Phylogenetic Relationship, Divergence Times, and Rates of Molecular Evolution for Camarodont Sea Urchins[1]

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The phylogenetic relationships of 21 relatively common and well-studied genera of camarodont echinoids were established using a numerical cladistic approach. This combines data about test morphology, pedicellarial structure, tooth ultrastructure, and larval morphology. The fossil record of the group was reappraised in the light of this analysis, and times of divergence for taxa were estimated. Camarodont families are considered to have diverged much more recently than has previously been suggested, and all except the paraphyletic Temnopleuridae have originated between 65 and 35 Myr ago. Estimates of rates of molecular evolution established on the basis of both thermal stability of heterologous single-copy DNA duplexes and gene sequence data were recalculated using the revised divergence times. Rate of nucleotide divergence, as measured by thermal stability of single-copy DNA heteroduplexes, was calculated to be 0.65–0.85 degrees C/Myr, while sequence data on histone genes indicated a rate of silent substitution of 0.70%–0.85%/Myr. Times of divergence estimated from the fossil record remain too poorly constrained to prove whether molecular evolution proceeds at a stochastically constant rate, but the results are wholly consistent with such a model.

Introduction

Most of the common, shallow-water, regular sea urchins alive today belong to the group Camarodonta. This group, which is almost certainly now more diverse than at any time in the past, was believed by Mortensen (1943*a*, 1943*b*) to comprise some 146 species and 44 genera currently extant, and few new species have been described since then. Camarodonts form a well-defined monophyletic group characterized by (1) their lantern structure, with epiphyses meeting above the foramen magnum, (2) echinoid-style ambulacral plate compounding (see Jensen 1981), and (3) a poison groove on the distal part of the blades of globiferous pedicellariae. However, taxonomic relationships within the Camarodonta are not so clearly established, and Mortensen (1943*a*, 1943*b*) had to rely on the fine structure of globiferous pedicellariae to differentiate family groupings. As a result, although fossil species can generally be identified as Camarodonta on the basis of features of the test alone, relatively few can be placed with any certainty into subgroups within Mortensen's classification scheme, basically because of a lack of data. Furthermore, regular echinoids are known to have a relatively poor fossil record (Kier 1977), so that paleontological data have been of little use in unraveling the evolutionary history of camarodonts.

Because of their difficult taxonomy and their poor fossil record, little attention has been paid to the phylogenetic history of the Camarodonta. This state of affairs

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would almost certainly have continued were it not for the spotlight that has been focused on this group by molecular biologists over the past decade. Camarodont sea urchins are a particularly favorable group for molecular study, principally because of the depth of knowledge now attained concerning their gene expression, especially during embryological development. Also, genetic material can be readily obtained from a number of easily available species. In recent years interest in the molecular evolution of sea urchins has grown, and histone and actin gene clusters, active early in the embryonic development of camarodonts, are classic examples of the parallel or tandem evolution of multigene families (Busslinger et al. 1982; Johnson et al. 1983; Lee et al. 1984).

Various workers have attempted to establish an absolute time scale for rates of molecular substitution (the "molecular clock") calibrated with reference to divergence times of camarodont genera. Angerer et al. (1976) estimated the rate of sequence change in camarodont nuclear DNA by using heteroduplex melting temperatures (T_m's) calibrated against divergence times based on the fossil record. Their estimate was vague (because of uncertainties over divergence times) but implied a change of heteroduplex melting temperature (ΔT_m) of 0.08–0.35 degrees C/Myr.

Hall et al. (1980) refined and improved on this technique and developed a low-criterion method for establishing heteroduplex mismatch. They also proposed that median divergence temperature (ΔT_{med}) was a better measure of evolutionary relationship because it provides an inclusive measure of the divergence of all of the single-copy DNA and, where it can be applied, gives an answer that is independent of the criterion of precision of duplex formation in the measurement. Using this approach they concluded that the rate of molecular divergence for camarodont sea urchins was ~0.5%/Myr.

Using sequence data Busslinger et al. (1982) calculated the rate of silent substitution (substitutions at the third coding position) for homologous sequences within the histone gene family of various camarodonts. Their results suggest a rate of change for silent sites in these genes of 0.22%–0.90%/Myr. Grula et al. (1982) calculated the average rate of divergence of single-copy sequences of DNA to be 1%/Myr. All these measurements of absolute rate of change hinge on the accuracy of the fossil record in dating divergence times. Yet estimates of the time of divergence of *Strongylocentrotus* and *Lytechinus* used by molecular biologists can vary from 180 Myr before the present (Mybp) (Lee et al. 1984) to 80 Mybp (Jacobs and Grimes 1986), and both of these are probably overestimates (see below).

Genetic distances between some species of camarodont echinoid have also been calculated by electrophoretic analysis of certain enzymes (Matsuoka 1987). Using this technique Matsuoka estimated the time of divergence of Strongylocentrotidae and Toxopneustidae at 6.2 Mybp.

Other workers have used the estimates of molecular rates of evolution to date specific molecular events. Molecular data alone can provide a relative scheme of evolutionary events affecting large gene families such as the actin gene family (Lee et al. 1984) or the histone gene family (Busslinger et al. 1982; Raff et al. 1984), but ultimately one or more absolute divergence times have to be established to calibrate events. Jacobs and Grimes (1986), for example, have demonstrated in the nuclear DNA of several species of camarodont the existence of a pseudogene transposed from mitochondrial DNA, and they have attempted to date this transposition event in various ways. Busslinger et al. (1982) used divergence times to support their thesis that hori-

zontal gene transfer in the histone gene family had occurred between distally related species of camarodont.

With so much work now being done on the molecular evolution of the camarodont genome, there is a clear need to reassess the phylogenetic history of this group on the basis of morphological and paleontological evidence. In particular, it is crucial that divergence times for genera and families be bracketed as accurately as possible. This paper then sets out to (1) establish phylogenetic relationships between the common genera of camarodont echinoids in a rigorous manner, (2) use this analysis to highlight the level at which test characters discernible in fossil species are apomorphous (derived), (3) use the fossil record to bracket divergence times, and (4) reexamine rates of molecular evolution on the basis of these new data.

Phylogenetic Relationships of Extant Camarodont Genera

Previous Classifications

The Camarodonta was first recognized as a natural group through Jackson's (1912) pioneering work on lantern structure. Groups within the Camarodonta, however, remained poorly conceived prior to the work of Mortensen (1943*a*, 1943*b*), and differentiation of them was based largely on test sculpture, the perforate or nonperforate nature of primary tubercles, and the number of ambulacral plates combined together into a compound plate. Mortensen (1943*a*, 1943*b*) paid meticulous attention to detail and drew together a vast amount of morphological information about this group, much of it new. His revision of the group led to the classification outlined in table 1. The families he recognized within the Echinina were distinguished almost entirely on the basis of differences in the fine structure of the globiferous pedicellariae.

Most later workers have accepted Mortensen's groupings without question. Durham and Melville (1957) admitted ignorance about the group and recognized all Mortensen's families and higher groupings, though they raised Temnopleurina and Echinina to the categorial rank of order. However, they did not accept Jackson's group Camarodonta, believing this to be a polyphyletic group. Their phylogenetic diagram (Durham and Melville 1957, fig. 6) shows Echinoida originating from phymosomatoids at the end of the Cretaceous and Temnopleuroida originating from the same group near the start of the Cretaceous. Later, Durham (1966) revised his views, extending divergence dates back in time. He showed Echinoida branching from phymosomatoids at the start of the Cretaceous (~130 Mybp), while Temnopleuroida he considered to have derived from hemicidaroids sometime in the Late Triassic (~180 Mybp). It is this phylogeny that was used later by molecular biologists such as Angerer et al. (1976) and Lee et al. (1984) to calibrate their molecular clock.

Philip (1966) did not agree with Durham and Melville but used Mortensen's classification without change or discussion. Smith (1981) also used Mortensen's classification, though recognizing Echinoida and Temnopleuroida at the rank of order.

The only worker to have critically examined the taxonomy of camarodonts since Mortensen is Jensen. Jensen (1974) carried out a detailed scanning electron microscopical investigation both into the ultrastructure of pedicellariae and into tooth structure for species of Strongylocentrotidae and later expanded her study to the tooth ultrastructure of other echinoid families (Jensen 1979). Two years later Jensen (1981) published an extensive analysis of echinoid relationships and produced a new classification (see table 1). This was presented as a cladistic treatment, but in fact Jensen only identified autapomorphies for her families and did not justify her scheme by identifying more than a handful of synapomorphies. Surprisingly, in this analysis of

Table 1

Classifications of Camarodont Genera Discussed in This Paper

Mortensen 1943a, 1943b	Jensen 1981	Present Paper
Order Camarodonta Jackson	Order Echinoida Claus	Order Echinoida Claus
Suborder Temnopleurina Mortensen	Family Temnopleuridae Agassiz	Suborder Temnopleurina Mortensen
Family Temnopleuridae Agassiz	Genus *Amblypneustes* Agassiz	Family Temnopleuridae Agassiz
Subfamily Temnopleurinae Mortensen	Genus *Holopneustes* Agassiz	Genus *Temnopleurus* Agassiz
Genus *Amblypneustes* Agassiz	Genus *Mespilia* Desor	Genus *Salmacis* Agassiz
Genus *Holopneustes* Agassiz	Genus *Microcyphus* Agassiz	Genus *Mespilia* Desor
Genus *Mespilia* Desor	Genus *Salmacis* Agassiz	Genus *Microcyphus* Agassiz
Genus *Microcyphus* Agassiz	Genus *Temnopleurus* Agassiz	Genus *Amblypneustes* Agassiz
Genus *Salmacis* Agassiz	Family Parechinidae Mortensen	Genus *Holopneustes* Agassiz
Genus *Temnopleurus* Agassiz	Genus *Paracentrotus* Mortensen	Suborder Echinina Mortensen
Subfamily Trigonocidarinae Mortensen	Genus *Psammechinus* Agassiz and Desor	Family Echinidae Gray
Genus *Desmechinus* Clark	Family Echinidae Gray	Subfamily Echininae Gray
Family Toxopneustidae Troschel	Genus *Echinus* Linnaeus	Genus *Echinus* Linnaeus
Genus *Lytechinus* Agassiz	Family Toxopneustidae Troschel	Subfamily Parechininae Mortensen
Genus *Pseudoboletia* Troschel	Genus *Desmechinus* Clark	Genus *Paracentrotus* Mortensen
Genus *Sphaerechinus* Desor	Genus *Lytechinus* Agassiz	Genus *Psammechinus* Agassiz and Desor
Genus *Toxopneustes* Agassiz	Genus *Parasalenia* Agassiz	Family Echinometridae Gray
Genus *Tripneustes* Agassiz	Genus *Pseudoboletia* Troschel	Subfamily Strongylocentrotinae Gregory
Suborder Echinina Mortensen	Genus *Sphaerechinus* Desor	Genus *Allocentrotus* Mortensen
Family Echinidae Gray	Genus *Toxopneustes* Agassiz	Genus *Strongylocentrotus* Brandt
Subfamily Echininae Gray	Genus *Tripneustes* Agassiz	Subfamily Echinometrinae Gray
Genus *Echinus* Linnaeus	Family Echinometridae Gray	Genus *Parasalenia* Agassiz
Subfamily Parechininae Mortensen	Genus *Anthocidaris* Lutken	Genus *Echinometra* Gray
Genus *Paracentrotus* Mortensen	Genus *Colobocentrotus* Brandt	Genus *Anthocidaris* Lutken
Genus *Psammechinus* Agassiz and Desor	Genus *Echinometra* Gray	Genus *Heterocentrotus* Brandt
Family Echinometridae Gray	Genus *Heliocidaris* Agassiz and Desor	Genus *Colobocentrotus* Brandt
Genus *Anthocidaris* Lutken	Genus *Heterocentrotus* Brandt	Subfamily Toxopneustinae Troschel
Genus *Colobocentrotus* Brandt	Genus *Zenocentrotus* Clark	Genus *Lytechinus* Agassiz
Genus *Echinometra* Gray	Family Strongylocentrotidae Gregory	Genus *Pseudoboletia* Troschel
Genus *Heliocidaris* Agassiz and Desor	Genus *Allocentrotus* Mortensen	Genus *Sphaerechinus* Desor
Genus *Heterocentrotus* Brandt	Genus *Strongylocentrotus* Brandt	Genus *Tripneustes* Agassiz
Genus *Zenocentrotus* A. H. Clark		Genus *Toxopneustes* Agassiz
Family Strongylocentrotidae Gregory		
Genus *Allocentrotus* Mortensen		
Genus *Strongylocentrotus* Brandt		
Family Parasaleniidae Mortensen		
Genus *Parasalenia* Agassiz		

camarodont relationships Jensen considered all obvious morphological characters except pedicellarial features, used so extensively by Mortensen. The two schemes are therefore to some extent complementary in the data used. Significant changes made by Jensen (1981) included the transfer of Toxopneustidae from the Temnopleuroida to the Echinoida and the elevation of the subfamilies Parechininae and Echininae of the family Echinidae to family status. Smith (1984, p. 170) followed Jensen in assigning Toxopneustidae to the Echinoida and presented a tentative phylogeny in which extant camarodont families were post–Upper Cretaceous in origin.

Recent immunological work by Matsuoka (1980, 1985, 1986, 1987) on camarodont sea urchins has clarified the position of *Pseudocentrotus* and provided new data on the biochemical phylogeny of the group. He has calculated genetic distances between pairs of species on the basis of electrophoretic patterns for 15 enzymes. The resulting similarity dendrogram suggests that *Pseudocentrotus* is a member of the Strongylocentrotidae and not of the Toxopneustidae, in which it had previously been placed. An enzyme-inhibition method has been used (Matsuoka 1986) to test the immunological relatedness of species within different camarodont families and suggests that Strongylocentrotidae and Toxopneustidae are more closely related to one another than either is to Temnopleuridae or Echinometridae.

A Cladistic Analysis of Camarodonts

A comprehensive search for putative homologies has been undertaken for 27 of the most common and widespread genera of camarodont. This included the suite of characters relating to pedicellarial structure, used by Mortensen (1943*a*, 1943*b*), and a suite of characters relating to tooth ultrastructure, used by Jensen (1981). Six of these genera were eventually excluded from the analysis because of a lack of data on tooth ultrastructure. A further three pairs of genera (*Temnopleurus/Salmacis, Sphaerechinus/Pseudoboletia,* and *Heterocentrotus/Colobocentrotus*) were found to have almost identical suites of characters and were treated as single operational taxonomic units for the purposes of this analysis. Thus, in all, 18 operational taxonomic units were used (see fig. 1).

A total of 20 characters, six of them multistate, were eventually used (see Appendix). A numerical cladistic package, PAUP (*p*hylogenetic *a*nalysis *u*sing *p*arsimony; Swofford 1985), was run using these data to establish the most parsimonious arrangement of taxa. No weighting was applied, and *Temnopleurus* was used as outgroup for the purposes of rooting.

The characters used in this analysis and their polarity are discussed in the Appendix. Most multistate characters were left unordered unless there was good reason to believe that they represented arbitrary divisions within a spectrum whose polarity was known.

Results

Analysis of the data produced six equally parsimonious trees each with a consistency index of 0.64. These trees differed in the positioning of two genera, *Lytechinus* and *Echinus. Lytechinus* was placed either as primitive sister group to other toxopneustids (*Sphaerechinus,* etc.) or as primitive sister group to both toxopneustids and echinometrids (between *Strongylocentrotus* and *Desmechinus* in fig. 1). The latter arrangement, however, is not preferred, since it demands that deep buccal notches be evolved then immediately lost from Echinometridae. Treating *Lytechinus* as primitive

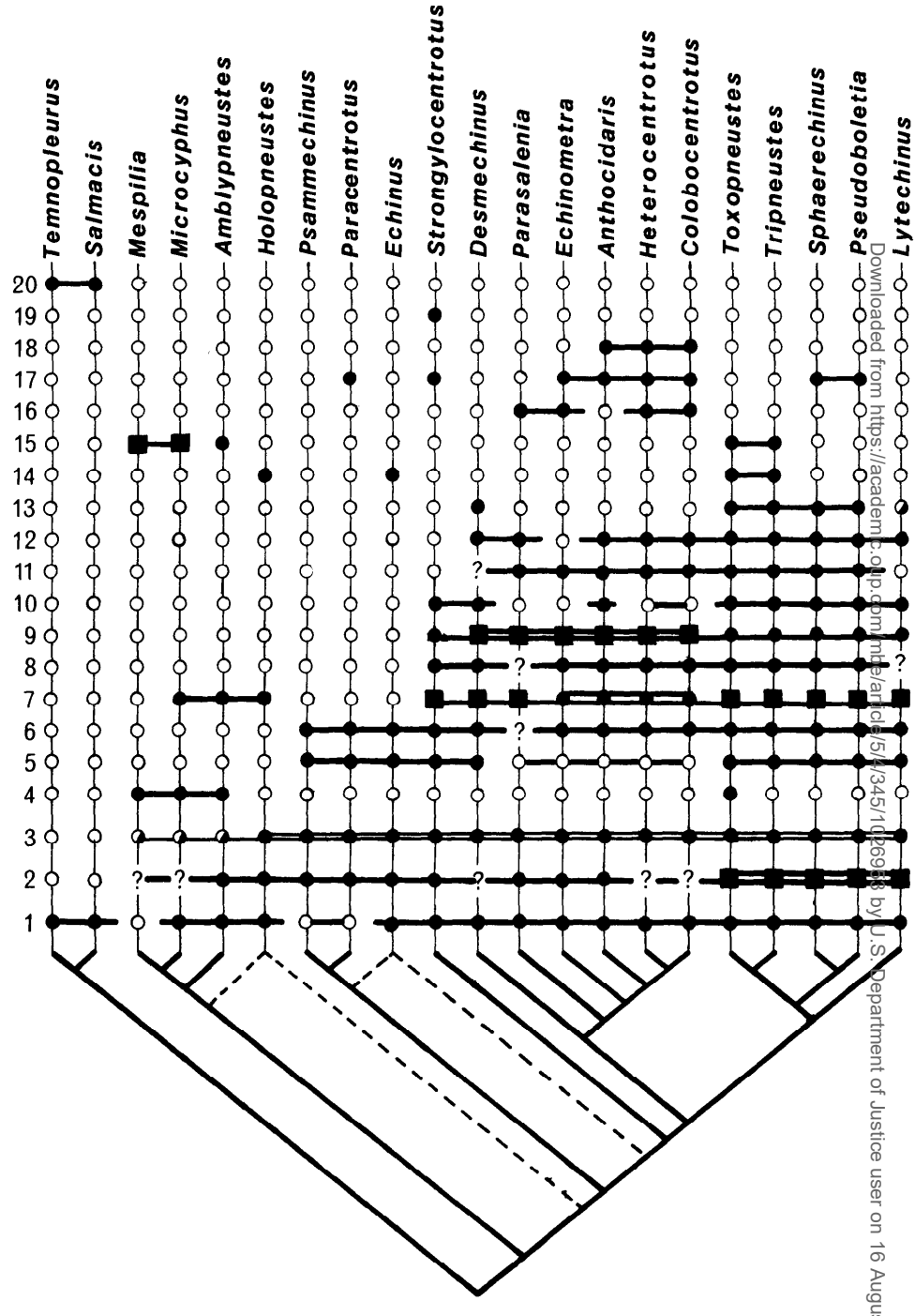

FIG. 1.—Cladogram and character matrix for genera of camarodont echinoids. Open symbols = primitive characters; solid symbols = derived characters; double bars = multiple-state characters for which one state is more inclusive than an alternative; ? = character state unknown. Derived characters 1–20 are as follows: 1, blade of globiferous pedicellariae compact and coalesced; 2, primary tooth plate with distance from umbo to lateral edge (compare distance from umbo to oral edge in the range 0.8–1.2 [circles] or 1.3+ [squares]);

sister group to Toxopneustidae alone implies that the absence of a pluteus larva with a basket-like skeletal structure in *Lytechinus* is a secondary reversal.

The analysis places *Echinus* in one of three positions, primitive to the *Psammechinus/Paracentrotus* branch, derived compared with the *Psammechinus/Paracentrotus* branch, or as primitive sister group to *Psammechinus/Paracentrotus* on that branch. The first of these options can be rejected because it demands that the presence of one primary ambulacral tubercle on every second or third plate be homologous in both *Echinus* and *Holopneustes* and that this character was evolved and then subsequently lost from all subsequent groups. This seems highly implausible. However, there are no synapomorphies to determine whether *Echinus* belongs to the branch containing *Psammechinus/Paracentrotus* or to its sister group. *Echinus* has therefore been placed in both positions in the cladogram (fig. 1).

One further change has been made, and that is to link *Holopneustes* to two positions. This is because the single attribute that links *Holopneustes* with Echinoida rather than with Temnopleuroida is its feebly crenulate tuberculation; and this is not considered to be a very reliable criterion. Crenulation is variably developed within temnopleuroid genera, and more work on temnopleuroid relationships is needed before definitive conclusions can be drawn about which genera are more closely related to Echinoida. A classification consistent with the results of this analysis is presented in table 1.

The Fossil Record of Camarodonta

Problems

As Mortensen (1943*a*, p. 63; 1943*b*, pp. 15, 20) pointed out, many fossil species of regular echinoid have been assigned to genera and families for spurious reasons. Small fossil camarodonts with imperforate noncrenulate tubercles and trigeminate plate compounding have generally been placed in the genus *Psammechinus,* but their taxonomic position is, in reality, indeterminate. There are relatively few test characters that can be used to identify taxa within the Camarodonta, most taxa being defined on the basis of characters of the globiferous pedicellariae or tooth ultrastructure. As few fossils are preserved with even their complement of apical disc plates, let alone their lantern, spines, and pedicellariae, many fossils must remain unclassifiable.

However, there are a number of useful test characters that allow some fossils to be placed within genera or families. The earliest appearance of such characters in the fossil record provides a latest date for divergence of the taxon that they characterize. These characters are discussed in detail below.

Placing a lower limit on the timing of divergence is a much more difficult task

3, primary tubercles weakly crenulate (half-filled circles) or noncrenulate (solid circles); 4, test with broad naked interradial and perradial bands adapically; 5, globiferous pedicellariae with single poison glands; 6, CLNP tooth system with oral lamellae that are branched or forked; 7, globiferous pedicellariae with a single asymmetrical side tooth (circles) or no side teeth (squares); 8, CLNP tooth system with a comb of tines; 9, stalk of globiferous pedicellariae solid (squares) or tubular (circles); 10, apical disc with oculars I and V insert; 11, larvae with a basket-type skeleton; 12, globiferous pedicellariae with stalk glands; 13, buccal notches sharp and deep, extending level to the fourth ambulacral plate; 14, ambulacra with a primary tubercle only on every second or third compound plate; 15, ambulacral pores arranged in two (squares) or three (circles) discrete columns on each compound plate; 16, test elliptical in outline; 17, ambulacra polyporous; 18, polyporous ambulacra with eight or more component elements; 19, globiferous pedicellariae with muscular neck; and 20, sutural pits present on coronal plates.

and cannot be done rigorously. This is because the absence of a taxon from the fossil record may be genuine or may result from preservation failure or inadequate sampling. Furthermore, there is no criterion by which ancestors can be distinguished from plesiomorphic primitive sister groups. Thus it is not possible to say for certain that a fossil species is "ancestral" to later groups even when it predates them, though one can speculate. Earlier dates of divergence must, therefore, remain equivocal. The quality of the fossil record of echinoids also varies through time (see Kier 1974), and there are some time periods for which we know we have a very poor representation of the fauna. Conversely, there are times for which large and extensive faunas are reported from around the world and from which we might expect to have sampled a reasonable proportion of the fauna of that period. Thus we probably have a moderately good record of echinoid faunas from the Middle and Upper Eocene and Lower Miocene but not from the Palaeocene, Lower Eocene, Oligocene, or Upper Miocene. The absence of species with distinctive camarodont traits from periods from which reasonably large faunas of regular echinoids have been reported suggests that the clade had not yet evolved—although the danger of relying on negative evidence is obvious. To some extent, the confidence with which one treats such negative evidence depends on the time span for which no evidence exists. Few people would seriously consider the fossil record of camarodonts to stretch back into the Palaeozoic, and many would question extending their range much before the Cretaceous. In this situation, earlier brackets on the timing of divergence are no more than informed speculation based on negative evidence and a working knowledge of the quality and apparent diversity of the fossil record of regular echinoids. I can see no alternative that would provide more rigorous results.

The Evidence

Temnopleuridae

Temnopleurids can conveniently be divided into two groups, those with test sculpturing (Mortensen's Trigonocidarinae and Gonocidarinae) and those with test pitting (Temnopleurinae) (Philip 1969). The only camarodonts that are known from the Cretaceous belong to the *Glyptocyphus-Echinopsis-Zeugopleurus* lineage (Cenomanian to Maastrichtian) and have weakly sculptured tests. *Orthologhus,* from the Upper Eocene to Late Miocene of Australia and New Zealand (Philip 1969), is virtually indistinguishable from *Zeugopleurus* and almost certainly represents the Tertiary continuation of this lineage. Sculpture in *Orthologhus* is very variably developed. Other representatives of sculptured temnopleurids (e.g., *Opechinus;* Duncan and Sladen 1884) appear in the Miocene and continue through to the present day. The earliest representatives with pits at plate sutures are also Upper Miocene (*Temnopleurus and Microcyphus;* see Lambert and Jeannet 1935; Mortensen 1943*a*, pp. 84, 150), while the earliest record of *Salmacis* is Pliocene (Currie 1930). Divergence of genera within the Temnopleurinae is therefore almost certainly post-Eocene—and probably post-Oligocene—whereas Trigonocidarinae represent a much older line and probably include part of the stem group for all Camarodonts.

Parechininae

Although many species have been assigned to the genus *Psammechinus,* there is no evidence that any of them are valid. Reasonably reliable records of *Paracentrotus* extend back into the Upper Miocene ("*Toxopneustes*" *bouryi* Cotteau [1883] from the Upper Miocene of France conforms closely to this genus, as noted by Mortensen

[1943*b*, p. 197]). Similarly, there is good evidence for *Psammechinus* from the Pliocene/Pleistocene of Britain and northwest Europe. All earlier records of this family must be treated as unproved, though small species that have trigeminate plate compounding and that are probably members of the Echinoida extend back to the Lutetian (Middle Eocene—i.e., "*Psammechinus*" *biarritzensis* [Cotteau]). No Cretaceous records can be confirmed.

Echininae

As with Parechininae, fossil representatives attributed to this genus are generally indeterminate. Mortensen (1943*b*, pp. 21–24) accepted valid records of *Echinus* only as far back as the Pliocene. "*Psammechinus*" *cailliaudi* Desor, described by Cotteau (1883) from the Upper Miocene of France, shows the characteristic development of primary ambulacral tubercles on every second plate only and is almost certainly a species of *Echinus*. The same is true of "*Rotulechinus*" *fischeri* (Cotteau) from the Pliocene of Rhodes. It seems likely, though impossible to prove without better-preserved material, that fossil species attributed to both *Stirechinus* and *Isechinus* from both the Miocene and Pliocene also belong here.

Strongylocentrotinae

The oldest record of *Strongylocentrotus* is *S. antiquus* Philip, from the Longfordian (=Aquitanian, Lower Miocene) of Australia (Philip 1965). The relationship of this species to extant species is not clear, but it has polygeminate plate compounding with five or six component plates at the ambitus but only four component plates adorally. On this criterion it would seem to be less specialized than any extant species. Isolated spines supposedly belonging to *S. purpuratus* have been recorded from the Late Miocene and Pliocene of western North America by Kew (1920) and Grant and Hertlein (1938); identifications based on spines alone are, however, extremely suspect. Tests from the Pliocene and Pleistocene of California are known (Kew 1920; Hertlein and Grant 1960). *Strongylocentrotus franciscanus* is known from the Middle and Upper Pliocene of California (see Kew 1920; Hertlein and Grant 1960), *S. pallidus* from the Pliocene of Holland (Geys and Marquet 1979), and *S. droebachiensis* from the Pliocene of Japan (Nisiyama 1966). Records of *S. droebachiensis* from the Pliocene/Pleistocene of northern Europe and Greenland are given by Mortensen (1943*b*, p. 214). *Allocentrotus* has been reported from the Pliocene of Japan (Nisiyama 1966).

Toxopneustinae

Species with deep buccal notches are known from the Middle and Upper Eocene, but there remains some doubt as to whether these species are really camarodonts. *Triplacidia* Bittner, from the Middle and Upper Eocene, was reported to have echinoid-style ambulacral compounding, but it appears to be more closely comparable to Paleogene species of the phymosomatoid *Thylechinus* which have equally extensive buccal notches (see Roman and Gorodiski 1959), and the two groups of species have often been confused. Similarly, the species "*Lytechinus*" *florianus* Cooke (1959) from the Late Eocene may be a camarodont, but its style of plate compounding has never been determined and there remains doubt as to whether it is a camarodont. *Scoliechinus axiologus* Clark from Jamaica (Arnold and Clark 1927) has echinoid-style compounding and deep buccal notches and clearly belongs to the Toxopneustidae. However, its geological horizon has never been determined, and although it is referred to as Cretaceous in age, it could easily come from the extensive Tertiary deposits of that island.

Philip (1965) attributed some fragments of test from the Oligocene of Australia to the Toxopneustidae, but the basis for this is tenuous.

The oldest undoubted records of Toxopneustidae come from the Late Oligocene Scotts Mills Formation of Oregon, where a species of *Lytechinus* (*Lytechinus pictus*?) has recently been discovered (R. A. Linder, personal communication) has also been reported, together with more dubious records of *?Lytechinus* species from both the Lower Miocene of California (H. L. Clark, in Grant and Hertlein 1938) and the Pliocene of California (Hertlein and Grant 1960). The earliest records of Toxopneustidae from Europe are Burdigalian (Lower Miocene) in age, when both *Schizechinus* and *Tripneustes* occur. *Schizechinus* has a rather generalized morphology, with simple trigeminate ambulacra and multiple primary tubercles on each interambulacral plate. *Schizechinus pentagonus* Kier comes from the Burdigalian of Saudi Arabia (Kier 1972), *S. ducei* Wright from the Tortonian of the Mediterranean, and *S. angularis* Pomel from the Pliocene of Algeria.

Tripneustes is easily recognized by its three discrete columns of ambulacral pores. *Tripneustes parkinsoni* Agassiz comes from the Burdigalian of southern France and the Mediterranean (Negretti 1984), and a similar species is also known from the Lower Miocene of the Caribbean (Podubiuk and Rose 1986). *Tripneustes gahardensis* Seunes (see Lambert 1906) comes from the Tortonian of Europe, and *T. californicus* Kew from the Pliocene of California (Kew 1920).

Other genera are known from more recent strata. Nisiyama (1966) records *Pseudocentrotus stenoporus* from an unspecified Miocene horizon in Japan. This has polygeminate ambulacra and sharply defined buccal notches. Mortensen (1943*a*, p. 525) also recorded *Sphaerechinus* from Pliocene deposits.

Echinometrinae

Archiac and Haime (1853, p. 207) described the species *Echinometra thomsoni* from the Upper Eocene of India. Examination of the holotype and only known specimen (BMNH E78562) shows that this is a slightly distorted test with phymosomatoid-style plate compounding. It is therefore a phymosomatoid, possibly *Porosoma,* and not a camarodont. The earliest valid record of an echinometrid is "*Echinometra*" *prisca* (Cotteau) from the Upper Oligocene of the Caribbean and Lower Miocene of the Caribbean (Podubiuk and Rose 1986). This species has an elliptical test, but, unlike extant *Echinometra* species, it has trigeminate plate compounding. Since in no specimen examined do there remain any apical disk plates by which to determine the orientation of the long axis, this species could be either a *Parasalenia* or a member of the common lineage of *Echinometra* and *Parasalenia. Parasalenia* itself has been recorded from the Aquitanian of France (Negretti 1984) and the Lower Miocene of Micronesia (Cooke 1957), though again without preserved apical disk plating. The oldest undoubted *Echinometra* with polyporous ambulacra is *E. miocenica* Loriol from the Lower Tortonian (Upper Miocene) of France (Loriol 1902). Further records of polyporous species of *Echinometra* come from the Late Miocene and Pliocene of Java, Ceram, Gulf of Suez, etc. (Lambert and Jeannet 1935).

Polyporous forms with more than eight component plates first appear in the Lower Miocene (Longfordian or Batesfordian) of Australia. Philip (1965) described *Heliocidaris ludbrookae* and *Zenocentrotus peregrinus* that were from here. The latter has large, massive spines and a doubling of pore pairs in each arc, both characteristic features of *Heterocentrotus.* There seems little doubt that these species are closely related to *Heterocentrotus* and possibly ancestral. *Heterocentrotus* is recorded from

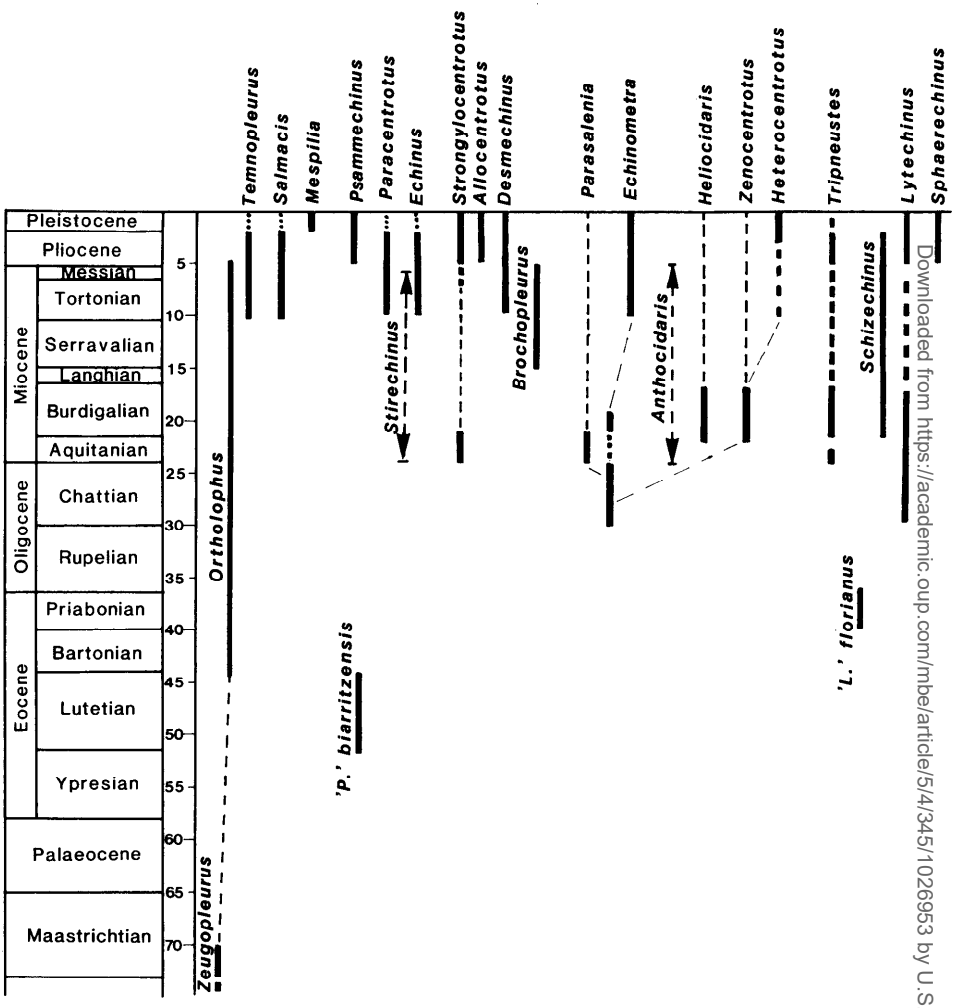

FIG. 2.—Known stratigraphical distribution of camarodont genera discussed in the text. The geological time scale is that of Snelling (1985).

the Pliocene and Pleistocene of the Indo-Pacific (Mortensen 1943*b*). Nisiyama (1966) reported a questionable specimen of *Anthocidaris* from the Miocene (horizon unspecified) of Saipan. Figure 2 summarizes the reliable stratigraphical distribution of camarodont genera.

Divergence Times

Combining the phylogenetic analysis with the known fossil record of camarodont echinoids provides at least some constraints on the latest time of divergence for certain groups. In this paper I have used the geological time scale of Snelling et al. (1985). The strongest evidence relates to members of the Echinometrinae. Echinometrinae were established by ~28 Mybp, which is when the earliest elliptical tested species are found. The divergence between *Echinometra* and *Parasalenia* appears to have taken place by approximately the start of the Miocene (~24 Mybp), and, in the absence of any evidence for elliptical or polyporous camarates in the Eocene, a reasonable lower

estimate of divergence time would be 35 Mybp (the Oligocene record of fossil regular echinoids is not good). Furthermore, the presence in the Lower Miocene of Australia of polygeminous species with more than 10 component elements—and the recognition of one of these species as having the biserial arrangement characteristic of *Heterocentrotus/Colobocentrotus/Zenocentrotus*—indicates that this clade had diverged by at least 17 Mybp. Because such highly characteristic test morphologies are unrecorded from the fossil record prior to this time, a reasonable earliest date of divergence might be ~25 Mybp.

The earliest record of a toxopneustid (*Lytechinus* from the Upper Oligocene of Oregon) coincides with the earliest record of an echinometrid ("*Echinometra*" *prisca* from the Upper Oligocene of the Caribbean) and places a latest limit of ~30 Mybp on the divergence time for these two families. Possible toxopneustids with deep peristomial notches have been reported from the Late Eocene, but these records need reexamining. A conservative earliest time of divergence might be ~40 Mybp, in the absence of definite Eocene representatives of either family. The record of *Tripneustes* in the basal Lower Miocene suggests that the latest date for divergence of this genus from *Lytechinus* and *Sphaerechinus* is ~24 Mybp. Divergence of polyporous toxopneustinae appears to be a relatively recent event, possibly from *Schizechinus* in the Late Miocene, since such forms have not been reported prior to the Pliocene.

As for other groups, the evidence is sparse. *Strongylocentrotus* can be traced back to the Lower Miocene. Recent species of *Strongylocentrotus* from before the Middle Pliocene are not known for certain; nor is *Allocentrotus*. The Lower Miocene species comes from Australia, whereas all extant species are found in the north Pacific or north Atlantic, suggesting that the group might have diverged after it extended its range into the North Pacific. Furthermore, the Lower Miocene species has a fairly general test morphology and is probably the primitive sister group to most, if not all, extant species. Divergence times for species within the genus *Strongylocentrotus* are therefore likely to lie within the range of 3.5–20 Mybp.

If *Stirechinus* is closely related to *Echinus,* as Mortensen believed, then the Echininae can be traced back to the mid Miocene (~15 Mybp). However, it has not proved possible to resolve the phylogenetic relationships of Echininae and Parechininae in this analysis. Echininae may have diverged from Parechininae relatively recently, after their common lineage had separated from the echinometrid line. This would imply a divergence time between ~15 Mybp and ~30 Mybp. Conversely, Echinidae may represent an independent line that diverged somewhat earlier as one of the first dichotomies after the divergence of Temnopleurina and Echinina (i.e., ~30–50 Mybp). The absence of any fossil forms definitely attributable to the Echininae prior to the Late Miocene makes the former inference more likely.

The constraints on Parechininae are no better. Many records of *Psammechinus* exist back to the Cretaceous, but none of these stand up to rigorous scrutiny, except possibly those from the Pliocene. The absence of records of polyporous parechinids prior to the Late Miocene suggests that the divergence of *Psammechinus* and *Paracentrotus* was probably a relatively recent event but certainly prior to 10 Mybp. Tentative limits to the timing of the divergence of these two species are 10–35 Mybp.

As generalized species of Echinina do appear to have been around from the Lutetian (Middle Eocene) onward, the divergence of Echinoid families from Temnopleurina presumably took place by at least 45 Mybp. There is no evidence for any member of the Echinina being older than Middle Eocene; thus, a conservative earlier

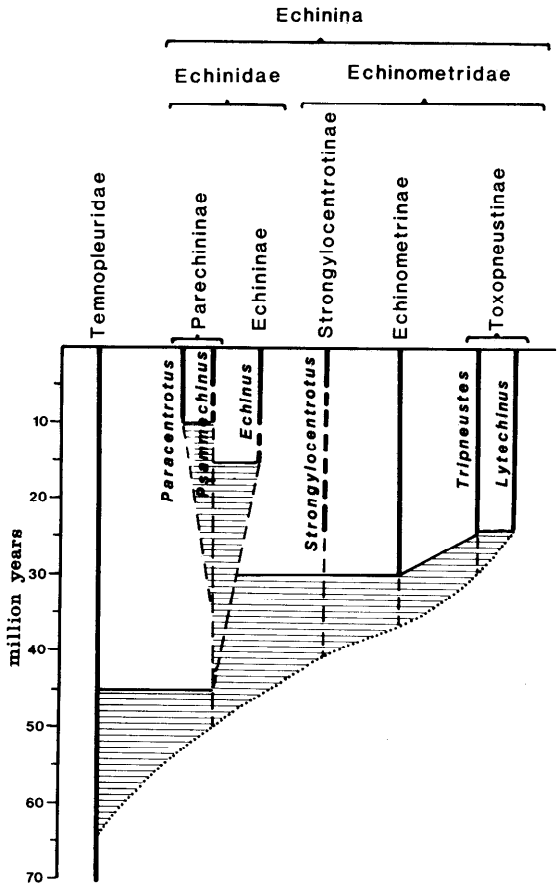

FIG. 3.—Best estimate of divergence dates for camarodont echinoid groups when data from the phylogenetic analysis and known stratigraphical ranges are combined. Shaded area indicates the possible range of error.

date of divergence could be taken to be 65 Mybp (the end of the Cretaceous), and a more realistic estimate could be taken to be 55 Mybp.

The subfamilies Parechininae and Strongylocentrotinae must have diverged at some time between the divergence of Echinina from Temnopleurina but before the divergence of Echinometrinae and Toxopneustinae. In effect this suggests a divergence time that is between, say, 55 Mybp and 35 Mybp. Figure 3 summarizes the times of divergence for higher taxa of Camarodonta.

Rates of Molecular Evolution

Divergence times for the camarodont families given above differ markedly from those used previously by molecular biologists. In particular, there seems to be no justification for extending any family, save the paraphyletic Temnopleuridae, back into the Cretaceous. Estimates for the divergence of *Strongylocentrotus* and *Lytechinus* at 180 Mybp (Durham 1966) are wrong, and a more realistic estimate is 30–40 Mybp. Both Angerer et al. (1976) and Hall et al. (1980) commented on the fact that a small but significant percentage of high-stability thermal duplexes formed between *Strongylocentrotus purpuratus* and *Lytechinus pictus* "in spite of the great separation between

Table 2
Rates of Molecular Evolution as Estimated from Reduced Thermal Stability of Heterologous Single-Copy DNA Duplexes

	ΔT_m (°C)	Median T Divergence	Divergence (Ma)	Median T/2Ma
Strongylocentrotus purpuratus/S. droebachiensis	6.8	7.7 (7)	3.5–20	0.19–1.1
S. purpuratus/S. franciscanus	13.2	21 (19)	3.5–20	0.53–3.0
S. purpuratus/Lytechinus pictus	8.5	51 (46)	30–40	0.64–0.85

SOURCE.—Hall et al. 1980.
NOTE.—The technique involved 2.4 M tetraethylammonium chloride solvent and digestion with S1 nuclease at low criterion (55 C). *S. purpuratus* was used as tracer. Figures in parentheses in the "Median T Divergence" column = average as based on hydroxyapatite and S1 assay combined (see Hall et al. 1980, p. 109).

these species" (Hall et al. 1980, p. 107) and found the similarity of their single-copy DNA sequences highly perplexing. Johnson et al. (1983, p. 1832) were also surprised by the similarity of actin gene structure in *Lytechinus* and *Strongylocentrotus,* postulating that "some process-(es) in addition to natural selection at the protein level may be acting to stabilize the DNA sequences of actin genes in sea urchin species."

Although the small amount of highly conserved genome shared between *Strongylocentrotus* and *Lytechinus* is still puzzling, there is now closer agreement between molecular rates of evolution calculated from different pairs of echinoid species. The estimated range of the rate of molecular substitution based on T_m's for single-copy DNA of *Strongylocentrotus/Lytechinus* lies within the range of estimates based on T_m's between species of *Strongylocentrotus.* Table 2 gives the relative thermal stabilities of interspecific heteroduplexes, as measured by Hall et al. (1980).

Times of divergence for species within *Strongylocentrotus* cannot be gauged from the fossil record. However, we know that *S. purpuratus, S. droebachiensis,* and *S. franciscanus* were all established within the Pliocene (2–5 Mybp), so that the latest divergence date for any pair is ~3.5 Mybp (the middle of the Pliocene). Similarly, it seems unlikely that divergence could have taken place much before 20 Mybp. To estimate the possible range for the rate of molecular evolution, one can assume that the most closely related pair (*S. purpuratus/S. droebachiensis*) could not have diverged later than 3.5 Mybp and that the most distantly related pair probably diverged subsequent to 20 Mybp. This assumption is supported by the observations of Kier (in Roberts et al. 1985), which showed that *S. purpuratus* and *S. droebachiensis* share a number of morphological traits that suggest they are more closely related to one another than either is to *S. franciscanus.* This gives an estimate of ΔT_{med}, as calculated by Hall et al. (1980), of 0.53–1.1 degrees C/Myr. By comparison, taking the divergence of *Lytechinus* and *Strongylocentrotus* as being 30–40 Mybp gives an estimated ΔT_{med} of 0.64–0.85 degrees C/Myr. Thus rates of molecular change estimated from *Lytechinus/Strongylocentrotus* data lie within the range estimated from interspecific differences within *Strongylocentrotus.* Because the divergence date of *Lytechinus/Strongylocentrotus* is rather better constrained than species divergences within *Strongylocentrotus,* the former may give a more accurate measure of the rate of molecular change. However, the smaller amount of DNA hybridization between *Lytechinus* and *Strongylocentrotus* makes estimates of ΔT_{med} somewhat less reliable, and this may have a counterbalancing effect.

These results imply that thermal stability measurements of single-copy DNA

Table 3
Rate of Molecular Evolution as Based on Sequence Data of H3 and H4 Histone Genes

	1	2	3	4	5
Psammechinus miliaris/Paracentrotus lividus	46	7.2	10–35	0.66–2.3	0.10–0.36
Psammechinus miliaris/ Strongylocentrotus purpuratus	70	11.2	35–50	0.7–1.0	0.11–0.16
Psammechinus miliaris/ Strongylocentrotus droebachiensis	70	11.1	35–50	0.7–1.0	0.11–0.16
Psammechinus miliaris/Lytechinus pictus	78	12.5	35–50	0.78–1.1	0.12–0.18
S. purpuratus/S. droebachiensis	6	1.0	3.5–20	0.15–0.86	0.03–0.14

SOURCE.—Busslinger et al. 1982.

NOTE.—Column 1 = % divergence for substitutable bases in silent sites corrected for multiple substitutions; column 2 = observed % divergence at all sites; column 3 = times of divergence (maximum and minimum); column 4 = rate of divergence at silent sites; and column 5 = rate of divergence at all sites.

duplexes are consistent in establishing phylogenetic relationships at least as far back as 40 Mybp and that the rate of change is in the range 0.65–0.85 degrees C median divergence/Myr.

Another approach to estimating rates of molecular substitution is to compare sequence data for homologous stretches of DNA and calculate percentage differences. Busslinger et al. (1982) did this using sequences within the histone genes H3 and H4 of *Strongylocentrotus, Psammechinus,* and *Lytechinus* (table 3). These authors calculated the range for rate of interspecific silent substitutions as being 0.22%–0.92%/Myr. Using the divergence dates estimated here gives a range of substitution rates of 0.70%–1.0%/Myr (*Psammechinus/Strongylocentrotus*), 0.78%–1.1%/Myr (*Psammechinus/Lytechinus*), 0.15%–0.86%/Myr (*S. purpuratus/S. drobachiensis*), and 0.66%–2.3%/Myr (*Psammechinus/Paracentrotus;* divergence poorly constrained). Although the range of individual rates is greater when taken together, because of the uncertainty of dating divergence times, all four estimates overlap. This overlap defines a range—0.78%–0.86% base changes in the silent position/Myr—for the rate of nucleotide substitution that is mutually consistent with all the data.

Busslinger et al. (1982) also give figures for observed percentage differences at all sites (table 3). When calibrated against divergence times, these give a rate of overall change of 0.11%–0.16%/Myr for *Psammechinus/Strongylocentrotus,* 0.12%–0.18%/Myr for *Psammechinus/Lytechinus,* 0.10%–0.36%/Myr for *Psammechinus/Paracentrotus,* and 0.03%–0.14%/Myr for *S. purpuratus/S. droebachiensis.* Again all four estimates overlap and define a mutually consistent rate of 0.12%–0.14% base changes/Myr.

Since most single-copy DNA sequences do not code for protein and are not subject to selection pressure, their rate of molecular divergence should approximate the rate of silent substitution within gene-coding regions of the genome. The correlation between reduction in thermal melting temperature of single-copy DNA and nucleotide mismatch is ~1 degree C = 1% mismatch (Hall et al. 1980). It is thus reassuring to find that estimates of rates of silent substitution in the camarodont histone gene (~0.78%–0.86%/Myr) and median reduction temperatures of heteroduplexes (~0.65–0.85 degrees C/Myr) are in good agreement.

In conclusion, rates of molecular evolution in camarodont sea urchins are con-

sistent when measured between different pairs of taxa, and previous major anomalies are the product of mistaken assumptions about divergence times taken from the fossil record. Morphological and paleontological data provided here on divergence times are still too poorly constrained to demonstrate that molecular rates of evolution conform to a stochastically constant rate, but they are wholly consistent with such a model.

Acknowledgments

I should like to thank Dr. Howy Jacobs both for providing the stimulus for this work to establish tighter constraints on divergence times within regular echinoid groups and for helping with the literature. I am most grateful to Professor Roy Britten and Dr. Howy Jacobs for their helpful suggestions and constructive criticism of an earlier draft of this paper.

APPENDIX

The Morphological Characters and Their Polarity

The characters used as putative homologies in the cladistic analysis (fig. 1) are discussed individually below.

A. Test Features

1. Test Shape

Whereas most camarodont genera have tests that are circular in outline, a few have tests that are elliptical in outline. The long axis of the test is not identical: in *Parasalenia* it runs through the III-5 axis (ambulacrum III–interambulacrum 5), in *Echinometra* through the I-3 axis, and in *Heterocentrotus* and *Colobocentrotus* through the II-4 axis. However, some variation of axis orientation exists within populations (Mortensen 1943*b*). These alternative states were scored separately and entered as unordered, but the PAUP program suggests that the tendency toward an elliptical test outline might be a homologous feature. If this were so, then the circular test of *Anthocidaris* may be interpreted as a reversal. Polarity was set by outgroup comparison with other regular echinoid groups (character 16 in fig. 1).

2. Primary Tubercles

These may be crenulate or noncrenulate; and those that are crenulate may be strongly so or may have only feebly developed crenulation. The possession of crenulate tubercles was treated as the primitive condition by outgroup comparison with Glyphocyphidae, the fossil stem group of Camarodonta. Genera were scored as either strongly crenulate, feebly crenulate, or noncrenulate, and the two derived states were treated as an ordered transformation series (character 3 in fig. 1).

3. Buccal Notches

The buccal notches (sometimes referred to as gill slits) found around the margin of the peristome mark the position of expansion sacs to the peripharyngeal coelom. In most camarodonts these notches are small and insignificant, penetrating to a depth no greater than the first ambulacral compound plate. However, in certain genera the buccal notches are deep and sharply defined, penetrating to a depth level with the third or fourth compound ambulacral plate, or sometimes further. This is considered to be the derived condition by outgroup comparison with other regular echinoids (character 13 in fig. 1).

4. Apical Disk

The position of the periproct within the apical disk varies between genera of camarodont. Those whose periproct lies centrally within the apical disk have a dicyclic arrangement of plates, and all oculars are exsert. In some genera the periproct is displaced toward the rear of the apical disk, and one or more oculars become insert. Genera were therefore scored as having either dicyclic apical disk plating or ocular plates I and V insert. The latter state was treated as derived by outgroup comparison with *Temnopleurus* and on grounds of development. However, *Zeugopleurus,* an advanced member of the camarodont stem-group lineage, has oculars I and V insert. The polarity of this character must therefore remain doubtful, though the PAUP analysis did not reverse the polarity decision made here (character 10 in fig. 1).

5. Pits at Plate Sutures

The presence of deep sutural pits between coronal plates was treated as a derived condition by outgroup comparison with other groups of regular echinoid (character 20 in fig. 1).

6. Naked Interradial and Perradial Zones

In a few genera there is a characteristic naked, tubercle-free zone adapically along the interradius and perradius. This is treated as derived by comparison with *Temnopleurus* and glyphocyphids (character 4 in fig. 1).

B. Ambulacral Features

1. Plate Compounding

All camarodonts have compound plates that are formed in the echinoid style (terminology follows Jensen 1981), but the number of individual plates incorporated into each compound plate varies. Most genera have just three components to each compound plate (trigeminous compounding), and this is treated as primitive by outgroup comparison with the stem group Glyphocyphidae and other primitive regular echinaceans (see Smith 1984, p. 33). A number of genera have developed polyporous compounding, in which more than three components are incorporated into one compound plate. Usually there are some four to six components in each compound plate, but in a few, including some species of *Strongylocentrotus,* there are 8–15 components. Genera were scored as having either trigeminous (primitive) or polygeminous ambulacral compounding, and polygeminate forms were further divided into those with four to six component plates and those with eight or more. These were treated as separate characters (characters 17 and 18 in fig. 1).

2. Arrangement of Pores

Certain arrangements of the ambulacral pores are highly distinctive and provide potentially useful characters. Most genera have a uniserial or arced arrangement of ambulacral pores, but, in some cases, multiserial arrangements are found. Thus, in *Tripneustes, Toxopneustes,* and *Amblypneustes* ambulacral pores are arranged into three quite discrete vertical rows. In *Mespilia, Microcyphus, Heterocentrotus,* and *Colobocentrotus* ambulacral pores are arranged into two discrete vertical series. Both of these conditions are treated as derived by outgroup comparison with *Temnopleurus,* Glyphocyphidae, and other regular echinoid groups (character 15 in fig. 1).

3. Ambulacral Tuberculation

Whereas most camarodonts have a primary tubercle developed on each compound ambulacral plate, a few do not. In these genera only every second or third trigeminous ambulacral plate bears a primary tubercle. This is treated as a derived state, by outgroup

comparison with *Temnopleurus,* Glyphocyphidae, and other regular echinoid groups (character 14 in fig. 1).

C. Structure of the Globiferous Pedicellariae

1. Number of Lateral Teeth on the Blade

On either side of the needle-like point of each valve there may be developed small, subsidiary teeth. These may be paired, with one or a number of such teeth developed on each side; or there may be a single asymmetrical tooth on one side alone; or such teeth may be lacking altogether. These three alternatives were scored and entered unordered. By outgroup comparison with the globiferous pedicellariae of other groups of regular echinaceans, it seems probable that the presence of paired lateral teeth is primitive, and this is the polarity produced by PAUP (character 7 in fig. 1).

2. Blade an Open or Fused Structure

The blade of globiferous pedicellariae above the base is usually a slender, compact cylindrical structure leading to the distal point. However, in some genera (*Psammechinus* and *Paracentrotus*) the blade has a more open, reticulate structure and is broader (see Mortensen 1943*b,* p. 7). The broad, open blade was treated as primitive in the analysis on account of its closer similarity to the structure of the valves of other kinds of pedicellariae, but the results of the PAUP analysis suggest that the broad, open valve is either a reversal or a derived state (character 1 in fig. 1).

3. Stalk

The calcite stalks of globiferous pedicellariae differ in their structure. In all Temnopleuridae the stalks are composed of a bundle of calcite rods or fibers, united only at their distal and proximal ends. This is treated as the primitive condition. In other groups the stalk may consist of either a solid meshwork of calcite or a hollow, tubular rod. These were scored separately and entered as unordered (character 9 in fig. 1).

4. Muscular Neck

Most camarodont genera have globiferous pedicellariae that lack a neck. *Strongylocentrotus,* however, has a muscular neck to its globiferous pedicellariae, and this is treated as a derived state by outgroup comparison with Temnopleuridae (character 19 in fig. 1).

5. Poison Glands

Globiferous pedicellariae have either a single or a double poison gland to each valve. A single gland per valve was treated as derived by outgroup comparison with the Temnopleuridae (character 5 in fig. 1).

6. Mucous Glands

Some genera have mucous stalk glands prominently developed, whereas others lack these glands or have them incorporated into the valves. The presence of stalk glands is treated as the derived state by outgroup comparison with Temnopleuridae, and their absence in *Echinometra* is interpreted as a secondary reversal (character 12 in fig. 1).

D. Tooth Ultrastructure

1. Shape

The shape of primary tooth plates can be expressed by the ratio of the distance between the umbo and the lateral edge of the central section to the distance from the

umbo to the oral edge (see Jensen 1981). This ratio varies from ~0.5 for species of Temnopleuridae to 0.8–1.2 for Echininae, Parechininae, and Echinometrinae to 1.3–1.5 for Toxopneustinae. The condition seen in Temnopleuridae was treated as primitive, and genera were scored as having this ratio as <0.7 (primitive), 0.8–1.2, or ≥1.3. This was entered as an ordered character transformation series (character 2 in fig. 1).

2. CLNP System

The CLNP system comprises a series of calcite needles and prisms developed between primary tooth plates and whose arrangement varies between genera. Jensen (1979, 1981) demonstrated the usefulness of this character for taxonomy but made no attempt to group the different types of CLNP system hierarchically. Here two distinctions are made:

1. The CLNP system is composed of oblique lamellae only along the oral part of the tooth, or the oblique lamellae are branched and develop forks or tines at right angles to the plate edge. In both cases flabelliform elements are usually developed away from the oral edge. The presence of oblique lamellae only is primitive by outgroup comparison with other regular echinoid groups (stirodonts, diadematoids, and cidaroids) that have this arrangement only (see Jensen 1981) (character 6 in fig. 1).

2. The branched oral ends of the CLNP system may be irregular or may be arranged into a highly organized comblike structure (tines). The presence of the comblike tines is treated as the derived state, as it is the more complex arrangement (character 8 in fig. 1).

E. Larval Features

The pluteus larvae of camarodonts have a series of skeletal rods that support their arms. These rods may be unconnected at their bases or may be interconnected so as to form a basket-like structure (see Mortensen 1943*a*, p. 389). The presence of a basket-like pluteus skeleton is taken to be derived, as this arrangement is unknown in any other group of echinoids (character 11 in the analysis).

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