



OXFORD
BIOLOGY



the **TIMETREE** *of* **LIFE**

edited by **S. BLAIR HEDGES** *and* **SUDHIR KUMAR**
foreword by James D. Watson

Sea urchins (Echinoidea)

Andrew B. Smith

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK (a.smith@nhm.ac.uk)

Abstract

The Echinoidea (sea urchins) is one of the five classes of the Phylum Echinodermata and includes ~900 living species in 50 families. Their traditional taxonomy, based on skeletal characters, has been largely corroborated by recent molecular phylogenetic analyses with one marked exception: clypeasteroids are not found to be monophyletic. The echinoid timetree deduced from molecular data is largely concordant with the fossil record, placing the basal divergence in the late Paleozoic (265 million years ago, Ma). Echinoids diversified during the Mesozoic (251–66 Ma) and there is a good match between paleontological and molecular estimates of divergence times, with clypeasteroids again proving to be an exception.

The Phylum Echinodermata is a clade of marine invertebrate deuterostomes that includes such well-known animals as the starfishes and sea urchins. All echinoderms possess a calcitic endoskeleton with a distinctive and unique three-dimensional structure, a stereom, and they all undergo an unusual asymmetrical development in which right larval coelomic components are suppressed and lost. There are five living classes of echinoderm, of which the Echinoidea or sea urchins (Fig. 1) is probably the best known and certainly the one that has left the most complete fossil record. Living echinoids have a mesodermal skeleton constructed of 10 columns of plates, all of which bear tubercles and spines. The modern taxonomy of echinoids was established by Mortensen (1), based primarily on the detailed arrangement of plates making up the skeleton. This has the great advantage of allowing fossils to be placed with confidence into any taxonomic scheme constructed for the living species. About 900 living species of echinoids have been described and placed in ~50 families (1, 2), not all of which are considered monophyletic. Here, I review the relationships and divergence times of the major echinoid groups.

It has long been recognized that the cidaroids differ in several fundamental ways from other echinoids

(Euechinoidea), and this division is reflected at the subclass level (1, 2). Cidaroids and euechinoids differ in their style of ambulacral plating, and have different jaw apparatus morphologies and musculature. Whereas cidaroids remained rather conservative in their morphology, the euechinoids have given rise to a wide diversity of forms (3), currently classified into 13 orders. There are a number of small, early branching groups but about 80% of the modern diversity lies in two major clades, the Irregularia and the Echinacea. Irregular echinoids are so named because their pentamerous symmetry is disrupted by migration of the anus from an apical to a posterior position during ontogeny, and most live infaunally. Echinacea are regular echinoids with a derived lantern morphology and keeled teeth and all are epifaunal.

The classification of the Echinacea has been particularly difficult and relies on small differences rarely preserved in fossils (4). The taxonomy of irregular echinoids, on the other hand, has been much less problematic with the long-standing major groups (spatangoids, holasteroids, clypeasteroids, and cassiduloids) readily differentiated



Fig. 1 An echinoid (*Arbacia punctulata*) from Carrie Bow Cay, Belize, viewed from above. Credit: A. B. Smith.

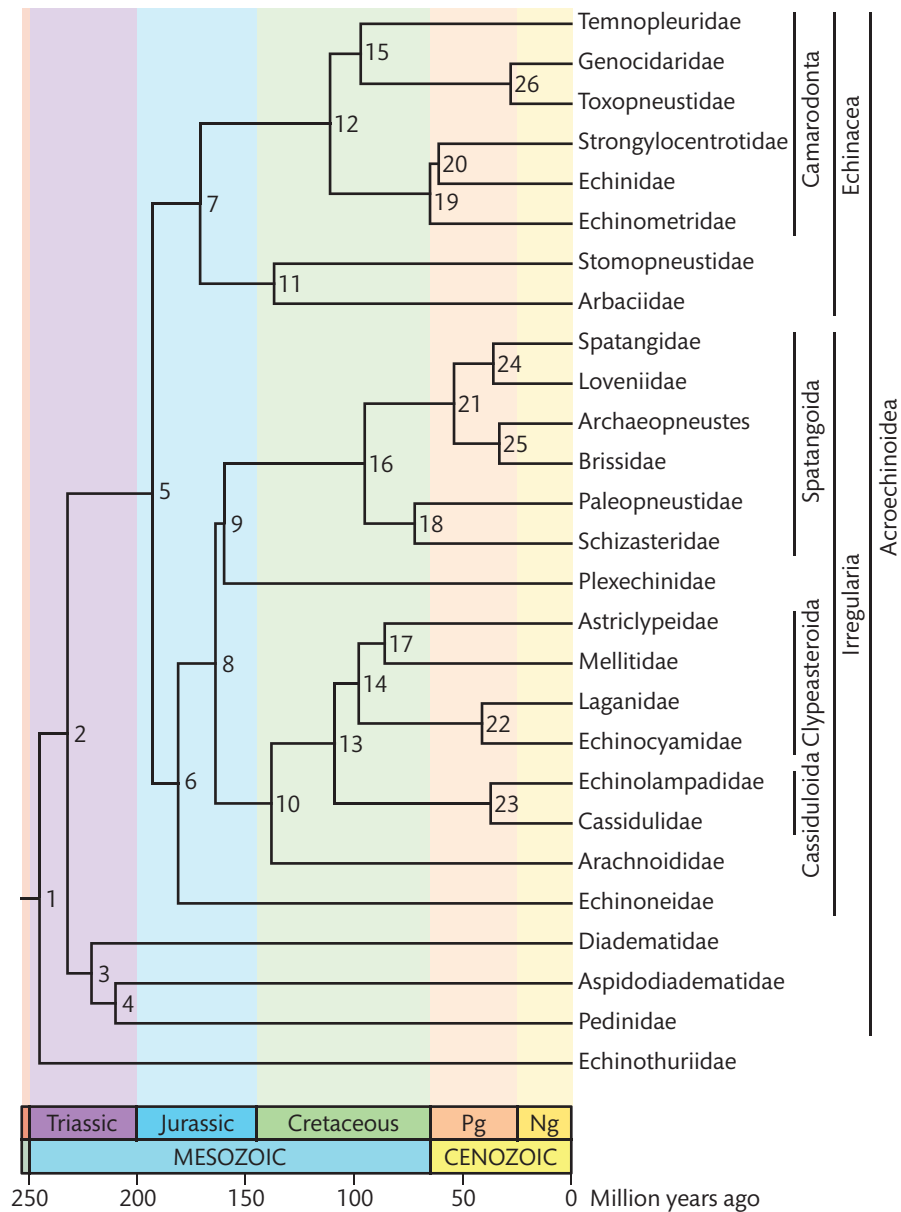


Fig. 2 A timetree of sea urchins (Echinoidea). Divergence times are from Table 1. *Abbreviations:* Ng (Neogene) and Pg (Paleogene).

on morphological grounds (1, 2). The monophyly of the clypeasteroids, a group characterized by the unique synapomorphy of multiple tube feet (and pores) on each ambulacral plate, has never been disputed from morphological grounds (5), though the cassiduloids, from which they emerged, are now recognized to be a paraphyletic grade (6).

Molecular phylogenies for the Echinoidea that encompassed a number of different families started to appear from 1992 onward (6–10). These have all been constructed

from nuclear and mitochondrial ribosomal RNA genes (18S, 28S, and 16S rRNA), sometimes with the addition of sequence data from three subunits of mitochondrial cytochrome oxidase genes (COI, COII, and COIII). The first studies achieved only a very sparse taxonomic coverage and failed to find convincing evidence for the cidaroid–euechinoid basal dichotomy (6). By 1995, however, the first analysis that could claim reasonable taxonomic coverage appeared (7) and showed good correspondence with morphology-based phylogenetic trees. In the latest

Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) among sea urchins (Echinoidea), based on ref. (10).

Timetree	
Node	Time
1	245
2	232
3	221
4	210
5	193
6	181
7	171
8	164
9	160
10	138
11	137
12	111
13	109
14	98
15	97
16	95
17	86
18	72
19	65
20	61
21	54
22	41
23	37
24	36
25	33
26	28

Note: Molecular dates are the means of estimates obtained from the analysis of concatenated *18S rRNA*, *28S rRNA*, and *COII* partial gene sequences using different methodologies: LF (Langley-Fitch), NPRS (nonparametric rate smoothing), PL-A (penalized likelihood with additive penalty function, PL-L (penalized likelihood with logarithmic penalty function), and Bayesian.

analysis (10), the molecular phylogeny is now based on gene sequence data from almost 50 taxa, with representatives from 13 of the 14 extant orders. In addition to these studies addressing the higher-level relationships of echinoids, detailed molecular phylogenies have appeared outlining the phylogenetic relationships of specific groups at

genus level (e.g., temnopleuroids (11), spatangoids (12), stronglylocentrotids (13)) and species level [e.g. *Eucidaris* (14), *Diadema* (15)].

From the beginning, phylogenetic studies have often analyzed morphological and molecular data in parallel and in combination, and have used the rich fossil record for dating divergences. The basic taxonomic framework for echinoids established from skeletal morphology has stood up well to this molecular scrutiny (1). Cidaroids consistently turn out to represent the deepest branch in the echinoid tree and echinothurioids the deepest branch on the euechinoid side, exactly as predicted by morphology. The next few branches are very closely spaced and branching order of pedinoids and diadematoids is not clear. There is a monophyletic Irregularia, within which the echinoneid *Echinoneus* represents the basal branch, and holasteroids and spatangoids are closest relatives. There is one major surprise—molecular data suggest that clypeasteroids are not monophyletic. The two suborders (Clypeasterina and Scutellina) are recognized, but they are not identified as closest relatives. Instead, representatives from two families of cassiduloid are the closest relatives of the Scutellina. The very short branches leading to the cassiduloid taxa suggest that this is not a long-branch attraction problem, and the inferred relationships are robust to addition or removal of taxa. However, it is hard to reconcile this observation with the strong morphological evidence for clypeasteroid monophyly.

Only one study has estimated divergence times among echinoid families from molecular data (10). This study examined 26 internal nodes and compared molecular estimates based on ribosomal gene divergence with paleontological estimates (Fig. 2). In order to generate a semilinearized tree one taxon was selected from each family, avoiding extremely long or short terminal and branches. Bayesian and nonparametric rate smoothing semiparametric penalized likelihood methods were all used for estimating divergence times along with the Langley-Fitch strict clock method, and error bars calculated. A selection of taxa from the other echinoderm classes formed the outgroup, with a prior depth of the root node set at 480 My based on the fossil record. Four internal calibrations were set as minimal divergence times from across the tree topology to provide constraints on local rate variation.

Molecular estimates of divergence times derived from applying both molecular clock and relaxed molecular clock models are concordant with estimates based on the fossil record for 70% of the nodes. Mismatch is confined to three areas of the tree, the most serious of which

concerns the clypeasteroids, where a late Jurassic divergence (156 ± 24 Ma) for Clypeasterina from Scutellina was predicted from molecular data. In contrast, the fossil record provides no evidence for any clypeasteroid before 60 Ma (Middle Paleocene) (2, 16).

The fact that so much of the molecular phylogeny matches what is known from morphology and the fossil record is encouraging, and should allow for a more confident integration of data. For example, the divergence of many of the basal euechinoid clades apparently occurred in the Triassic (251–200 Ma), during the very earliest stages of the breakup of Pangea (17) as marine conditions started to spread over the continental shelves after a major sea-level low stand (18). By comparative analysis it is possible to show that the mismatch between molecular clock and paleontological estimates of divergence increases as the marine rock record deteriorates in quality (17).

Acknowledgment

Support was provided by a grant from the Leverhulme Foundation.

References

1. T. Mortensen, *A Monograph of the Echinoidea*, 5 volumes (C. A. Reitzel, Copenhagen, 1928–1951).
2. A. B. Smith, *The Echinoid Directory*, <http://www.nhm.ac.uk/research-curation/projects/echinoid-directory> (The Natural History Museum, London, 2006).
3. A. B. Smith, in *Evolving Form and Function—Fossils and Development*, D. E. G. Briggs, Ed. (Yale University Press, New Haven, 2005), pp. 181–194.
4. A. B. Smith, *Mol. Biol. Evol.* **5**, 345 (1988).
5. R. Mooi, *Paleobiology* **16**, 25 (1990).
6. A. B. Smith, *Paleobiology* **27**, 392 (2001).
7. A. B. Smith, B. Lafay, R. Christen, *Phil. Trans. Roy. Soc. Lond. B* **338**, 365 (1992).
8. D. T. J. Littlewood, A. B. Smith, *Phil. Trans. Roy. Soc. Lond. B* **347**, 213 (1995).
9. A. B. Smith, D. T. J. Littlewood, G. A. Wray, *Phil. Trans. Roy. Soc. Lond. B* **349**, 11 (1996).
10. A. B. Smith, D. Pisani, J. A. Mackenzie-Dodds, B. Stockley, B. L. Webster, D. T. J. Littlewood, *Mol. Biol. Evol.* **23**, 1832 (2006).
11. C. H. Jeffery, R. B. Emlet, D. T. J. Littlewood, *Mol. Phylogenet. Evol.* **28**, 99 (2003).
12. B. Stockley, A. B. Smith, D. T. J. Littlewood, H. A. Lessios, J. A. MacKenzie-Dodds, *Zool. Scripta* **34**, 447 (2005).
13. Y.-H. Lee, *Mol. Biol. Evol.* **20**, 1211 (2003).
14. H. A. Lessios, B. D. Kessing, D. R. Robertson, G. Pauley, *Evolution* **53**, 806 (1999).
15. H. A. Lessios, B. D. Kessing, J. S. Pearse, *Evolution* **55**, 955 (2001).
16. P. M. Kier, *Palaeontology* **25**, 1 (1982).
17. A. B. Smith, *Paleobiology* **33**, 311 (2007).
18. A. B. Smith, A. J. McGowan, *Palaeontology* **50**, 765 (2007).

