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Evolution and extinction of Partulidae, endemic Pacific island land snails

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SUMMARY

The broad outline of the systematics of the endemic Pacific island land snail family Partulidae has been understood for some time. The family is divided into three genera: *Eua* has four species, confined to Tonga and Samoa; *Samoana* has about 23 species, widely but sporadically distributed in Polynesia and the Mariana Islands; *Partula* has about 100 species, distributed from Belau to the Society Islands.

This review integrates this systematic and biogeographic knowledge with work on ecology, population genetics and speciation that has concentrated especially on the recently speciated *Partula* spp. of Moorea in the Society Islands. Explanations of Moorean diversity (much of which seems unrelated to ecological factors) based on parapatric speciation and the evolution of morph ratio clines in the absence of isolation have predominated, although without incontrovertible support. Unitary explanations are probably not appropriate.

Rather little is known of the basic biology of partulids. They are generally arboreal; feed on a wide range of partially decayed and living plant material; and are relatively long-lived, slow reproducing, ovoviviparous, cross- or self-fertilizing hermaphrodites.

The phylogenetic and geographical origins of the three genera are unknown. *Partula* may have evolved, somewhere unknown, from *Samoana*, which evolved from *Eua* in the Tonga–Samoa region, this being the region of origin of *Eua*; but the opposite sequence has also been postulated. The question is unresolved.

Origins of the Moorean species are better understood as their inter-relationships are relatively clear. Rather few dispersal events probably took place and the Society Island fauna as a whole may be derived from but two colonization events – first by a *Samoana* sp. and later by a *Partula* sp., both of which then speciated *in situ* – with a few intra-archipelago colonization events taking place subsequently, predominantly in a southwesterly direction from the older to the younger islands.

Many of the questions posed by the group may never be answered. Some species, notably those of Moorea, are already extinct in the wild; others are severely threatened. Artificial introductions of both plants and animals, combined with urban and agricultural development, have had significant impacts,

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but ill-conceived biological control programmes, targeted at the Giant African Snail, *Achatina fulica*, constitute currently the most serious threat.

However, significant areas are still open to research. Analysis of DNA variation, combined with modern ideas of Pacific biogeography, should allow the whole range from the broad origins of the fauna to the detailed evolution within groups of species to be addressed. Some species may yet be relatively secure in the wild and allow field studies, but extraction of DNA from museum specimens provides an exciting opportunity to continue unravelling the evolutionary history of these endangered snails and to contribute further to our understanding of evolutionary processes and the biogeography of the Pacific.

1. INTRODUCTION

The biotas of islands, especially tropical islands, and in particular the myriad islands of the Pacific Ocean have been, since at least Darwin's time (Cain 1984*a*), of considerable interest to biogeographers and evolutionary biologists (e.g. Allee & Schmidt 1951; Carlquist 1965, 1974; Darlington 1957; Gressitt 1963; Mayr 1963; Udvardy 1969; Watts 1971) and have generated a huge body of literature, both theoretical and empirical or observational (e.g. Bengtson & Enckell 1983; Diamond & May 1976; MacArthur & Wilson 1967; Simberloff *et al.* 1981; Williamson 1981, 1983). Perhaps the classic examples of adaptive radiation come from birds on Pacific islands – Hawaiian honeycreepers (Amadon 1950; Freed *et al.* 1987) and Galapagos finches (Grant 1986) – and intensive work on Hawaiian Drosophilidae (see Carson 1982, 1987*a*, *b*; DeSalle & Hunt 1987; Kaneshiro & Boake 1987), drawing on aspects of their behaviour, genetics, biogeography and ecology, has brought major new insights to our understanding of the process of speciation.

This importance of islands to evolutionary biologists is due especially to islands' geographical isolation and discreteness, the opportunity for successive re-invasions of particular islands, the potential for replication of observations on more than one island, and the very recent geological origin of many, particularly volcanic, islands (Carlquist 1965; Carson 1987*c*; Clarke & Murray 1969; Moulton & Pimm 1986; Peake 1973; Tillier & Clarke 1983). Tropical islands, in particular, have assumed special significance because, in general, they have more complex faunas and fewer catastrophic climate-related extinctions than temperate islands, and because animals invading a tropical island with many geographical and floral niches, especially with steep mountains and valleys as found in many of the high islands of the Pacific, are subject to isolation and disruptive selection leading potentially to local speciation (Clarke & Murray 1969; Moulton & Pimm 1986; Zimmerman 1948).

Although much of the land snail diversity on Pacific islands is of small, relatively drab species, a number of major families are involved (Solem 1976, 1981, 1983), some of which have radiated spectacularly. However, it is the four families Endodontidae, Amastridae, Achatinellidae and Partulidae, endemic to Pacific islands and generally not found in regions around the rim, that have attracted most interest from evolutionary biologists. (Extensions of the distributions of *Tornatellinops* and, especially, *Elasmias* (both Achatinellidae) into Australia, south east Asia and islands of the Indian Ocean may be explained as artificial introductions if the species involved ultimately prove to be synonyms of Pacific species (Zimmerman 1948), although Cooke & Kondo (1960), despite implying human agency in extending the distributions of these genera, kept these extra-Pacific species distinct.) Among these Pacific endemic groups, the often visually polymorphic, predominantly arboreal Achatinellinae (Achatinellidae) and Partulidae have been most studied.

More than 200 species names have been applied in the genus *Achatinella* (Achatinellinae), which is endemic to the small Hawaiian island of Oahu; *Achatinella* offers one of the most spectacular examples of local radiations among land snails world wide. While this genus, and the other Hawaiian Achatinellinae, have attracted extensive and detailed work on their taxonomy and distribution (e.g. Cooke & Kondo 1960; Pilsbry & Cooke 1912–14; Welch 1958 and references therein), their rapid demise during the twentieth century (Hadfield 1986) has precluded thorough modern evolutionary and population genetic analysis, although some work on their growth, demographics and population dynamics (Hadfield 1986; Hadfield & Mountain 1980; Hadfield & Miller 1989; Severns 1981) has been accomplished, with a view, in part, to providing basic data for their conservation. As first suggested by Gulick (1872, 1873, 1905), whose ideas on isolation were acknowledged by Sewall Wright (e.g. 1978) as a significant contribution to the development of evolutionary thought (see Carson 1987*c*), much of the variation in these snails may well have been related to stochastic events, including founder effects and genetic drift, as small propagules became isolated in the numerous steep-sided valleys of the Hawaiian islands, rather than to finely tuned adaptation (see, in addition, Carlquist (1974)).

The Partulidae, although on the whole not as dramatically speciose over small areas as the Achatinellinae, have a much wider overall distribution (figure 1) throughout the high volcanic islands (not atolls) of the tropical Pacific, from Belau and the Marianas in the northwest to the Marquesas, Austral and Society Islands in the southeast (Kondo 1968; Kondo & Burch 1972). (Island names follow Motteler (1986).) Well over 200 species names have been applied in the family (Richardson 1990). Kondo (1968) listed, with their distributions, all species he considered valid (120 species), and, combined with some earlier, more detailed information (Kondo 1955; Pilsbry 1909–10) and a small number of subsequent additions and revisions (Johnson *et al.* 1986*a*; Kondo 1970, 1973, 1980; Kondo & Burch 1983, 1989), this

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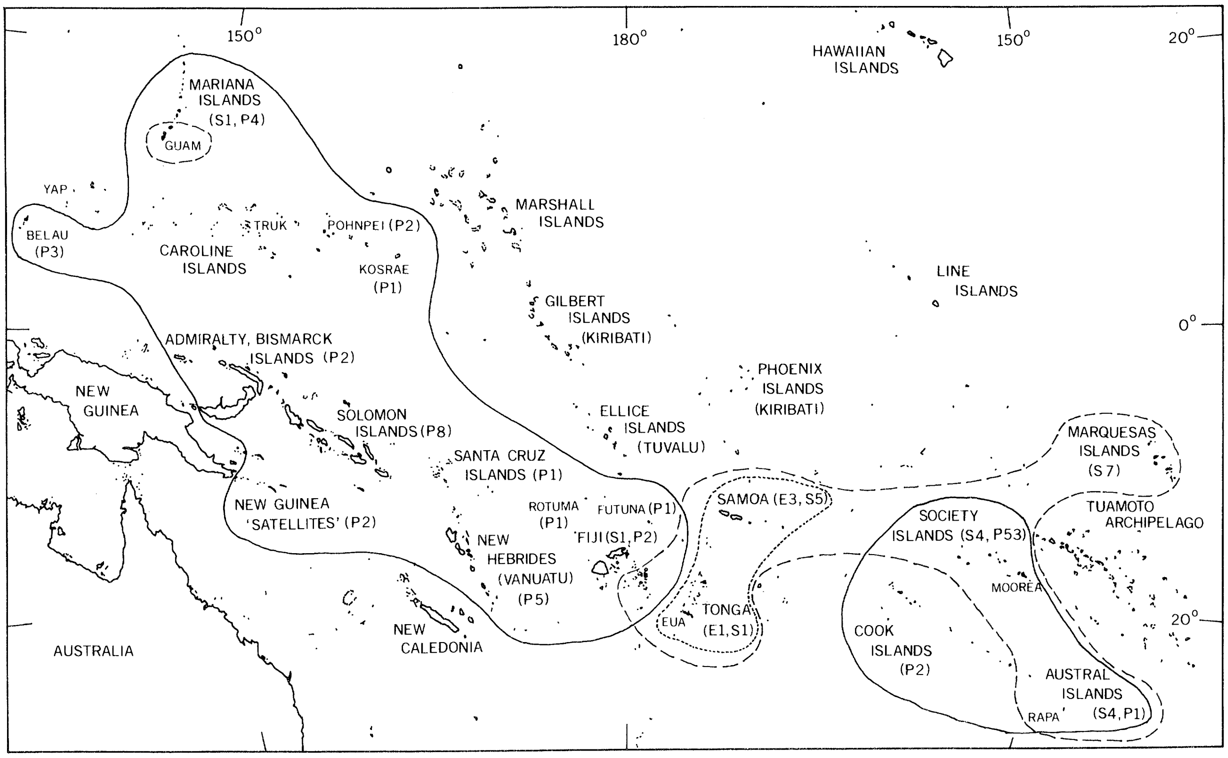

Figure 1. Distribution of Partulidae: *Eua* (dotted line), *Samoana* (dashed line) and *Partula* (solid line). The numbers of species of *Eua* (E), *Samoana* (S) and *Partula* (P) on each island or island group are shown in parentheses. Distribution details and number of species for each island or island group are based on the list of Kondo (1968) with modifications and further detail derived from Johnson *et al.* (1986*a*), Kondo (1955, 1970, 1973, 1980), Kondo & Burch (1983, 1989), Pilsbry (1909–10), and from the status of the Moorean species as discussed in this review. The doubtful records of *P. newcombiana* from Talaud and *P. grisea* and *P. bulimoides* from New Guinea are omitted. Subspecies are ignored. *P. hyalina* is counted in the Society, Cook and Austral Islands; all other species are endemic to the island or island group indicated.

list provides the basis for figure 1. Kondo (1968) implicitly lumped a significant number of taxa, notably those considered by Solem (1959) from the New Hebrides, and suggested that continued study would result in further lumping (notably of the Solomon Islands species; Clench 1941); his list may be a more biologically meaningful representation of diversity in the family, although far less comprehensive or systematically informative, than the list of Richardson (1990), which included 143 species.

The purpose of this review is to draw together the considerable body of research that, on the one hand, has dealt with the taxonomy, systematics and to some extent the biogeography of the Partulidae as a whole, and on the other hand, has asked detailed questions of population genetics and speciation within a small subset of species endemic to the Society Islands of French Polynesia.

Many of the 120 or more species of Partulidae, representing but three genera, are confined to single islands. All bear more or less conical shells (figure 2) with adult shell height ('length' of some authors) ranging from about 11 mm (e.g. *P. arguta* of Huahine) to 30 mm (e.g. *P. calypso* of Belau) but with most species intermediate in size (Kondo 1955; Pilsbry 1909–10). Although new species continue to be discovered and described (e.g. Kondo 1980; Kondo & Burch 1989), the broad taxonomic outline of the family has been understood for some time (Kondo 1955, 1968; Pilsbry 1909–10; Pilsbry & Cooke 1934).

With this high diversity and, in some species, striking levels of shell colour and pattern polymorphism, the group has attracted the interest of evolutionary biologists since the work of Garrett (1884). In particular, considerable information on both inter- and intraspecific variation in the family, based on extensive collecting activity, was accumulated early this century by H. E. Crampton (1916, 1925*a*, 1932). Although this early work was carried out without the advantages of a modern background in population genetics and evolutionary biology (see Cowie 1989), it nevertheless laid the foundation for an extensive research programme, carried out over the last three decades, focusing primarily on the *Partula* spp. of Moorea in the Society Islands of French Polynesia, a body of research that has had a significant impact on our understanding of speciation and reproductive isolation and has fuelled debate on adaptation and the maintenance of polymorphism in natural populations (see, for example, Barton 1988; Barton & Charlesworth 1984; Butlin 1989; Endler 1977; White 1978*a*).

The special value of the Partulidae to students of evolution is due to a combination of characteristics (Clarke & Murray 1969): the family is widespread, speciose, and displays high levels of intraspecific diversity; frequently, closely related species occur in

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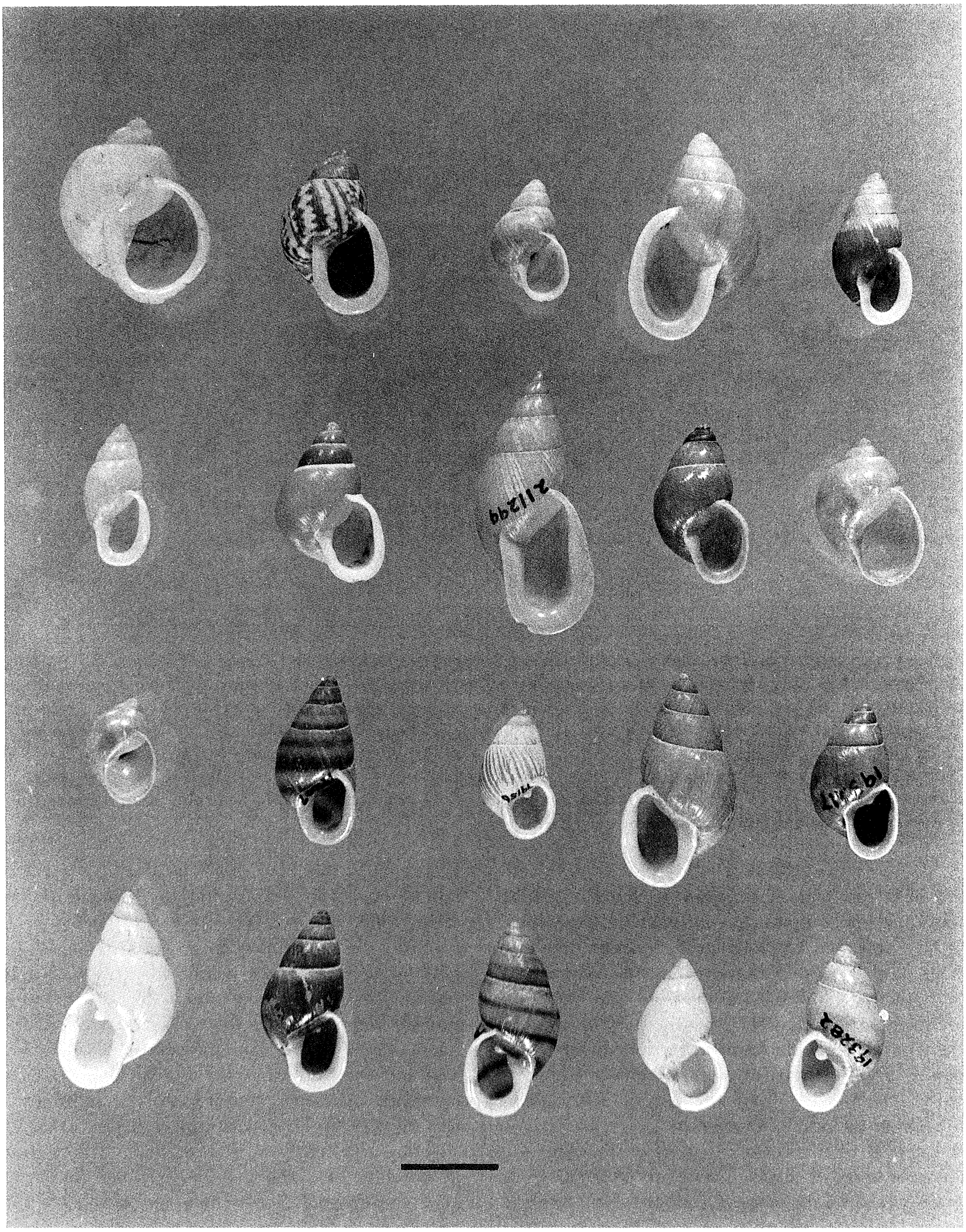

Figure 2. Some of the Partulidae mentioned in the text to illustrate the range of shell shape, size and colour and pattern in the family. The scale bar represents 1 cm. Top row, left to right: *Eua globosa*, Eua, Tonga (Bishop Museum catalogue number: BPBM 108558); *E. zebrina*, Tutuila, Samoa (BPBM 84457); *Samoana fragilis*, Guam, Mariana Islands (BPBM 153051); *S. conica*, Tutuila, Samoa (BPBM 85475); *S. burchi*, Tahiti, Society Islands (BPBM 206915). Second row, left to right: *S. attenuata*, Tahaa, Society Islands (BPBM 139749); *Partula gibba*, Guam (BPBM 152740); *P. calypso*, Oreor, Belau (BPBM 211299); *P. assimilis*, Raratonga, Cook Islands (BPBM 95426); *P. turgida*, Raiatea, Society Islands (BPBM 136085). Third row, left to right: *P. arguta*, Huahine, Society Islands (BPBM 142379); *P. producta*, Tahiti, Society Islands (BPBM 79207); *P. filosa*, Tahiti (BPBM 79156); *P. otaheitana*, Tahiti (BPBM 193821); *P. mirabilis*, Moorea, Society Islands (BPBM 193217). Bottom row, left to right: *P. tohiveana*, Moorea (BPBM 193763); *P. suturalis* (dextral), Moorea (BPBM 193310); *P. suturalis* (sinistral), Moorea (BPBM 193333); *P. taeniata*, Moorea (BPBM 193512); *P. mooreana*, Moorea (BPBM 193284).

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complex patterns of sympatry and parapatry, sometimes with only partial reproductive isolation; their low vagility leads to genetic differences between populations only short distances apart; and their growth is determinate, adulthood marked by the formation of a flared lip at the shell aperture (cf. Gould 1989). These features are superimposed on the more general characteristics of land snails that make these animals amenable to ecological and evolutionary investigation (Clarke 1978): among others, the ease with which they can be sampled without the need for trapping, the ease with which they can be marked permanently, and the fact that the shell, even in the dead animal, provides a record of its own development and growth. Partulids are also, in contrast to Achatinellinae (M. G. Hadfield, personal communication), easy to maintain in the laboratory (Clarke & Murray 1969). Thus far, studies on *Partula* spp., particularly on the French Polynesian island of Moorea, 'have revealed in exceptional detail the pattern of interactions between incipient species, and have presented some fascinating paradoxes' (Murray & Clarke 1980); such examples of partial speciation have been significant in development of ideas on the origin of species (e.g. Mayr 1963); and indeed, the group offers 'both a museum and a laboratory of speciation' (Murray & Clarke 1980).

2. EXTINCTION

Tragically, the fate of most of these and other Pacific land snails is in the balance; for some it is already too late. Although habitat destruction, over-collecting by shell collectors and predation by accidentally introduced animals (notably rats, but perhaps also ants; Solem 1973; Tillier & Clarke 1983) have certainly been factors in the extinction of some Pacific island land snails, e.g. many Hawaiian *Achatinella* spp. (Hadfield 1986) and some of the Partulidae of Guam (Hopper & Smith 1992), the deliberate introduction of carnivorous snails (most significantly *Euglandina rosea* but also *Gonaxis* spp.) on many Pacific islands (and elsewhere; Woodward 1989; Wells 1990) since the early 1950s (Davis & Butler 1964; Eldredge 1988; Funasaki *et al.* 1988; Hopper & Smith 1992; Howarth 1991; Mead 1961, 1979; Takeuchi *et al.* 1992; Tillier & Clarke 1983) in well-intentioned but ill-conceived attempts to control the introduced Giant African Snail, *Achatina fulica*, considered a pest of crops and gardens, has intensified dramatically the threat to the remaining species. *E. rosea* was the precipitous cause of the extinction of Moorean *Partula* spp., the process taking only 10 years from introduction to complete destruction in the wild (Clarke *et al.* 1984; Murray 1989; Murray *et al.* 1988); the partulids of Tahiti and Guam are either extinct or close to extinction for the same reason (Wells 1990; Eldredge 1988; Hopper & Smith 1991; Pointier & Blanc 1982; Tillier & Clarke 1983).

There is no good evidence for the efficacy of these carnivorous snails in controlling *A. fulica*, whose populations on most islands, following initial explosion, seem to decline naturally (although the proximate cause of this decline can only be speculated upon) (Christensen 1984; Mead 1955, 1961, 1979; Pointier & Blanc 1982; Takeuchi *et al.* 1991; Tillier & Clarke 1983; Waterhouse & Norris 1987). For instance, *A. fulica* populations have declined on Huahine-Nui in the Society Islands just as they have on Moorea and Tahiti, also in the Society Islands, although *E. rosea* was not introduced to Huahine; and *A. fulica* declined prior to the spread of *E. rosea* into certain valleys on Moorea (Pointier & Blanc 1982; Tillier & Clarke 1983). Populations of *A. fulica* in Hawaii have declined dramatically over the last 30 years or so, and, whereas some argue, from the coincidence of this decline with the introduction of carnivorous snails, that the biological control programme has been successful (Davis & Butler 1964), neither adequate preliminary evaluations nor control experiments were ever done and the purported impact of predation by the introduced snails on *A. fulica* (Nishida & Napompeth 1975) remains unproven. There is no established causal link (Christensen 1984; Hadfield & Kay 1981; Tillier & Clarke 1983; Woodward 1989); and indeed, experiments suggest that, in fact, *E. rosea* prefers small snails, perhaps such as *Achatinella* spp., to large ones like *A. fulica* (Cook 1989). Various other factors have been suggested as responsible for this characteristic population decline (following initial explosion), which may be something of a general phenomenon associated with at least some introductions of non-native species (see, for example, King (1990); Williams (1987)). Diseases, from which the initial introductions escaped, but which ultimately caught up with the expanding populations, causing their decline, have perhaps been most frequently invoked (e.g. Mead 1955; Pointier & Blanc 1982; Tillier & Clarke 1983), although genetic effects akin to inbreeding depression may also play a part (cf. Sailer 1978; Simberloff 1986), as may predation by subsequently introduced organisms (Eldredge 1988; Tillier & Clarke 1983), but competition with later introductions (cf. examples given by Clausen (1978)) is so far probably unimportant.

Nevertheless, despite this lack of evidence supporting the control programmes, yet abundant evidence of their negative effects on native snail faunas, the carnivorous snails are still considered of potential utility by some (Leehman 1981; Schreiner 1989) and deliberate introductions continue (e.g. of *E. rosea* to American Samoa and Belau in the last decade or so; Eldredge 1988; Hadfield & Kay 1981; L. G. Eldredge, personal communication), giving immediate cause for serious concern (Tillier & Clarke 1983).

The plight of the partulids, in particular, has attracted considerable attention because of the significant body of evolutionary and systematics research they have generated (see, for example, the popular article by Gould (1991)). Sixteen species (along with 48 Achatinellidae) are listed in the *1990 IUCN Red List of Threatened Animals* (IUCN 1990); no doubt many others are under threat, but for most no assessment of their current status has been made. A number of institutions around the world are engaged in captive breeding of some of the *Partula* spp., a holding

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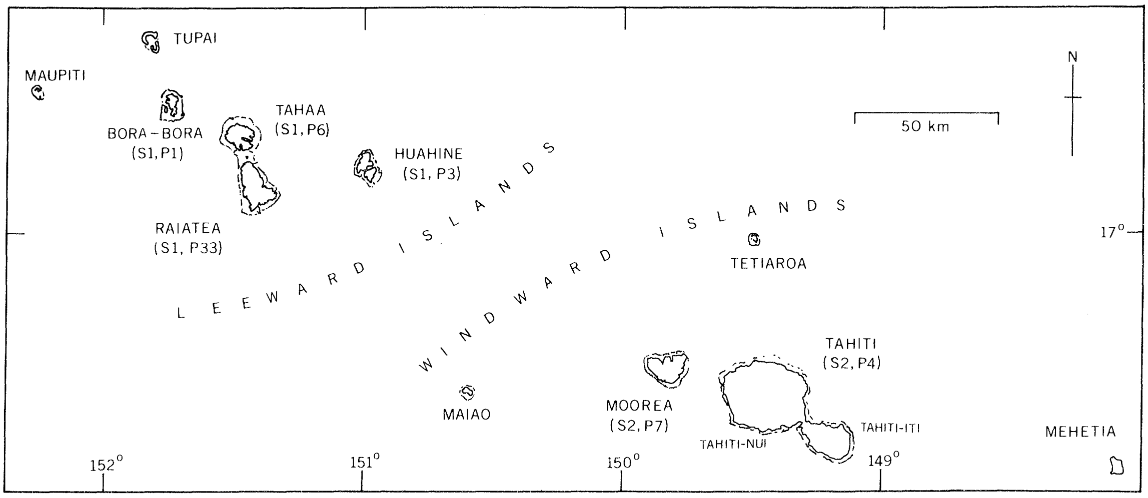

Figure 3. Distribution of partulid diversity in the Society Islands. The numbers of species of *Samoana* (S) and *Partula* (P) on each island are shown in parentheses. Details are based on the list of Kondo (1968) with modifications derived from Johnson *et al* (1986*a*), Kondo (1973), Kondo & Burch (1983), and from the status of the Moorean species as discussed in this review. Subspecies are ignored. *S. attenuata* is counted on Bora-Bora, Tahaa, Raiatea, Moorea and Tahiti; *P. faba* is counted on both Bora-Bora and Raiatea; otherwise, all species are endemic to single islands. (The three northwesternmost islands in the archipelago (Maupihaa, Manuae and Motu One) are atolls, support no Partulidae and are not shown).

operation in the hope that, one day, they will be released back into the wild (Tillier & Clarke 1983; Wells 1990; Woodward 1989; and see the popular article by Meadows (1989)).

3. ORIGINS AND BIOGEOGRAPHY

Four major families of land snails, the Endodontidae, Achatinellidae (including Tornatellinidae; Cooke & Kondo 1960), Amastridae and Partulidae, are the dominant and endemic groups of the inner Pacific (excluding surrounding Pacific rim regions) (Kondo 1956; Kondo & Burch 1972; Solem 1981). The origins of these families are not clear but the Achatinellidae, Amastridae and Partulidae are thought to be ancient families (order Orthurethra) derived from the earliest pulmonate snails to have come out on to land during the late Palaeozoic (Kondo & Burch 1972; Pilsbry 1900*a*), whereas the Endodontidae are considered to be the most primitive of the 'higher' pulmonates (order Sigmurethra) (Solem 1976). The phylogenetic relationships of the Endodontidae are well understood (Solem 1976, 1983; Tillier 1989), but those of the three more ancient, and very distinct, families remain somewhat speculative: the Amastridae may be close to the Holarctic Cochlicopidae or Palaearctic Ferussaciidae; the Partulidae seem to be related to and perhaps derived from the Old World Enidae; and the Achatinellidae have no known nearest relatives although they seem to group with the Pupillidae, Valloniidae and Pyramidulidae (Solem 1959, 1979, 1981; Tillier 1989).

Prior to the wide acceptance of the theory of plate tectonics and the consequent better understanding of the geological history of the Pacific basin, and the discovery of significant fossil material, the current endemic Pacific distributions of these three orthuréthran families were explained either (i) by postulating an ancient origin, perhaps in the Pacific (Kondo 1956), followed by diversification within the Pacific (Kondo & Burch 1972), perhaps on large hypothetical mid-Pacific land masses (Pilsbry 1900*b*, 1909–10, 1916), or (ii) by a more recent peripheral continental origin and subsequent overseas dispersal (Vagvolgyi 1975). However, the discovery of 'modestly diverse' achatinellid faunas, represented by the genus *Anthracopupa*, in the late Palaeozoic of North America and Europe (Solem 1979, 1981; Solem & Yochelson 1979), combined with modern knowledge of continental drift, implies an ancient, probably Pangean origin for the Achatinellidae (although the family affinities of *Anthracopupa* are somewhat controversial; Solem & Yochelson 1979). Fossil Achatinellidae (*Protornatellina isoclina*) are known subsequently only from the Cretaceous of Wyoming (Solem 1979, 1981; Solem & Yochelson 1979) and the sequence of events leading to the continental demise and present Oceanic distribution of the Achatinellidae is unknown. Endodontid fossils ranging back to the lower Miocene are known from the Marshall Islands and Pleistocene fossils have been found at Midway (Ladd 1958, 1960; Ladd *et al.* 1967; Solem 1976, 1977). Otherwise, these endemic Pacific families have no fossil record and their ages and geographic origins cannot be elucidated further (see, in addition, Peake (1981)). That Pacific islands could have served as refugia for ancient faunal segments, even within the context of plate tectonics, has been suggested by Kay (1980), both generally and specifically with regard to the pre-Mesozoic ancestors of present day land snails.

The phylogenetic relationships and geographic origins of the Partulidae are, then, unknown. The family comprises but three genera, *Eua*, *Samoana* and *Partula*, distinguished, in increasing order of complexity, on

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the basis of their penial anatomy (Pilsbry & Cooke 1934; Kondo 1970; Kondo & Burch 1972). *Eua*, with four species is narrowly confined to Tonga and Samoa; *Samoana*, with about 23 species is distributed sporadically from the Mariana to the Marquesas Islands; and *Partula*, with 90 or more species, is the most widespread, found from Belau and the Marianas (and perhaps even Talaud) to the Society Islands (Kondo 1968, 1980; Kondo & Burch 1972; Richardson 1990) (figure 1). Of the major groups of high islands in the Pacific, Partulidae are absent only from the Hawaiian archipelago (where the Achatinellinae seem to replace them in some respects). It is in the Society Islands that the family expresses its greatest diversity (figure 3): between 50 and 60 *Partula* spp. (close to half the total number of species in the family) and four *Samoana* spp. are endemic to these islands (Crampton 1956; Crampton & Cooke 1953; Johnson *et al.* 1986a; Kondo 1968, 1973, 1980). Whereas the *Partula* spp. of the Society Islands are endemic to particular islands, the fewer *Samoana* spp. of these islands are not all so confined; *S. attenuata*, for instance, is known from Tahiti, Moorea, Tahaa, Raiatea and Bora-Bora (Kondo 1973).

Two hypotheses of the generic-level evolution of the group have been put forward (Kondo 1968; Kondo & Burch 1972):

1. *Eua*, with the simplest penial morphology, evolved from the ancestral stock in the Samoa–Tonga region; *Samoana* evolved from *Eua*, also in this region; and *Partula*, with the most complex penial morphology, evolved from *Samoana* in an unknown region (perhaps somewhere in Polynesia; Peake 1968). Support for this was considered to derive (Kondo 1968; Kondo & Burch 1972) from the co-existence of *Eua* and *Samoana* in Tonga-Samoa to the exclusion of *Partula*, the displacement of *Samoana* (see Clarke & Murray 1969; Johnson *et al.* 1986a; Kondo 1973; Murray & Clarke 1980) to the tops of tall trees or to mountain tops on islands where it does co-exist with *Partula*, and the occurrence of *Eua globosa* on one of the oldest islands in the Pacific (Eua in the Tonga group).
2. The more widespread genus (*Partula*) is the more primitive and the more restricted genera (*Eua*, *Samoana*) more specialized. Evolution was thus in the reverse direction to that suggested in (1), above, from the more complex to the simpler morphology. Support for this scenario is said to come from serological studies (Kondo & Burch 1972).

None of these arguments is convincing and the question remains open, despite further speculation (Kondo 1973, 1980) on the dispersal of *Samoana* and *Partula*, harking back to early ideas (see above) of large, mid-Pacific land masses (Pilsbry 1900*b*, 1909–10, 1916) that have been resurrected, but also severely criticized, with the advent of vicariance biogeography (Miller & Naranjo-García 1991; Nelson & Platnick 1981; Nelson & Rosen 1981; Thornton 1983), and speculation (Ladd 1960; Solem 1959, 1976) that many of the now submerged seamounts formerly projected above the ocean surface, providing more stepping stones for dispersal than are currently above sea level. Indeed, there is no reason to presume that evolution of the three genera was sequential; for instance, *Partula* might be ancestral, having spread eastwards across the Pacific (as have other organisms: see, for example, papers in Gressitt (1963), Kay (1980), Peake (1969) and Zimmerman (1948)), and have given rise to both *Samoana* and *Eua*. We simply do not have adequate information on the number, direction and chronology of colonization events during the history of the Partulidae (White 1978*a*) nor on the detailed phylogenetic relationships within the largest genus, *Partula*; and the geological and eustatic history of the Pacific remains controversial (papers in Nelson & Rosen 1981; Paulay & McEdward 1990). Furthermore, the division of the family into these three genera and the allocation of species among them, based almost entirely on variation in genital morphology, may be inaccurate. Genital anatomy may be subject to convergence (Johnson *et al.* 1986*a*), although allozyme studies (Johnson *et al.* 1986*b*) suggest that the broad generic distinctions are legitimate. Why, for instance, are there only four species of *Eua*, confined to the single Tongan island of Eua and to Samoa, yet 90 or so *Partula* spp., spread across the whole of the Pacific? Why are there no *Eua* in the Fijian archipelago, and no *Partula* in Tonga, Samoa or the Marquesas? Why is the distribution of *Samoana* disjunct, with all *Samoana* spp. found in Polynesia, except for *S. fragilis*, which is endemic to Guam near the western edge of the distribution of the family; is *S. fragilis* really a species of *Samoana*; and is *Samoana* a legitimate genus? Why is *Partula* found in Pohnpei, Kosrae, the Marianas and Belau, but not on Truk or Yap? And why is the family not represented in New Caledonia and New Guinea? More detailed, multivariate studies combining analysis of both soft anatomy and shell characteristics are probably needed, despite the implications of Kondo (1980) that shell characters may be insignificant; and, just as molecular data had begun to provide a clearer understanding of the evolutionary origins of the Moorean species (Murray *et al.* 1991), questions relating to the wider origins of the whole family throughout the Pacific will probably only be answered by augmenting morphological studies with modern analyses of molecular, especially DNA, variation, and setting this within the context of modern ideas of biogeography, geology and eustatics in the Pacific.

4. ECOLOGY AND ECOLOGICAL DIFFERENTIATION

The ecology of partulids has been rather little studied, most workers having concentrated on systematics and population genetics. Crampton's monographs (Crampton 1916, 1925*a*, 1932) contain much anecdotal natural history, although his focus was more on the quantification of morphological variation and the mechanisms controlling it. We know little about population dynamics, life-history strategies, food preferences, inter- and intraspecific competition, predators and so on. None the less, such basic information is essential to a full understanding of the evolution of the group and what little is known has proved significant in this endeavor.

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(*a*) *Breeding system*

Partulidae are ovoviviparous hermaphrodites in which the eggshell is resorbed by the parent before birth (Clarke 1968; Murray & Clarke 1966). Gravid animals contain anything from one to ten (usually two to three) eggs or juveniles in the brood pouch (Mayer 1902; Crampton 1916, 1925*a*, 1932). Most of those species thus far studied directly (*Partula* spp. only, in laboratory breeding experiments) cross-fertilize almost exclusively, although at least five species of Moorean *Partula* are capable of low levels of self-fertilization (Murray & Clarke 1966). The two most studied species do, however, differ in detail. Self-fertilization in *P. taeniata* is responsible for about 20% of production in the early part of reproductive life, declining to undetectable levels later, and averaging about 2% throughout life (Murray & Clarke 1976*a*). In *P. suturalis*, there is no evidence of changes in selfing frequency through life, the rate being about 1–2%, but possibly with significant levels of individual variation, for which there is no explanation (Murray & Clarke 1976*b*). In contrast, *P. gibba* from Saipan near the western boundary of the distribution of Partulidae, appears to be predominantly, if not entirely, self-fertilizing, isolated virgin snails in the laboratory producing offspring at the same rate as those with mates (Johnson *et al.* 1977); and this laboratory behaviour is, no doubt, a good indicator of the behaviour of *P. gibba* in the wild, as, in common with other selfing organisms including other terrestrial Mollusca (see, for example, Foltz *et al.* (1984)), it shows lower (in fact zero) allozymic variability than known outcrossers (Johnson *et al.* 1977). On the basis of low allozyme variability, the four *Samoana* spp. of the Society Islands may be predominantly selfers, contrasting with *S. conica* of Tutuila (American Samoa) (Johnson *et al.* 1986*a*).

Nothing is known of the distribution of selfing in other partulids and the hints that *Partula* spp. are generally outcrossers and *Samoana* spp. tend to be selfers may be misleading. Assessments from laboratory breeding experiments of the relative significances of selfing and outcrossing in the wild must be viewed with some caution as possible reduced availability of mates in the wild may lead to increased levels of selfing compared to levels detected in laboratory experiments in which mates are readily available. Confirmatory evidence from DNA or allozyme studies, or at least evidence of the level of selfing in isolated animals, should be sought, as above.

Although those partulids whose behaviour has been studied directly, appear to be predominantly outbreeding hermaphrodites, as many other land snails (Tompa 1984), they contrast with the admittedly rather few snail species that have been studied in detail in that mating is not reciprocal. Behavioural studies of *P. taeniata* and *P. suturalis* (Lipton & Murray 1979) show that during mating one individual acts as a male and the other as a female; sometimes, once mating is complete, the roles are reversed and a further courtship sequence takes place, although this may be less successful.

(*b*) *Life history*

Compared with the Achatinellinae (e.g. *Achatinella* spp. and *Partulina* spp.; Hadfield 1986; Hadfield & Miller 1989; Hadfield & Mountain 1980), partulids are faster-growing and produce young at a more rapid rate (table 1). For instance, in the laboratory *Partula suturalis* and *P. taeniata* reach maturity (formation of a reflected shell lip and enlargement of the reproductive organs) in about a year or less, produce their first offspring from about four months to a year later, and give birth to a single juvenile on average about every 20 days thereafter (Murray & Clarke 1966). *P. taeniata* in the wild lives for at least 5 years after achieving maturity (Murray & Clarke 1984); Achatinellinae live up to at least 18 years (table 1).

None the less, both the Achatinellinae and the Partulidae are relatively slow-growing, long-lived and slow-reproducing land snails, relatively ‘K-selected’ compared to more ‘r-selected’ egg-laying generalist species such as *Achatina fulica* (Kekauoha 1966; Mead 1961) or the helicid *Theba pisana* (Cowie 1984*a*), which reach maturity more quickly and produce a larger number of relatively smaller hatchlings over a shorter adult life (table 1). These aspects of the life histories of Achatinellinae and Partulidae almost certainly have been significant in the vulnerability of these species to over-collecting and unnaturally high levels of predation by introduced organisms (Hadfield 1986).

(*c*) *Predation*

The natural predators of partulids are largely unknown; they may well have included extinct species of birds (Clarke 1968). Crampton (1916) considered there to be virtually no predation on the partulids of Tahiti (although he did note some rat predation), and indeed this may well be close to the truth as far as natural predation is concerned. Clarke (1968) speculated that a native kingfisher might be a predator of *Partula* on Moorea but felt that its impact would be unimportant.

Partulid evolution, and perhaps achatinelline evolution more so, may well have occurred in the absence or near absence of predation, thus allowing the evolution of the life-history strategies indicated above. However, because of this evolution in the absence of natural enemies, introduced predators, including those introduced for biological control of *Achatina fulica* (see above), constitute a major threat to the survival of many, if not all, of these snails, which are unable to withstand such intense pressure.

Kondo (1973) noted shell damage to *Samoana burchi* due to an unknown predator, possibly introduced rats, and G. A. Solem (according to Emberton (1982)) considered Tahitian partulids to suffer extensive rat predation. Clarke (1968) suggested that feral jungle fowl, rats and pigs might be predators of *Partula* on Moorea but that rats were perhaps its only important enemies. Introduced rats and ants have probably had a serious impact on other Pacific land snails (Hadfield 1986; Solem 1973; Tillier & Clarke 1983). The

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Table 1. *Comparative life-history characteristics of Achatinellinae, Partulidae and two contrasting land snail species, Achatina fulica (Achatinidae) and Theba pisana (Helicidae: Helicinae)*

variable	Achatinellinae	Partulidae	*A. fulica*	*T. pisana*
age at first reproduction/years	4–7[4,5,6]	< 1[12]	0.4–2[10,11,15]	1–2[1]
length of reproductive life/years	2.3– > 12[4,5,6]	> 5[13]	> 4.25[11]	0.25[1]
total life-span/years	5– > 18[4,5,6,14]	> 5[13]	> 5[11]	1–2.5[1]
offspring per year	0.4–6.2[4,5,6]	18[12]	> 600[7,11]	339[1]
total lifetime offspring	1–74[4,5,6]	> 90[12,13]	> 3,000[7,9,11]	339[1]
shell size[a] at birth/mm	3.0–4.5[5,6,14]	3.0–3.5[2,3]	5–5.5[7,9,10]	2[1]
adult shell size/mm	17.0–21.3[5,6,14]	15.3–16.6[2,3]	89–133[7,9,10]	12–25[1,8]
relative shell size at birth[b]	0.18–0.24[5,6,14]	0.20–0.21[2,3]	0.04–0.06[7,9,10]	0.11[1]

(Data derived from: [1]Cowie (1984*a*), and R. H. Cowie (unpublished data), *Theba pisana*; [2]Crampton (1916), *Partula hyalina*; [3]Crampton (1925*a*) *Partula radiolata*; [4]Hadfield (1986), *Achatinella mustelina*, *Partulina redfieldii*; [5]Hadfield & Miller (1989), *Partulina proxima*; [6]Hadfield & Mountain (1980), *Achatinella mustelina*; [7]Kekauoha (1966), *Achatina fulica*; [8]Kerney & Cameron (1979), *Theba pisana*; [9]Kondo (1964), *Achatina fulica* [10]Lange (1950), *Achatina fulica*; [11]Mead (1961), *Achatina fulica*; [12]Murray & Clarke (1966), *Partula suturalis*, *Partula taeniata*; [13]Murray & Clarke (1984), *Partula taeniata*; [14]Severns (1981), *Achatinella lila*; [15]Takeuchi *et al.* (1991), *Achatina fulica*.)

[a] Shell size is defined as the maximum dimension (height or width) of the shell.

[b] Relative shell size at birth is defined as shell size at birth divided by adult shell size.

introduced terrestrial flatworm *Platydemus manokwari* seems to have reduced populations of *Achatina fulica* on Guam but will also feed on native snails including partulids (Eldredge 1988; Hopper & Smith 1992).

(*d*) *Food and habitat*

Partulids are predominantly nocturnal, arboreal and herbivorous, and, in favourable habitats, may achieve densities of up to 10 individuals per square metre, although 1–2 m^{-2} is more usual (Murray 1972). They live on a wide variety of tree species, and, whereas Crampton (1916, 1932) stated that they descend to the ground at night to feed on decaying plant material, which he considered to constitute the major part of their diet, later work (Murray *et al.* 1982) indicates that they eat a wide variety of both partially decayed and fresh plant material, and that most species spend all their time in the trees, both resting and active, only a few species (e.g. *Partula taeniata* of Moorea) sometimes descending to the ground to forage. Some species, however, are largely ground-dwelling (e.g. *P. producta* of Tahiti; Crampton 1916). Dispersal is limited, most snails remaining within an area of a few square metres throughout their lives (Murray & Clarke 1984).

Although comparable to the Achatinellinae in their arboreal habit, the generalist food preferences of partulids contrast dramatically with the very precise requirements of, for example, *Achatinella* and *Partulina*, which feed on fungi and perhaps algae associated with the leaves of native plants in Hawaii (see Carlquist 1974; Pilsbry & Cooke 1912–14; Welch 1938; M. G. Hadfield personal communication). Many of these native plants are severely threatened or already extinct (Wagner *et al.* 1990) and are being replaced by non-native plants that are unsuitable for the snails, an additional factor contributing to the snails' extinction.

Niche partitioning among species, in terms of both habit and habitat, has been documented to some extent. Cooke (1928) indicated different microhabitat preferences of three species on Tutuila (American Samoa): *Samoana conica* and *S. abbreviata* tended to be associated more with trunks and branches than with leaves, whereas *Eua zebrina* showed the opposite trend. Cooke (1928) also found snails on the ground, and although his published statement is ambiguous, his field notes (archived at the Bishop Museum, Honolulu) confirm that this referred to *E. zebrina*. Cooke did not quantify these observations, and whether they can be generalized and indicate more profound differences between the two genera is unknown. His most interesting observation was that *E. zebrina* eats other (non-partulid) snails (soft parts and shells), in contrast to the two *Samoana* spp., which do not. Cooke postulated that the need for calcium for the growing juvenile shell was the explanation of this behaviour, *E. zebrina* having a thicker shell than the *Samoana* spp. Most of the snail species eaten were ground-living rather than arboreal, again suggesting a somewhat terrestrial habit for *E. zebrina*. Carnivorous behaviour has not been reported for any other partulid.

Leaving aside the early and largely unquantified ecological work of Crampton and of Cooke, only the *Partula* spp. of Moorea have been studied in any depth ecologically. As many as four of the seven species (table 2, and see below) occur together, and while there is considerable overlap in habitat among these species, there are nevertheless some consistent differences in host plant preference and height above ground at which the snails are found (Murray & Clarke 1980; Murray *et al.* 1982). In general, the two dominant and most widespread species on Moorea, *P. suturalis* and *P. taeniata*, are distinct ecologically, as they are taxonomically (see below), with *P. mirabilis* intermediate both ecologically and taxonomically. *P. suturalis* exhibits a relative preference for the trunks and branches of the main canopy tree *Hibiscus tiliaceus*, being found predominantly above 3–4 m and as high as over 15 m above ground, whereas *P. taeniata* is

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Table 2. *The Partulidae of Moorea, as considered by various authors and indicating major taxonomic changes that have taken place since the work of Crampton (1932)*

Crampton (1932)	Crampton & Cooke (1953)	Kondo (1968)	Kondo (1973)	Murray & Clarke (1980)
	Partula diaphana	*Samoana diaphana*	*S. diaphana*	
Partula solitaria		*Samoana solitaria*	*S. attenuata*	
Partula exigua		*P. exigua*		*P. exigua*
P. tohiveana		*P. tohiveana*		*P. tohiveana*[a]
P. olympia		*P. olympia*		
P. aurantia		*P. aurantia*		*P. aurantia*
P. mirabilis		*P. mirabilis*		*P. mirabilis*
P. mooreana		*P. mooreana*		*P. mooreana*
P. suturalis		*P. suturalis*		*P. suturalis*[a]
P. dendroica		*P. dendroica*		
P. taeniata		*P. taeniata*		*P. taeniata*

[a] *P. tohiveana* and *P. olympia* were considered conspecific by Murray & Clarke (1980), as were *P. suturalis* and *P. dendroica*, although neither pair was formally synonymized.

found predominantly on low woody shrubs but also on climbing pandanus (*Freycinetia demissa*) and a large fern (*Angiopteris* sp.). *P. mooreana* and *P. tohiveana* (including *P. olympia*; see below), both of which belong to the group of species closely associated with *P. suturalis* (see below) and whose distributions are completely overlapped by that of *P. suturalis*, have parapatric distributions with respect to each other and seem to occupy equivalent ecological niches, both being found predominantly on climbing pandanus. *P. mirabilis* and *P. aurantia* are also associated with climbing pandanus, but to a lesser degree, the former, at least, having a more general distribution including woody shrubs and *Angiopteris* sp. In addition to these interspecific differences, juveniles, at least of *P. suturalis* and perhaps of *P. mirabilis*, show differences compared to adults, being associated less with *Hibiscus tiliaceus* and *Freycinetia demissa* respectively, and (*P. suturalis*) being found lower in the vegetation (Clarke & Murray 1971; Murray *et al.* 1982).

In general, the *Partula* spp. of Moorea exhibit spatial differences, which may reflect trophic differences, but appear not to partition their habitat temporally, as activity seems to be closely associated with rainfall in all species (Murray *et al.* 1982), although subtle temporal differences in behaviour related to weather patterns have not been investigated.

Although this detailed work on the Moorean species has not included the *Samoana* spp. of that island, scattered comments in the literature consistently mention the tree-top habits of members of this genus when sympatric with *Partula* spp. (Clarke & Murray 1969; Crampton 1932; Kondo 1973; Kondo & Burch 1972), further emphasizing the evolution of niche partitioning in the family.

Local partulid diversity depends, then, on partitioning of both taxonomic and structural floral diversity; it also appears linked to altitude (Murray & Clarke 1980). The explanation of the increasing diversity with altitude, however, may be that floral diversity is linked to climate, especially rainfall and humidity, both of which also increase with altitude on Moorea. The trend is more pronounced if the two *Samoana* spp. of Moorea, *S. attenuata* and *S. diaphana*, are included, as these are restricted to altitudes greater than 300 m on Moorea (Kondo 1973; Murray & Clarke 1980).

The possibility that the partulids of Moorea compete with each other and that this competition is, at least in part, responsible for their disjunct local distributions, their partitioning of the available habitat, and the maximum diversity sustainable at a particular locality, has not been tested. Demonstration of competition is notoriously difficult (Connell 1983; Schoener 1983); even the seemingly much less complex contention that competition is involved in maintaining the disjunct distributions of the helicid land snails *Cepaea nemoralis* and *C. hortensis* in western Europe remains essentially unanswered (e.g. Cowie & Jones 1987; Perry & Arthur 1991) after years of study (Arthur 1982*a*; Cain 1983).

Although the Moorean *Partula* spp. are more or less distinct both morphologically and ecologically, they are nevertheless very closely related, gene flow being theoretically possible between all the species (see below) and interspecific allozyme variation among them being very low (Johnson *et al.* 1977, 1986*c*, 1987; Murray & Clarke 1980). Ecological divergence, just as reproductive isolation (see below), appears not to be linked to allozyme divergence, implying that behavioural differentiation does not require extensive genetic change (Johnson *et al.* 1986*c*; Murray *et al.* 1982).

5. INTRASPECIFIC VARIATION

W. D. Hartman (see Mayer 1902; Smith 1902), Andrew Garrett (1884), with his immense collecting effort in the Society Islands, and A. G. Mayer (1902), laid the foundation for future studies of partulid variation. Garrett was the first to consider seriously the profusion of forms in the Partulidae, noting especially *Partula otaheitana* of Tahiti and *P. taeniata* of Moorea, and to speculate on the boundaries between

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species, mentioning what he considered to be clear cases of hybridization (see, in addition, Mayer (1902); Pilsbry (1909–10)). Acknowledging his debt to Garrett and to Mayer, Crampton, in his three major monographs covering Tahiti (Crampton 1916), Guam and Saipan (Crampton 1925*a*), and Moorea (Crampton 1932) and a number of shorter papers (e.g. Cooke & Crampton 1930; Crampton 1924*a*, *b*, 1925*b*, 1928), investigated the variation in detail, especially concentrating on shell shape and shell colour and pattern, and for the first time asking questions regarding the causes of the variation. However, although one of Crampton's aims was to show that intraspecific variation was genetically controlled, he did not approach his material from a sophisticated background in population genetics, a subject then still in its infancy. His effort, rather than being aimed at elucidating the mechanisms by which natural selection might control the variation, was directed more at detecting direct environmental influences on the phenotype and the possible inheritance of acquired characteristics, which of course he did not find (Cowie 1989).

None the less, Crampton's work set the scene for a major body of later research (including re- analysis of his own data; Bailey 1956; Clarke 1962; Emberton 1982; Gould *et al.* 1985; Lundman 1947) undertaken against the background of the 'Modern Synthesis' (Huxley 1943) and concentrating on *Partula* of Moorea and, to a lesser extent, Tahiti.

(*a*) *Genetics of shell colour and banding*

Shell colours and patterns are very variable in the Partulidae. Although some species show rather little intraspecific variation, others manifest a range of variation from dark brown and purple through pinks and yellows to almost white, with or without spiral banding or transverse striations. Colours of the lip (formed at the aperture of the adult shell) and the spire of the shell may also vary. This variability was one of the key factors attracting early workers to the family. From his field studies, Crampton (1932) deduced that the variation was almost entirely genetically controlled but it was not until the laboratory breeding experiments of Murray & Clarke (1966, 1976*a*, *b*), on *Partula taeniata* and *P. suturalis*, that the mechanisms of this genetic control were elucidated.

The parallels and contrasts with *Cepaea*, the only other land snail group for which the genetic mechanisms controlling shell colour and pattern have been more thoroughly worked out (see reviews by Jones *et al.* (1977); Murray (1975)), are striking and prompt much speculation. In *P. taeniata*, overall shell colour, banding pattern, spire colour and lip colour are controlled by multiple alleles at six or more tightly linked loci, a supergene (Murray 1975; Murray & Clarke 1976*a*); in *P. suturalis* shell colour and banding are controlled by multiple alleles at a single locus that may be complex and therefore also deserve the 'supergene' epithet (Murray 1975; Murray & Clarke 1976*b*). The close linkage of the genes controlling shell colour and pattern in *Partula taeniata* and *P. suturalis* is strongly reminiscent of the supergene in *Cepaea nemoralis* and *C. hortensis* (Jones *et al.* 1977; Murray 1975), inviting the speculation that, because these genera are so distantly related, the genetic systems have evolved convergently in response to similar environmental problems (Murray & Clarke 1976*a*). What these problems are remains unknown, but close linkage provides a method for maintaining selectively appropriate combinations of alleles in cases where complex polymorphisms are controlled at a number of loci, and there is some evidence of supergene control of shell colour and pattern in a number of other land snail species (Clarke *et al.* 1978; Murray 1975). However, data for these other species are scanty compared to those for *Partula* and, even more so, *Cepaea*; and recent information on *Helix aspersa* (Albuquerque de Matos 1984*a*, *b*) and *Theba pisana* (Cain 1984*b*; Cowie 1984*b*) suggests that the complex polymorphisms in these species may not be controlled by a supergene of tightly linked loci, although some linkage has been demonstrated. To suggest that such a mechanism is ubiquitous in visually polymorphic land snails would be premature.

The details of these genetic systems in *Partula* (Murray 1975; Murray & Clarke 1966, 1976*a*, *b*) also differ from those in *Cepaea*. Whereas alleles for darker shell colours in *P. taeniata* tend to be dominant, although not always completely, to those for paler colours, as in *Cepaea*, alleles for banding (in *P. taeniata* at two loci) are dominant to those for lack of banding, contrasting with *Cepaea* (Jones *et al.* 1977; Murray 1975). The lip formed at the aperture of the adult shell in both *Partula* and *Cepaea* may also vary in colour, independently of overall shell colour, and this variation is controlled by a single locus linked to the shell colour locus or loci. The allele for pink (i.e. dark) lip colour in *P. taeniata* is dominant to that for white, just as darker lip colour (from pinkish through to dark brown, controlled by multiple alleles) is dominant to white in *Cepaea*. The allele for dark spire in *P. taeniata* is dominant to that for pale spire, a feature not comparable to the documented variation in *Cepaea*, but contrasting with the admittedly rather different variation in apex (in fact the protoconch, or embryonic shell) colour in *Theba pisana*, the locus for which is linked to the banding locus, with pale apex dominant (Cain 1984*b*; Cowie 1984*b*).

Segregation and dominance in *P. suturalis* is more complicated than in *P. taeniata*, because the variation in the former cannot be broken down into a simple hierarchy of dark to pale colours but has been described (Murray & Clarke 1966, 1976*b*) by referring to Crampton's (1932) varietal classification (see, in addition, Cain (1988)), which recognized particular combinations of shell pattern and colour (cf. description of the complex variation in *Theba pisana* by using a series of codes describing characteristic phenotypes – Cain 1984*b*, 1988; Cowie 1984*b*). Alleles for the darkest of these forms appear intermediate in the dominance hierarchy, while the top dominant and bottom recessive alleles result in similar phenotypes (Murray & Clarke 1976*b*).

Too few species in too few land snail families have been studied to allow any generalization from these

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comparisons, except to say that shell colour and banding pattern are frequently controlled by multiple alleles in a dominance hierarchy at two or more loci (one or more loci for colour, one for banding) (Murray 1975). The fine detail frequently differs among species. However, it is interesting, in the family Helicidae, that alleles for banding are recessive to those for reduced or lack of banding in all Helicinae for which this information is known (Albuquerque de Matos 1984*a*; Cain 1984*b*; Cowie 1984*b*; Murray 1975; A. J. Cain & R. H. Cowie, unpublished results), but that the reverse applies in certain other helicid subfamilies: Helicigoninae (*Arianta arbustorum*, see Murray 1975) and Helicellinae (*Cochlicella acuta*, Lewis, referred to by Murray (1975); *Cernuella virgata*, A. J. Cain & R. H. Cowie, unpublished results). This suggests that some features of these genetic systems may be conserved throughout the evolution of certain higher taxa, but that others are flexible and malleable over short periods of evolutionary time; convergence of the broad structure of the genetic control may result from constraints imposed by the overall way of life of a snail, but the details will be influenced by the specific aspects of the ecological and evolutionary history of particular species. The differences between the genetic control of the polymorphism in *P. taeniata* and *P. suturalis* contrast with the apparent complete homology between *Cepaea nemoralis* and *C. hortensis*. This implies that the evolution of the polymorphism in *Cepaea* antedates the rather recent divergence of the two *Cepaea* species (Murray 1972), and suggests that the polymorphism in *P. taeniata* evolved independently from that in *P. suturalis*, and, perhaps, that the two *Partula* species diverged rather earlier than did the *Cepaea* spp.

(*b*) *Control of shell colour and pattern gene frequencies in the wild*

Crampton (1932) considered that mutation and migration, not natural selection, were the causes of the extensive variation in morph frequency he encountered among the *Partula* spp. of Moorea. However, it is now known that mutation rates are not sufficient, and the widespread migration he postulated does not occur (Johnson *et al.* 1988; Murray & Clarke 1984); his deductions are attributable to his large-scale sampling methods which obscured small-scale differences (over but a few metres) in morph frequency (Clarke 1968; see also Zimmerman (1948, p. 170)); and morph frequencies appear to be stable over long periods in at least one species, *Partula suturalis* (Clarke & Murray 1971).

Attempts to correlate morph frequencies with environmental variables, including physical, climatic and biotic factors, and even with the presence of other partulid and non-partulid snail species, have met with little success (Clarke 1968; Clarke & Murray 1969, 1971; Murray 1972). There is a slight hint that snails with striated patterning, such as var. *strigata* of the Moorean sub-species *P. suturalis vexillum*, are concentrated somewhat on climbing pandanus (Clarke & Murray 1971), and populations of *P. otaheitana* of Tahiti seem to have higher frequencies of unbanded shells in drier, sunnier valleys (Emberton 1982). The former association admits no explanation, but the latter is in accord with explanations of shell colour and pattern variation in other land snails, in which climatic selection favours paler shells in sunnier, more exposed habitats as a means of reducing heat load by reflecting solar radiation (Cain 1983; Jones *et al.* 1977). But otherwise there appears to be no relation of genotype distributions to environmental variables, areas of uniform gene frequencies frequently crossing ecological boundaries, yet changing abruptly within a seemingly uniform habitat (Clarke 1968; Clarke *et al.* 1978; Clarke & Murray 1969, 1971; Murray 1972).

Again, the comparison with *Cepaea* is unavoidable. Although natural selection due to visual predation and climatic variation plays a significant role in certain localities in controlling colour and pattern variation in both shell and soft parts of both *Cepaea* (Cain 1983; Cowie & Jones 1985; Jones *et al.* 1977) and other species (see, for example, Cowie (1990); Heller (1981); Johnson 1981), the most controversial feature of genotype distribution in *Cepaea* has been the discovery, especially in *C. nemoralis*, of large areas, greater than the panmictic unit, characterized by uniform gene frequencies apparently bearing no relation to any environmental variable, and termed 'area effects' in a seminal paper by Cain & Currey (1963*a*). The discovery of area effects led to the recognition of similar phenomena in other species of land snails (Clarke 1978; Clarke *et al.* 1978) and perhaps in other organisms (White 1978*a*, *b*), and resulted in considerable discussion as to their cause(s). The history of area effects in *Cepaea* has been reviewed by Gould & Woodruff (1990), who summarize the main explanations that have been put forward (see also Ochman *et al.* (1983)) as: (i) immediate selection by cryptic environmental factors (Cain & Currey 1963*a*, *b*); (ii) secondary contact between populations in which genetic differences became established following a founder event and subsequent genetic co-adaptation (Goodhart 1963, 1973); and (iii) differentiation within large populations initiated by random effects and maintained by co-adaptation (Clarke 1966; Wright 1978). Clarke (1968), Clarke & Murray (1969, 1971), Murray (1972) and White (1978*a*) favoured the third explanation for the distribution of morphs in the *Partula* spp. of Moorea. In particular, Clarke (1968) and Murray (1972) argued that the concordance with the abrupt change in allele frequencies in *P. taeniata* in northwest Moorea of (i) changes in population density not related to ecological factors, (ii) changes in shell size, (iii) disturbance of dominance relationships, and (iv) fecundity variations, combined with the apparent selection against homozygous banded *P. taeniata* in laboratory breeding experiments (Murray & Clarke 1966) but the lack of apparent selective agents in the wild, supported the contention, considered a 'black box' by Schindel & Gould (1977), that 'internal factors [i.e. co-adapted gene complexes] may be important in determining morph frequencies'. (The supposed selection against homozygotes – heterozygote advantage – was shown in a later paper

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(Murray & Clarke 1976*a*) not to be significant.) However, none of these authors convincingly discounted an explanation based on the founder effect and frequent local isolation of small populations, an explanation of the *Cepaea* area effects that is now gaining considerable support (Cameron Carter & Palles-Clark 1980; Cameron & Dillon 1984; Cameron Down & Pannett 1980; Ochman *et al.* 1983). Cain (1983) interpreted the *Partula* area effects as due to former separation of populations, current overlap and selection against hybrids, although Clarke (1968) and Clarke & Murray (1971) believed that isolation was not necessary and that the steep clines in morph frequency could have come about *in situ*, which is theoretically possible (Clarke 1966; Endler 1977). However, the causes of area effects may be as diverse as the phenomena are themselves heterogeneous (Gould & Woodruff 1990; Jones *et al.* 1980) and, with their extinction on Moorea, the real explanation for the area effects in the *Partula* spp. of that island will probably never be known.

More generally, geographic (both large and small scale) structuring of frequencies of alleles controlling the shell polymorphism in natural populations of partulids, including both area effects and other patterns, results, no doubt, from as many complex factors as it does in natural populations of *Cepaea* (Jones *et al.* 1977). Such complexity is probably ubiquitous and attempts to explain variation of this kind, not only in land snails but also in other organisms, will likely founder if this is not understood.

(*c*) *Coiling and its genetics*

The Partulidae are relatively unusual among land snail families in having species with dextrally coiled shells and others with sinistrally coiled shells. Furthermore, some species, such as *Partula suturalis* of Moorea, *P. otaheitana* of Tahiti and *P. gibba* of the Mariana Islands are amphidromic, i.e. having both dextral and sinistral individuals (Johnson 1982; Kondo 1970; Murray & Clarke 1966). In *P. suturalis*, direction of coil is genetically determined, with sinistrality dominant to dextrality (Murray & Clarke 1966, 1976*b*) and sinistrality presumed to be the ancestral condition (Clarke & Murray 1969). The genetic control of chirality in a predominantly, and presumably ancestrally, dextral species such as *P. taeniata* is unknown (although there are hints that dextrality is dominant in *P. mirabilis*; Johnson *et al.* 1990), but would be of great interest (Clarke & Murray 1969), given the general consensus that wild-type alleles tend to be dominant over new alleles arising by mutation (e.g. Futuyma 1986, pp. 211–212; Murray 1972).

As suggested by Crampton (1916, 1924*b*, 1932) and confirmed by Murray & Clarke (1966, 1969, 1976*b*), the coiling phenotype in *P. suturalis* is determined by the maternal genotype, just as in the clausiliid land snail *Laciniaria biplicata* (Degner 1952) and the extensively studied freshwater snail *Lymnaea peregra*, although in the latter species dextrality is dominant (Boycott & Diver 1923; Boycott *et al.* 1930; Diver & Anderson-Kottö 1938; Diver *et al.* 1925; Freeman & Lundelius 1982; Sturtevant 1923). Expression of the coiling genotype is, then, delayed one generation. In *P. suturalis*, sporadic offspring are produced of opposite coil to that which would be expected (Crampton 1924*b*; Murray 1975; Murray & Clarke 1976*b*), for reasons as yet unknown, although perhaps due to complex patterns of crossing over between two extremely tightly linked (but otherwise undistinguished) loci, as suggested by Freeman & Lundelius (1982) for the appearance of such apparently anomalous individuals in *L. peregra*. Chirality is determined early in development, the cleavage pattern in the early embryo being opposite in dextral and sinistral individuals. In *L. peregra*, dextrality (dominant) is due to the effect on the cleavage pattern of a cytoplasmic product of the dominant allele (Freeman & Lundelius 1982).

The chirality locus in *P. suturalis* is not linked to the colour and pattern locus (Murray & Clarke 1976*b*). However, re-analysis of Crampton's (1916, 1932) data on *P. suturalis* and *P. otaheitana* by Gould *et al.* (1985) and further analysis by Johnson (1987) of breeding experiments first reported by Murray & Clarke (1966) showed that variation in shell shape in these two species is associated with chirality, sinistral shells being relatively wider than dextrals. While Gould *et al.* (1985) felt that the difference in shape was due to a developmental constraint imposed by the chirality, Johnson (1987) showed convincingly that the association is due rather to pleiotropic effects of the chirality gene (or of other genes very tightly linked to the chirality gene).

Although *P. suturalis* can be either dextral or sinistral, the two morphotypes only co-occur within a population in a few narrow transitional areas (Murray & Clarke 1976*b*). Variation in chirality is not related to topography or flora, transition zones crossing valleys and ridges regardless of changes in ecological features (Clarke & Murray 1969). It appears to be related more to character displacement associated with reproductive isolation (see below).

(*d*) *Shell size and shape*

Although shell size and shape have been important in the description of the large number of species of Partulidae (Pilsbry 1909–10), nothing is known of the factors responsible for determining specific limits on these characters. Questions on the ecological and phylogenetic deployment of land snail shell shape have been addressed on a world-wide faunal scale by Cain (1977, 1978*a*, *b*, 1980, 1981; and related papers by Cameron & Cook (1989), Heller (1987) and Solem & Climo (1985)) but, although patterns have emerged suggesting that interspecific differences in shell shape are connected to niche partitioning within a fauna (see, in addition, Peake (1973)), and some studies have hinted at the proximate causes of such differences (Cain & Cowie 1978, Cameron 1978; Cook & Jaffar 1984), these fundamental questions of gastropod evolution remain unanswered. Specific studies on Partulidae have not been done.

Little more is known of the factors influencing

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intraspecific variation in shell shape and size in the Partulidae. High heritability of shell size has been demonstrated in *Partula taeniata* and *P. suturalis*, and stabilizing selection has been inferred tentatively from these laboratory breeding experiments, which also showed that there is no maternal effect on shell size and no association of shell size and shell pattern (Murray & Clarke 1968*a*).

The relationships of shell shape and size to environmental variables have received but little attention. Clarke & Murray (1971) indicated complex interrelations among altitude, population density and 'shell-length' (a measure of overall size) in *P. suturalis* and *P. taeniata* on Moorea, but gave no details, although Clarke (1968) had earlier mentioned a negative correlation of shell length and altitude in *P. taeniata* of northwest Moorea (see also Emberton 1982). On the basis of these rather few correlations and the relatively high heritability of shell size, Johnson (1987), while accepting that the evidence was circumstantial, considered variation in shell shape of Moorean *P. suturalis* to be adaptive.

In Tahiti, as demonstrated by a multivariate analysis (Emberton 1982) of Crampton's (1916) data, populations of the widespread and variable species *Partula otaheitana* in wetter, more shaded valleys tend to have more elongate shells, a higher frequency of banded shells, and shells with a lesser development of a parietal barrier in the aperture than populations from drier, more sunlit valleys. Both similar and different trends appear in other *Partula* spp. of Tahiti (Emberton 1982) and Moorea (Emberton 1982; Lundman 1947). If these trends were all in the same direction, there would be good circumstantial evidence for the direct action of natural selection, although the specific causes of the variation – for instance, why an elongate shell is favoured in wetter habitats – would not be illuminated. That the trends are not consistent, leaves us without a good explanation of their causes.

There does seem to be a general intraspecific association of larger size with wetter conditions in land snails and most interpretations of this are based on direct ecophenotypic effects of the environment on growth rate, wetter habitats allowing faster growth (Goodfriend 1986). But the negative relation of shell length to altitude in Moorean *Partula*, indicated above (Emberton 1982), and indeed in *Achatinella* on Oahu (Welch 1958), seems to contradict this generality, because humidity increases with altitude on both these islands. (For a further counter-example, see Peake (1973).) The high heritability of shell size in *Partula* of Moorea (see above) suggests that selection, rather than direct environmental effects on the phenotype, plays an important role.

The role of apertural denticles in *Partula* 'is a mystery' (Goodfriend 1986). Speculation on the adaptive roles of conchological structures (denticles, lamellae, etc.) within the apertures of land snails (reviewed by Goodfriend (1986)) has stressed protection from predation and reduction of evaporative water loss. Emberton (1982) seemed to favour the former explanation for the presence of an apertural tooth in *P. otaheitana* in Tahiti, although accepting that the case was very weak since the tooth is so small; and no likely predator was suggested as the selective agent. He did not comment on his finding that the size of the tooth tends to be greater in drier, sunnier valleys, a finding that at least does not contradict an explanation based on prevention of desiccation.

In the absence of consistent trends, other than those hinted at above, reasons for variation in shell size and shape in the Partulidae can only be speculated upon. Emberton (1982) suggested that correlations between environment and shell shape occur either (i) fortuitously as a by-product of clines in shell shape produced, for example, by restricted gene flow, or (ii) by way of direct causal relationships (due either to natural selection or to non-selected direct environmental action on the phenotype) that are masked by rapid migration, interspecific competition or other factors; some of these suggestions, especially those related to ecophenotypic effects, could be tested experimentally. Interspecific interactions involving character displacement and reproductive isolation may well also provide part of the explanation (see below). But perhaps the most likely explanation, a recurring pattern in land snail population biology, is that no one explanation is adequate, either for the family as a whole or for any one species (cf. Jones *et al.* 1977).

(*e*) *Character displacement*

In general, on Moorea, morphologically similar taxa do not coexist (Murray & Clarke 1980). *Partula tohiveana* increases in size where it approaches overlap with *P. mooreana*, with which it is sympatric at only one locality; and *P. taeniata* is more elongate as it becomes sympatric with short broad forms of *P. mirabilis* and *P. suturalis* (Murray & Clarke 1980). The reasons for these changes in shape and size in relation to sympatry and allopatry are unknown and can only be speculated upon in the most general terms of habitat partitioning and avoidance of competition (Arthur 1982*b*). Habitat partitioning has been documented among species of *Partula* (see above) but competition has not; and, although there is some evidence for both phenomena in *Cepaea*, character displacement in *Cepaea* has not been demonstrated (Cowie & Jones 1987), despite extensive efforts and speculation in this direction. Character displacement and its causes are notoriously difficult to demonstrate convincingly (Grant 1972; Harvey & Ralls 1985; Schindel & Gould 1977). The apparent character displacement among 'varieties' and 'sub-varieties' of *P. taeniata*, indicated by Bailey's (1956) re-analysis of Crampton's (1932) data, prompted the former to suggest that these forms were close to being reproductively isolated and 'truly species'. However, this conclusion depended on Crampton's now discounted ideas of large-scale migration of snails within Moorea (Clarke 1968; Murray & Clarke 1980), and Bailey's findings are probably artefacts of the extensive variation within *P. taeniata* and Crampton's variable collecting regime.

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On Tahiti, character displacement in areas of sympatry between the two subspecies *Partula otaheitana affinis* and *P. o. rubescens*, which may deserve the rank of full species (Lundman 1947; Kondo & Burch 1979, 1983) or may be in the process of speciating, is possibly related to reproductive isolation between the two forms (Emberton 1982): *P. o. affinis* is smaller, sometimes banded and predominantly dextral, while *P. o. rubescens* is larger, always unbanded and always sinistral. However, this possibility remains speculative as detailed work has not been undertaken, and, with the imminent extinction of Tahitian partulids due to *Euglandina rosea* (Pointier & Blanc 1982; Tillier & Clarke 1983), the question may never be resolved.

In contrast, detailed work on variation in chirality in the *Partula* spp. of Moorea, clearly implicates reproductive isolation. No two sinistral taxa coexist in sympatry, with the single exception of the otherwise allopatric *P. mooreana* and *P. tohiveana* at one locality (Murray & Clarke 1980). The most telling evidence comes from *Partula suturalis*, which is widespread on Moorea, overlaps the distributions of a number of other species and can be either sinistral or dextral. Particular populations of *P. suturalis*, excepting those in transition zones, are, however, entirely dextral or entirely sinistral, due to positive frequency-dependent selection (Johnson 1982; Johnson *et al.* 1990), and assume the opposite coil to that of the most closely related sympatric congener. For instance, *P. suturalis* is dextral where it is sympatric with sinistral *P. mooreana*. Assuming that hybrids between these two species (Murray & Clarke 1980) are less fit, selection acting to prevent hybridization is the likely explanation of the character displacement (Clarke & Murray 1969). Related patterns are known in other Pacific land snails, such as the Diplommatinidae, in which similar-sized forms do not co-exist unless they differ in chirality, and have been explained in terms of habitat partitioning and reproductive isolation (Peake 1973; Tillier 1981).

6. REPRODUCTIVE ISOLATION, SPECIATION AND THE ORIGINS OF THE SOCIETY ISLAND PARTULIDS

(*a*) *Reproductive isolation*

Selection acting on direction of coil to prevent hybridization between closely related species (see also Peake (1973)) is supported by intraspecific studies on mating behaviour, in the chirally polymorphic *Partula suturalis*, that have provided detailed descriptions of the sequence of events leading to copulation (Lipton & Murray 1979). Just as in entirely dextral or entirely sinistral species, dextral and sinistral individuals of *P. suturalis* have the reproductive pore on opposite sides of the body. During courtship, one individual of the pair adopts the male role, the other the female role. Penial probing by the acting male is on that side of the acting female appropriate if both individuals were of the same chirality. Courtship between two dextral individuals is a mirror-image of that between two sinistrals. But when the couple consists of one individual of each coil, penial probing by the acting male is on the side of the acting female appropriate for the acting male's own chirality. Although the acting female modifies its behaviour in an attempt to accommodate the acting male, and although cross-fertilization producing viable offspring is possible (Murray & Clarke 1966, 1976*b*), assortative mating in natural populations of *P. suturalis* does occur to some degree (Clarke & Murray 1969) and, in laboratory studies, snails of differing coil mated only 20% as frequently as those of like coil, producing 28% fewer offspring (Johnson 1982). Although production of only 28% fewer offspring from 80% fewer matings is a more efficient rate of production per mating, the overall reduction in production implies reduced fitness. In addition, sinistral snails collected from areas with low frequencies of sinistrals in the wild produced fewer young than dextrals from the same populations (Johnson 1982). Partial incompatibility during courtship may be the cause of this reduced reproductive output and leads to the suggestion that mating behaviour is at least one factor involved in reproductive isolation among the Partulidae of Moorea and that selection to prevent interspecific hybridization between *P. suturalis* and its sympatric congeners has resulted in the character displacement and hence coil polymorphism in this species.

Reproductive isolation between species of *Partula* on Moorea is, however, far from simple. For instance, on the basis of multivariate analyses of variation in shell shape, shell size, parietal tooth size, shell colour and banding pattern, chirality, penial morphology and egg calcification, Murray & Clarke (1968*b*) showed that reproductive isolation between *P. suturalis* and *P. aurantia* and between *P. taeniata* and *P. exigua* was incomplete, but that the level of isolation varied from place to place. Electrophoretic studies (Schwabl & Murray 1970) confirmed the close relationship between *P. suturalis* and *P. aurantia* and their ability to hybridize freely. Hybridization within both these species pairs occurs in some but not other localities, and the pattern of isolation has been postulated as having arisen from previous separation and allopatric speciation (or partial speciation) of the now adjacent or overlapping populations or from parapatric speciation with no prior isolation (see below). With their demise in the wild (Murray *et al.* 1988), the question of whether these species will merge or speciate fully (Murray & Clarke 1968*b*) will never be answered. Of the *Partula* spp. of Moorea, only *P. mooreana* is well isolated reproductively from its congeners, although even it shows some possibility of crossing with *P. suturalis*, *P. mirabilis* and *P. tohiveana* (considered to include *P. olympia*; see below) (Murray & Clarke 1980). A number of localized (less than 2 km and up to 5 km diameter) 'ring species' or 'circular overlaps' (Cain 1971; Mayr 1963) seem to occur in which two forms behave as good species (reproductively isolated) in their area of overlap but are connected by a ring of inter-breeding or inter-grading forms (Clarke & Murray 1969; Murray & Clarke 1980). Nevertheless, although localized introgression occurs between some of the Moorean *Partula* spp., they coexist in most

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places without hybridizing (Johnson *et al.* 1977) and are, in general, distinguishable morphologically. It is, therefore, of considerable interest that, despite great allozyme polymorphism within populations (at 18 of 20 loci studied, and with Mendelian inheritance shown for some), there is, in general, little interpopulation or interspecific allozymic differentiation not only within and among the Moorean *Partula* spp. but also between them and Tahitian species; and this interspecific variation is low compared to that found in other studies of closely related species (Johnson *et al.* 1977, 1986*c*, 1987). (*P. gibba* of Saipan stands apart electrophoretically from the Society Island species; Johnson *et al.* 1977). In addition, the species thus far studied (*P. mooreana*, *P. olympia* (now included in *P. tohiveana*; see below), *P. aurantia*, *P. suturalis*, *P. taeniata* and *P. mirabilis*, all from Moorea) have the same chromosome number (Scvortzoff quoted by Johnson *et al.* (1986*b*), Murray & Clarke (1980) and Murray *et al.* (1982)). However, there is a degree of large scale patterning in allozyme frequencies, with a particular anomaly of one population of *P. taeniata* showing considerable divergence from the remainder of the species, despite possessing the common mitochondrial DNA (mtDNA) genotype and lacking clear morphological distinction (Johnson *et al.* 1986*c*, 1987, 1988; Murray *et al.* 1991). This implies that the morphological divergence, allozyme divergence, reproductive isolation and mtDNA variation are evolving independently (see also Clarke 1978); reproductive isolation may have evolved by means of relatively simple behavioural differences determined by but a few genes, and post-mating isolation may not be well-developed (Johnson *et al.* 1977, 1986*b*). This and related phenomena are beginning to be observed more and more widely; other studies on groups of closely related animals and plants (see, for example, Avise 1990; Carr 1987; Dowling *et al.* 1989; Mayer 1991; Meyer *et al.* 1990; Palumbi & Metz 1991; Woodruff & Solem 1990), as well as intraspecific studies (e.g. Johnson *et al.* 1984; Nixon & Taylor 1977), show similar decoupling of the evolution of morphology, behaviour, molecular variation and reproductive isolation, and contrast with studies (e.g. Ashley & Wills 1989; Warwick & Gottlieb 1985) in which allozyme, DNA and morphological evolution have occurred in concert (see also Hillis (1987) who discusses variability in rates of morphological and molecular evolution and the problems this causes for systematics).

(*b*) *Speciation*

Crampton (1932) and Crampton & Cooke (1953) recognized 11 *Partula* spp. on Moorea (table 2). Kondo (1968) reduced this to nine with the removal of *P. diaphana* and *P. solitaria* to *Samoana* (the latter species subsequently synonymized (Kondo 1973) with the widespread Society Island species *S. attenuata*). The informal synonymizing of *P. dendroica* with *P. suturalis* and *P. olympia* with *P. tohiveana* (Johnson *et al.* 1986*b*, *c*; Murray & Clarke 1980; Schwabl & Murray 1970) reduced the number further to seven (table 2). Formally, *P. dendroica* Crampton, 1924*a* thus becomes a junior synonym of *P. suturalis* Pfeiffer, 1855. The formal taxonomic position with regard to *P. olympia* Crampton, 1924*a* and *P. tohiveana* Crampton, 1924*a* is less clear as both were described at the same time in the same publication and neither name is given precedence clearly by Murray & Clarke (1980). However, subsequent usage (first by Murray *et al.* (1982, p. 324)) includes *P. olympia* within *P. tohiveana* (see also, for example, Johnson *et al.* (1986*b*)), giving senior synonymy to the name *tohiveana* over *olympia* under the Principle of the First Reviser (*International Code of Zoological Nomenclature*, 3rd edn, 1985, Article 24, p. 53) and complies with Recommendation 24A of the *Code* that the name appearing first (*tohiveana*) be selected.

The relationships of these species are so complex that Murray & Clarke (1980) considered there 'to be no reasonable way to accommodate the group within a conventional Linnaean scheme', suggesting that it 'would be easy to argue for as few as four or as many as ten "true" species'. In all but a few cases, concepts of subspecies or geographical races are inappropriate, although some early authors did attempt to apply them.

The seven Moorean *Partula* spp. fall into two groups, both of which are widespread across the island, with a single species linking the groups, and as many as four species co-existing without hybridizing (Clarke & Murray 1969; Murray & Clarke 1980; Murray *et al.* 1982). The *P. suturalis* complex comprises four species: *P. suturalis* (including the geographically isolated but morphologically, electrophoretically and reproductively indistinguishable and therefore conspecific *P. dendroica*; Murray & Clarke 1980; Schwabl & Murray 1970; and see above), *P. tohiveana* (including *P. olympia*, with which it is connected clinally, hybridizes freely and is now considered conspecific; see above), *P. aurantia*, and *P. mooreana*. The *P. taeniata* group includes only the variable and widespread *P. taeniata* and the much more restricted *P. exigua*. (Prior to their removal to *Samoana* (Kondo 1968), *S. diaphana* and *S. solitaria* (= *S. attenuata*; see Kondo 1973) were included in the *P. taeniata* group, although their distinctiveness was appreciated; Clarke & Murray 1969). *P. mirabilis* links the two groups (although it was formerly included in the *P. taeniata* complex; Clarke & Murray 1969).

The relationships within the two groups are complex (Murray & Clarke 1968*b*, 1980) and range from the almost complete isolation of *P. mooreana* as a good species within the *P. suturalis* group, to the locally variable relationships between *P. suturalis* and *P. aurantia* and between *P. taeniata* and *P. exigua* (see above). In some localities *P. aurantia* hybridizes with *P. suturalis*, whereas in others it seems distinct and isolated; laboratory crosses are fertile. At the centre of these complex relationships within the *P. suturalis* group stands *P. tohiveana* (particularly the form known previously as *P. olympia* but now considered conspecific with *P. tohiveana*; see above). This species can hybridize with *P. aurantia*, *P. suturalis* and *P. mooreana*, and also with *P. mirabilis* to form a link with the *P. suturalis* group, and even with *P. otaheitana* of Tahiti

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(Murray & Clarke 1980). The relationships between *P. taeniata* and *P. exigua* are comparable in that these two members of the *P. taeniata* group behave as distinct species in one place but intergrade or hybridize in another (Murray & Clarke 1968*b*; Clarke & Murray 1969). Murray & Clarke (1980) summarized these relationships very clearly in diagrammatic form. It is theoretically possible for gene flow to take place between all members of each group, either directly or through another species, and, through *P. mirabilis*, between the two groups; all the Moorean *Partula* spp. can thus be linked genetically (Clarke & Murray 1969; Murray & Clarke 1980).

These complex relationships have been interpreted in terms of previous allopatric speciation (or almost speciation), followed by introgression to different degrees in different places (Murray & Clarke 1968*b*; Schwabl & Murray 1970), or by parapatric speciation with no isolation (Clarke 1978; Clarke & Murray 1969; Murray & Clarke 1980). Despite its intuitive attraction, allopatric speciation may have been uncommon, as geographical barriers seem to have been unimportant in the evolution of variation on Moorea, barriers being just as frequent within as between the ranges of particular forms (Clarke & Murray 1969), and as secondary contact between previously isolated and currently divergent populations should lead theoretically to concordance of clines in several different traits (Barton & Hewitt 1985), a feature for which there is but little evidence (Clarke 1968) in the *Partula* spp. of Moorea (Johnson *et al.* 1987). This seems to contrast with variation in *Achatinella* spp. in which different forms seem often (but with major exceptions) to be confined to specific valleys and ridges (Welch 1958, and references therein). The notion that area effects, as seen for instance in shell colour variation in *P. taeniata* (Clarke 1968) and *Cepaea* (Cain & Currey 1963*a*, *b*) and postulated (e.g. Clarke *et al.* 1978) as due to genetic co-adaptation within adjacent populations (derived either allopatrically or parapatrically), represent incipient speciation – 'area effect speciation' (White 1978*a*) – has been generally discounted because of the lack of concordance between patterns of variation at different loci (see, for example, Jones *et al.* (1980); Ochman *et al.* (1983)).

Although allopatric and area effect speciation have been largely discounted for the Moorean *Partula* spp., parapatric speciation has gained favour, although without substantial justification. Parapatric speciation seems theoretically possible (Endler 1977), but it remains difficult to distinguish between (i) previous isolation followed by secondary contact and (ii) primary divergence without isolation, as explanations for present patterns of variation, especially of hybrid zones between closely related forms (Barton & Hewitt 1985; Endler 1977). But whereas there is some justification for explaining morph frequency differences in *Partula* in terms of parapatric differentiation (Clarke 1968; Clarke & Murray 1971), to extend this to an explanation of speciation by arguing that 'if groups of populations within taxa evolved parapatrically it is economical to postulate that the taxa themselves do so' (Murray & Clarke 1980), is to fall into a similar trap to that which led to the proposal of area effect speciation: arguing from polymorphism to speciation. Furthermore, the argument is a negative one depending for its strength (Murray & Clarke 1980) on the lack of apparent relation between environmental variation and the distribution of the forms.

Sympatric (or 'micro-allopatric'; White 1978*a*) speciation generally remains controversial (Otte & Endler 1989). It can only occur under very specific circumstances in which morphs in a polymorphic population select particular microhabitats or niches and become strongly associated with them so that assortative mating is virtually complete and reproductive isolation and thence speciation ensue (Futuyma 1986; Grant & Grant 1989). Gittenberger (1988) suggested that polymorphism for coil in snails, combined with a degree of assortative mating and behavioural incompatibility between individuals of differing coil, might lead to sympatric speciation into entirely dextral and entirely sinistral species. However, models of the chiral polymorphism in *Partula suturalis*, which is controlled by a single locus (see above), show that speciation by this mechanism is highly unlikely, essentially because assortative mating is not complete, due in part to the delaying by one generation (see above) of the expression of the chirality genotype (Johnson *et al.* 1990). Furthermore, allozyme frequencies among dextral and sinistral individuals from the same populations of *P. suturalis* do not differ (Johnson *et al.* 1987) and neither is there any apparent ecological differentiation (Johnson *et al.* 1990). That chirality cannot act as a genetic barrier has been confirmed by studies of mtDNA (Murray *et al.* 1991).

Speciation based on the chiral polymorphism or on other current patterns of polymorphism in the Moorean *Partula* spp. seem, therefore, to be unlikely. A combination of models – allopatric and parapatric – probably provides the best explanation, but discerning their relative importance is difficult and may now be impossible with the extinction of these species in the wild.

(*c*) *Origins of the Society Island partulids*

In general, land snail diversity on Pacific Islands, in common with diversity of other elements of the fauna and flora (see, for example, Holloway 1983; Zimmerman 1948), probably has resulted from dispersal and speciation, although involving rather few colonization events (Solem 1981) and, indeed, the Moorean *Partula* spp. are so closely inter-related that it seems probable that they have evolved and speciated on Moorea rather than being the results of more than one species level invasion (Clarke & Murray 1969; Johnson *et al.* 1986*b*; Murray & Clarke 1980).

The Society Islands (figure 3), as other island chains in the Pacific, were formed in succession as the Pacific plate moved northwestwards over a fixed hot spot in the Earth's mantle; Maupiti, the northwestern-

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most high island (not atoll) is somewhat over 4 million years (Ma) old, Moorea is around 2 Ma old, Tahiti-nui and Tahiti-iti are, respectively, about 1 Ma and less than 0.5 Ma old, and Mehetia, the easternmost island is even more recent (Duncan & Clague 1985; Jackson 1976). The suggested single invasion of Moorea by *Partula* probably came, therefore, from the older Leeward Islands to the northwest of Moorea (Johnson *et al.* 1986*b*; Murray & Clarke 1980), not, as Bailey (1956) suggested, from the younger Tahiti. Colonization by drosophilids of islands in the Hawaiian chain, also formed by the passage of the Pacific plate over a hot spot, also has been predominantly from older to younger islands, although a few colonization events in the reverse direction have been suggested (Carson 1987*a*). The *Partula* spp. of Tahiti, which are monophyletic on the basis of allozyme studies, are probably in turn derived from those of Moorea through a single colonization event (Johnson *et al.* 1986*b*). Although the morphological similarities between three pairs of Tahitian/Moorean species – *P. otaheitana*/*P. olympia* (the latter now considered conspecific with *P. tohiveana*; see above), *P. filosa*/*P. taeniata*, *P. nodosa*/*P. suturalis* – are suggestive of more than one colonization event (Murray & Clarke 1980), interpretation of the complex patterns of mtDNA variation in a wide range of *Partula* spp. of Moorea, Tahiti and Huahuine suggests that both the morphological and mitochondrial similarities may, at least in part, be due to reversed, parallel or convergent evolution and that, indeed, the Tahitian species are monophyletic and derived from a single colonization (Murray *et al.* 1991). That the position regarding the above pairs of morphologically similar species is confusing, is further illustrated by the reduction of *P. filosa* and *P. nodosa* to subspecies of *P. affinis* (Kondo & Burch 1983; Richardson 1990). As in many other organisms, such non-concordance of morphological and molecular variation poses a problem for biologists attempting to unscramble their evolutionary history. Crampton's (1916) view was that both the Moorean and Tahitian species were derived from a common stock that inhabited both islands during times when they formed a contiguous land mass (cf. Hyatt *et al.* (1911) for related ideas on the Hawaiian islands). However, the whole archipelago was probably never joined together in this way; despite the complex interactions of island subsidence and glacio-eustatic sea level fluctuations (Paulay & McEdward 1990), only Raiatea and Tahaa could ever have formed a single land mass, being currently within a single lagoon (G. Paulay, personal communication).

The biogeographic relations of the other Society Island species have been addressed by Johnson *et al.* (1986*b*) in an extensive allozyme study of large (mostly) samples of 24 *Partula* spp. (including 22 from the Society Islands), five *Samoana* spp. (including the four Society Island species) and *Eua globosa* from the Tongan island of Eua. This study showed that the *Partula* spp. of the leeward group of islands are monophyletic, as are those of the windward island group, suggesting that the windward species are derived from just a single colonization from the leeward islands. The species on each island within the two main groups of islands are also monophyletic (with the single, awkward exception of *P. turgida* of Raiatea, which seems more closely related to *P. assimilis* of Rarotonga in the Cook Islands; and see above for Tahiti/Moorea). Ambiguities in the data did not allow a definite conclusion on the sequence of colonizations among Huahine, Raiatea and Bora-Bora. However, because the ages of the Society Islands are known, it was possible to estimate rates of evolution within the group, and although these rates vary considerably, they are not extraordinarily high and do not demand an explanation based on colonization from even older islands now submerged to the northwest, an argument that, in any case, cannot be invoked because of the apparent monophyletic nature of the species groups on each island (cf. Hawaiian drosophilids; Beverley & Wilson 1985; but see DeSalle & Hunt 1987).

If it is assumed that (i) dispersal has been highly significant in Pacific land snail biogeography (Peake 1969; Vagvolgyi 1975), (ii) the general direction of partulid dispersal across the Pacific has been from west to east, as seems well established for both land snails and other organisms (for example, papers in Gressitt (1963); Kay (1980); Peake (1969); Zimmerman (1948), and (iii) *Partula* is younger than *Samoana* and derived from it (Kondo 1968), then it is possible to speculate on the origins of the Society Island species (Kondo 1973). Thus, a *Samoana* progenitor – *S. burchi* or something like it – was suggested by Kondo (1973) as initially being widely distributed on a large single Society island. (Although such an island probably never existed (see above), this does not fatally invalidate the following hypothetical sequence of events.) *S. burchi* (and not *S. jackieburchi*, which has now been shown (Johnson *et al.* 1986*a*) to be synonymous with *Partula otaheitana*, despite its penial morphology resembling that of *Samoana* (Kondo 1980)) then gave rise to *S. attenuata* which usurped the former, forcing it to retreat to small isolated high altitude localities. *Partula* then arrived, following one or a few colonizing events, and the large island subsided, becoming fragmented into the present smaller islands. While *Partula* speciated, *Samoana attenuata* was forced to high altitudes, following *S. burchi*, and isolated populations evolved into *S. diaphana* on Moorea and *S. annectens* on Huahine. This scenario, set out by Kondo (1973, 1980), may well have some truth in it, despite its foundation on the distribution of a single *Samoana* progenitor across a conjectured single large island that subsided and its ignoring of the sequential production of the Society Islands as the Pacific plate moved over the hot spot. If *Samoana* is generally less prone to speciation than *Partula*, and the seemingly slower rate of allozyme evolution (Johnson *et al.* 1986*b*) and the suggestion that self-fertilization may be more common in Moorean *Samoana* (Johnson *et al.* 1986a) support this, then it is reasonable to suppose that this single *Samoana* progenitor colonized a number of islands without speciating (cf. Carson 1987*b*). *Partula* might then have arrived on one (or a few) island(s) and dispersed to others, following the initial colonizing event(s), the

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demise of *Samoana* and speciation of *Partula* then taking place as suggested above by Kondo (1973).

However, even with the detailed information we have on Society Island, and especially Moorean, partulids, the evolutionary sequence of events remains speculative. And the phylogenetic origins of the family as a whole, its constituent genera, and the multitude of species, especially of *Partula*, remain completely unknown. Multivariate phylogenetic analysis of shell and soft part morphology and molecular, especially DNA, variation, combined with explanations of distribution derived from both dispersalist and vicariance theories of biogeography (cf. Diamond 1982; Gittenberger 1984; Van Bruggen 1987) – although because of the presumed oceanic island origin of the family, greater significance being attached to dispersal (cf. Kay 1980; Peake 1981; Thornton 1983) – will probably lead to the best reconstruction of partulid origins in the Pacific. No doubt, as with more and more evolutionary phenomena that are addressed in detail, a single model will be inadequate (see also Zimmerman (1948, p. 137)). Whereas, in general, seeking a unitary explanation should be the first, most parsimonious attempt, the temptation to be constrained by such an explanation of the complex inter-relationships among these snails should be avoided.

7. CONCLUSION

The Society Islands exhibited the greatest partulid diversity of any Pacific archipelago, and only Raiatea had greater diversity than Moorea (Kondo 1968; but see Johnson *et al.* (1986*c*), who suggest that the Raiatea species have been over-split by earlier taxonomists). The elucidation of many aspects of the inter- and intraspecific relationships of the Moorean species provides a framework for understanding all but the most complex aspects of partulid biology as a whole. These studies have not only advanced our knowledge of land snail population biology and become one of perhaps only three major bodies of work in this area – the others being the work on *Cepaea*, reviewed by Cain (1983), Clarke *et al.* (1978) and Jones *et al.* (1977), and *Cerion* (Gould & Woodruff 1990, and references therein) (but see also the work on camaenids by Heatwole & Heatwole (1978) and the growing body of work on *Liguus* (e.g. Hillis *et al.* 1987, 1991; Roth & Bogan 1984)) – but have also provided significant insights into many aspects of our understanding of evolution. It is a tragedy that the Moorean *Partula* spp. are now extinct in the wild and that many other members of the family are seriously threatened, if not also extinct.

Murray & Clarke (1980) considered that molecular studies were the way forward in attempts to understand more fully the origins and evolution of the *Partula* spp. of Moorea, and especially to answer questions about single or multiple invasions. The first study of DNA variation in partulids has now appeared (Murray *et al.* 1991) and, while once again emphasizing the complexity of the variation among the Society Island species, has both answered and posed significant questions about their evolution. Although partulids are under threat throughout the Pacific it may yet be possible to study their DNA more extensively by using not only the surviving laboratory colonies of living snails but, covering the family much more widely, by investigating those species that remain unthreatened and using alcohol-preserved specimens in museum collections. Clarke's (1968) vision of the value of museum specimens is endorsed by the recent discovery of the possibility of obtaining DNA from preserved material (see Arnheim *et al.* 1990). The origins of the family Partulidae, its constituent genera and especially the many individual species of *Partula* and *Samoana* may still be open to investigation, extending the contribution of this ancient family to our modern understanding of evolution.

It is becoming a common theme of twentieth century biology that island species, especially endemics, are highly vulnerable, particularly to introduced organisms, and that their rate of extinction far exceeds extinctions of continental species (Atkinson 1989; Carlquist 1974; Diamond 1984). Efforts to publicize the precarious position of this unique land snail fauna, to prevent further introductions of carnivorous snails for biological control, and to conserve those populations that remain, are crucial if these fascinating animals are to continue to give up their secrets and not become another sad statistic in the march of progress.

This review is dedicated to Yoshio Kondo (1910–1990) who spent a lifetime working on the Pacific land snail fauna. I thank Arthur Cain, Daniel Chung, Lu Eldredge, Mike Hadfield, David Hopper, Alison Kay and Dan Polhemus for comments on earlier drafts, Neal Evenhuis for taxonomic advice and Gustav Paulay for discussion of Pacific island formation. Bryan Clarke, Jim Murray and Mike Johnson were gracious in response to my writing a review dwelling heavily on their work. The Cooke Foundation provided financial support.

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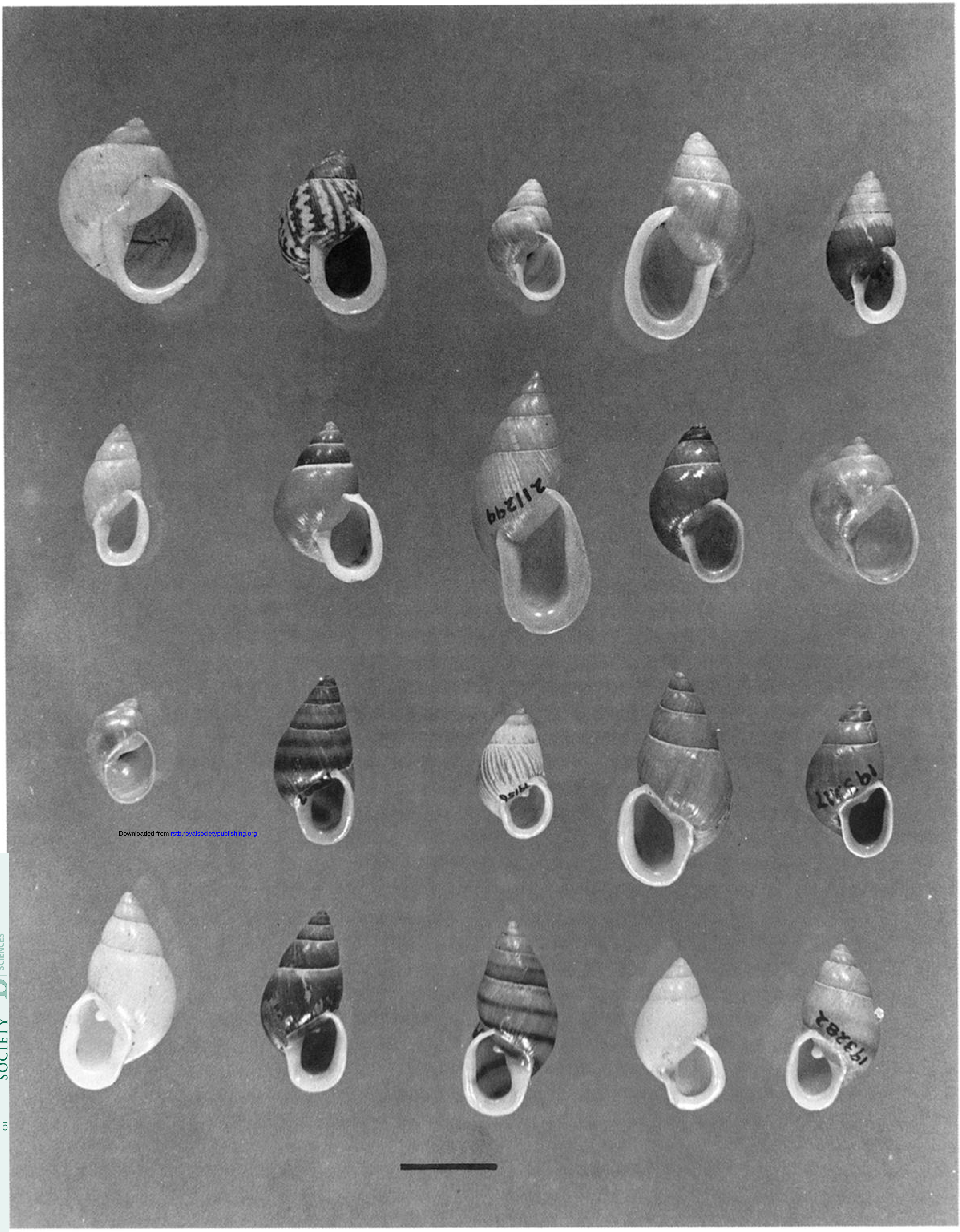

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Figure 2. Some of the Partulidae mentioned in the text to illustrate the range of shell shape, size and colour and pattern in the family. The scale bar represents 1 cm. Top row, left to right: *Eua globosa*, Eua, Tonga (Bishop Museum catalogue number: BPBM 108558); *E. zebrina*, Tutuila, Samoa (BPBM 84457); *Samoana fragilis*, Guam, Mariana Islands (BPBM 153051); *S. conica*, Tutuila, Samoa (BPBM 85475); *S. burchi*, Tahiti, Society Islands (BPBM 206915). Second row, left to right: *S. attenuata*, Tahaa, Society Islands (BPBM 139749); *Partula gibba*, Guam (BPBM 152740); *P. calypso*, Oreor, Belau (BPBM 211299); *P. assimilis*, Raratonga, Cook Islands (BPBM 95426); *P. turgida*, Raiatea, Society Islands (BPBM 136085). Third row, left to right: *P. arguta*, Huahine, Society Islands (BPBM 142379); *P. producta*, Tahiti, Society Islands (BPBM 79207); *P. filosa*, Tahiti (BPBM 79156); *P. otaheitana*, Tahiti (BPBM 193821); *P. mirabilis*, Moorea, Society Islands (BPBM 193217). Bottom row, left to right: *P. tohiveana*, Moorea (BPBM 193763); *P. suturalis* (dextral), Moorea (BPBM 193310); *P. suturalis* (sinistral), Moorea (BPBM 193333); *P. taeniata*, Moorea (BPBM 193512); *P. mooreana*, Moorea (BPBM 193284).

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