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Species of marine invertebrates: a comparison of the biological and phylogenetic species concepts

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ABSTRACT

Traditional morphological approaches have substantially underestimated species diversity in living marine invertebrates, as assessed by either the biological or phylogenetic species concepts. The degree to which these concepts succeed individually or agree with each other depends on the group and the biogeographic context. In sympatry, the biological and phylogenetic species concepts should yield the same result, because reproductive incompatibility implies at least one diagnostic difference between isolated forms. Hybridization in sympatry between partially isolated forms may be a problem for both species concepts in some groups, although evidence for this in the field is limited. It is often difficult to find qualitative morphological differences between forms that can be unambiguously recognized by other characters, so that a phylogenetic species concept that depends on morphological characters will miss many reproductively isolated forms. In allopatry, the differences between the two species concepts are potentially much greater, because the phylogenetic species concept has the potential to recognize any diagnosably distinct population at the species level, regardless of its triviality. In groups with extensive dispersal ability, there may be predictable relationships between genetic and reproductive divergence that allow taxonomic decisions to be made using either species concept. In groups with limited dispersal ability and a propensity for founder events and local extinction, substantial and complex patterns of genetic variation will prove challenging for both species concepts. The phylogenetic species concept makes no special distinction between species and higher level

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taxa, while the biological species concept places species at the boundary between reticulation and cladogenesis. This appears to be an important and well-defined boundary for many marine invertebrates, and thus merits special taxonomic recognition.

10.1 INTRODUCTION

Morphologically defined species remain the rule in nearly all groups of marine invertebrates, but recent work has revealed that many so-called species are in fact complexes of taxa that can be most readily distinguished using genetic, behavioural or ecological characters (Knowlton, 1993). Nevertheless, most of these sibling species exhibit subtle (and sometimes not so subtle) morphological differences that were previously ascribed to intraspecific variation, based on a priori assumptions of wide geographic range or extensive non-genetic plasticity.

How much variability should a single species encompass? The taxonomic response to this question will depend upon the nature of the species concept to be employed. Two classes of options currently dominate the literature (Claridge *et al.*, 1997: Chapter 1). The first class is epitomized by the biological species concept (Mayr and Ashlock, 1991). Species are defined in principle on the basis of reproductive compatibility, although indirect evidence for the existence of reproductive barriers marking species boundaries is acceptable with this approach (Avise and Ball, 1990). Templeton's (1989) cohesion species concept is related in accepting the biological species concept for those groups for which it works well, but it also utilizes criteria that can be applied to groups that are asexual, subdivided, or that hybridize extensively. The second class of species concepts consists of a group of cladistically based approaches, all of which have been loosely referred to as the phylogenetic species concept (Mishler and Theriot, 1997). In its least restrictive usage (Cracraft, 1989, 1997: Chapter 16), a phylogenetic species is simply the minimum diagnosable taxonomic unit based on any qualitative character. Some workers, however, insist that minimum units must be strictly monophyletic and thus defined by derived characters (reviewed by Smith, 1994), and others argue that some monophyletic groups are too trivial to merit recognition at the species level (Mishler and Theriot, 1997).

The purpose of this chapter is to compare the implications of these two classes of approaches for the definition of species in marine invertebrates in practice, without getting overwhelmed by the alpha taxonomy of the species concepts themselves. For simplicity, we will focus primarily on the biological species concept of Mayr (Mayr and Ashlock, 1991) and Cracraft's (1989, 1997: Chapter 16) version of the phylogenetic species concept. We shall not consider the special problems raised by obligately clonal or selfing life-histories, since these are rare in marine invertebrates.

The comparison between the biological and phylogenetic approaches is clarified by considering sympatric and allopatric taxa separately. In sympatry, the two approaches make the same recommendations in principle, for taxa that are reproductively isolated in sympatry are also by definition diagnosably distinct in at least the character that generates the isolation. However, as the title of this symposium (*The Units of Biodiversity: Species in Practice*) implied, the translation of theory into practice is not always straightforward. Reproductively isolated, sympatric taxa can generally be distinguished by ecological, behavioural, genetic or morphological differences, but these differences may be quantitative rather than qualitative, and thus not diagnosable in practice by the criteria of phylogenetic species concepts. Moreover, reproductive isolation is itself a quantitative character when isolation is not complete, and can thus be a problem for both species concepts in deciding the status of morphs that are partially interfertile in sympatry. In allopatry, the differences between these approaches are potentially much more marked, since for the phylogenetic species concept any geographically isolated population with a diagnosably distinct characteristic can be recognized at the species level. Founder populations begun by a small number of individuals may often be diagnosably distinct at the genetic level, and thus would be species using the approach favoured by Cracraft (1989), regardless of the triviality of the difference.

10.2 CORALS AND SHRIMPS AS CASE STUDIES

The differences between the biological and phylogenetic species concepts for practical taxonomy are best evaluated by considering real organisms rather than hypothetical situations. Below we discuss the implications of these approaches for corals and snapping shrimp. These two groups share a bad reputation among practising taxonomists trying to define species, but the problems they pose for these alternative species concepts are quite different.

10.2.1 Reef-building corals and the problem of quantitative characters

With few exceptions, alpha taxonomy of corals is entirely based on skeletal characters (but see Lang, 1984). Most reef-building corals are colonial, and characteristics of the skeletal cups secreted by individual polyps, called corallites, play a major role in defining species boundaries in many genera (Budd *et al.*, 1994a). Because corallites often vary considerably within a colony (a genetic individual), species boundaries were traditionally defined to encompass much of this variation (Wood Jones, 1907). Colony growth form is also known in some cases to exhibit phenotypic plasticity in response to wave energy and light level (Willis, 1985), the latter a consequence of the obligate symbiosis between reef-building

corals and photosynthetic dinoflagellates. These features have led most coral taxonomists to accept large amounts of intraspecific variation at the level of both the corallite and the colony.

The problems with this approach are well illustrated by the coral *Montastraea annularis*. This 'species' is the most abundant and best studied coral on Caribbean reefs. It exhibits enormous variability in colony morphology, ranging from massive heads to columns to plates. Computer models and transplant experiments designed to evaluate the effect of depth on growth form (Graus and Macintyre, 1976; Dustan, 1979) made it a text-book case of the importance of phenotypic plasticity. Nevertheless, the different morphologies can be found side by side, and intermediates between the major types of colony morphology are rare (Graus, 1977).

Recently, a number of features have been found that are strongly concordant with the different patterns of colony growth. These include corallite morphometrics, skeletal density and growth rate, stable isotope signatures, aggressive behaviour, allozymes, and reproductive biology (Knowlton *et al.*, 1992, and in press; Van Veghel and Bak, 1993; Van Veghel and Kahmann, 1994; Weil and Knowlton, 1994; A.F. Budd and N. Knowlton, in preparation). However, most of these differences, including those likely to be useful in identifying skeletal material, are quantitative rather than qualitative.

The response of coral systematists to these findings has been mixed. Because numerous and presumably unrelated characters were concordant, Weil and Knowlton (1994) resurrected two previously synonomized names to recognize the three common shallow water forms. Van Veghel and Bak (1993), in contrast, referred to them as morphotypes rather than species, based on the absence of qualitative differences in the same set of data. Reviewing this situation, Veron (1995: 33) concluded that there may be no correct answer because species are arbitrary. The species level taxonomy of many other corals is comparably problematic (Veron, 1995).

There are several general and somewhat inter-related explanations for this failure to find reliable qualitative differences. First, reproductively isolated species may be genuinely similar in genetic or morphological characters, either because divergence is slow or because the species are relatively young. Recently or slowly diverging species may still share the same polymorphisms across much of the genome, so that finding qualitative or fixed differences can be equivalent to searching for a genetic needle in a haystack (Avise and Ball, 1990). Romano (1995), for example, found comparatively little genetic divergence even between groups whose fossil record indicates a long history of isolation, suggesting that the molecular 'clock' of corals ticks slowly. Some corals have long generation times, which other things being equal, should act to slow the rate of divergence (Gillespie, 1991).

Second, coral species, like plants, may be particularly prone to hybridization (Veron, 1995). The morphological simplicity of corals may underlie the successful production of hybrids in the laboratory (Wallace and Willis, 1994), and the annual simultaneous spawning of congenerics documented for many corals could provide regular opportunities for interspecific hybridization in the field (Wallace and Willis, 1994; Veron, 1995). Even when hybrids are less fit than the products of intraspecific matings, selection to avoid such matings is ultimately constrained by the fact that even a severely inferior hybrid is fitter than an unfertilized egg.

However, it should be emphasized that hard evidence for rampant natural hybridization in corals is lacking. Indeed, the three described species of the *M. annularis* species complex show considerable overlap in the date of spawning, but appear nevertheless to be reproductively isolated by a combination of barriers to fertilization or development and differences in the hour of peak spawning (Knowlton *et al.*, in press). Moreover, in *Acropora*, there are several examples of incompatibility between morphologically similar colonies that are supposed to be conspecific (Wallace and Willis, 1994), suggesting that the importance of breeding barriers may have been underestimated as well as overestimated.

Molecular techniques have revolutionized the detection of sibling species in many groups, but in corals, apart from protein electrophoresis, they have been little used due to technical difficulties. These difficulties are likely to be resolved in the coming years, and clearly defined species may emerge from these studies. On the other hand, if closely related species of corals diverge slowly and hybridize frequently, there may be no magic molecular bullet for recognizing hybrids or defining species, even in sympatry.

In summary, corals can be problematic for a variety of species concepts, even in sympatry, due to the scarcity of diagnostic differences and a poorly understood potential for hybridization. In the absence of a consensus in sympatry, the situation in allopatry or even in different reef habitats is, of course, more problematic. In the *M. annularis* species complex, for example, deeper water forms converge on a plate-like morphology, making it difficult to distinguish species or evaluate relationships between shallow and deeper water forms. The three basic morphologies can be recognized throughout the Caribbean, but show differences from site to site which are also hard to interpret. Veron (1995) described many comparable situations for Pacific corals.

10.2.2 Snapping shrimp and the problem of allopatric variation

Species of snapping shrimp in the genus *Alpheus* (Alpheidae) are numerous and often difficult to distinguish using conventional morphological characters in preserved material. In sympatry, however, many morpho-

logically similar species can be readily identified by their colour patterns when alive (Knowlton and Mills, 1992), as well as by fixed allozyme differences and substantial divergence in mitochondrial DNA (mtDNA) sequences (Knowlton *et al.*, 1993 and unpublished data). It is also possible directly to assay reproductive cohesion, because males and females are often found paired, and are usually aggressive to all individuals except potential mates. Interspecific pairings are not observed in the field and are almost impossible to establish in the laboratory, suggesting that hybridization is uncommon. Thus, in contrast to corals, both the biological and phylogenetic species concepts have little difficulty in defining species boundaries in sympatry when the appropriate characters are employed.

Neotropical alpheids from opposite sides of the Isthmus of Panama are particularly useful for exploring the nature of species in allopatry. The Isthmus now divides what was once a continuous tropical sea, and the faunas of the eastern Pacific and Caribbean contain numerous examples of transisthmian sister taxa (Knowlton *et al.*, 1993). Detailed geological and palaeontological analyses provide strong support for dating the final closure of the Isthmus at approximately 3 million years ago (Coates *et al.*, 1992). While the biological history of the region is more complex than commonly assumed (see below), it nevertheless represents the best marine example of the classic form of geographic isolation – one large population being divided into two still large populations that subsequently slowly diverge through time.

Seven pairs of transisthmian sister taxa have been examined using a suite of molecular and behavioural techniques (Knowlton *et al.*, 1993). They show considerable but concordant variation in the degree of divergence exhibited, suggesting that some pairs were isolated more recently than others. Although the most similar transisthmian pairs show little aggression when males from one ocean are placed with females from the other ocean, they almost never produce fertile clutches of eggs. This contrasts with the routine production of fertile clutches when conspecifics from the same ocean are paired under identical laboratory conditions. The general conclusion to be drawn from these experiments is that 3 million years is long enough to result in substantial reproductive isolation in these organisms.

Can we use the information obtained from transisthmian pairs to interpret other patterns of divergence in allopatry where it has not been possible to study reproductive compatibility directly? This appears to be a reasonable procedure for two reasons. First, the relatively large number of transisthmian pairs studied strengthens our confidence in the relationship between molecular and reproductive divergence. Second, the classical or dumb-bell mode of geographic isolation is probably the most sluggish way of generating new species, based on theory (Templeton, 1981), empir-

ical observations in other groups (Coyne and Orr, 1989), and limited observations for the alpheids themselves (unpublished data). Thus, we may underestimate reproductive isolation for a given level of molecular divergence by using the transisthmian data as a null model, but we are not likely to overestimate it.

The widely scattered island groups of the Pacific provide an appropriate arena for comparing the biological and phylogenetic species concepts in a more complex pattern of allopatry. To this end, we here summarize preliminary data on *Alpheus lottini*, an obligate symbiont of the corals *Pocillopora* and *Stylophora* that ranges in distribution from the eastern Pacific to the Red Sea. It is a conspicuous and well-studied snapping shrimp, but no attempt has previously been made to evaluate variability across its wide range.

Examination of living material from a variety of sites across the Pacific immediately revealed two clearly distinct colour patterns: animals were characterized by either a solid black stripe down the carapace and paired blotches down the abdomen (type A), or by speckles scattered across both regions (type B). Limited collections from Panama, Pohnpei, Clipperton and Moorea contained only type A, those from Hawaii and Guam only type B, while both types were found in Palau (mated assortatively).

Mitochondrial DNA sequences from types A and B (for the same gene region as was studied for transisthmian taxa; see caption of Table 10.1 for methods) had an average corrected sequence divergence of 10–13% (Table 10.2). This corresponds to an estimated time of divergence of 4–5 million years, based on the transisthmian taxa (Figure 10.1). This degree of sequence divergence was always associated with reproductive isolation across the Isthmus, and the finding of assortatively mated pairs at the one site where they were found together (Palau) also supports an interpretation of strong reproductive isolation. Thus, both the biological and phylogenetic species concepts would recognize types A and B as specifically distinct.

The molecular data also reveal more subtle allopatric structuring within these two types, however. The clearest is that between the Hawaiian and other type B taxa, which differ by about 4.5% in corrected sequence divergence. This is less than that seen between seven transisthmian sister species (Knowlton *et al.*, 1993), but still substantial, particularly in light of the fact that even the least divergent of these (6.6%) never successfully interbred in laboratory experiments. From the perspective of the biological species concept, these taxa are likely to be specifically distinct, but explicit tests of their compatibility to further refine the relationship between genetic and reproductive divergence at the low end of the divergence scale are necessary. For the phylogenetic species concept, however, there is no ambiguity, because the Hawaiian shrimp can be distinguished genetically from the other type B shrimp (20 transitions and three silent transversions

Table 10.1 Aligned sequence haplotypes for variable positions within the 564 bp area of analysis of the CO1 mtDNA gene of *Alpheus lottini* complex (parentheses indicate multiple individuals with same halotype)

	000000000000000000011111111112222222222222222233333333333344444444444444555555555555
Position	011222333445666799900112467890122233445778889900133455677003344567788990011223344 55
	628147039281369503628470421984625814087392581409203245058585814321709581706581403 25
B-PALAU1	AATGCCCTAGTCAAGGACGGTAAGATGTCTCTCACGAGAACCCGCTAGCAGTATATCACGGCCCTACACTCCAAACCCGTGCG
B-PALAU2	.....
B-GUAM1	.....T.....T.....
B-GUAM2	.....T.....
B-GUAM3(2)	.....G.....T.....
B-HAWAII1(2)	G..A..T.G...G.AA....C..A..A.....TG...A.....AT.A.T.GC.G.CT.....T.....A.A..
B-HAWAII2	G..A..T.G.C.G.AA....C..A..A.....TG...A.....AT.A.T.GC.G.CT.....T.....A.A..
B-HAWAII3	G..A..T.G...G.AA....C..A..A.....TG...A.....AT.A.T.GC.G.CT.....T.....A.A..
A-PALAU1	.GCATAGCCACTGGAAGTA.CGGAGCAATCTG...AG.GG.TTCACGA.GACCC.CTG.CCAT.CG.CGCA.GG...TAC..A
A-PALAU2	.GCATAGCTACTGGA..TA.CGGAGCAATCTG...AG.GG.TTCACGA.GACCC.CTG.CCAT.CGTCGCA.GG...TAC..A

A-POHNPEI1	.GCATAGCCACTGGA..TA.CGGAGCAATCTG...AG.GG.TTCACGA.GACCC.CTG.CCAT.CG.CGCA.GG...TAC..A
A-POHNPEI2	.GCATAGCCACTGGA..TA.CGGAGCAATCTG...AG.GG.TTCACGA.GACCC.CTG.CCAT.CG.CGCA.GG...TAC..A
A-POHNPEI3	.GCATAGCCACTGGA.?TAACGGAGCAATCTGT..AG.GG.TTCACGA.GACCC.CTG.CCAT.CG.CGCA.GG...TAC..A
A-MOOREA1	.GCATAG.CACT.....TA.CGGAGCAAT.TG....G..G.TTCAC.A..ACCC.CT..CCAT.CG.CGCA.GG...TAC..A
A-MOOREA2	.GCATAG.CACT.....TA.CGGAGCAAT.TG....G..G.TTCAC.A..ACCC.CT..CCAT.CG.CGCA.GG..T.AC..A
A-MOOREA3	.GCATAG.CACT.....TA.CGGAGCAAT.TG....G..G.TTCAC.A..ACCC.CT..CCAT.CG.CGCA.GGG..TAC..A
A-CLIPPERTON1	.GCATAG.CACT.....TA.CGGAGCAAT.TG....G..G.TTCAC.A..ACCC.CT..CCAT.CG.CGCA.GGG..TAC..A
A-CLIPPERTON2	.GCATAG.CACT.....TA.CGGAGCAAT.TG....G..G.TTCAC.A..ACCC.CT..CCATT.GTCGCA.GGGT.TAC.TA
A-PANAMA1	.GCATAG.CACT..T.GTA.CGGAGCAAT.TG..TAG..G.TTCAC.A..ACCC.CT.TCCAT.CG.CGCA.GGG..TAC..A
A-PANAMA2(2)	.GCATAG.CACT..T.GTA.CGGAGCAAT.TG...AG..G.TTCAC.A..ACCC.CT..CCAT.CG.CGCA.GGG..TAC..A
A-PANAMA3	.GCATAG.CACT..T.GTA.CGGAGCAAT.TG...AG..G.TTCAC.A..ACCC.CT..CCAT.CG.CGCA.GG...TAC..A

Dots represent concordance with the top sequence. Mitochondrial DNA methods as in Knowlton *et al.* 1993 with the following modifications: primers (5′–3′ positions in the amplification product) PCR and sequencing = COI (1–20) and *Alpheus* specific primer 1 [5′ CAT TTA GGC CTA AGA AGT GTT G 3′ (619–640)]; internal sequencing: light strand – ALP7 [TGA CTT GGA ACC CTC CAT GG 3′ (304–323)] and ALP5 [5′ ATT GCY CAC TGA TTC CCC YTA TT 3′ (514–536)]; heavy strand – ALP2 [5′ CCR TGG AGG GTT CCR AGT CA 3′ (304–323)]. Double stranded sequencing as in method 2 of Kessing *et al.* (1989). Sequences in Genbank (u76428–u76455).

Table 10.2 Kimura (1980) corrected percent sequence divergence values* (calculated by Sequencer 3.0; Kessing, 1995) averaged by site for two types of *Alpheus lottini*

	B-PALAU	B-GUAM	B-HAWAII	A-PALAU	A-POHNPEI	A-MOOREA	A-CLIPPERTON	A-PANAMA
B-PALAU	1 0.0 XXX–XXX							
B-GUAM	8 0.4 0.2–0.4	6 0.3 0.2–0.5						
B-HAWAII	8 4.7 4.6–4.8	16 4.6 4.4–4.8	6 0.1 0.0–0.2					
A-PALAU	4 12.7 12.6–12.8	8 13.0 12.8–13.2	8 11.8 11.5–12.0	1 0.7 XXX–XXX				
A-POHNPEI	6 12.5 12.4–12.8	12 12.7 12.6–13.0	12 11.7 11.5–11.8	6 0.5 0.4–0.7	3 0.3 0.0–0.4			
A-MOOREA	8 10.3 10.2–10.4	12 10.5 10.4–10.8	12 10.7 10.6–11.1	6 2.4 2.2–2.5	9 2.1 1.8–2.6	3 0.4 0.2–0.5		
A-CLIPPERTON	4 10.8 10.4–11.1	8 11.0 10.6–11.5	8 11.4 10.9–11.7	4 2.8 2.4–3.3	6 2.5 2.0–3.3	6 0.7 0.0–1.4	1 0.9 XXX–XXX	
A-PANAMA	8 11.1 10.8–11.5	16 11.3 11.0–11.9	16 11.5 11.1–11.9	8 2.2 1.8–2.7	12 2.1 1.8–2.5	12 0.8 0.5–1.4	8 1.1 0.5–1.8	6 0.3 0.2–0.5

Top value is number of pairwise comparisons, bottom values indicate range. See text for details.

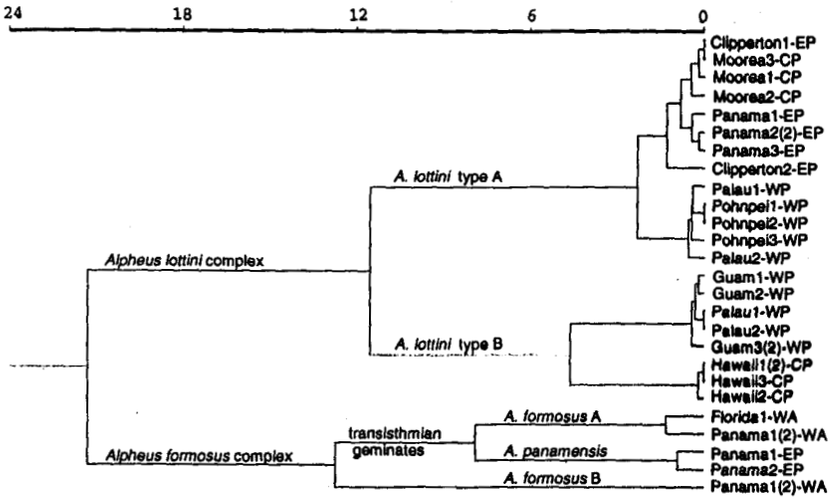

Figure 10.1 UPGMA tree for *Alpheus lottini* and the *A. formosus* sister clade (unpublished data) complex within the genus. The latter includes a pair of geminate (transisthmian) species that apparently diverged at the final closure of the Isthmus approximately three million years ago (Knowlton *et al.*, 1993). EP, eastern Pacific; CP, central Pacific; WP, western Pacific; WA, western Atlantic.

at third position sites; Table 10.1). The Hawaiian individuals also have a distinct egg colour that would permit their recognition on that basis.

The potential conflict between the two species concepts becomes clearer as we consider more similar populations. Within the type A form, maximum corrected sequence divergence between sites is only 2.8% (Table 10.2). This value is substantially less than that exhibited across the Isthmus and is not much more than apparently intraspecific differences between Panama and Florida or even within Panama (Figure 10.1). Nevertheless, within the type A clade, fixed third position genetic differences distinguish a Palau/Pohnpei taxon (nine transitions), a Panama taxon (one silent transversion), and a Clipperton–Moorea taxon (two transitions) (Table 10.1). If confirmed by more extensive sampling, this would result in the elevation of each of these to specific status using the phylogenetic species concept of Cracraft (1989, 1997: Chapter 16), but the slight sequence divergence would argue against such a distinction using the biological species concept in the absence of other evidence.

Thus, the biological and phylogenetic species concepts provided rather different results when applied to variability in allopatric *Alpheus*, although both support recognition of several taxa that had been missed in traditional morphological analyses. Their treatment of the transisthmian taxa is comparable, for Pacific and Caribbean forms are both reproductively isolated and diagnosably distinct. For the pan-Pacific *A. lottini*, however, the

biological species concept clearly supports the existence of only two or three species, while the phylogenetic species concept would recognize five based on the samples available (Figure 10.2).

10.3 OTHER MARINE INVERTEBRATES

In the discussion above we focused on two genera and ignored the vast majority of marine invertebrates. While we cannot do justice in a brief review to the diversity represented by over 30 phyla, we can try to assess the generality of the patterns we highlighted.

10.3.1 Quantitative characters in sympatry

The absence of qualitative morphological differences between closely related species is a fact of life for many groups of marine invertebrates, including those that are clearly reproductively isolated (Langan-Cranford and Pearse, 1995). Multivariate analyses of quantitative morphological characters (Budd *et al.*, 1994a; Jackson and Cheetham, 1994) often clearly define taxa, however, and molecular techniques can confirm their status. This approach is compatible with the phylogenetic species concept *sensu* Cracraft (1989) when fixed genetic differences can be found, and concordance of independent characters provides strong indirect evidence for reproductive isolation (Avise and Ball, 1990).

However, as argued above, there are no easy practical solutions for species that are either extremely similar across much of the genome or for species that sporadically hybridize. How common are such cases likely to be? Although natural hybridization is often inferred from the ability to produce viable hybrids in the laboratory and the occurrence of 'intermediates', we generally lack the genetic data to test the inference. Lessios and Pearse (in press) show for Indo-Pacific sea urchins in the genus *Diadema* that genetic data do not support the idea of common hybridization, despite the absence of conspicuous pre- or post-zygotic isolating mechanisms and the presence of morphologically intermediate specimens.

We may be fortunate to be doing systematics now, rather than two million years ago, when many new species emerged during the turnover event that created much of the modern tropical marine invertebrate fauna (Budd *et al.*, 1994b; Jackson, 1994). Since that time, comparatively little appears to have happened in terms of speciation, thereby increasing the probability that lineage sorting will have created qualitative genetic differences between species (Avise and Ball, 1990). Very recently diverged species of marine invertebrates (Palumbi and Metz, 1991; Johannesson *et al.*, in press) seem to be the exception rather than the rule, although the

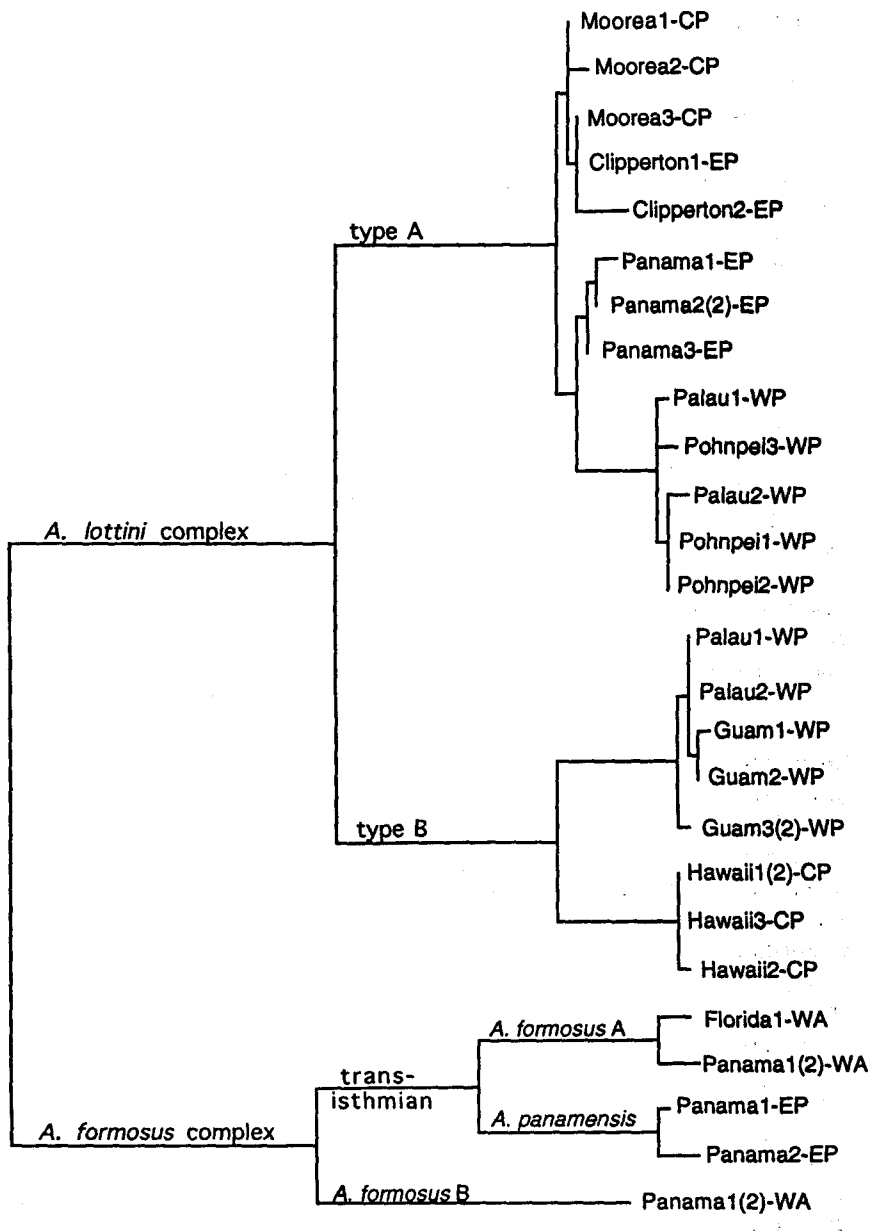

Figure 10.2 One of 144 equally parsimonious trees. (PAUP analysis as in Knowlton *et al.*, 1993, for the same taxa as in Figure 10.1.)

difficulty of identifying recently diverged species may contribute to our perception of their rarity.

10.3.2 Divergence in allopatry

While problems with corals may represent an atypically pessimistic view of species definitions in sympatry, the snapping shrimp case may give an overly optimistic view of the potential for understanding and categorizing allopatric variation. The dispersal of most *Alpheus* larvae is moderate in range (with a development time of several weeks), and rafting is probably not a regular feature of their dispersal biology. While many marine invertebrates share these features, many others do not (Jackson, 1986). Of particular concern are the numerous sessile or sedentary groups with limited larval dispersal. These taxa as currently defined often have very large geographic ranges relative to their dispersal ability, and exhibit extensive and complex patterns of variation.

Several well-studied, small crustaceans provide examples of problems that are likely to plague many such groups. In the tide pool dwelling copepod *Tigriopus californicus*, six of nine study sites analysed in the less than 800 km of coastline between San Francisco and San Diego are diagnosably distinct based on allozymes and DNA sequences (Burton and Lee, 1994; R.S. Burton, personal communication). Some of these differences appear to represent divergence times of 7 million years, but there is no predictable relationship between genetic divergence and post-zygotic compatibility, or between different molecular measures of divergence (Burton, 1990; Burton and Lee, 1994; Ganz and Burton, 1995). Similarly complex patterns have also been reported for the intertidal, beach-dwelling isopod *Excirolana braziliensis*, whose current range, based on traditional morphological criteria, extends from the Gulf of California to southern Chile in the eastern Pacific, and from the Gulf of Mexico to southern Brazil in the Atlantic. Just within Panama, populations from 10 of 11 sites could be distinguished by fixed allozyme differences (Lessios and Weinberg, 1993), and nearby populations sharing the same morphology were typically almost as genetically divergent as populations of different morphologies isolated by the Isthmus of Panama for at least 3 million years (Lessios and Weinberg, 1994). There were also marked genetic changes at one site over a 2-year period.

Organisms like these are going to be a problem for both the biological and phylogenetic species concept. If there are no predictable relationships between potential for interbreeding and other measures of divergence, there are going to be no short-cuts such as the Isthmus for *Alpheus* in defining species boundaries based on the biological species concept. For the phylogenetic species concept, sufficiently detailed genetic information could result in every sample (including samples over time from the same

site) being diagnosably distinct. Even the biological species concept may result in a staggering increase in species level diversity in such taxa.

10.4 BROADER IMPLICATIONS

Taxonomy does not operate in an intellectual vacuum, unconnected with other fields of science. Thus, the species concept embraced by students of marine invertebrates is likely to have substantial consequences both within taxonomy and across other disciplines. Here we consider a few examples.

10.4.1 Nomenclature

Rigorous application of either the phylogenetic or the biological species concept will inevitably result in the future recognition of numerous sibling species within marine invertebrates. Regardless of the species concept that is ultimately employed, use of terms such as 'species complex' or 'species group' allows one to recognize informally clusters of similar and apparently related forms. This seems a more useful approach than splitting up speciose genera (see also Mayr and Ashlock, 1991) or designating numerous subgenera without a phylogenetic analysis.

Application of the phylogenetic species concept as defined by Cracraft (1989, 1997: Chapter 16) could result in orders of magnitude increases in species level diversity in some cases (Avise and Ball, 1990), effectively replacing a taxonomic entity with a geographic one. Cracraft (1989) has scorned the 'how many names can you learn' concern, but names that cannot be readily used by non-specialists will not be used at all. There is likely to be little sympathy beyond the ranks of a subset of systematists for a system that gives species names to every genetically distinct population, regardless of its potential transience and the triviality of its divergence. Indeed, Mishler and Theriot (in press), while arguing for their version of the phylogenetic species concept, suggest that monophyletic groups that are evolutionary trivial, cryptic or poorly supported not be given formal recognition. This solution, however, negates the chief virtue of Cracraft's approach, namely its unambiguous universality.

10.4.2 Ecology

Sympatric sibling species, once recognized, generally exhibit ecological differences that have important implications for understanding community structure (Knowlton, 1993). For example, previous conclusions that corals were generalists (Connell, 1978) are suspect in light of recent taxonomic discoveries which suggest that niche divergence may be more important than previously realized (Knowlton and Jackson, 1994).

Diversity recognized by adherents of both the biological and phylogenetic species concepts could result in a substantial change in the taxonomic database upon which ecologists rely.

10.4.3 Biogeography

Both the biological and the phylogenetic species concepts are likely to result in greater estimates of endemism, particularly with the use of genetic data. For example, only 30% of Hawaii's marine invertebrates are thought to be endemic (Kay and Palumbi, 1987), but *Alpheus lottini* is apparently a false member of the remaining 70%, despite its ability to disperse via planktonic larvae. Based on the studies of *Excirolana* and *Tigriopus* summarized above, essentially all of Hawaii's brooding marine invertebrates are likely to be endemic.

10.4.4 Conservation

In the era of the Rio Convention on Biodiversity, species boundaries have important political as well as biological implications. Fine scaled allopatric splitting, as promoted by the phylogenetic species concept, would facilitate national 'ownership' of biodiversity resources. On the other hand, if such splitting were unwarranted, it could inhibit the development of international cooperation in the conservation of interconnected populations whose survival depends on regional approaches (Committee on Biological Diversity in Marine Systems, 1995).

10.4.5 Palaeontology

While this book focuses deliberately on living species, many marine invertebrate species living today have extensive fossil records. Species concepts that work in the present but not in the past are particularly problematic for these groups. Smith (1994), for example, argued that quantitative statistics are an inappropriate tool for recognizing species, yet they are an essential and powerful technique for recognizing living species morphologically for many of the groups with the best fossil records, such as corals, bryozoans and molluscs. Felsenstein (1988) argued that the biological difference between quantitative and qualitative characters was more illusory than real, and that the focus on qualitative characters in parsimony analysis was primarily a reflection of computational constraints. Thus, there seems to be little justification for abandoning these fossil species as unrecognizable. Rather, genetic data for species in the present should be used to evaluate quantitative morphometric methods for application in the past (Jackson and Cheetham, 1994).

10.4.6 Phylogeny

Phylogenetic analyses have largely ignored the problem of species boundaries. A recent study of cheilostome bryozoans, however, showed that accurate resolution at the species level greatly improved the quality of phylogenetic analyses in terms of parsimony, consistency, and concordance between morphological and genetic data (Jackson and Cheetham, 1994). For species that are readily distinguished by qualitative characters, rigorous discrimination of species by either concept will lead to an improved understanding of relationships. However, in these cheilostomes, as with the corals discussed earlier, quantitative statistical methods were required to resolve the species level taxa, so that many of the species discriminated in this study would not be recognized by most supporters of the phylogenetic species concept.

10.5 CONCLUSIONS

The traditional, morphological species concept, as applied to marine invertebrates, has been unduly conservative. In sympatry, application of both the biological species concept and the phylogenetic species concept will result in the recognition of numerous new species that reflect previously undetected reproductive barriers between morphologically similar forms. However, insistence on qualitative morphological characters by some advocates of the phylogenetic species concept will make it impossible to recognize many species, because morphological differences are often quantitative.

In allopatry both approaches would again result in an increase in the number of species, but the differences between the two approaches are more marked because any distinctive population can become a phylogenetic species. There are two problems here. First, the difference between allopatry and sympatry is less clear-cut in the sea because of the variable and difficult to measure dispersal of larvae. Over what spatial scale does one assess reproductive cohesion, an essential step if one is 'to avoid assigning species status to individual organisms, to different sexes and morphs, or to developmental stages' (Cracraft, 1989)? Second, sporadic recruitment events are likely to create trivial and sometimes transient (Lessios and Weinberg, 1994) but diagnosable groups. Mishler and Theriot (in press) recommend ignoring these minor monophyletic units, but then we are left with the question, how minor is minor enough? This is no less subjective than trying to assess how much differentiation is likely to be associated with reproductive barriers were the allopatric taxa to come together, one of the primary objections raised against the biological species concept. Moreover, the subjectivity of the assessment of

reproductive compatibility is declining with the appearance of theory (Orr, 1995) and empirical studies (Coyne and Orr, 1989; Knowlton *et al.*, 1993) that relate divergence in allopatry to reproductive isolation (although some groups, like *Tigriopus*, may prove difficult to evaluate in this fashion).

Thus, it would appear that all reasonable species concepts require the use of scientific judgement. If we are going to have to use judgement, what principle should guide it? The warring species concepts give us two alternatives from which to choose. The phylogenetic species concept argues for systematic consistency: species should be defined in a manner analogous to all higher taxa. The biological species concept, on the other hand, suggests that species are special, because they lie at the boundary that divides the realm of reticulation from the realm of cladogenesis. We strongly prefer the latter approach, because we find the reticulate/cladistic boundary, even if fuzzy (Mishler and Theriot, in press), to be too biologically important to ignore. Most cladists, however, strongly disagree. Ironically, it is not at all clear where Willi Hennig would stand were he to participate in today's debate.

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