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Sex and darts in slugs and snails (Mollusca: Gastropoda: Stylommatophora)

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Abstract

In the final stages of an elaborate courtship, many slugs and snails shoot calcareous 'love' darts into each other. While darts improve the reproductive success of the shooter, by promoting sperm survival in the recipient, it is unclear why some species have darts and others do not. In fact, dart use has barely been studied, except in the garden snail *Cantareus aspersus* (*Helix aspersa*). An evolutionary approach was therefore taken to attempt to understand the origin and use of darts, by investigating mating behaviour in a wide range of species. The prediction was that, because darts could have arisen out of an escalating cycle of sperm digestion and investment in sperm, then darts should be found in taxa that enforce simultaneous reciprocity during mating. Likewise, they should not be found in taxa that mate unilaterally, because the co-evolutionary cycle is absent or reduced. Mating behaviour in 60 genera (28 families) of land snails and slugs was recorded, and compared against dart use across the whole of a stylommatophoran phylogeny. 'Face-to-face' simultaneous reciprocal-mating behaviour is restricted to three monophyletic groups of snails and slugs, and dart-bearing species are a subset within the same clades, which suggests a link, though not necessarily a causal one. As yet, we are unable to quantify the extent to which darts or mating behaviour, as well as several other correlated characters, are determined by common ancestry or regimes of natural or sexual selection, because the current phylogeny lacks resolution. However, the results emphasize that to understand the use of darts, then data are required from a wide range of species. The realization that several characters are correlated may stimulate further research, and could eventually lead to some testable models for dart and mating behaviour evolution.

Key words: love dart, mating behaviour, sexual conflict, simultaneous hermaphrodite

INTRODUCTION

Pulmonate land snails and slugs are especially interesting, because in the final stages of an often elaborate courtship involving circling, touching and biting, many species shoot calcareous 'love' darts into each other (Baur, 1998). Although this can injure the recipient, and reputedly even kill them, in the garden snail *Cantareus aspersus* (*Helix aspersa*) it has been shown that darts improve the reproductive success of the shooter by promoting sperm survival in the recipient (Koene & Chase, 1998; Landolfa, Green & Chase, 2001; Rogers & Chase, 2001, 2002). In *Cantareus*, mucus introduced with the dart induces a muscular contraction that closes the entrance to a specialized sperm digestive organ (the bursa copulatrix), while at the same time speeding uptake of the spermatophore into a blind-ended organ of the female digestive tract (Koene & Chase, 1998). The effect of successful dart-shooting is to improve fertilization success (Koene & Chase, 1998; Landolfa *et al*., 2001; Rogers & Chase, 2002).

One theory is that darts evolved from sexual conflict (i.e. differences in male and female interests; Chapman *et al*., 2003), because dart-shooting promotes donor sperm survival at a cost to the receiver. Alternatively, heightened sperm competition between males could mean that the main function of darts is to improve the survival of a male's own sperm compared against sperm from other males (Pomiankowski & Reguera, 2001). A final consideration is that females might favour successful dart shooters, because they then have fitter offspring, either via higher reproductive success (Fisher's runaway process) or higher viability (good genes) (Pomiankowski & Reguera, 2001).

Ultimately, however, the reason why darts evolved at all in stylommatophoran slugs and snails remains unclear,

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and also why some species have darts and others do not. Dart use has barely been studied outside of *Cantareus*, and there has been only one brief and incomplete survey of darts in different species (Tompa, 1980). It was therefore decided to record the occurrence of darts in the stylommatophoran land snails and slugs, and in particular, to investigate whether there is a link between mating system and dart use.

In the past, many authors have tended to assume that genital intromission during mating is simultaneous and reciprocal (with a few exceptions such as *Partula*; Lipton & Murray, 1979), because stylommatophoran snails and slugs are *simultaneous* hermaphrodites. This is erroneous because many species mate unilaterally (e.g. *Liguus*; Cook, 1985). Asami, Cowie & Ohbayashi (1998) have recently shown that there is a strong correlation between mating position, and whether mating is reciprocal or not. They found that, with some obvious exceptions (e.g. *Limax*, references within Baur, 1998), taxa either mate 'face-to-face' or by 'shell-mounting'. Species that mate face-to-face almost always mate simultaneously and reciprocally, whereas shell-mounting species mate unilaterally. Although Asami *et al*. (1998) are not explicit in their explanation, the essential difference is that in simultaneous reciprocal face-to-face mating both individuals in a mating pair use both their male and female organs at the same time, whereas in unilateral shell-mounting mating, each snail has a defined and distinct role, either as a male or a female in each mating. Finally, unilateral mating can sometimes be sequential, where individuals switch sex roles after one round of unilateral mating. An essential difference is that in unilateral mating, an individual cannot be forced to reciprocate. In contrast, in simultaneous reciprocal-mating, copulation is conditional on reciprocity, hence both mating partners are obliged to act as male and female at the same time (insemination is also reciprocal; Baur, 1998; Rogers & Chase, 2002). Given an insistence on reciprocal insemination, it is possible to 'cheat' (i.e. not use your partner's sperm to fertilize your own eggs) only after intromission has occurred. One way to achieve this might be to either expel or digest your partner's sperm.

Generally, multiple mating and sperm digestion are common in hermaphrodites that mate simultaneously and reciprocally (Michiels, 1998; Greeff & Michiels, 1999). Since sperm digestion reduces the fertilization success of a given ejaculate, this can select for increased sperm investment, leading to a co-evolutionary cycle in which both the amount of sperm digested and investment in sperm increase until eventually, individuals will invest equally in male and female gametes (Greeff & Michiels, 1999). Fitness through the male function should then become more dependent on the total resources devoted to sperm, rather than on the number of matings, thus reducing Bateman's principle (Bateman, 1948), which is that male reproductive success is limited by the number of matings, and female reproductive success by investment in eggs. Once ejaculates are large and costly, reciprocity will be further enforced, because individuals that insist on reciprocal sperm transfer will be favoured as they receive an energetic compensation for their investment, through the digested sperm (Greeff & Michiels, 1999). However, alternative evolutionary responses are likely, because an individual that reduces sperm digestion in their partner will be able to father more offspring. This could be achieved by packing sperm in spermatophores, or, using darts to inject a substance that could promote sperm survival in the recipient.

Given the above theory, we speculated that the nature of the differences between mating systems would predict the more frequent occurrence of darts in simultaneous reciprocal-mating species. This is because only they are potentially locked into an escalating cycle, which could promote the evolution of alternative responses such as darts. This is exactly what we found: darts invariably occur in association with face-to-face simultaneous reciprocal-mating. Moreover, it has been shown previously that mating behaviour is correlated with shell shape, and that there is also a complicated correlation with shell and body asymmetry (chirality; Asami *et al*., 1998). Thus, while it is far from proven that the relationship between darts and mating behaviour is a causal one, the realization that they are correlated may stimulate further research.

Note: for clarity it is still often convenient to use the terms 'male' or 'female' when referring to specific behavioural or anatomical features of hermaphrodites.

MATERIALS AND METHODS

The literature on darts and especially reproductive behaviour in stylommatophoran land snails and slugs is sparse. In particular, no study has investigated the relationship between both dart use and mating behaviour. The only comparable study is that of Asami *et al*. (1998), where data from 17 stylommatophoran familes were used to investigate the relationship between mating behaviour, shell-shape and chirality (no molecular phylogeny was available at the time).

Most prior research on darts has been in *Cantareus aspersus* (Koene & Chase, 1998; Landolfa *et al*., 2001; Rogers & Chase, 2002), with a few investigations in closely related species (Baminger, Locher & Baur, 2000). While the details of dart use differ (e.g. used before or after genital intromission), in all the species that have been investigated darts are hard calcareous or chitinous structures that pierce a partner during mating. It was possible to infer whether individual species possess darts from a knowledge of the internal anatomy, and by reference to standard descriptive texts.

Original publications were also sourced, and our personal knowledge as well as that of colleagues used to categorize slug and snail mating behaviour as: (1) 'unilateral' or 'simultaneous reciprocal'; (2) 'shell-mounting' or 'face-to-face' (see Introduction for explanation of categories as well as Asami *et al*. 1998 for further information on mating positions). The degree to which individuals mate unilaterally rather than unilateral sequentially was impossible to verify, because detailed behavioural observations do not exist for most species. It was therefore not possible to distinguish between 'true' unilateral mating and unilateral sequential mating. This should not affect the prediction that darts would be found in simultaneous reciprocal-mating taxa, because the enforced aspect of reciprocity is lacking in both types of unilateral mating. The main references used for mating behaviour were Dasen (1933), Künkel (1933), Pilsbry (1939–40), Moreno (1950), Webb (1951, 1953, 1968), Quick (1960), Hecker (1965), Plummer (1975), Woodruff (1978), Lipton & Murray (1979), Tompa (1980), Cook (1985), Adamo & Chase (1988), Tomiyama (1994), Schilthuizen & Lombaerts (1995), Asami *et al*. (1998), Rodriguez & Gomez (1999) and Stringer *et al*. (2003), with additional information on *Amphidromus* from Menno Schilthuizen, and *Trichotoxon* from Bernard Verdcourt. At the same time whether snail shell-shape is low- or high-spired was also recorded. The division into 1 of 2 types of shell was possible, because it has been shown previously that snails have a bimodal distribution of shell shapes (Cain, 1977).

Full details of the specimens used, collection localities, dart use and shell shape are given in the appendix. The detailed description and analysis of the phylogenetic relationship between species will be published elsewhere (Wade, Mordan & Naggs, in press). Briefly, an approximately 1460 nucleotide region of the 5.8S, ITS-2 and 28S rRNA gene was amplified for 160 species in 144 genera (56 new, GenBank accession numbers AY841280 to AY841349; for the remainder see Wade, Mordan & Clarke, 2001). PCR amplification and DNA sequencing were carried out as in Wade & Mordan (2000). Sequences were assembled and aligned manually. Evolutionary trees were constructed using the neighbour-joining method in Paup* (version 4.0d65, Swofford, 2002), with distances corrected for multiple hits by using the general time-reversible (GTR) model and between-site rate heterogeneity accounted for by incorporating a proportion of invariant sites (I) and gamma-distributed rates (G) into the model. The rate matrix, base frequencies, proportion of invariant sites (pinvar) and shape parameter (α) of the gamma distribution were estimated using likelihood by iteration from an initial neighbour-joining tree. The parameters estimated from the initial tree were then used to build a new neighbour-joining tree and the parameters re-estimated. This process was repeated until there was no further improvement in likelihood. As an alternative phylogenetic method, Bayesian analysis was undertaken using MrBayes v3.0b4 (Huelsenbeck & Ronquist, 2001). A GTR plus gamma model was used and the tree space was explored using four chains of a Markov Chain Monte Carlo algorithm for 25 million generations, sampling every 2500 generations. To ensure adequate chain swapping, the heating parameter was set to 0.025 and the dirichlet of the state frequency priors set to 600. A consensus tree was built from the last 1000 trees (burn in = 9001 samples).

Possession of darts, shell shape and mating behaviour were then mapped onto the resulting phylogeny. Unfortunately, poor resolution at several important nodes prevented a strict, phylogeny controlled, comparative analysis (e.g. CAIC, Purvis & Rambaut, 1995). Furthermore, while multiple taxa from the Limacoidea have darts, there was material from only one specimen.

RESULTS

In total, the mating behaviour of 60 stylommatophoran slug and snail genera in 28 families was discovered. It was found that unilaterally mating snails in 11 families mate by shell-mounting, and none have darts (Table 1). In contrast, simultaneous reciprocal-mating species in 15 out of 18 families mate face-to-face, with the exception of the families Achatinidae and Discidae and *Albinaria* (Table 2). Dart-bearing species are a subset within the simultaneous reciprocal, face-to-face mating group, and are restricted to two superfamilies, the Helicoidea (at least four familes) and Limacoidea (at least four families; three for which the mating behaviour is known plus the Dyakiidae), as well as the slug family Philomycidae (Table 2). The tables show a further correlation, that both helicoid and limacoid superfamilies predominantly have low-spired shells (Table 2; 26 of 28 helicoid genera and 4 of 4 limacoid genera), or are else slugs, whereas shell-mounting species tend to be high-spired (11 of 15 genera examined; Table 1).

Table 1. Unilateral mating snails and slugs. Genera that mate unilaterally mate by shell-mounting and none have darts. Most are also high-spired (11/15 genera). Only one of the genera is from a dart-containing clade (*Oreohelix*, Helicoidea), and it is also low-spired. *Cerion* mate unilaterally but no further information is available (Woodruff, 1978). FF, face-to-face mating; SM, shell-mounting; L, low-spired; H, high-spired

	Mating behaviour	Shell-shape
Acavidae		
Helicophanta	SM	L
Clausiliidae		
Euphaedusa	SM	H
Luchuphaedusa	SM	H
Stereophaedusa	SM	H
Haplotrematidae		
Haplotrema	SM	L
Oreohelicidae		
Oreohelix	SM	L
Orthalicidae		
Liguus	SM	H
Ceriidae		
Cerion	?	H
Partulidae		
Partula	SM	H
Rhytididae		
Paryphanta	SM	L
Spiraxidae		
Euglandina	SM	H
Strophocheilidae		
Strophocheilus	SM	H
Succineidae		
Catinella	SM	H
Oxyloma	SM	H
Succinea	SM	H

Table 2. Simultaneous reciprocal-mating snails and slugs. Genera that mate simultaneous reciprocally usually do so face-to-face, with the exception of the Achatinidae, Discidae and *Albinaria*. Dart-bearing species are a subset within the face-to-face mating group, and are in three separate monophyletic groups, the Helicoidea, Limacoidea and Philomycidae (see Fig. 1). Genera with low-spired shells are also much more common in the Helicoidea and Limacoidea (Fig. 1, Cain, 1977). Both *Cochlicella* and *Monacha* have dart sacs but lack darts, so must have secondarily lost darts. FF, face-to-face mating; SM, shell-mounting; L, low-spired; H, high-spired

Superfamily Family	Genus	Mating behaviour	Darts or dart-sac	Shell-shape
Helicoidea				
Bradybaenidae	*Bradybaena*	FF	Y	L
	Euhadra	FF	Y	L
	Mandarina[a]	FF		L
Camaenidae	*Caracolus*	FF		L
	Satsuma	FF		L
	Amphidromus	FF		H
Helicidae	*Cepaea*	FF	Y	L
	Cantareus	FF	Y	L
	Theba	FF	Y	L
	Arianta	FF	Y	L
Helminthoglyptidae	*Cepolis*	FF	Y	L
	Helminthoglypta	FF	Y	L
	Humboldtiana	FF	Y	L
	Monadenia	FF	Y	L
	Sonorella	FF		L
	Polymita	FF	Y	L
Hygromiidae	*Cochlicella*[b]	FF	Y	H
	Monacha	FF	Y	L
Polygyridae	*Allogona*	FF		L
	Ashmunella	FF		L
	Cryptomastix	FF		L
	Mesodon	FF		L
	Neohelix	FF		L
	Polygyra	FF		L
	Stenotrema	FF		L
	Trilobopsis	FF		L
	Triodopsis	FF		L
	Vespericola	FF		L
Limacoidea				
Agriolimacidae	*Deroceras*	FF		slug
Arionidae	*Arion*	FF		slug
	Geomalacus	FF		slug
Ariophantidae	*Ariophanta*	FF	Y	L
Gastrodontidae	*Oxychilus*	FF		L
Milacidae	*Tandonia*	FF		slug
Urocyclidae	*Trichotoxon*	FF	Y	slug
Vitrinidae	*Semilimax*	FF	Y	slug
	Vitrinobrachium	FF		slug
Zonitidae	*Mesomphix*	FF		L
	Ventridens	FF		L
Other				
Clausiliidae[c]	*Albinaria*	SM		H
Philomycidae	*Philomycus*	FF	Y	slug
Achatinidae	*Achatina*	SM		H
	Archachatina	SM		H
	Lissachatina	SM		H
Discidae	*Anguispira*	SM		L

[a] Of ~100 *Mandarina* matings, we recently observed one that was unilateral, not simultaneous reciprocal.
[b] Most other genera of Hygromiidae are low-spired.
[c] Mating is normally simultaneous reciprocal, but occasionally may be unilateral, as in other Clausiliidae.

The use of darts and shell-shape were scored for 160 species, then mapped onto a molecular phylogeny and compared with mating behaviour, all of which are summarized in Fig. 1 (see Appendix for further details). While the mating behaviour was not known for some of these taxa, mating behaviour does not vary much within taxonomic and phylogenetic groups (families or superfamilies), e.g. all helicoid species are simultaneous reciprocal face-to-face mating, except *Oreohelix*; all clausilids mate by shell-mounting. Thus, we were confident in making generalizations for monophyletic groups in the phylogeny. Similarly, both the well-supported Limacoidea and Helicoidea correspond to pre-existing superfamilies, based on morphological evidence, so taxa such as *Ariophanta* can be confidently placed in the Limacoidea, even though DNA evidence is lacking.

Simultaneous reciprocal face-to-face mating was found to be confined to three monophyletic groups, the Limacoidea, Helicoidea and the Philomycidae. Dart-bearing species are a subset of genera within the three groups (Fig. 1). The monophyly of the three groups is beyond doubt, because each is well supported using both neighbour-joining and Bayesian methods, but the relationship between them is uncertain (Fig. 1). The molecular phylogenetic analysis is suggestive, although not statistically significantly so, of a relationship between the Limacoidea and Philomycidae (39% neighbour-joining bootstrap support; $P = 0.99$ with MrBayes). Unfortunately, the phylogeny is poorly supported at the base, so it is not possible to estimate reliably the number of times that darts evolved.

None the less, there is some phylogenetic evidence for character evolution. There is firm evidence for dart loss. Both *Cochlicella* and *Monacha* lack darts but have dart-sacs, and are nested with two taxa that have darts, *Cernuella* and *Trichia* (Fig. 1). Furthermore, *Amphidromus* is nested within a large dart-containing clade, though the position is not well supported. There are also two well supported monophyletic dart-bearing groups within the Helicoidea, one comprising only *Sagda* and another, the remaining taxa, which could in theory mean that darts have evolved more than once within the Helicoidea (Fig. 1).

The mapping of shell shape onto the molecular phylogeny (Fig. 1) confirms that several large monophyletic groups have the same kind of shell and mate in the same manner, with only a few exceptions. In the phylogeny, the Helicoidea and Limacoidea have low-spired shells, except *Cochlicella* and *Amphidromus*. The Orthurethra, Clausilioidea, and Achatinoidea are almost entirely composed of high-spired species, again with a few exceptions (e.g. *Pyramidula*, *Thyrophorella*).

DISCUSSION

In our study, a previously unrecognized and striking association between three characters was discovered: the use of darts, mating behaviour and shell shape. Dart-bearing genera are in eight different families that always mate face-to-face and are usually low-spired snails, or

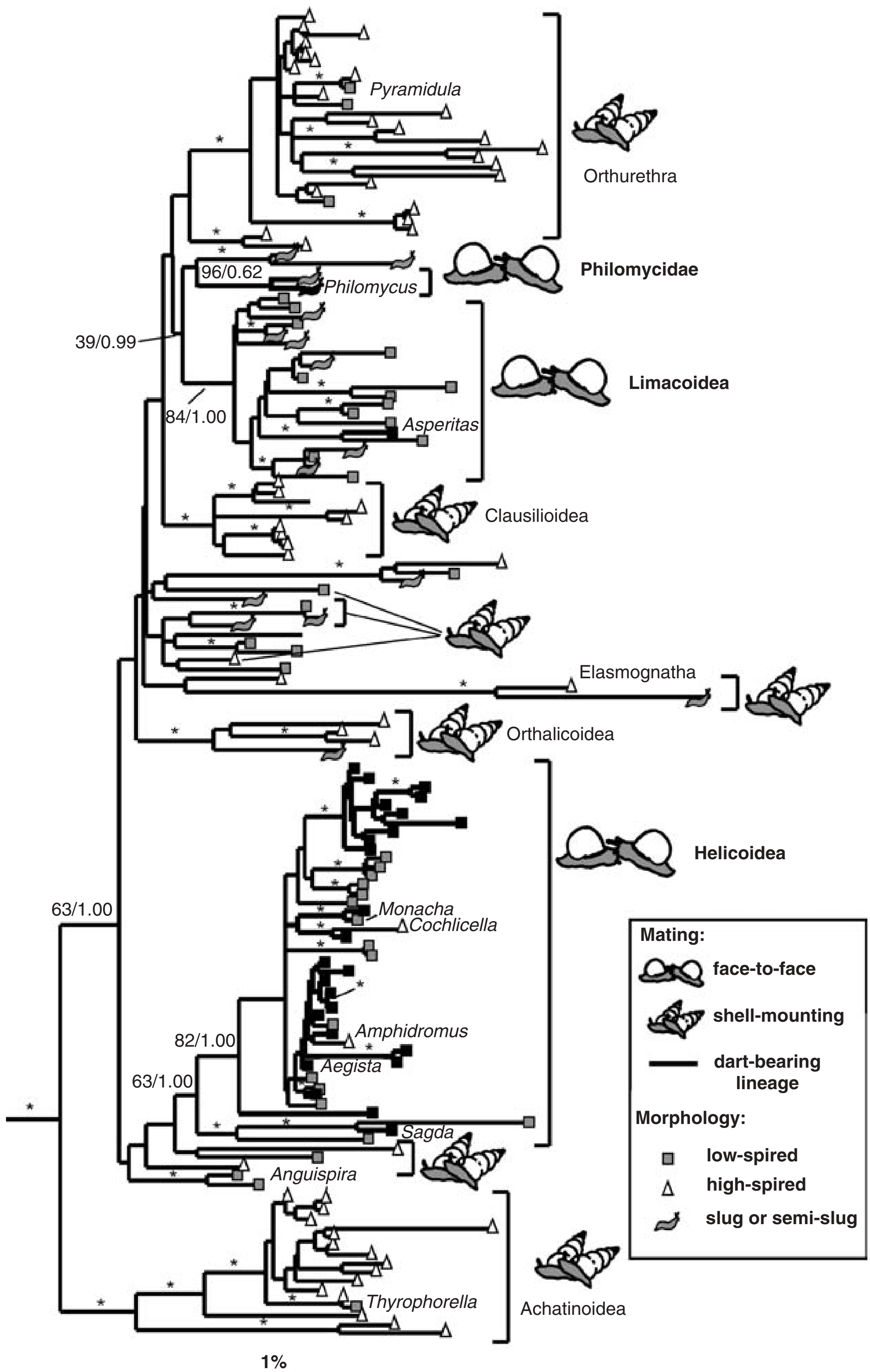

Fig. 1. Neighbour-joining phylogeny showing the association between mating position, the use of darts and shell shape in slugs and snails. Only reciprocal face-to-face mating species have darts and are found in three monophyletic groups, the Helicoidea, Limacoidea and Phylomycidae. Face-to-face mating species nearly always have low-spired shells, or else are slugs. In contrast, species that mate by shell-mounting are often high-spired, especially the large monophyletic groups of the Orthurethra, Clausilioidea, and Achatinoidea. The neighbour-joining phylogeny is rooted using a non-stylommatophoran pulmonate outgroup; genera that are specifically discussed in the main text are labelled. *, support value > 70% (neighbour-joining) and $P > 0.95$ (MrBayes). Precise support values (neighbour-joining/MrBayes) are shown at several important nodes.

else slugs. Darts and simultaneous reciprocal face-to-face mating are both confined to three monophyletic groups, the Helicoidea, Limacoidea and Philomycidae (Fig. 1). In contrast, many of the other families contain only high-spired species that mate by shell-mounting, and it is genera within those groups that are most frequently variable for their body asymmetry (Asami *et al*., 1998). Because all the characters are strongly correlated with phylogeny, it cannot be determined exactly how natural or sexual selection are implicated in the evolution of darts and mating behaviour. Moreover, while there is a definite relationship between dart use and mating behaviour, it is not necessarily a causal one. The results, however, emphasize that in order to understand the use of darts, data are required from a wide range of species.

In general, the results seem to corroborate the expectations of mating systems theory (Greeff & Michiels, 1999). The digestion of sperm in the recipient will promote the evolution of large (expensive) ejaculates, which in turn will bring about higher levels of sperm digestion and an even higher investment in sperm (Greeff & Michiels, 1999). Sperm digestion should be a greater problem for donors in simultaneously reciprocal mating species (rather than unilateral). Consequently, strategies to mitigate the effects of sperm digestion should be stronger in simultaneously reciprocal mating species, because of the heightened investment in sperm (Greeff & Michiels, 1999).

An intriguing question that could affect dart evolution is whether individuals are able to recognize the dart status of their mating partner. Variation in status is to be expected for a variety of reasons: virgins do not usually produce a dart; once a dart has been shot, it may take up to a week to generate another; finally, some populations within otherwise dart-bearing species lack both darts and dart-sac (e.g. *Aegista mikuriyensis* from Japan). If individuals can recognize dart-bearing individuals, then they may refuse to mate with them, because it would allow the 'female' to regain control over fertilization of her own eggs, and not be penetrated by a potentially damaging dart.

Ultimately, however, aside from recent progress in *Cantareus aspersus*, we remain relatively ignorant as to the function of darts (Koene & Chase, 1998; Pomiankowski & Reguera, 2001; Rogers & Chase, 2001, 2002). One means to progress might be to incorporate the data on reciprocity and multiple mating into models or simulations, to try to determine the evolutionarily stable strategy. The knowledge gained could be used to determine how different situations may favour the evolution and maintenance of darts. Further empirical tests will then be required, based on the outcome of the models.

Reciprocity

Although simultaneous reciprocity was used as the predictor of dart use, the correlation of mating behaviour with dart use is stronger if the criterion is face-to-face mating, because the Achatinoidea (e.g. giant African snail *Lissachatina fulica*) and *Anguispira* do not have darts, even though they mate in a simultaneous reciprocal manner. We speculate that the reason for this is that it is more difficult to enforce reciprocity when mating is by shell-mounting. Again, models or simulations are required, but it is possible that if a low proportion of matings are not reciprocal, then the escalating co-evolutionary cycle is broken, removing the selection pressure to manipulate the partner. However, while it is possible that loss of reciprocity has led to the loss of darts in some species and populations, there is presently no direct evidence for this as the cause, and probably many factors are involved. For example, a number of taxa within the large dart-bearing helicoid group lack darts (e.g. *Cochlicella*), so have, presumably, secondarily lost them, but they still mate in a face-to-face reciprocal manner. One testable prediction is that simultaneous reciprocal-mating snails, especially those that shoot darts, should have larger spermatophores or ejaculates, because they are locked in an escalating co-evolutionary cycle.

Correlations with shell-shape

Previously, Cain (1977) showed that pulmonate land snail shell-shape has a bimodal distribution, and argued that this is largely independent of taxonomic position, providing strong indirect evidence for the action of natural selection on shell-shape. Subsequent studies have largely confirmed and extended his original hypothesis (Cain & Cowie, 1978; Cook & Jaffar, 1984). Although it could be argued that the general relationship between shell-shape and phylogeny that was found in our study contradicts the findings of Cain (1977), the results are consistent if closely related species by phylogeny tend to be under the same selective pressure, because they live in similar niches. Some of the correlation of dart use with shell shape could be explained if high-spired species are more commonly found on vertical surfaces, and reciprocal mating is more difficult in that position.

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Appendix

Family	Taxon	Dart?	Shell shape or slug	Collection/location	Collector
Stylommatophoran pulmonates (Phylum Mollusca, Class Gastropoda, Subclass Pulmonata, Order Eupulmonata, Suborder Stylommatophora)					
Infraorder Orthurethra					
Achatinellidae	*Elasmias luakahaense* (Pilsbry and Cooke, 1915)	No Dart	High	Koolau Range, Oahu, Hawaii	R. Rundell & K. Olival
	Partulina proxima (Pease, 1862)	No Dart	High	Maui, Hawaii	B. Holland
Cochlicopidae	*Cochlicopa lubrica* (Müller, 1774)	No Dart	High	Box Hill, Dorking, U.K.	P. Mordan & E. Platts
	Cochlicopa lubricella (Porro, 1838)	No Dart	High	São Miguel, Azores	P. Mordan
Amastridae	*Leptachatina lepida* Cooke, 1910	No Dart	High	Hawaii Island, Hawaii	P. Mordan & R. Cowie
Pupillidae	*Pupoides albilabris* (Adams, 1841)	No Dart	High	Wilson County, Tennesse, U.S.A.	J. Slapcinsky & B. Coles
Lauriidae	*Lauria cylindracea* (da Costa, 1778)	No Dart	High	Mullaghmore, Co. Sligo, Ireland	E. Platts
	Lauria fasciolata (Morelet, 1860)	No Dart	High	São Miguel, Azores	P. Mordan
Valloniidae	*Vallonia costata* (Müller, 1774)	No Dart	Low	São Miguel, Azores	P. Mordan
	Vallonia eccentrica Sterki, 1892	No Dart	Low	São Miguel, Azores	P. Mordan
Vertiginidae	*Vertigo antivergo* (Draparnaud, 1801)	No Dart	High	Chuett, Arnoldstein, Austria	P. Miltner
	Pronesopupa acanthinula Ancey, 1892	No Dart	High	Koolau Range, Oahu, Hawaii	R. Rundell & K. Olival
	Gastrocopta armifera (Say, 1821)	No Dart	High	Wilson County, Tennesse, U.S.A.	J. Slapcinsky & B. Coles
Orculidae	*Orcula austriaca* Zimmerman, 1932	No Dart	High	Kuhberg, Austria	P. Miltner
Strobilopsidae	*Eostrobilops nipponica* (Pilsbry, 1908)	No Dart	Low	Osaka, Japan	I. Matsumura
Pyramidulidae	*Pyramidula rupestris* (Draparnaud, 1801)	No Dart	Low	Mullaghmore, Co. Sligo, Ireland	E. Platts
Chondrinidae	*Chondrina avenacea* (Bruguière, 1792)	No Dart	High	Verdon Gorge, France	H. Selvadaurai
	Chondrina clienta (Westerlund, 1883)	No Dart	High	Villach, Austria	P. Miltner
	Solatopupa similis (Bnuguière, 1792)	No Dart	High	Verdon Gorge, France	A. Davison
Enidae	*Buliminus labrosus* (Olivier, 1804)	No Dart	High	Saladin's Castle, Syria	P. Mordan
	Pene sidonensis (Férussac, 1821)	No Dart	High	Saladin's Castle, Syria	P. Mordan
	Luchuena reticulata (Reeve, 1849)	No Dart	High	Kikai Island, Ryukyu, Japan	S. Chiba
	Napaeus pruninus (Gould, 1846)	No Dart	High	São Miguel, Azores	A. Polasczek
	Macaronapaeus vulgaris (Morelet & Drouet, 1857)	No Dart	High	São Miguel, Azores	P. Mordan
	Mastus pupa (Bruguière, 1792)	No Dart	High	Sicily	A. Davison
Draparnaudia	*Draparnaudia singularis* (Reeve, 1854)	No Dart	High	Mont Koghis. Grande Terre, New Caledonia	C. Wade & K. Bowman
Cerastidae	*Cerastus schweinfurthi* (Martens, 1895)	No Dart	High	Al-Mahuit, N. Yemen	P. Mordan
	Pachnodus silhouettanus van Mol & Coppois, 1980	No Dart	High	Silhouette Island, Seychelles	J. Gerlach
Partulidae	*Partula suturalis* Pfeiffer, 1855	No Dart	High	Moorea	B. Clarke
	Samoana conica (Gould, 1848)	No Dart	High	Samoa	R. Cowie
	Eua zebrina (Gould, 1848)	No Dart	High	Samoa	R. Cowie
Infraorder Mesurethra					
Clausiliidae	*Cochlodina laminata* (Montagu, 1803)	No Dart	High	South Downs, East Sussex, U.K.	B. Clarke
	Albinaria xantostoma (Boettger, 1883)	No Dart	High	Crete	D. Thomaz
	Papillifera papillaris (Müller, 1774)	No Dart	High	Sicily	A. Davison
	Clausilia bidentata (Ström, 1765)	No Dart	High	Kirkdale, Derbyshire, U.K.	C. Wade
	Macrogastra rolphii (Turton, 1826)	No Dart	High	South Downs, East Sussex, U.K.	B. Clarke
	Pinguiphaedusa platydera (Martens, 1876)	No Dart	High	Sendai, Japan	S. Chiba & A. Davison
	Stereophaedusa japonica (Crosse, 1871)	No Dart	High	Yamaguchi City, Japan	P. Callomon
	Mundiphaedusa decapitata (Pilsbry, 1902)	No Dart	High	Osaka City, Japan	P. Callomon
	Nenia tridens (Schweigger, 1820)	No Dart	High	El Yunque, Puerto Rico	A. Davison
Infraorder Elasmognatha					
Succineidae	*Succinea putris* (L., 1758)	No Dart	High	Southampton, U.K.	C. MacDonald
	Sucinea striata (Krauss, 1848)	No Dart	High	Mambassa Hu, Natal	M. Harmer & R. Miller
Athonacophoridae	*Athoracophorus bitentaculatus* (Quoy & Gaimard, 1832)	No Dart	Slug	Mere Mere, New Zealand	G. Barker
Infraorder Sigmurethra					
Orthalicidae	*Placostylus ambagiosus* Suter, 1906	No Dart	High	Manaaki Whenua, New Zealand	D. Gleeson
	Placostylus eddystonensis (Pfeiffer, 1855)	No Dart	High	Mont. Koghis, New Caledonia	C. Wade & K. Bowman
	Bulimulus guadalupensis (Bruguière, 1789)	No Dart	High	San Juan Viejo, Peurto Rico	A. Davison
	Bulimulus sporadicus (d'Orbigny, 1835)	No Dart	High	Natal, Brasil	P. Rainbow
	Drymaeus discrepans (Sowerby, 1833)	No Dart	High	Guatemala	Unknown
Amphibulimidae	*Gaeotis nigrolineata* Shuttleworth, 1854	No Dart	Semislug	El Yunque, Puerto Rico	A. Davison
Cerionidae	*Cerion incanum* (Binney, 1851)	No Dart	High	Florida Keys, U.S.A.	J. Taylor
Ferussaciidae	*Ferussacia foilliculus* (Gmelin, 1791)	No Dart	High	Los Alcornales, Prov Cadiz, Spain	M. Seddan
Subulinidae	*Subulina striatella* (Rang, 1831)	No Dart	High	Kew Gardens (introduced)	F. Naggs
	Bocageia sp.	No Dart	High	Sao Thomé	A. Gascoigne
	Riebeckia sp.	No Dart	High	Samha, Sokotra Archipelago	E. Neubert
	Rumina decollata (L., 1758)	No Dart	High	Sicily	A. Davison
	Xerocerastus sp.	No Dart	High	Otjiwarongo, Namibia	W. Sirgel
	Zootecus insularis (Ehrenberg, 1831)	No Dart	High	Dubai, United Arab Emirates	S. Green
Glessulidae	*Glessula ceylanica* (Pfeiffer, 1845)	No Dart	High	Colombo, Sri Lanka	P. Karunaratne
Achatinidae	*Lissachatina fulica* (*Achatina*) (Bowdich, 1822)	No Dart	High	Unknown (Zool. Soc. Lond. colln.)	P. Pearce-Kelly
	Archachatina marginata (Swainson, 1821)	No Dart	High	Nigeria (NHM collection)	Unknown
	Atopocochlis exarata (Müller, 1774)	No Dart	High	Nr. Balem, Sao Thomé	A. Gascoigne
	Limicolaria kambeul (Bruguière, 1789)	No Dart	High	Somalia (NHM collection)	M. Leng
Coeliaxidae	*Coeliaxis blandii* (Pfeiffer, 1852)	No Dart	High	New Bradford, South Africa	N. Smith
	Pyrgina umbilicata Greeff, 1882	No Dart	High	Sao Thomé	A. Gascoigne
Thyrophorellidae	*Thyrophorella thomensis* Greeff, 1882	No Dart	Low	Zampala, Sao Thomé, West Africa	A. Gascoigne
Spiraxidae	*Euglandina rosea* (Férussac, 1821)	No Dart	High	Moorea (Zool. Soc. Lond. colln.)	P. Pearce-Kelly
Testacellidae	*Testacella scutulum* Sowerby, 1821	No Dart	Slug	North London, U.K.	R. Hurst
Streptaxidae	*Gonaxis quadrilateralis* Preston, 1910	No Dart	High	Reunion	O. Griffiths
	Gonospira sp.	No Dart	High	Mauritius	O. Griffiths
Megalobulimidae	*Megalobulimus oblongus* (Müller, 1774)	No Dart	High	Antigua (Zool. Soc. Lond. colln.)	P. Pearce-Kelly
Dorcasiidae	*Dorcasia alexandri* Gray, 1938	No Dart	Low	Windhoek, Namibia	C. Boix-Hinzen
	Trigonephrus globulus (Müller, 1774)	No Dart	Low	Natal, South Africa	W. F. Sirgel
Acavidae	*Acavus phoenix* (Pfeiffer, 1854)	No Dart	Low	Kitulgala, Sri Lanka	P. Karunaratne
	Leucotaenius proctori (Sowerby, 1894)	No Dart	High	Beheloa, Madagascar	O. Griffiths
Caryodidae	*Caryodes dufresnii* Leach, 1815	No Dart	High	Mt Wellington, Hobart, Tasmania	B. Smith

Appendix. Continued.

Family	Taxon	Dart?	Shell shape or slug	Collection/location	Collector
Rhytididae	*Rhytida stephenensis* Powell, 1930	No Dart	Low	Manaaki Whenua, New Zealand	D. Gleeson
	Schizoglossa sp.	No Dart	Semislug	Kaikarangi, New Zealand	G. Barker
Chlamydephoridae	*Chlamydephorus burnupi* (Smith, 1892)	No Dart	Slug	Pevensey, Natal	D. Herbert
Haplotrematidae	*Haplotrema vancouverense* (Lea, 1839)	No Dart	Low	Eugene, Onegon	D. Taylor
Corillidae	*Corilla adamsi* Gude, 1914	No Dart	Low	Sri Lanka	D. Raheem
Punctidae	*Laoma* sp.	No Dart	High	Mannacau Harbour, New Zealand	P. Mordan
Charopidae	*Suteria ide* (Gray, 1850)	No Dart	Low	Waitomo, New Zealand	P. Mordan
Otoconchidae	*Otoconcha dimidiata* (Pfeiffer, 1853)	No Dart	Semislug	Waitakere New Zealand	P. Mordan
Discidae	*Discus rotundatus* (Müller, 1774)	No Dart	Low	Kirkdale, Derbyshire, U.K.	C. Wade
	Anguispira alternata (Say, 1816)	No Dart	Low	Wilson Co. Tennessee, U.S.A.	J. Slapzinsky & B. Coles
(Limacoidea)					
Euconulidae	*Euconulus fulvus* (Müller, 1774)	No Dart	Low	New Forest, Hampshire, U.K.	P. Mordan
	Louisia barclayi (Benson, 1850)	No Dart	Low	Mauritius	O. Griffiths
	Hiona sp.	No Dart	Low	Moorea	P. Pearce-Kelly
Helicarionidae	*Fastosarion brazieri* (Cox, 1873)	No Dart	Semislug	Mossman, Queensland, Australia	J. Stanisic
	Rhysotina hepatizon (Gould, 1848)	No Dart	Low	Sao Thomé	A. Gasgoine
	Harmogenanina argentea (Reeve, 1852)	No Dart	Low	Reunion	O. Griffiths
	Plegma caelatura (Férussac, 1821)	No Dart	Low	Reunion	O. Griffiths
Ariophantidae	*Cryptozona bistrialis* (Beck, 1837)	No Dart	Low	Sri Lanka	P. Karunaratne
	Euplecta gardeneri (Pfeiffer, 1846)	No Dart	Low	Sri Lanka	D. Raheem
	Ratnadvipia sp.	No Dart	Semislug	Sri Lanka	D. Raheem
Dyakiidae	*Asperitas inquinata* (v.d. Busch, 1842)	Dart	Low	Java	J. Reynolds
	Craterodiscus pricei McMichael, 1959	No Dart	Low	Ravenshoe, NE Old, Australia	J. Stanisic
Trochomorphidae	*Trochomorpha pallens* Pease, 1870	No Dart	Low	Faatoai Valley, Moorea	Unknown
	Videna gouldiana (Pilsbry, 1901)	No Dart	Low	Amami Island, Ryukyu, Japan	S. Chiba
Vitrinidae	*Vitrina pellucida* (Müller, 1774)	No Dart	Semislug	Kirkdale, Derbyshire, U.K.	C. Wade
	Plutonia laxata (Morelet, 1860)	No Dart	Semislug	São Miguel, Azores	P. Mordan
Pristilomatidae	*Vitrea crystallina* (Müller, 1774)	No Dart	Low	New Forest, Hampshire, U.K.	P. Mordan
Zonitidae	*Oxychilus alliarius* (Miller, 1822)	No Dart	Low	Deepdale, Derbyshire, U.K.	C. Wade
	Oxychilus helveticus (Blum, 1881)	No Dart	Low	Kirkdale, Derbyshire, U.K.	C. Wade
	Oxychilus cellarius (Müller, 1774)	No Dart	Low	Co. Kerry, Ireland	Unknown
Milacidae	*Tandonia budapestensis* (*Milax*) (Hazay, 1881)	No Dart	Slug	Kirkdale, Derbyshire, U.K.	C. Wade
Limacidae	*Deroceras reticulatum* (Müller, 1774)	No Dart	Slug	Kirkdale, Derbyshire, U.K.	C. Wade
(Helicoidea)					
Polygyridae	*Mesodon thyroides* (Say, 1816)	No Dart	Low	York Co. Pennsylvania, U.S.A.	F. Thompson
	Triodopsis alleni (Wetherby, 1883)	No Dart	Low	Williams Creek, Iowa, U.S.A.	R. Cameron
	Vespericola columbiana (Lea, 1838)	No Dart	Low	Eugene, Oregon	D. Taylor
Camaenidae	*Amphidromus* sp.	No Dart	High	Unknown	D. Reid
	Nipponchloritis bracteatus (*Chloritis*) (Pilsbry, 1902)	No Dart	Low	Sendai, Japan	S. Chiba
	Mandarina ponderosa (Pilsbry, 1901)	No Dart	Low	Hahajima, Bonin Islands, Japan	S. Chiba & A. Davison
	Thelidomus asper (*Eurycratera*) (Férussac, 1821)	No Dart	Low	Windsor, Jamaica	S. Chiba
	Pleurodonte sinuata (Müller, 1773)	No Dart	Low	Green Grot Cave, Jamaica	S. Chiba
	Polydontes undulata (Férussac, 1821)	No Dart	Low	Dominican Republic	G. Seal
	Polydontes lima (Ferussac, 1821)	No Dart	Low	Dorado, Puerto Rico	A. Davison
	Satsuma japonica (Pfeiffer, 1847)	No Dart	Low	Osaka City, Japan	P. Callomon
	Coniglobus mercatorius (*Satsuma*) (Pfeiffer, 1854)	No Dart	Low	Kikai Island, Ryukyu, Japan	S. Chiba
	Sphaerospira fraseri (Griffith and Pigeon, 1833)	No Dart	Low	Brisbane, Queensland, Australia	J. Stanisic
	Zachrysia auricoma (Ferussac, 1821)	No Dart	Low	Nr. Dorado, Puerto Rico	A. Davison
	Obba rota (Broderip, 1841)	No Dart	Low	Bohol Island, Phillippines	S. Chiba
	Moellendorffia diminuta (Pilsbry and Hirase 1905)	No Dart	Low	Ryukyu, Japan	S. Chiba
Hygromiidae	*Trichia striolata* (Pfeiffer, 1828)	Dart	Low	Deepdale, Derbyshire, U.K.	C. Wade
	Trichia hispida (L., 1758)	Dart	Low	Deepdale, Derbyshire, U.K.	C. Wade
	Cochlicella acuta (Müller, 1774)	Dart sac (no dart)	High	Porthcurnick, Cornwall, U.K.	E. Bailes
	Cernuella virgata (Da Costa, 1778)	Dart	Low	Porthcurnick, Cornwall, U.K.	E. Bailes
	Monacha cantiana (Montagu, 1803)	Dart sac (no dart)	Low	Pulpit Down, Buckinghamshire, U.K.	P. Mordan
Helicidae	*Helix pomatia* L. 1758	Dart	Low	Pulpit Down, Buckinghamshire, U.K.	P. Mordan
	Helix lucorum L. 1758	Dart	Low	Unknown	Unknown
	Cantareus aspersus (*Helix aspersa*) (Müller, 1774)	Dart	Low	Kettering, Northants., U.K.	C. Wade
	Cantareus apertus (Born, 1778)	Dart	Low	Sicily	A. Davison
	Cepaea nemoralis (L., 1758)	Dart	Low	Marlborough Downs, Wiltshire, U.K.	A. Davison
	Cepaea hortensis (Müller, 1774)	Dart	Low	Marlborough Downs, Wiltshire, U.K.	A. Davison
	Eremina desertorum (Forskål)	Dart	Low	Unknown	Unknown
	Marmorana scabriuscula (Deshayes, 1830)	Dart	Low	Sicily	A. Davison
	Otala lactea (Müller, 1774)	Dart	Low	Unknown	Unknown
	Theba pisana (Müller, 1774)	Dart	Low	Sicily	A. Davison
	Arianta arbustorum (L., 1758)	Dart	Low	Deepdale, Derbyshire, U.K.	C. Wade
	Helicigona lapicida (L., 1758)	Dart	Low	Deepdale, Derbyshire, U.K.	C. Wade
Bradybaenidae	*Bradybaena similaris* (Férussac, 1821)	Dart	Low	Sri Lanka	P. Karunaratne
	Acusta despecta chinensis (*Bradybaena*) (Sowerby, 1839)	Dart	Low	Japan	S. Chiba
	Ainohelix editha (*Bradybaena*) (A. Adams, 1868)	Dart	Low	Shimamaki, Hokkaido, Japan	S. Chiba
	Ezohelix gainesi (*Bradybaena*) (Pilsbry, 1900)	Dart	Low	Sapporro, Hokkaido, Japan	S. Chiba
	Aegista vulgivaga (Schumacher & Boettger, 1890)	Dart	Low	Osaka City, Japan	P. Callomon
	Paraegista takahidei (Kuroda and Azuma, 1951)	Dart	Low	Hokkaido, Japan	S. Chiba
	Euhadra amaliae (Kobelt, 1875)	Dart	Low	Osaka City, Japan	P. Callomon
	Euhadra sandai Pilsbry, 1928	Dart	Low	Osaka City, Japan	P. Callomon
	Nesiohelix bipyramidalis Kurodo and Emura, 1943	Dart	Low	Ryukyu, Japan	S. Chiba
	Helicostyla lignaria (Pfeiffer, 1842)	Dart	Low	Bohol island, Phillipines	S. Chiba
	Chloraea intorta (Sowerby, 1840)	Dart	Low	Bohol island, Phillipines	S. Chiba
	Trishoplita hachijoensis (Pilsbry, 1902)	Dart	Low	Niijima Island, Izu Islands, Japan	S. Chiba

Appendix. Continued.

Family	Taxon	Dart?	Shell shape or slug	Collection/location	Collector
Helminthoglyptidae	*Monadenia fidelis* (Gray, 1834)	Dart	Low	Oregon	D. Taylor
	Cepolis streatori (Pilsbry, 1889)	Dart	Low	Grand Cayman	S. Chiba
Sagdidae	*Sagda* sp.	Dart	Low	Windsor, Jamaica	S. Chiba
(Philomycidae)					
Arionidae	*Arion hortensis* Férussac, 1819	No Dart	Slug	Kirkdale, Derbyshire, U.K.	C. Wade
	Arion ater (L., 1758)	No Dart	Slug	Kirk Ireton, Derbyshire, U.K.	C. Wade
	Geomalacus maculosus Allman, 1843	No Dart	Slug	Unknown	P. Wisniewsky
Philomycidae	*Meghimatium bilineatum* (Benson, 1842)	No Dart	Slug	Mauritius	O. Griffiths
	Philomycus carolinianus (Bosc, 1802)	Dart	Slug	Wake Co., North Carolina, U.S.A.	A. Braswell
Non-stylommatophoran pulmonates (Phylum Mollusca, Class Gastropoda, Subclass Pulmonata)					
Order Eupulmonata					
Ellobiidae	*Melampus luteus* (Quoy & Gaimard, 1832)			Souilla, Mauritius	O. Griffiths
	Laemodonta sp.			Suralaya, W. Java	B. Dharma
Carychiidae	*Carychium tridentatum* (Risso, 1826)			Abelheira, Sao Miguel, Azores	P. Mordan
Order Basommatophora					
Siphonariidae	*Siphonaria pectinata* (L., 1758)			Zamara Los Atunes, Spain	S. Hawkins
Order Systellomatophora					
Veronicellidae	*Laevicaulis alte* (Férussac, 1823)			Dubai, United Arab Emirates	A. Green
Rathouisiidae	*Atopos australis* (Heynemann, 1876)			Malanda, Queensland, Australia	J. Stanisic
Phylum Mollusca, Class Gastropoda, Subclass Opisthobranchia, Order Anaspidea					
Aplysiidae	*Aplysia punctata* (Cuvier, 1803)			Bessaker, Trondelag, Norway	J. Evertsen & T. Bakken