significant ( $P < 0.05$ ) correlations of clade and age data, whereas 30% show highly significant ( $P < 0.01$ ) correlations. Distributions are not significantly different (Kolmogorov-Smirnov test). **C** and **D:** Comparison of relative completeness index (RCI) values for echinoderms and continental vertebrates. In both cases, many more cladograms have RCI values  $>50\%$  (i.e., more known record than cladistic minimum implied gap, MIG) than  $<50\%$ . Of echinoderm cladograms (**C**), 78% show higher RCI values (RCI  $> 50\%$ ), compared to 95% of continental vertebrate cladograms (**D**).



and D, 3), although the frequency distributions cannot be distinguished statistically. This surprising discovery matches the findings of the SRC test.

The echinoderm fossil record may seem poorer because the test cladograms are generally smaller (mean number of terminal taxa = 6.3) than are those of continental vertebrates ( $n = 10.7$ ). It is unclear whether there is a relation between cladogram size and RCI values: for echinoderms there is no correlation, but for vertebrates the RCI value is inversely proportional to cladogram size ( $P < 0.01$ ). When smaller echinoderm cladograms ( $n = 4$ ) were culled from the comparative sets, the distributions of RCI values for both groups still could not be distinguished statistically (Fig. 3).

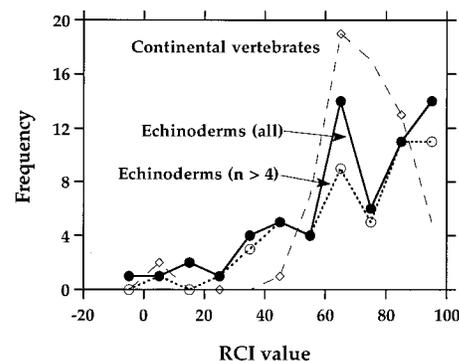
### CONTINENTAL RECORDS AS GOOD AS MARINE?

These results show that studies of the relative abundance of specimens of different phyla in fossiliferous sites are not a guide to their value in larger scale studies of phylogeny and macroevolution. In marine shelf sites, echinoderm fossils may be immensely abundant, whereas continental vertebrate fossils are typically sparse. Nevertheless, the amount of error inherent in the fossil records of both groups is not significantly

different, when assessed on a global scale. The macroevolutionary quality of the fossil record is determined by the number of stratigraphic horizons at which identifiable finds have been made, and improvements can occur only by discovery of new sections.

The surprisingly good quality of the continental vertebrate fossil record may reflect the fact that it has been exploited more intensively than has that of echinoderms. The number of active taxonomists working on tetrapods is much greater than the number studying any invertebrate phylum (Gaston and May, 1992). Thus, it is probable that a higher proportion of fossilized tetrapod taxa than echinoderm taxa has been identified. This may explain the counterintuitive discovery that continental tetrapods have a better fossil record than echinoderms, but it in no way detracts from that finding. Ultimately, when an equivalent number of hours of study has been devoted to both groups, echinoderms may prove to have a more complete fossil record than continental tetrapods at the family and/or stage level.

The discovery that continental vertebrates have a fossil record of quality equivalent to that of echinoderms, despite enormous differences in local abundance of fossils in both settings, vindicates the value of the fossil record for large-scale studies of



**Figure 3.** Comparison of relative completeness of fossil record of echinoderms and continental vertebrates, based on distribution of relative completeness indices (RCI). In all cases, most cladograms show RCI values  $>50\%$ . Sample of cladograms of all echinoderms ( $n = 63$ ) has mean RCI = 66%; for echinoderm cladograms with more than four terminal taxa ( $n = 50$ ), mean RCI = 70%; and for continental vertebrate cladograms ( $n = 63$ ), mean = 70%. Continental vertebrates do not have fossil record significantly different (Kolmogorov-Smirnov test) from that of echinoderms, whether all echinoderm cladograms, or larger echinoderm cladograms only.

phylogeny. Dinosaur fossils may be rare on the ground, but their fossil record is no worse than that of skeletonized marine invertebrates for large-scale studies.

### ACKNOWLEDGMENTS

Supported in part by the Leverhulme Trust. We thank Derek Briggs, Glenn Storrs, Karl Flessa, and Doug Erwin for helpful comments.

### REFERENCES CITED

- Behrensmeier, A. K., and Hill, A. P., 1980, Fossils in the making: Vertebrate taphonomy and paleoecology: Chicago, University of Chicago Press, 338 p.
- Benton, M. J., 1985, Mass extinction among non-marine tetrapods: *Nature*, v. 316, p. 811–814.
- Benton, M. J., 1993, *The fossil record 2*: London, Chapman and Hall, 839 p.
- Benton, M. J., 1994, Palaeontological data, and identifying mass extinctions: *Trends in Ecology and Evolution*, v. 9, p. 181–185.
- Benton, M. J., 1995, Testing the time axis of phylogenies: *Royal Society of London Philosophical Transactions*, ser. B, v. 349.
- Benton, M. J., and Storrs, G. W., 1994, Testing the quality of the fossil record: Paleontological knowledge is improving: *Geology*, v. 22, p. 111–114.
- Benton, M. J., and Storrs, G. W., 1995, Diversity in the past: Comparing cladistic phylogenies and stratigraphy, in Hochberg, M. E., et al., eds., *The genesis and maintenance of biological diversity*: Oxford, United Kingdom, Oxford University Press.
- Blake, D. B., 1987, A classification and phylogeny of post-Palaeozoic sea stars (Asterozoa: Echinodermata): *Journal of Natural History*, v. 21, p. 481–528.
- David, B., 1988, Origins of the deep-sea holasteroid fauna, in Paul, C. R. C., and Smith, A. B., eds., *Echinoderm phylogeny and evolutionary biology*: Oxford, United Kingdom, Clarendon Press, p. 331–346.

- Donovan, S. K., 1988, The early evolution of the Crinoidea, in Paul, C. R. C., and Smith, A. B., eds., Echinoderm phylogeny and evolutionary biology: Oxford, United Kingdom, Clarendon Press, p. 235–244.
- Durham, J. W., 1966, Clypeasteroids, in Moore, R. C., ed., Treatise on invertebrate paleontology, Part U, Echinodermata 3(2): Boulder, Colorado, Geological Society of America (and University of Kansas Press), p. U450–U491.
- Emlet, R. B., 1988, Crystallographic axes of echinoid genital plates reflect larval form: Some phylogenetic implications, in Paul, C. R. C., and Smith, A. B., eds., Echinoderm phylogeny and evolutionary biology: Oxford, United Kingdom, Clarendon Press, p. 299–310.
- Feral, J.-P., and Derelle, E., 1990, in Yanagisawa, T., et al., eds., Echinoderm biology: Rotterdam, Netherlands, A. A. Balkema, p. 331–338.
- Flessa, K. W., 1990, The “facts” of mass extinctions, in Sharpton, V. L., and Ward, P. D., eds., Global catastrophes in Earth history: Geological Society of America Special Paper 247, p. 1–7.
- Fürsich, F. T., 1990, Fossil concentrations and life and death assemblages, in Briggs, D. E. G., and Crowther, P. R., eds., Palaeobiology; a synthesis: Oxford, United Kingdom, Blackwell Scientific, p. 235–239.
- Gale, A. S., 1987, Phylogeny and classification of the Asterozoa (Echinodermata): Linnean Society Zoological Journal, v. 89, p. 107–132.
- Gaston, K. J., and May, R. M., 1992, Taxonomy of taxonomists: Nature, v. 356, p. 281–282.
- Gauthier, J., Kluge, A. G., and Rowe, T., 1988, Amniote phylogeny and the importance of fossils: Cladistics, v. 4, p. 105–209.
- Huelsenbeck, J. P., 1994, Comparing the stratigraphic record to estimates of phylogeny: Paleobiology, v. 20, p. 470–483.
- Jablonski, D., 1991, Extinctions: A paleontological perspective: Science, v. 253, p. 754–757.
- Jensen, M., 1981, Morphology and classification of the Euechinozoa Bronn, 1860—A cladistic analysis: Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn, v. 143, p. 7–99.
- Kidwell, S. M., 1986, Models of fossil concentrations: Paleobiologic implications: Paleobiology, v. 12, p. 6–24.
- Matsumura, T., Hasegawa, M., and Shigei, M., 1979, Collagen biochemistry and phylogeny of echinoderms: Comparative Biochemistry and Physiology, v. 62B, p. 101–105.
- Milsom, C., Simms, M. J., and Gale, A. S., 1994, Phylogeny and palaeobiology of *Marsupites* and *Uintacrinus*: Palaeontology, v. 38, p. 595–607.
- Mooi, R., 1990, Paedomorphosis, Aristotle's lantern, and the origin of the sand dollars (Echinodermata: Clypeasteroidea): Paleobiology, v. 16, p. 25–48.
- Norell, M. A., 1992, Taxic origin and temporal diversity: The effect of phylogeny, in Novacek, M. J., and Wheeler, Q. D., eds., Extinction and phylogeny: New York, Columbia University Press, p. 89–118.
- Norell, M. A., 1993, Tree-based approaches to understanding history: Comments on ranks, rules, and the quality of the fossil record: American Journal of Science, v. 293A, p. 407–417.
- Norell, M. A., and Novacek, M. J., 1992a, The fossil record and evolution: Comparing cladistic and paleontologic evidence for vertebrate history: Science, v. 255, p. 1690–1693.
- Norell, M. A., and Novacek, M. J., 1992b, Congruence between superpositional and phylogenetic patterns: Comparing cladistic patterns with fossil records: Cladistics, v. 8, p. 319–337.
- Paul, C. R. C., 1988, The phylogeny of the cystoids, in Paul, C. R. C., and Smith, A. B., eds., Echinoderm phylogeny and evolutionary biology: Oxford, United Kingdom, Clarendon Press, p. 199–213.
- Paul, C. R. C., and Smith, A. B., 1984, The early radiation and phylogeny of the echinoderms: Biological Reviews, v. 59, p. 443–481.
- Raff, R. A., and eight others, 1988, Molecular analysis of distant phylogenetic relationships in echinoderms, in Paul, C. R. C., and Smith, A. B., eds., Echinoderm phylogeny and evolutionary biology: Oxford, United Kingdom, Clarendon Press, p. 29–41.
- Raup, D. M., 1979, Biases in the fossil record of species and genera: Carnegie Museum of Natural History Bulletin, v. 13, p. 85–91.
- Retallack, G., 1984, Completeness of the rock and fossil record: Some estimates using fossil soils: Paleobiology, v. 10, p. 59–78.
- Sadler, P. M., 1981, Sediment accumulation rates and the completeness of stratigraphic sections: Journal of Geology, v. 89, p. 569–584.
- Seilacher, A., 1979, Constructional morphology of sand dollars: Paleobiology, v. 5, p. 191–221.
- Simms, M. J., 1988, The phylogeny of post-Palaeozoic crinoids, in Paul, C. R. C., and Smith, A. B., eds., Echinoderm phylogeny and evolutionary biology: Oxford, United Kingdom, Clarendon Press, p. 269–284.
- Simms, M. J., 1993, Echinodermata, in Benton, M. J., ed., The fossil record 2: London, Chapman and Hall, p. 491–528.
- Simms, M. J., 1994, Reinterpretation of thecal plate homology and phylogeny in the Class Crinozoa: Lethaia, v. 26, p. 303–312.
- Simms, M. J., and Sevastopulo, G. D., 1993, The origin of articulate crinoids: Palaeontology, v. 36, p. 91–109.
- Smiley, S., 1988, The phylogenetic relationships of holothurians: A cladistic analysis of the extant echinoderm classes, in Paul, C. R. C., and Smith, A. B., eds., Echinoderm phylogeny and evolutionary biology: Oxford, United Kingdom, Clarendon Press, p. 69–84.
- Smith, A. B., 1984a, Classification of the Echinodermata: Palaeontology, v. 27, p. 431–459.
- Smith, A. B., 1984b, Echinoid palaeobiology: London, George Allen and Unwin, 190 p.
- Smith, A. B., 1985, Cambrian eleutherozoan echinoderms and the early diversification of edrioasteroids: Palaeontology, v. 28, p. 715–756.
- Smith, A. B., 1988a, Fossil evidence for the relationships of extant echinoderm classes and their times of divergence, in Paul, C. R. C., and Smith, A. B., eds., Echinoderm phylogeny and evolutionary biology: Oxford, United Kingdom, Clarendon Press, p. 85–97.
- Smith, A. B., 1988b, Patterns of diversification and extinction in early Palaeozoic echinoderms: Palaeontology, v. 31, p. 799–828.
- Smith, A. B., 1990, Echinoid evolution from the Triassic to Lower Liassic: Cahiers de l'Université Catholique de Lyon, Séries Scientifique, v. 3, p. 79–117.
- Smith, A. B., 1992, Echinoderm phylogeny: Morphology and molecules approach accord: Trends in Ecology and Evolution, v. 7, p. 224–229.
- Smith, A. B., and Arbizu, M. A., 1987, Inverse larval development in a Devonian edrioasteroid from Spain and the phylogeny of Agelacrinitinae: Lethaia, v. 20, p. 49–62.
- Smith, A. B., and Hollingworth, N. T. J., 1990, Tooth structure and phylogeny of the Upper Permian echinoid *Miocidaris keyserlingi*: Yorkshire Geological Society Proceedings, v. 48, p. 47–60.
- Smith, A. B., and Wright, C. W., 1989, British Cretaceous echinoids. Part 1, General introduction and Cidaroida: Palaeontographical Society Monographs, v. 141, p. 1–101.
- Smith, A. B., and Wright, C. W., 1990, British Cretaceous echinoids. Part 2, Echinothurioida, Diademodontoida and Stirodonta (1, Calycina): Palaeontographical Society Monographs, v. 143, p. 101–198.
- Smith, A. B., and Wright, C. W., 1993, British Cretaceous echinoids. Part 3, Stirodonta 2, Hemicidaroida and Phymosomatoida, Part 1: Palaeontographical Society Monographs, v. 147, p. 199–267.
- Smith, A. B., Lafay, B., and Christen, R., 1992, Comparative variation of morphological and molecular evolution through geologic time: 28S ribosomal RNA versus morphology in echinoids: Royal Society of London Philosophical Transactions, ser. B, v. 338, p. 365–382.
- Sprent, P., 1989, Applied nonparametric statistical methods: London, Chapman and Hall, 259 p.
- Valentine, J. W., 1969, Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time: Palaeontology, v. 12, p. 684–709.

Manuscript received December 27, 1994  
 Revised manuscript received March 23, 1995  
 Manuscript accepted March 29, 1995