

## How good was the fossil record? Clues from the Californian Pleistocene

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**Abstract.**—The living members of 113 families of bivalves and gastropods of the Californian Province include 698 species living at shelf depths, of which 538 or 77% are known as Pleistocene fossils from the same region; another 113 fossil species are extralimital, and 98 are extinct. Living species not found as fossils are chiefly rare today, and/or minute, fragile, and/or from deeper shelf habitats. Sampling of the Pleistocene record has been biased towards shallow-water assemblages. Fragile and minute forms are probably underrepresented in the record. Rare forms, however, are still appearing as new studies are conducted, and many rare species are yet to be discovered. At least 85% of durably skeletonized living species may have been captured in the record. It is probable that most durably skeletonized invertebrate species were represented in lithostratigraphic units throughout the Phanerozoic, but that this record is lost owing to erosion, burial, and destruction of skeletons *in situ*. The bulk of the marine invertebrate fossil record does not represent a series of unusual skeletal accumulations, but rather the preserved remnants of an excellent original record formed through ordinary though episodic processes.

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### Introduction

The problems of assessing the quality of the fossil record have never been more pressing than at present, when paleontologists are making concerted efforts to infer processes of ecology and evolution from fossil data. Darwin's (1859) famous treatment of the fossil record emphasized its incompleteness and biases, and many subsequent workers have also laid stress upon the difficulties of inferring past biological processes or conditions from a patchy record. However, efforts to understand the record have been increasingly fruitful and indicate that the fossil record can yield a great deal of biological information if the nature of the biases is understood. Here I am concerned with marine benthic communities, which yield our longest and most diverse record of animal life.

Three major sorts of studies contribute to our understanding of the nature of the benthic marine record, of which only a few examples are cited. The first sort involves studies of the modern fauna, to estimate or observe the way in which potentially fossilizable skeletons are recruited into dead shell assemblages (Cadée 1968; Lawrence 1968; Warme

1971; MacDonald 1976; Stanton 1976; Warme et al. 1976; Schopf 1978; Cummins et al. 1986a, b; Meldahl 1987; Miller 1988). To summarize the main findings of this sort of study, the composition of the dead assemblages commonly reflects fairly closely the durably skeletonized species that inhabit the environments where they are found, and in some cases rather fine spatial gradients and variations in living associations are mirrored in the dead assemblages. Indeed, as dead assemblages often accumulate over time periods spanning many generations, they frequently include species that have not lived together at the sampled area, but that have appeared there successively. The dead assemblage is a sample from a pool of species that can usually inhabit the area and associate with the community, but that do not all happen to co-occur, perhaps owing to stochastic fluctuations in recruitment and in microenvironmental conditions. Thus the dead assemblages are sometimes significantly more diverse than the easily fossilized fauna that is observed living, for they are "time-averaged" (Walker and Bambach 1971). Of course, some dead assemblages have been mixed from more than a

single living association, particularly in wave- or current-swept environments. Despite the close resemblance of some live and dead species associations, recruitment of dead individuals into shell assemblages appears to be a sporadic rather than an ongoing process, perhaps concentrated in rather discrete episodes. Steps leading from a living fauna to the accumulation of a diverse shell bed seem not to have been observed. The completeness of an assemblage of dead shells is difficult to specify, because the ultimate pool of fossilizable species that can be associated within the living community is not known.

The second sort of study involves the interpretation of fossil assemblages as to their mode of formation, completeness, and accumulation span (Johnson 1960; Kidwell 1982; Fürsich and Flessa 1987). A particular difficulty in assessing the completeness of fossil assemblages is that, as for modern dead assemblages, the pool of potentially fossilizable species is unknown, so that it is not even certain just how or whether any standing live community of the past is represented. Some fossil assemblages are clearly only fragmentary remnants of large living associations of easily fossilized species, degraded by winnowing, differential transport, or by mechanical or chemical destruction and dissolution. Another consideration is that very rare species, which must form a large fraction of the species present in any given community, probably have a correspondingly small chance of contributing to a fossil assemblage. Even if present, the rare species have a low probability of being completely sampled by a paleontologist (see Koch 1987).

A third sort of study involves increasingly quantitative assessments of the completeness and resolution of the lithostratigraphic (Schindel 1980, 1982; Sadler 1981; Crowley 1984; Anders et al. 1987) and biostratigraphic record (Paul 1982; McKinney 1986; Springer and Lilje 1988). These studies may inform us as to how frequently fossils and fossil assemblages, of whatever completeness, are incorporated into the record.

The marine benthic Pleistocene fauna of the Californian Province is diverse, and most of the species (about 87%) are still represented

by living populations in the eastern Pacific. As a first approximation, then, the living fauna may be taken as the pool from which the fossils were assembled, regardless of the associations of living species found at any one time. From this basis I evaluate the completeness with which the entire fauna of the Californian Province has entered the fossil record during approximately the last million years. By thus employing a stratagem to overcome some of the problems encountered in estimating fossil completeness by other methods, this study may complement those approaches in attempting to understand the nature of the fossil record in general.

### Materials and Methods

*The Living Fauna.*—The first step in this study was to establish a sample pool of easily fossilizable living species from which the fossil fauna may have been drawn. This step was accomplished by using a representative sample of the living shelled mollusks of the classes Gastropoda and Bivalvia, which are relatively well studied and with which I have experience. To qualify for the pool, species had to live within the Californian Province (Fig. 1), which lies between the more northerly Oregonian Province (boundary taken as Point Conception, California) and the more southerly Surian Province (boundary taken as Punta Eugenia, Baja California Sur; see Valentine 1966). A further requirement for pool membership is that the species be recorded as living at shelf depths (taken as 180 meters or less for this region; Shepard 1963). Species from appropriate depths around the islands off southern California and northern Baja California were also included, as these areas are part of the Californian Province. Species known only from Isla Cedros and southward were excluded, as were species known only from the subtropical fauna of Laguna Scammon and southward.

The list of marine mollusks edited by Burch (1944–46) was used as a basis for the compilation, with revisions and additions from later works, including Grau (1959); Keen (1971); Coan (1971, 1973a–c, 1977, 1979); Kennedy (1974); McLean (1978); DuShane (1979); and Bernard (1983). Two families, the ectoparasit-

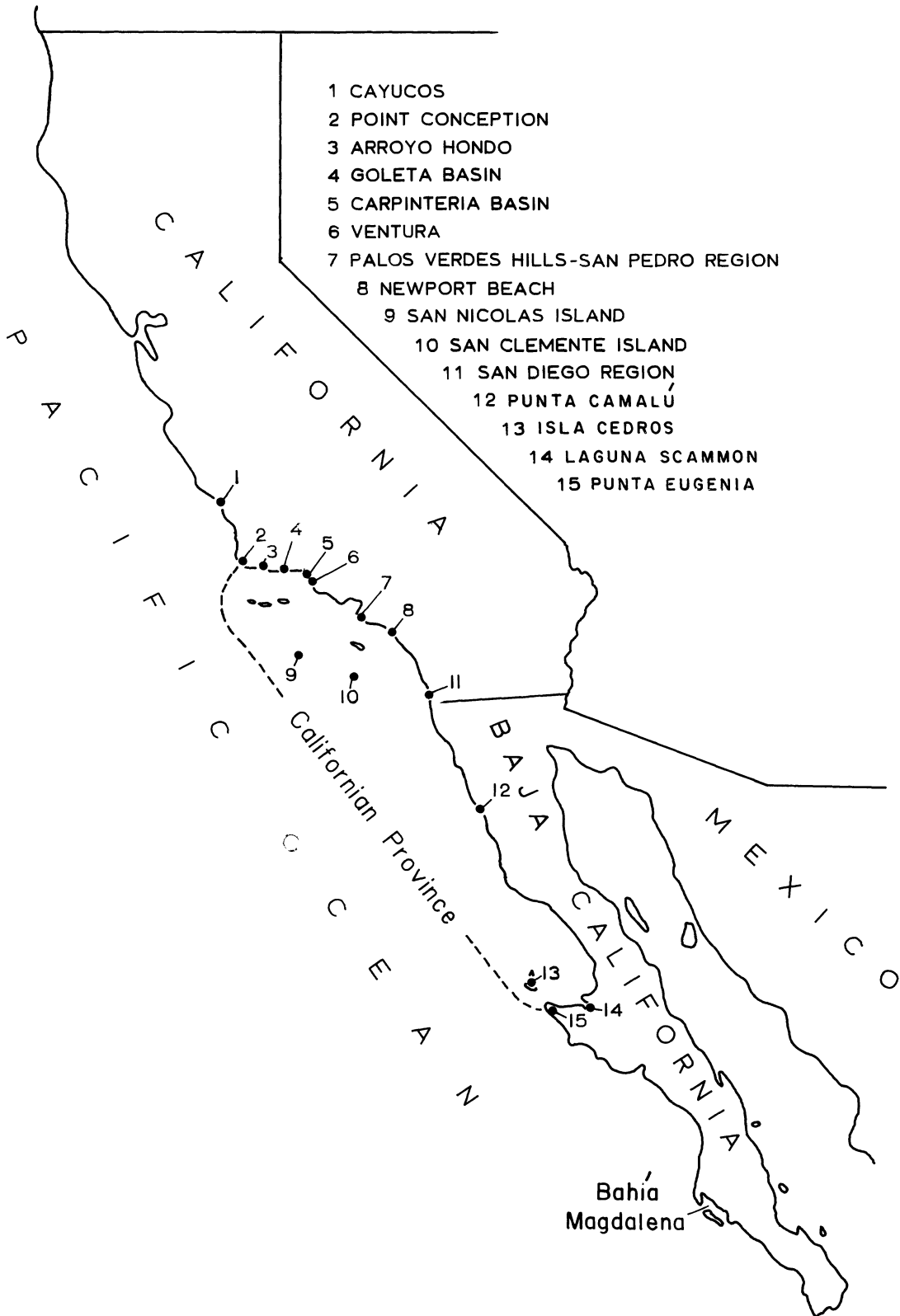


FIGURE 1. Map of principal localities mentioned in the text.

ic Melanellidae and Pyramidellidae, were excluded because they are particularly in need of taxonomic revision. A few species were recorded only once from the province by Dall (1921) or previous workers and have not been reported again. Most of these records are from San Pedro, San Diego, and Catalina Island, and most of these species are tropical. It seems unlikely that these species are now represented by living populations within the Californian Province. Many of the records are probably erroneous, but species' ranges are dynamic, and it is possible that some species have retreated from (or entered into) the province since extensive collecting began during the last century. Zinsmeister (1974) has pointed out that northward flowing currents occasionally bring tropical larvae into southern California and that populations of normally tropical species might have become temporarily established in this region. Species considered to be ephemeral, however, have not been included in the pool. Another small group of species not included in the pool are deep-sea forms largely confined to the continental slope, but found rarely on the outer edge of the continental shelf. However, species known only from outer shelf depths were included in the pool. The final pool includes 698 species, representing 201 genera, and placed in 113 families (Appendix).

*The Pleistocene Fauna.*—Pleistocene records of species of these 113 families from localities within the Californian Province were compiled for comparison with the living species pool. I arbitrarily decided to try to restrict the Pleistocene records to those of the last one million years. The faunas from the marine terrace deposits along the Californian mainland and on islands within the Californian Province generally fall within this range.

Coral-based uranium series ages (Valentine and Veeh 1969; Ku and Kern 1974; Omura et al. 1979; Muhs and Szabo 1982; Muhs and Rosholt 1984; Muhs et al. 1987; Kennedy et al. 1987) and amino-acid racemization ages calibrated from these datums (Wehmiller et al. 1977; Kern 1977; Kennedy 1978; Lajoie et al. 1979; Valentine 1980; Kennedy et al. 1982; Muhs 1985; Kennedy and Wehmiller 1986; Kennedy et al. 1986) have demonstrated that

most of the richly fossiliferous Californian terraces, which are now found chiefly at lower elevations, date from about 80 and 125 thousand-year-old (Ka) sea levels. Older terraces from higher present elevations have yielded fewer fossiliferous localities; most higher terrace fossils are from flights of terraces on Palos Verdes Hills (Woodring et al. 1946; 12 mapped terraces) and San Nicolas Island (Vedder and Norris 1963; 14 mapped terraces). The highest fossiliferous terrace of Palos Verdes Hills may be near 1,000 Ka (Muhs and Rosholt 1984). The age of the highest fossiliferous terrace on San Nicolas Island has been estimated by extrapolation of the rates of elevation as indicated by well-dated lower terraces and may be over 1,000 Ka (Muhs 1985). However, no species not known elsewhere in the Californian Pleistocene record are reported from this terrace. So far as is known, all other terrace localities are younger than one million years.

Non-terrace Pleistocene faunas have been described from the San Pedro Sand, Timms Point Silt, and Lomita Marl in Los Angeles Basin. Uranium-series dates based on molluscan material from these units have been considered unreliable (Kaufman et al. 1971). The San Pedro Sand appears to include the youngest sediments of this succession, and the age of its upper portion has been estimated by amino-acid racemization as 350 to 450 Ka; the Timms Point Silt, older and perhaps laterally equivalent to the Lomita Marl in part, yields estimates of 500 to 700 Ka or older (Wehmiller et al. 1977). The fauna of the Lomita Marl has not been completely described. Molluscan species recorded from these three units and their equivalents were used in the compilation.

In Ventura Basin, Pleistocene faunas that could be younger than a million years are known from two formations that have been mapped under a variety of names. Bailey (1935) mapped them as a lower "Santa Barbara Formation" and an overlying and partially interfingering "San Pedro Formation"; neither of the named units has its type locality in Ventura Basin, but the names are used in recent literature and are repeated here (in quotes) to avoid compounding the con-

fusion. The "Santa Barbara Formation" contains volcanic ash beds that have been dated by fission-track methods supported by potassium-argon dates. North of Ventura, the Bailey Ash occurs near the base and the Bishop Ash near the top of the "Santa Barbara Formation" (Sarna-Wojcicki et al. 1987); these ash beds have yielded fission-track ages of 1,200 Ka and 740 Ka, respectively (Izett et al. 1974; Izett 1981; see also Dalrymple 1980). Fossils from stratigraphically above the Bailey Ash in Ventura Basin were included in the compilation. It is possible that a few localities may be older than a million years. However, this does not present a problem, because no species in the living pool occur there that are not known elsewhere in the Pleistocene.

The Santa Barbara Formation proper is known from the small coastal Carpinteria and Goleta Basins (see Upson 1951), which were structurally isolated from Ventura Basin during deposition of the Santa Barbara Formation (Jackson and Yeats 1982). The type locality of the Santa Barbara Formation is in Goleta Basin, and the age relations of the sediments in the small coastal basins and those mapped as "Santa Barbara Formation" in Ventura Basin (see for example Bailey 1954) are uncertain. The Bailey Ash has not been identified in the smaller basins, so the Santa Barbara Formation proper may be younger than that unit, although it is possible that some of the assemblages are over one million years old. The fauna of the Santa Barbara Formation proper was included in the compilation, however.

The main effort in establishing the Pleistocene list was to achieve consistency in species identification with the living fauna. Shell morphology provided the sole criterion, so the comparison is strictly between morphospecies. Nominal subspecies or "varieties" were not recognized as separate entities. Fossil species qualified by either "cf." or "aff." were included. The list was based on an earlier compilation (Valentine 1958) summarized in Valentine (1961). Subsequent records of Californian Pleistocene species occurrences have been reviewed and used, and the earlier records have been revised when required by later work. The more inclusive

later studies include those of Kanakoff and Emerson (1959); Orr (1960); Emerson (1960); Valentine and Meade (1961); Valentine (1962, 1980); Valentine and Lipps (1963); Vedder and Norris (1963); Addicott (1964); Meade (1967); Lipps (1967); Lipps et al. (1968); Valentine and Rowland (1969); Kern (1971, 1977); Kern et al. (1971); Wright (1972); Bishop and Bishop (1972); Kennedy (1974, 1975); and Marinovich (1976). Large, identified, but unpublished, collections from the Santa Barbara Formation (Valentine in preparation) were also used. From all of these sources, a total of 747 molluscan species are listed for the 113 families, somewhat more than are present in the living pool.

### Comparison of the Living with the Pleistocene Fauna

Comparisons between the living and fossil faunas are summarized in Table 1. There are 536 species found on both the living and the fossil lists, constituting 77% of the living pool and 72% of the fossils. Thus, 162 of the living species are not known as fossils in these Pleistocene units, and 211 of the fossil species are not known to be represented by living populations in the Californian region. The fossil list includes 98 species that are extinct. The remaining 113 do not now live in the Californian Province and so are not in the living pool, but they do live to the south (72 species) or to the north (41 species) at present. The presence of these "extralimital" species in the Pleistocene deposits is commonly taken as an indication that the marine thermal regime was at times warmer, at times cooler, or at least at times quite different during the Pleistocene than it is today. This inference seems to be supported by comparisons of the faunas of the various Pleistocene sea levels with oxygen-isotope curves from the deep-sea record (Shackleton and Opdyke 1973; see Wehmiller et al. 1977; Kennedy 1978). The molluscan faunas containing the southern (warm-water) extralimital species (but including some northern forms) are associated with sea levels matching the higher light-oxygen isotopic peaks, while molluscan assemblages that lack warm-water elements, but contain northern extralimital species, are associated with sea



TABLE 1. Summary of the living pool of molluscan species from the Californian region.

	Living	Known fossil	% Known fossil
<b>Bivalvia</b>			
Families	53	48	90.6
Genera	132	111	84.2
Species	230	184	80.1
<b>Gastropoda</b>			
Families	60	53	88.3
Genera	159	130	81.8
Species	468	354	75.6
<b>Total</b>			
Families	113	91	89.4
Genera	291	241	82.8
Species	698	538	77.1

levels matching lower light-oxygen isotopic peaks; presumably these indicate warmer- and cooler-water conditions, respectively. However, paleoclimatic reconstructions of global ocean temperatures (CLIMAP Project Members 1984) indicate that an isotopic substage (5e) represented by sediments containing numerous southern extralimital species was generally no warmer than today. Furthermore, oxygen-isotope paleotemperature estimates based on Californian terrace fossils dated as isotopic substage 5e suggest temperatures about 2.2°C cooler than today's in this region (Muhs and Kyser 1987 and references therein). If these estimates are confirmed by future work, it will obviously require re-evaluation of the climatic implications of the extralimital species.

Finally, there are 12 living species represented in the Pleistocene units that are known only from slope and deep-sea environments today. These forms were not included in either the living or fossil pools and are not involved in any subsequent tallies here. A few species that are not recorded in the Pleistocene are known from older rocks (chiefly outer-shelf forms), and a few are known as fossils in upper Pleistocene deposits outside the Californian region; none of these fossil records is considered further here. The percentages of genera and families from the living pool that were found as fossils are progressively greater than for species, with nearly 90% of the families appearing in the record (Table 1). The missing families are all poorly repre-

sented in the Californian Province; none has more than two species there. These genera and families do have species living elsewhere, however; the genera were not studied further; the families all have fossil records.

The species in the living pool that did not occur on the fossil list were reviewed individually to attempt to understand why they were not present in the Pleistocene units. In general, all of the common and well-known species in the living pool are known as fossils, and most of those are in fact common in the Pleistocene. Those species that are missing from the fossil record tend to be small or thin shelled or from outer-shelf habitats, or share two or more of these attributes. Among the Bivalvia, only the Mytilidae, Pectinidae, Montacutidae, and Cuspidariidae contain more than two missing species (Appendix). The cuspidariids are minute and are found chiefly below 100 meters on the outer shelf. The montacutids are also minute and are thin shelled, and some are rare, known only from one or two dredge hauls; one is essentially a northern species that qualified for the species pool because of a single record from off Santa Rosa Island. The missing pectinids include two cyclopectens from moderately deep water and the offshore islands. Finally, the missing mytilids are mostly small and rare, although one, the appropriately named *Modiolus neglecta* Soot-Ryen, is a good candidate for fossilization, but is not known as a fossil; perhaps it is present, but misidentified, among the Pleistocene records. All of the species in the important bivalve families Carditidae, Lucinidae, Cardiidae, Veneridae, Mactridae and Tellinidae in the living pool are represented as fossils.

Unlike the Bivalvia, only one important, diverse family of Gastropoda is completely represented in the fossil record (Calyptraeidae; see Appendix), and this class is generally less well represented than the bivalves (Table 1), perhaps because it is chiefly epifaunal. The most important gastropod families with significant numbers of missing species are as follows: Trochidae (the missing forms are from moderately deep water); Vitrinellidae (the missing forms are minute, mostly under 5 mm in their longest dimension); Epitoni-

idae (which include both small and exceedingly rare species, some not reported since their original descriptions); Muricidae (the missing species are from moderately deep water, especially species of *Trophonopsis*); Columbellidae (chiefly missing are small, off-shore forms, some of which are poorly known); and Turridae (many missing species are found only in moderately deep water on the outer shelf or around the offshore islands).

All of the species in the living pool that are likely to be of much importance in benthic communities have been found in the Pleistocene record. If there are exceptions, they are likely to be among species of the outer shelf environments, particularly around the offshore islands. This deeper environment is the one least well-represented by the fossils that were studied. Many of the missing forms are unknown or are found only rarely along the mainland shelf. If there are ecological reasons for such restrictions, then it may be that these species never did penetrate into the coastal basins from which our record of this depth zone has been recovered, and thus were not available to be incorporated into the fossil record that we have.

### Discussion

Clearly, species-rich accumulations of dead shells, such as are reported in taphonomic studies, have been captured by the fossil record commonly enough and over wide enough a range of shelf environments to form a surprisingly complete record of the easily fossilized fraction of the living fauna. The completeness of the species pool also implies that the living communities are well represented (see also Woodring et al. 1946; Valentine 1961; Valentine and Mallory 1965). This is true despite the episodic nature of shell-bed accumulations and an unknown rate and pattern of loss of these assemblages before being preserved in lithostratigraphic units.

The living species that are not found in the fossil pool are heavily biased towards minute, fragile, and rare forms, and those that live today in deeper water. Deeper-water Californian Pleistocene deposits have not been given as much attention as have shallow-water

deposits, and it is possible that the deeper-water record is significantly better than we know. In the same light, minute mollusks are probably not as well studied as are large ones, and this may also account for some of the bias. However, it is perfectly plausible that minute species simply have fossilized poorly (e.g., Cummins et al. 1986b).

As for the rare species, their appearance as fossils depends heavily upon sampling intensity, a problem reviewed recently by Koch (1987). If the abundances of fossil species are assumed to approximate a log-series distribution, such as has held for a number of cases (Williams 1964; Koch 1987), then it is possible to estimate the expected success of a given sampling program in recovering rare species. The Pleistocene fauna considered here has been recovered from about 400 localities that yielded an average of about 50 species each, for a total of about 20,000 occurrences (one occurrence being one species at one locality). If this considerable effort of sampling and identification were to be repeated a second time, it is expected that approximately the same number of fossil species would be recovered. However, some of the rarest species in the present fossil pool, found at one or a few localities, would probably not be found in the repeated samples. Instead, other species, so rare as to have been missed during the original sampling, would finally be discovered during the re-collection. If the frequency distribution of the fossil species does approximate a log series, about 10% of the species would be affected (Koch 1987: fig. 1); after doubling the sampling effort, then, about 590 of the 698 species in the living pool (85%) would be known as fossils. Of course it is not certain that a doubling of sampling effort would actually produce another 10% increase in the fossil species record: the samples are not from a homogeneous population, the sampling program is not systematically stratified, preservation bias (perhaps size-related) and other factors may cause significant departures of species frequency distributions from a log series, and so on. Nevertheless, there are clearly more species yet to be found as fossils in the Californian Pleistocene; new studies continue to yield previously undis-

covered forms. It does not seem implausible that the fossil record contains 85% or so of the living species pool, perhaps even a somewhat higher percentage for shallow-water environments. Other durably skeletonized invertebrate taxa besides the gastropod and bivalve families studied here (such as echinoids, bryozoans, ostracodes, and barnacles) should be essentially as well represented, although their records are not as well known, as these taxa are rarely studied.

### General Implications

The Californian Pleistocene benthic shelf record reviewed here holds some implications for the fossil record in general. Perhaps most interesting is that the record has captured all of the important species and species associations, and a very high percentage of all species, important or unimportant, in the families studied. There is no reason to believe that similar fractions of other durably skeletonized groups are not equally well fossilized. This rather good record has been recovered from deposits that represent only a fraction of the million-year interval studied; there are probably fewer than 20 terrace levels, with an average accumulation time of the fossil assemblages studied of perhaps no more than 5,000 years. Thus the terrace deposits may represent at most about 10% of the time span embracing all of the terraces. Indeed, a single terrace locality contains over half of the species in the fossil pool (Kanakoff and Emerson 1959), yet probably represents an accumulation time less than 1% of the million-year span. Several Californian Pleistocene localities contain over 100 species.

The amount of fossiliferous sediment available for collection clearly diminishes through time, because of tectonic destruction or burial (e.g., Gilluly 1949; Veizer and Jansen 1985) or because of erosion, and even within preserved sections, many of the fossils may not survive because of diagenesis. The present study suggests that it is this destruction, and not any lack of accumulation, that accounts for most of the deficiencies in the fossil record of durably skeletonized forms. A very large fraction of durably skeletonized benthic species appears to be captured as fossils in

deposits that become part of the geologic record. It is the deterioration of this good record that creates the gaps and blanks in fossil data.

Fortunately, the fossil record does not deteriorate at the same rate as the geological record, because there is considerable redundancy among localities, both in space and time, in both species composition and community representation. The preservation of only a few of the richer Pleistocene localities would provide a good sample of the fauna of an entire province for a million years—far from perfect, but adequate for many geological and paleobiological purposes. Terraces representing marine isotopic substage 5e are preserved widely around the world, and preservation of a scattering of localities would permit a reasonable reconstruction of global patterns of diversity and endemism of the shelf fauna during that time. Preservation of a similar pattern each million years or so would provide a superb fossil record.

The fossil record is not as good as all that, but this study suggests that it has been that good; that the occasional richly fossiliferous localities of durably skeletonized invertebrates, such as are not uncommon throughout the Phanerozoic column, are not due to especially unusual conditions of fossil accumulation or of fossilization, but to preservation of rich associations that may have been rather common originally, but have been largely destroyed or buried. Of course, shallow-water facies that accumulate as sedimentary veneers are quite vulnerable to erosion, while those that accumulate as sedimentary wedges in basinal deposits are more likely to have a longer geological life. However, rich shell beds are by and large not in the same category as the *lagerstätten* that have yielded rich and unusual assemblages of soft-bodied forms, such as the Burgess Shale or the Solnhofen Limestone. The point here is that the main loss in the numbers of durably skeletonized species that are fossilized does not occur during the incorporation of shells into dead assemblages or even of the dead assemblages into lithologic units as a fossil record, but in destruction of the fossil record itself. I am not sure whether or not this conclusion raises hopes for the discovery of additional



rich localities, but it does seem to be the more valid perspective, and it does seem to imply that in rich localities or locality clusters we may obtain good samples of the original, durably skeletonized faunas.

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## Appendix

The pool of living Californian shelf species and its fossil representation. For each family studied, the number of living species in the pool, the number of these species known as fossils in the selected Pleistocene units, and similar information on the genera, are indicated.

Family	Living species	Known fossil	Living genera	Known fossil
<b>Bivalvia</b>				
Solemyidae	2	0	1	0
Nuculidae	5	3	2	2
Nuculanidae	9	8	2	2
Arcidae	2	2	2	2
Glycymeridae	3	3	1	1
Nucinellidae	1	1	1	1
Philobryidae	1	1	1	1
Mytilidae	21	10	11	9
Pinnidae	1	0	1	0
Pteriidae	1	0	1	0
Pectinidae	11	8	8	7
Limidae	2	1	1	1
Anomiidae	3	2	2	2
Ostreidae	1	1	1	1
Crassatellidae	2	2	2	2
Carditidae	7	7	4	4
Bernardinidae	2	1	2	1
Lucinidae	6	6	5	5
Thyasiridae	3	3	2	2
Ungulinidae	2	2	2	2
Erycinidae	5	5	3	3
Leptonidae	1	1	1	1
Montacutidae	15	5	5	3
Chlamydoconchidae	1	1	1	1
Sportellidae	2	2	2	2
Tortonidae	1	1	1	1
Chamidae	3	3	2	2
Cardiidae	6	6	5	5
Veneridae	18	18	11	11
Petricolidae	3	3	1	1
Cooperellidae	1	1	1	1
Mesodesmatidae	1	0	1	0
Macridae	9	9	4	4
Tellinidae	16	16	3	3
Donacidae	2	2	1	1
Psammobiidae	4	4	3	3
Solecurtidae	2	2	1	1
Semelidae	6	6	2	2
Solenidae	2	2	1	1
Cultellidae	2	2	2	2
Myidae	3	3	3	3
Corbulidae	3	2	2	2
Spheniopsidae	1	1	1	1
Hiatellidae	3	2	3	2
Pholadidae	9	9	6	6
Teredinidae	1	0	1	0
Pandoridae	3	3	1	1
Lyonsiidae	4	2	3	2
Periplomatidae	3	2	1	1
Thraciidae	4	4	3	3
Cuspidariidae	8	2	3	1
Poromyidae	2	1	1	1
Verticordiidae	1	1	1	1
<b>Gastropoda</b>				
Scissurellidae	1	0	1	0
Haliotidae	7	6	1	1
Fissurellidae	14	11	8	6
Acmaeidae	20	17	4	4
Trochidae	33	27	9	9
Liotiidae	3	1	2	1
Skeneidae	4	2	1	1
Turbinidae	9	7	2	2
Phasianellidae	4	4	1	1
Littorinidae	2	2	1	1
Lacunidae	5	4	1	1
Rissoidae	21	20	7	7
Assimineidae	1	1	1	1
Rissoellidae	1	0	1	0
Rissoinidae	6	5	1	1
Truncatellidae	1	1	1	1
Caecidae	7	5	3	1
Cyclostremellidae	2	1	1	1
Vitrinellidae	16	7	6	2

## Appendix Continued.

Family	Living species	Known fossil	Living genera	Known fossil
Orbitestellidae	1	0	1	0
Turritellidae	7	4	3	3
Vermetidae	8	8	4	4
Cerithiidae	16	13	1	1
Cerithiopsidae	19	15	3	3
Diastomatidae	5	4	2	2
Triphoridae	4	3	1	1
Potamididae	1	1	1	1
Epitoniidae	24	18	2	2
Hipponicidae	2	2	1	1
Fossaridae	1	0	1	0
Calyptraeidae	13	13	4	4
Capulidae	1	0	1	0
Naticidae	7	6	5	4
Lamellariidae	4	3	3	2
Triviidae	5	5	2	2
Cypraeidae	6	1	2	1
Cymatiidae	2	1	2	1
Bursidae	1	1	1	1
Muricidae	38	23	11	7
Coralliophilidae	1	0	1	0
Rapanidae	1	1	1	1
Thaididae	5	5	2	2
Neptunidae	5	5	5	5
Columbellidae	20	13	4	4
Nassariidae	7	6	1	1
Fasciolaridae	5	5	1	1
Turbinellidae	1	0	1	0
Olividae	3	3	1	1
Marginellidae	5	5	3	3
Mitridae	3	2	1	1
Cancellariidae	6	4	2	2
Conidae	1	1	1	1
Terebridae	1	1	1	1
Turridae	55	38	18	14
Acteonidae	5	4	1	1
Haminoeidae	3	3	2	2
Retusidae	4	2	2	2
Scaphandridae	11	10	2	2
Melampidae	3	1	3	1
Siphonariidae	3	3	3	3