Character Analysis and the Integration of Molecular and Morphological Data in an Understanding of Sand Dollar Phylogeny

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Reconciling discordant morphological and molecular phylogenies remains a problem in modern systematics. By examining conflicting DNA-hybridization and morphological phylogenies of sand dollars, I show that morphological criteria may be used to help evaluate the reliability of molecular phylogenies where they differ from morphological trees. All available criteria for assessing the reliability of DNA-hybridization phylogenies suggest that the sand dollar DNA-hybridization phylogeny is robust. Standard homology-recognition criteria are used to assess the a priori reliabilities of the morphological attributes associated with the node drawn into question by the DNA data, and it is shown that these attributes are among the least phylogenetically informative of all the morphological characters. Moreover, the questioned node has the smallest number of supporting characters, and most of these characters are associated with the food grooves, which suggests that they may be functionally correlated. Thus, on the basis of the analysis of the morphological data and given the robustness of the DNA tree, the DNA phylogeny is preferred.

Further, paleobiogeographic data support the DNA tree rather than the morphological tree, and a plausible heterochronic mechanism has been proposed that may account for the homoplasious morphological evolution that must have occurred if the DNA tree is correct.

Introduction

How to integrate molecular and morphological data most effectively is one of the challenges of contemporary phylogenetics. Molecular and morphological phylogenies frequently exhibit broadly similar topologies, with disagreements restricted to the position of a few taxa. In these cases the reliability or robustness of both phylogenies is assessed (e.g., by bootstrapping), and the tree with the greatest support is favored. In some cases the molecular and morphological characters are combined in a single analysis (e.g., see de Sá and Hillis 1990), and the most parsimonious tree for the combined data, if statistically robust, is accepted.

Here I use an alternative approach to integrating discordant molecular and morphological phylogenies. The approach is based on the fact that characters established in morphological analyses represent testable hypotheses of relationship (Bryant 1989). Criteria exist for evaluating the relative informativeness or reliability of characters prior to their use in building evolutionary trees (Remane 1952), and it is the use of these criteria to establish the relative reliabilities of the characters drawn into question

1. Key words: character analysis, DNA hybridization, sand dollar phylogeny, homology recognition criteria, paleobiogeography, heterochrony.

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by molecular data that offers the possibility of using morphological data to help evaluate the robustness of molecular phylogenies. These homology-recognition criteria are traditionally used to establish phylogenetically informative characters in the initial stages of morphological analyses, and the process of applying the criteria is termed “character analysis” by some (e.g., Bryant 1989; Sluys 1989). As an example of the application of the second of the three major recognition criteria of Remane (1952) (“similarity between structures based on the correspondence between numerous separate features of these structures”; Sluys 1989, p. 353), architecturally very simple characters are more likely to reflect undetected homoplasies than are characters with highly intricate and complex architectures. Riedl (1978, pp. 34–36), Wiley (1981, pp. 130–131), and Sluys (1989) provide discussions of Remane’s (1952) criteria for recognizing homologies.

Marshall and Swift (accepted) provide a DNA-hybridization phylogeny of sand dollars that differs from phylogenies derived from morphological traits. Here I use the general principles of character analysis to establish a priori relative weights for the morphological characters. These weights are then used to assess the extent to which the morphological data are contradicted by the DNA phylogeny. It is shown that, while the DNA-hybridization phylogeny is essentially unanticipated by the morphological data, relatively few characters—and only those with relatively high a priori likelihoods of being undetected homoplasies—are drawn into question by the DNA phylogeny. Further morphological and paleobiogeographic data are presented that support the DNA tree where it differs from the morphological cladogram.

Sand dollars were selected for the present study because of their relatively complex morphology and excellent fossil record (Marshall 1988). An analysis of the fossil record of the group is being prepared which assesses the absolute rates of single-copy DNA evolution in the group and employs the methods outlined by Marshall (1990a, 1990b) to estimate both upper and lower bounds on the divergence times of the species studied.

**DNA-Hybridization Phylogeny**

Marshall and Swift (accepted) provide a DNA-hybridization phylogeny (fig. 1A) of four scutelline sand dollars, *Dendraster excentricus* (Eschscholtz), *Echinarchnus*...
parma (Lamarck), and the two mellitids *Leodia sexiesperforata* (Leske) and *Mellita tenuis* Harold and Telford. A sea biscuit, *Clypeaster rosaceus* (Linne), was used as an outgroup. Table 1 shows the averaged $\Delta T_m$ and $1/n$ (normalized % hybridization (NPH)) (used as an approximation for $\Delta T_m R$; see Marshall and Swift, accepted) values.

Reliability of the DNA-Hybridization Phylogeny

Three data sets [$\Delta T_m$ (both corrected for multiple hits and not corrected for multiple hits) and $1/n$NPH] were analyzed both with and without averaging reciprocal distances, both with and without the assumption of a molecular clock, and with the algorithms of Cavalli-Sforza and Edwards (1967) and Fitch and Margoliash (1967). The topology shown in figure 1A was obtained in all these analyses, as well as when the data were jackknifed (Marshall and Swift, accepted); it would appear that the phylogenetic signal is unambiguous. As a further test of the robustness of the phylogeny, a bootstrapping technique [of Krajewski and Dickerman (1990), as modified by Marshall (1991)] was applied. The tree found in the analyses described above (fig. 1A) was obtained in 94% ($\Delta T_m$, corrected for back mutations) and 86% ($1/n$PH) of the 500 pseudoreplicates performed for each set of data. The conflicting morphological tree (fig. 1B) was not found among any of the pseudoreplicate trees for the $1/n$PH data set and was found in just 1% of the $\Delta T_m$ pseudoreplicate trees (Marshall and Swift, accepted). The nonparametric Mann-Whitney $U$ test does not provide a reliable indication of the robustness of phylogenies derived from distance data (Marshall 1991) and was not used. Before the DNA data are considered further, two common misconceptions regarding the mode of analysis and nature of DNA hybridization data must be considered.

The Molecular Clock

It was initially thought that DNA-hybridization data had to exhibit clocklike behavior before they could be used to estimate phylogenies (e.g., see Sibley and Ahlquist 1981; Brownell 1983; Houde 1987a, 1987b; Marshall 1988). However, the assumption of a molecular clock is not required to retrieve phylogenetic information from distance data (see, especially, Springer and Krajewski 1989a; also see Sheldon 1987), and, in unusual cases, computing trees under the assumption of a molecular clock may actually lead to incorrect topologies (fig. 2).

The ability of distance algorithms to retrieve correct topologies is largely dependent

<table>
<thead>
<tr>
<th></th>
<th>Dendraster excentricus</th>
<th>Echinorachnius parma</th>
<th>Leodia sexiesperforata</th>
<th>Mellita tenuis</th>
<th>Clypeaster rosaceus</th>
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<tr>
<td>D. excentricus</td>
<td>14.7 ± 1.3</td>
<td>20.7 ± 1.0</td>
<td>20.1 ± 1.5</td>
<td>23.0 ± 2.1</td>
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<td>E. parma</td>
<td>0.029 ± 0.003</td>
<td>17.7 ± 2.0</td>
<td>16.2 ± 0.9</td>
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<td>L. sexiesperforata</td>
<td>0.072 ± 0.010</td>
<td>0.059 ± 0.004</td>
<td>13.7 ± 1.6</td>
<td>23.5 ± 1.2</td>
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<td>M. tenuis</td>
<td>0.061 ± 0.050</td>
<td>0.046 ± 0.002</td>
<td>0.022 ± 0.001</td>
<td>22.6 ± 1.5</td>
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<tr>
<td>C. rosaceus</td>
<td>0.150 ± 0.030</td>
<td>0.147 ± 0.006</td>
<td>0.166 ± 0.008</td>
<td>0.151 ± 0.006</td>
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**NOTE.—** Mean ± standard deviations, based on four determinations, are given for $\Delta T_m$ (in °C; above diagonal) and for $1/n$ (normalized % hybridization) values (below diagonal). The $\Delta T_m$ values have been corrected for multiple hits by using the formula of Jukes and Cantor (1969) and assuming that 1°C = 1% mismatch.

**SOURCE.—** Marshall and Swift (accepted).
FIG. 2.—Data showing that assumption of molecular clock is not required to recover correct topologies by using distance data. The data matrix was derived from the “correct” topology shown in i). i), Analysis with algorithm that does not assume molecular clock (FITCH program in PHYLIP 3.2; Felsenstein 1989) but recovers “correct” topology from data matrix. ii), Analysis under assumption that molecular clock (KITSCH in PHYLIP 3.2; branch tips are contemporaneous) does not recover correct topology from data matrix. In this hypothetical example, taxon A has been designated as the outgroup.

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on the distances being additive (Bledsoe and Sheldon 1989; Springer and Krajewski 1989a). Nonadditivity may result from measurement error and homoplasy (Springer and Krajewski 1989b; Bledsoe and Sheldon 1990), and while nonadditivity is more likely to result when rates of DNA sequence divergence are highly variable, rate variability per se does not negate the value of distance data.

Sympleisomorphies and DNA-Hybridization Distances

DNA-hybridization distances are a measure of the degree of mismatch between homologous strands of DNA. The word “distances” may raise the specter of “phenetics” for some, and it might be concluded that the phylogenetic value of DNA hybridization data is compromised because of the inclusion of shared primitive characters (sympleisomorphies) in computed distances. However, only substitutions that occurred after species have become separate contribute to interspecies distances measured by DNA-hybridization techniques. Sympleisomorphies do not result in mismatches and therefore do not contribute to interspecies distances (Sibley et al. 1987; Sarich et al. 1989; Bledsoe and Sheldon 1990).

Strengths and Weaknesses of DNA Hybridization

DNA hybridization is thought to be a reliable source of phylogenetic information, in part because of the enormous amount of information assayed. A $\Delta T_m$ of 1°C between two species is roughly equivalent to a 1% difference in their single-copy DNAs (Werman et al. 1990), or about 5,000,000 bp differences for sand dollars. Thus each internode distance in the DNA-hybridization phylogeny corresponds to a sequence divergence of $\sim 10^8$ point mutations. Even if single genomic “events” cause the simultaneous appearance of thousands of point mutations, a $\Delta T_m$ of even a few degrees (as is the case in the sand dollar phylogeny) would still correspond to differences in base sequence that were the result of thousands or tens of thousands of such events.

Further support for DNA hybridization comes from the empirical observation that DNA-hybridization phylogenies usually correspond well with other phylogenetic analyses [e.g., for birds, see Krajewski (1989) and Diamond (1990) for a perspective
on Sibley and Ahlquist's work; for hominoids, see Sibley and Ahlquist (1984) and
Caccone and Powell (1989); for cave crickets, see Caccone and Powell (1987); for
bears, see O'Brien et al. (1985); and for marsupials, see Springer et al. (1990). Dif-
fferences usually occur only where there has already been dispute in the morphological
literature (as is true for Echinarchninius and Dendraster). In birds, where most DNA-
hybridization data have been collected, not only do DNA-hybridization phylogenies
that differ from traditional phylogenies usually find some morphological support, but,
in some cases, they help clarify previously misunderstood biogeographic problems
(Diamond 1983).

However, a frustration with DNA-hybridization data is that it is effectively im-
possible to determine the exact nature of the mismatches that contribute to the mea-
sured interspecies distances. Thus it is difficult to critically examine the data to de-
termine whether any systematic biases or unanticipated properties of the DNA
renaturation kinetics exist to warrant rejection of the data as a source of reliable
phylogenetic information. This does not invalidate the use of DNA-hybridization
data, but it does suggest caution in interpreting the results gained from such exper-
iments.

In addition, our inability to determine the exact nature of the mismatches that
lead to DNA-hybridization distances means that DNA-hybridization data cannot easily
be combined with data derived from other sources, should such a combined analysis
be desired. However, this may not be a serious disadvantage, since combining molecular
and morphological data sets in a single analysis seems limited for two reasons; first,
as molecular data sets become increasingly large, they are likely to numerically swamp
the contribution of morphological characters. Second, and more important, combining
molecular and morphological data sets in a single analysis negates the major advantage
of utilizing independent data sets in evolutionary studies; by keeping the data separate,
hypotheses concerning the nature of morphological evolution can be carried out without
the circularity that accompanies testing hypotheses concerning morphological evolution
with morphologically derived phylogenies (Olmstead 1989), and vice versa. Given
both the robustness of the DNA-hybridization phylogeny vis-à-vis alternative methods
of analysis and the expectation, given our current knowledge of the nature of single-
copy DNA evolution, that DNA-hybridization data are phylogenetically informative,
the DNA phylogeny of sand dollars (fig. 1A) deserves serious consideration.

The Morphological Phylogenies

Most morphological clypeasteroid phylogenies (Seilacher 1979; Jensen 1981;
Smith 1984, p. 191; Mooi 1987) differ from the phylogeny derived from the DNA-
hybridization data (Marshall and Swift, accepted); in these morphological phylogenies,
Echinarchninius is the sister group of the other three sand dollars (fig. 1B), while in
the DNA-hybridization phylogeny it is the sister group of Dendraster alone (fig. 1A).
Of the morphological studies, only Durham's (1955, 1966) analysis gives results that
are the same as those given by the molecular phylogeny. However, no explicit criteria
were given by Durham (1955, 1966) in support of his evolutionary tree, and it is
difficult to evaluate the strength of his scheme in light of the other analyses, and his
phylogeny will be considered no further. Note that while Seilacher (1979), Jensen
(1981), Smith (1984, p. 191), and Mooi (1987) all agree over the branching pattern
of the four genera depicted in figure 1B, they differ from each other, often considerably,
with respect to the placement of other clypeasteroid taxa.

The most complete morphological analysis of the clypeasteroids is the thorough
study by Mooi (1987), and the discussion of the quality of the morphological data is primarily based on his cladistic analysis. The relevant characters used by Seilacher (1979) and Jensen (1981) are discussed subsequently. A. B. Smith's (personal communication) characters are encompassed by those of Seilacher (1979) and Mooi (1987).

**Quantity of Characters Contradicted**

Figure 1B shows the number of synapomorphies that support each node in Mooi's (1987, 1990) phylogenetic analysis of the clypeasteroids relevant to the present study. If the DNA-hybridization phylogeny is correct, then it is the characters that support the node indicated by the dot (●) that must have evolved homoplasiously. This is the least-supported node in figure 1B, with just four characters, compared with the 8, 19, and 14 characters that support the other nodes. Acceptance of the DNA-hybridization data does not require any modification in our interpretation of the bulk of the morphological characters. In the currency of numbers of characters, the node drawn into question by the DNA data is exactly the node where the morphological data are weakest.

**Quality of Characters Contradicted**

Despite the way characters appear in data matrices, not all characters are equally informative; that is, some characters, by virtue of either their relative complexity or their limited intraspecific variability, are more likely to represent true homologues than are others. The notion of character quality is difficult to quantify, yet it is relatively easy to demonstrate. Below I examine two highly informative characters. The first supports the monophyly of the four sand dollars, and the second supports the monophyly of *Mellita* and *Leodia*.

1. Lantern supports. In the outgroup *Clypeaster* (and all other Clypeastererines) the lantern supports are paired structures that attach to the ambulacral basicoronal plates (fig. 3Ai), while in the four scutellines (and in laganines and all other scutellines) the lantern supports are single elements that attach to the interambulacral basicoronaals (fig. 3Aii). This is a relatively complex character, involving not only the structure of the lantern supports themselves but also their position with respect to the underlying plates that make up the test.

2. Architecture of lunules. Lunules have evolved several times in sand dollars, in the rotulids, and in scutasterids, perhaps twice in the astriclypeids, and twice in the mellitids and nearest outgroups (Seilacher 1979). Figure 3B shows the position and architecture of the lunules in an astriclypeid and *Mellita*. Both have lunules in the posterior ambulacrals, but they are constructed differently in each species. Note that if one was unaware of the difference in the construction of these lunules, the presence of the lunules could be scored (mistakenly) as a synapomorphy between the two groups.

Unlike the characters described above, the characters drawn into question by the DNA phylogeny generally have less architectural complexity and little or no specific positional relations with respect to other morphological features and are thus, on a priori grounds, more likely to be unidentified homoplasies than characters such as those described above. If the DNA-hybridization phylogeny is correct, then these characters are homoplasies and must have been either gained in parallel in *Dendraster* and the mellitids or gained once in a common ancestor of *Dendraster, Echinarchnium,*
Complex characters

A

i

ii

B

i

ii

Simpler characters

C

i

ii

D

i

ii

E

i

ii

iii

Leodia, and Mellita and subsequently lost in Echinarchnius. The first four characters discussed are based on the original descriptions by Mooi (1987).

1. Sacs on miliary spine tips. In Clypeaster the tips of the miliary spines are covered with a thin layer of epithelium. In Echinarchnius (fig. 3Ci) there is a thickening of this epithelial layer. In Dendraster (fig. 3Cii) and the mellitids the basement membrane of the epithelium has become separated from the spine tip and has become inflated with fluid. This character is simple compared with the two characters described
above; there are no subtleties of topological position and only a little detailed architecture (associated with the distribution of collagen fibers that support the sac). Moreover, fluid-filled sacs are occasionally seen on the regular sea urchin *Lytechinus* (G. A. Wray, personal communication). The reliability of a character is decreased when the intraspecific variability begins to approach interspecies variability, and thus, even though *Lytechinus* is phylogenetically far removed from the sand dollars, the occasional presence of fluid-filled sacs in *Lytechinus* adds some strength to the possibility of independent acquisition of the character within the sand dollars. Secondary loss is also a possibility, which of course would leave very little trace (or is the thickened epithelial layer the remnant of the sac?). Other than its simple presence, there is little information available to make a strong case for a single origin of the character.  

2. Lengths of barrel-tipped podia. In *Clypeaster* and *Echinarachnius* the barrel-tipped podia are present in one length. In *Dendraster* and the mellitids there are both long and short barrel-tipped podia. As is the previous character, this is a simple character; there is neither positional information nor architectural detail that could be used to detect parallel or convergent evolution in this character, had it actually arisen homoplasiously.  

3. Geniculate spines. In *Dendraster* and the mellitids geniculate (bent) spines are found in fields associated with the food grooves, while in the outgroup *Clypeaster* and in *Echinarachnius* the spines are not bent (fig. 3D). Not only is this a simple character, like the two previous characters, but, as can be seen in figure 3D, there is not a lot to distinguish geniculate from nongeniculate spines (*Scaphechinus mirabilis* is shown, to emphasize that the nongeniculate spines also have a degree of bending). Homoplasy would be very difficult to detect in this character. The positional information (geniculates are only found in association with food grooves) adds some strength to the character, but the possibility that this association is a functional requirement offsets, to some extent, the importance of the positional information.  

4. Differentiation in spine fields. In *Dendraster* and the mellitids the spines of the oral interambulacrum are longer than those of the ambulacra and constitute a distinct locomotory field. In the outgroup *Clypeaster* and in *Echinarachnius* there is no significant differentiation in the oral spines. As is the previous character, this, too, is a simple character. It is interesting that differentiation of the oral spines has arisen at least twice within the outgroup genus *Clypeaster*, in *C. lamprus* from the Caribbean (T. S. Hopkins, personal communication), and independently in a Japanese species (personal observation). Thus there is some evidence that this character is especially prone to homoplasious evolution.  

Two other characters have been proposed that support the monophyly of *Dendraster* and the mellitids with respect to *Echinarachnius*.  

5. Food grooves. Seilacher (1979) placed *Echinarachnius* as the sister group to all other scutellines, rather than as the sole sister group to *Dendraster* (Durham 1955, 1966), on the basis of the relationships between the food grooves and underlying plates. In *Echinarachnius* (and outgroups) the primary trunk of the food groove runs suturally and extends well beyond the basicoronal (fig. 3Ei and ii). In all other scutelline sand dollars the food grooves bifurcate proximally (at the ends of the basicoronal plates) and then run in the middle of the plates, rather than suturally (fig. 3Eiii). However, *Echinarachnius* shows an unusual trifurcation of the food groove distally, and at this point the food grooves leave the sutures (fig. 3Eii). The phylogenetic value of this character in *Echinarachnius* is unclear; near the mouth the food groove shows the outgroup condition of sutural growth, but distally the food groove has the derived
condition of growth across plate sutures. Depending on which aspect of the food grooves is considered, the form of the grooves in *Echinarchnium* may be viewed as either a modification of the primitive or the advanced condition! Seilacher (1979) views the *Echinarchnium* condition as a modified symplesiomorphy, while Mooi (1987) suggests that it is a modification of the derived bifurcate condition. Note the difficulty in deciding whether the condition in *Echinarchnium* is derived from the *Clypeaster* or *Dendraster* condition or whether it is intermediate between the two. Difficulty in interpreting this character renders it of questionable phylogenetic value.

6. Jensen (1979, 1981) has provided a detailed scanning-electron microscopic analysis of the tooth structure of a wide range of echinoids. She noted that *Mellita* and *Dendraster* share a unique tooth-plate construction, while *Echinarchnium* shares a different state with some other clypeasteroids (Jensen 1981). The fine structure of the plates is quite complex, suggesting a relatively strong phylogenetic signal, though understanding the evolution of the character is made difficult by the large number of described character states. There are at least six types of tooth plates known in the clypeasteroids, and there are four types of needles-prisms systems. This represents the only relatively informative character drawn into question by the DNA-hybridization data.

**Correlated Characters?**

Characters 2–5 discussed above are all directly associated with the food grooves; the geniculate spines are only found in food groove–associated spine fields, as are the barrel-tipped podia. These four characters may well be part of the differentiation between the food-groove spine fields and the locomotory spine fields and thus, for phylogenetic purposes, perhaps should be more properly treated as a single character. Under this scheme, only two characters in Mooi’s analysis (fig. 1B) are drawn into question by the DNA-hybridization data! The sixth character is also associated with the feeding apparatus (the nature of the tooth plates) and thus may also be correlated with the food groove–associated characters.

**Independent Support for DNA-Hybridization Tree**

**Morphology**

From a morphological standpoint a major difficulty in accepting the DNA-hybridization phylogeny is the dearth of morphological features described in the systematic literature that support a clade of *Dendraster* plus *Echinarchnium*, to the exclusion of the mellitids. In fact, at first glance there seem to be several morphological differences between these two genera, even beyond those addressed above. However, Beadle (1989, 1990) presents a scenario where, by a simple heterochrony in test growth, the symmetrical echinarachniid-type test shape could be transformed into the asymmetrical dendrasterid-type test shape, or vice versa. Significantly, Beadle (1990) showed that, if a dendrasterid/echinarachniid transformation did occur by the proposed heterochrony, then the additional differences between the two genera alluded to above are exactly the differences one would expect to see.

Thus, while morphological characters, per se, are difficult to find that support the relationship of *Dendraster* and *Echinarchnium* [though the position of the periproct with respect to the ambulacral plates noted by Beadle (1990) is a good candidate], it is easy to see how one could be derived from the other, and this transformation is consistent with the differences in the architecture of the test observed between the two species. Further, if a major heterochronic event is responsible for the transformation
of one into the other, then it is entirely plausible that a whole suite of characters could either have been lost or have reappeared, as must have occurred if Dendraster and Echinarchinus are sister taxa with respect to the mellitids. Further analysis of all the relevant species (many of which are not discussed either here or by Beadle), with Beadle’s heterochronic mechanism kept in mind, may well produce morphological support for the topology derived from the DNA data.

Beadle’s (1989, 1990) arguments that Dendraster is the result of a heterochronic transformation of an echinarachniid are strengthened by an examination of the fossil record (Beadle 1990). There are numerous extinct taxa known from the northern Pacific that have been variously assigned to the Dendrasteridae, Echinarachniidae, or, under some phylogenetic schemes, to a third, closely allied family (Durham 1955; Nisiyama 1968; Wagner 1974; Mooi 1987). Part of the difficulty in reaching a consensus on how to classify the complex is the presence of several chimeric forms among the fossil taxa, which suggests a close relationship between the Echinarachniidae and the Dendrasteridae. A thorough revision of the northern Pacific taxa, as well as a reanalysis of the mellitids and their fossil sister groups in light of Beadle’s suggestion of heterochronic transformations between members of the Echinarachniidae and the Dendrasteridae, is required to secure Beadle’s morphological arguments in favor of Echinarchinus being more closely related to Dendraster than to either Mellita or Leodia.

Paleobiogeography

For the first half of their respective histories, the dendrasterid/echinarachniid clade and the lineage that led to the mellitids occupied widely separated geographic realms. In the Eocene the first echinarachiids (Kewia) are known from Oregon (Linder et al. 1988), and a now-extinct sister group to the mellitids, Monophoraster (see Mooi 1987), appears in southern South America (Larrain 1984). In the Oligocene, a period of poor fossilization for echinoids (Raup 1975), the echinarachiid Kewia is known from the northwestern United States, Sakhalin, and Japan (Nisiyama 1968; Linder et al. 1988), while Monophoraster is still restricted to South America (Patagonia; W. J. Zinsmeister, personal communication). In the Miocene the distributions begin to converge as the mellitids become centered in the Caribbean, and since the Pliocene there has been limited overlap between some mellitids (Encope and Mellita) and Dendraster in southern California and Baja California (Mooi 1989; Beadle, accepted).

Thus, if Dendraster is really the sister group to the mellitids, then dispersal of some primitive dendrasterids from the northwest Americas to southeast South America (during a time well before dendrasterids first appear in the fossil record!) needs to be hypothesized. While not impossible (the Panamanian Isthmus was open, and modern representatives of these groups all have feeding planktotrophic larvae), the spatially and temporally disjoint origins of the dendrasterids and mellitids present a major problem for the morphological cladogram—but not for the DNA-hybridization phylogeny or for Durham (1955, 1966) and Beadle (1989, 1990). For an explanation of the distribution of these sand dollars, it is more parsimonious to accept a vicariance model rather than a dispersal model.

Conclusions

In the present study I have compared the reliabilities of DNA-hybridization and morphological phylogenies of some clypeasteroids and have found that, where the two trees differ, the DNA phylogeny is more reliable. In other studies it may be found that morphological data are more reliable than are DNA data. For example, an 18S rRNA
phylogeny of amniote classes (Hedges et al. 1990) was found to differ from a robust paleontological phylogeny of the same taxa. An examination of the DNA sequences led to the identification of substantial substitution biases in the 18S rRNA sequences, and reanalysis of the sequences by the weighted parsimony algorithm of Williams and Fitch (1990) greatly improved the concordance between the paleontological and DNA phylogenies (Marshall 1992). In attempting to understand the nature of conflicting molecular and morphological phylogenies (rather than taking grand averages of the available information), one can gain insight into the nature of evolutionary changes in both morphological and molecular data sets.

With regard to the clypeasteroids, while I have argued that it is only a few of the weakest of characters that are drawn into question by the DNA tree, it does not follow that those characters should not have been used in the morphological analyses in the first place. In the absence of any other information—i.e., the conflicting DNA and biogeographic data, as well as the morphological analyses of Beadle (1989, 1990)—these characters represent good hypotheses of relationship. This examination of the quality of the morphological characters used by Mooi (1987) does not negate the fact that contradictory evidence exists on the affinities of *Dendraster* and *Echinarachnius* and that perhaps the DNA-hybridization phylogeny is in error, though I have argued that this latter possibility is unlikely. DNA sequence data are now being collected to test the veracity of the DNA-hybridization and morphological data, and further morphological analysis is also required.

The DNA-hybridization phylogeny implies that morphological evolution among the four sand dollars has proceeded in a (slightly) less than most parsimonious way. Parsimony is the most commonly used criterion for deciding between phylogenetic hypotheses, especially between competing morphological hypotheses. Thus, to some, the fact that the DNA data support a less than most parsimonious tree for the sand dollars may indicate some error in analysis of the DNA data. But it should be noted that there is no a priori reason for favoring the most parsimonious tree simply because it is the most parsimonious (see, especially, Sober 1988, p. 104; also see Wiley 1975; Johnson 1982; Marshall 1986; Sluys 1989). To quote a philosopher: “Unless we give more details, there is no more reason to give pride of place to a principle of parsimony than to a principle of plenitude” (Sober 1988, p. 104).

The DNA-hybridization data give reason to favor a little more plenitude in interpreting the morphological data than do the morphological data alone, and, as shown above, when standard criteria for recognizing homologies are employed to assess the relative informativeness of the morphological characters implied to be homoplasies by the DNA-hybridization phylogeny, the supposition that they represent undetected homoplasies is not unreasonable. Biogeographic data and a detailed analysis of the morphologies of *Dendraster* and *Echinarachnius* in the light of heterochronic mechanisms further support the probability of a little more plenitude.

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