

Shell shape and mating behaviour in pulmonate gastropods (Mollusca)

KURT JORDAENS^{1*}, LOBKE DILLEN¹ and THIERRY BACKELJAU^{1,2}

¹*Department of Biology, University of Antwerp, Groenenborgerlaan 171, B-2020 Antwerp, Belgium*

²*Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000 Brussels, Belgium*

Received 4 January 2008; accepted for publication 30 May 2008

Previous work suggests that low-spired hermaphroditic snails mate face-to-face and have reciprocal sperm exchange, whereas high-spired snails mate by shell mounting and have unilateral sperm exchange. This dichotomy lead others to speculate on the evolution of enigmatic mating behaviours and whole-body enantiomorphy. In the present study, we review the current literature on mating behaviour in pulmonate snails and show that: (1) several pulmonate species show considerable intraspecific variation in mating behaviour; (2) mating position does not predict reciprocity of penis intromission and sperm exchange; (3) dart-shooting may be correlated with reciprocity of sperm exchange but other factors must explain the gain or loss of darts; (4) it is unlikely that the degree of reciprocity is the most important factor in explaining the relationship of whole-body enantiomorphy and shell shape; and (5) the reciprocal intromission of penises does not necessarily involve the reciprocal transfer of sperm. Hence, our survey shows that current ideas on the evolutionary relationship between shell shape and reciprocity with sexual selection (including dart-use) and whole-body enantiomorphy in hermaphroditic snails should be refined. The results obtained demonstrate that our current knowledge on gastropod mating behaviour is too limited to detect general evolutionary trajectories in gastropod mating behaviour and genital anatomy. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 96, 306–321.

ADDITIONAL KEYWORDS: dart-shooting – freshwater snails – hermaphrodite – land snails – sexual selection – whole-body enantiomorphy.

INTRODUCTION

Pulmonate gastropods comprise a group of approximately 20 000 hermaphroditic species that produce sperm and eggs simultaneously, although, in some species, the sperm may mature before the ova (Heller, 1993). The majority of pulmonates belong to two suborders (i.e. the Stylommatophora and the Basommatophora). Pulmonates show diverse and very complex reproductive organs (e.g. sperm-digesting organ, allosperm-storage organ or spermatheca, stimulator, dart-sac, penial appendages) and mating behaviours (e.g. apophallation, dart-shooting, aerial mating with sperm exchange at the tips of highly extended penises) (Duncan, 1975; Tompa, 1984; Baur, 1998). Explaining the evolution of the complex

reproductive organs and behaviours in pulmonates proves challenging (Davison *et al.*, 2005b; Koene & Schulenburg, 2005; Schilthuizen, 2005; Beese, Beier & Baur, 2006).

Theoretically, during mating, hermaphroditic pulmonates may donate sperm (sperm donor or ‘male’), receive sperm (sperm receiver or ‘female’) or both donate and receive sperm at the same time. Asami, Cowie & Ohbayashi (1998), based on Cain’s (1977) observation that shells of pulmonates are either low-spired (flat) or high-spired (tall) with few intermediate, globular species, reviewed the courtship and mating behaviour of 17 stylommatophoran families and found an intriguing relationship between shell shape (i.e. low-spired versus high-spired) and mating behaviour. Low-spired species show a symmetrical courtship behaviour, mate face-to-face and have reciprocal penis intromission (Fig. 1A, B). By contrast, high-spired species show an asymmetrical courtship

*Corresponding author. E-mail: kurt.jordaens@ua.ac.be

behaviour termed shell mounting during which one individual (the 'male') mounts the shell of its partner (the 'female') (Fig. 1C). This is followed by unilateral penis intromission (i.e. the 'male' inserts its penis into the vagina of the 'female' and donates sperm). In some species, the first mating is followed by a second in which the partners reverse roles (i.e. sex role alternation) (Lipton & Murray, 1979; Koene & Ter Maat, 2005). Davison *et al.* (2005b) extended the list of Asami *et al.* (1998) to 60 genera (28 families) and confirmed the bimodality of mating behaviour that was observed by Asami *et al.* (1998). Hence, the most important outcome of the studies of Asami *et al.* (1998) and Davison *et al.* (2005b) is that low-spined species mate reciprocally and that high-spined species mate unilaterally, with there being only very few exceptions to this rule (Asami *et al.*, 1998). This bimodality in mating behaviour has led to speculation on the evolution of several striking phenomena in pulmonates (i.e. sexual selection, including the shooting of so-called 'love-darts' during mating; Davison *et al.*, 2005b; Schilthuizen, 2005) and intraspecific dimorphism in coiling (i.e. whole-body enantiomorphy; Asami *et al.*, 1998; Davison *et al.*, 2005a; Schilthuizen & Davison, 2005).

In the present study, we first show that the presumed relationship between shell-shape and mating behaviour (i.e. low-spined species mate face-to-face and reciprocally and high-spined species mate by shell mounting and unilaterally) is not so straightforward as is currently accepted. Then, we explore how these findings may affect our current ideas on: (1) sexual selection in pulmonates in general; (2) the evolution of dart-gain and dart-loss within the Pulmonata; and (3) the evolution of whole-body enantiomorphy. Finally, we propose several issues of snail mating behaviour that deserve further attention and that may allow the fine-tuning of our current ideas on the above mentioned topics. Because part of the misconceptions on the relationship between shell-shape and mating behaviour may result from ill-defined mating behaviours that cause confusion, we also provide definitions of some commonly used terminology of mating behaviour in pulmonates.

MATERIAL AND METHODS

Based on a detailed literature study of the mating behaviour of hermaphroditic pulmonate gastropods, we summarize the relevant terminology of pulmonate mating behaviour in Table 1. This terminology will be adopted throughout the present study. We surveyed shell shape, mating position, penis intromission or penis entwining, sperm exchange, the presence of darts (or dart-sacs), and whole-body enantiomorphy in six basommatophoran genera (three families), one

non-stylommatophoran eupulmonate genus, and 74 stylommatophoran eupulmonate genera (24 families) (see Supporting information, Appendix S1). Shell shape was categorized as high-spined (spire-index > 1) or low-spined (spire-index < 1). This was performed by calculating the ratio of shell height to shell width, which is known as the spire-index (Cain, 1977). Mating position was categorized as face-to-face or shell mounting. Penis intromission/entwining was categorized as reciprocal or unilateral and whether it occurs through intromission (i.e. internal sperm exchange) or through entwining (i.e. external sperm exchange) (Table 1; see also Supporting information, Appendix S1). Data on shell shape, mating position, penis intromission/entwining, sperm exchange, the presence of a dart(-sac), and whole-body enantiomorphy are provided in the Supporting information (Appendix S1). The main references used for dart-shooting were Davison *et al.* (2005b) and Koene & Schulenburg (2005). Data on intraspecific whole-body enantiomorphy were gathered from Asami (1993).

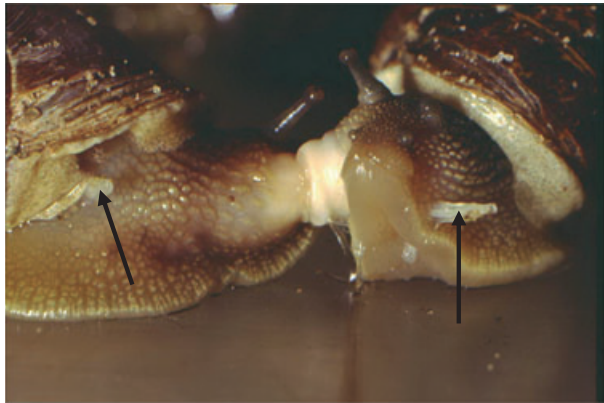
Shell width and shell height of species were gathered from the literature whenever available (a list is available by request from the authors) to examine the dichotomy in shell shape in the species for which enough data on the reproductive behaviour were available.

We redrew the Bayesian phylogenetic tree for the five well-supported stylommatophoran pulmonate clades of Wade, Mordan & Naggs (2006), whose Neighbour-joining analysis yielded virtually identical results. Some of the nodes with low Bayesian probabilities were collapsed to aid interpretation. Possession of darts, shell shape, mating behaviour, and penis intromission reciprocity were then mapped onto the phylogeny. The deep relationships between the 'non-achatinoidean' clades (Orthurethra, Limacoidea, Clausilioidea, Helicoidea, Orthalicoidea, and Elasmognatha) are not clear and there is poor resolution at several important nodes (Wade *et al.*, 2006). This poor resolution prevents a strict, phylogeny controlled, comparative analysis using independent contrasts (Purvis & Rambaut, 1995; see also Davison *et al.*, 2005b) of the results of Wade *et al.* (2006). An alternative method, which calculates character correlation using pairwise comparisons on a phylogeny, suggested by Maddison (2000) could not be used because we could not always judge the direction of change of the character and because this method yielded only very few comparisons so that a statistical analysis could not be performed.

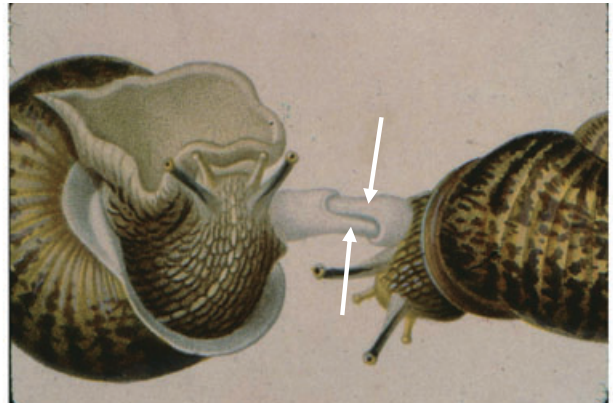
RESULTS

Figure 2 shows that the presumed dichotomy in shell shape with species either high-spined or low-spined

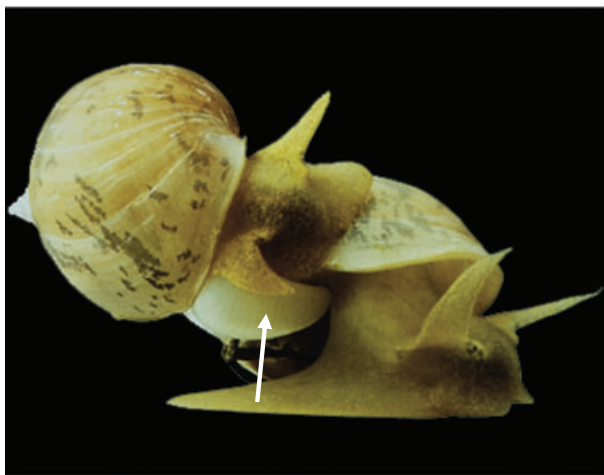
A



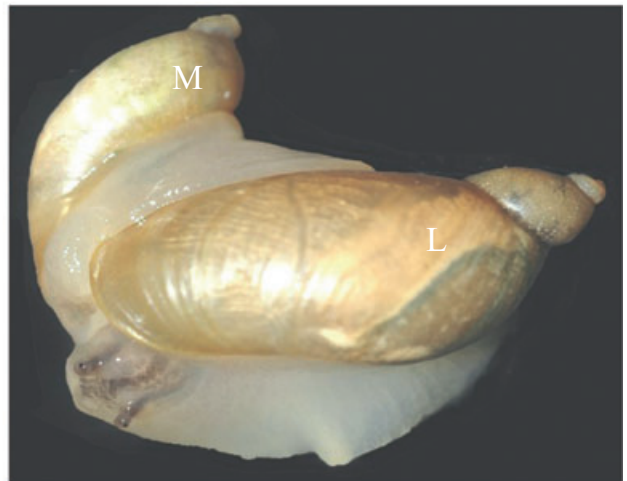
B



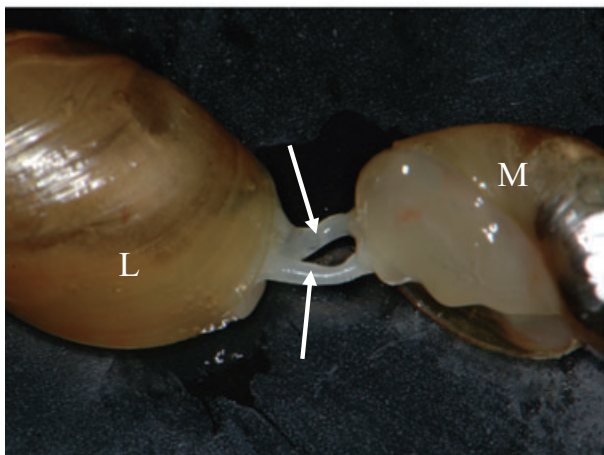
C



D



E



F



Figure 1. Photographs of copulating pulmonate snails. A, reciprocal, face-to-face mating in *Cornu aspersum* (photo: Ronald Chase; the black arrows indicate the darts that were shot). B, reciprocal, face-to-face mating in *Cornu aspersum* (drawing from Férussac, 1819). C, unilateral mating by shell mounting in *Lymnaea stagnalis* (photo: Joris M. Koene & Anton Pieneman). D, reciprocal mating by shell mounting in *Succinea putris* (photo: Lobke Dillen & Kurt Jordaens). E, a copulating pair of *S. putris* killed in liquid nitrogen while copulating (photo: Lobke Dillen & Kurt Jordaens). The shell-mounter (M) was removed from the lower individual (L) to show the reciprocally intromitted penises. The upper penis belongs to the shell mounter, the lower penis belongs to the lower individual of the mating pair. F, reciprocal mating in two high-spined individuals of *Amphidromus atricallosus* that probably started mating face-to-face but continued mating side-by-side (Sutcharit *et al.*, 2007). In all figures, white arrows indicate penises.

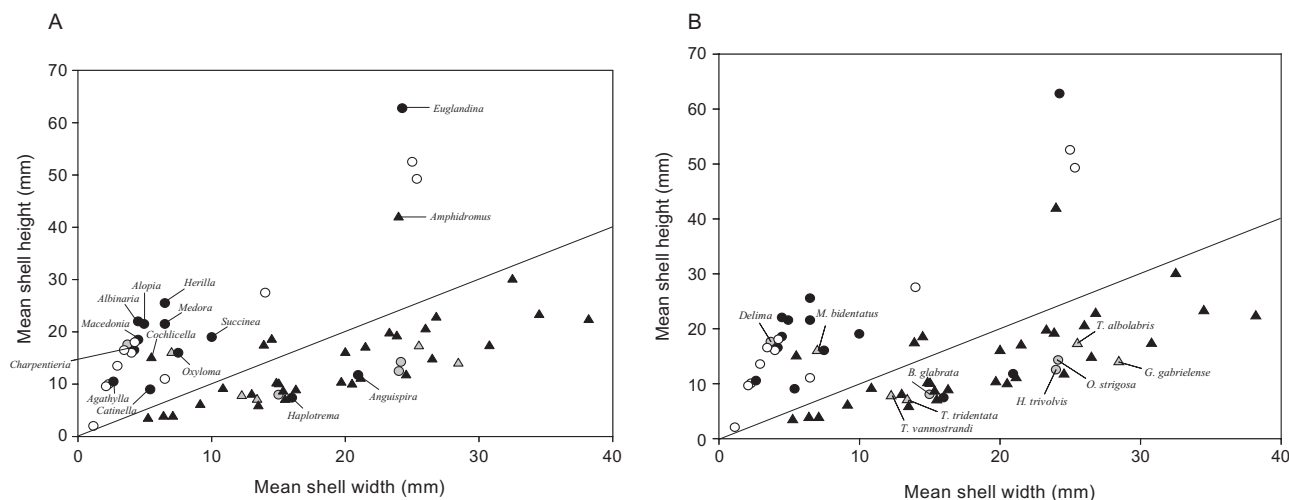


Figure 2. The relationship between shell shape, mating position (triangles, face-to-face; circles, shell mounting) and penis intromission/entwining (closed symbols, reciprocal intromission/entwining; open symbols, unilateral intromission). Grey symbols are genera/species in which both unilateral and reciprocal penis intromission/entwining have been recorded. The lines in (A) and (B) represent equal shell heights and widths. Species with a high-spined shell are above the diagonal, those with a low-spined shell are below the diagonal. A, with indication of genera that ‘deviate’ from the ‘high-spined (i.e. shell mounting and unilateral mating) and low-spined (i.e. face-to-face and reciprocal mating) rule. B, with indication of the genera/species in which both unilateral and reciprocal penis intromission/entwining have been recorded.

with few intermediates is not straightforward for the species for which substantial data on the mating behaviour are available. Although few species are globular (i.e. spire-index of approximately 1), several approach a globular shell shape (i.e. the data points near the diagonal lines of Fig. 2). This may be because many species for which some data on the mating behaviour are available (e.g. the Helicoidea) approach a globular shell shape. Nevertheless, species with a mating behaviour that ‘deviates’ from the general rule outlined above are either clearly low-spined or high-spined. For this, the division of low-spined and high-spined will be maintained throughout the present study.

RELATIONSHIP BETWEEN SHELL-SHAPE AND MATING POSITION

A summary of our results is given in Figure 2 and the Supporting information (Appendix S1). This shows

that, in general, low-spined species (42 out of 47 taxa) mate face-to-face and high-spined species (32 out of 34 taxa) mate by shell mounting (Fig. 2A). Yet, five out of the 47 low-spined taxa (*Helicophanta*, *Anguispira*, *Haplotrema*, *Oreohelix*, *Paryphanta*) mate by shell mounting and, in *Polydontes*, both face-to-face mating (two matings out of three) and mating by shell mounting (one mating out of three) has been recorded (Webb, 1970c). All these genera belong to different families (see Supporting information, Appendix S1) so that it is highly likely that the deviations in mating position represent independent evolutionary events. Two out of 34 high-spined taxa (*Amphidromus* and *Cochlicella*) generally mate face-to-face (in *Amphidromus* mating sometimes becomes side-by-side; Fig. 1F) (Sutcharit, Asami & Panha (2007). Both genera belong to different families (see Supporting information, Appendix S1) and thus likely represent independent evolutionary events. Basommatophorans all mate by shell-mounting. Although *Helisoma* and

Table 1. Definitions of some commonly used terminology of mating behaviour in hermaphroditic pulmonates

<i>Courtship behaviour</i>	Behaviour that mating partners show before one of the penises is intromitted into the partner in internal sperm exchanging species, or before penises get entwined in external sperm exchanging species. Courtship behaviour is also referred to as <i>pre-copulatory behaviour</i>
<i>External sperm transfer</i>	Sperm is transferred on the penis of the partner without intromission of the penis into the female reproductive system. During copulation, penises may be entwined or not
<i>Face-to-face mating</i>	Mating position whereby both individuals are faced opposite to each other so that the genital openings, which are situated on the right side (or left side in sinistral species) are opposed and mating can be achieved
<i>'Female' role</i>	The sperm receiver
<i>Internal sperm transfer</i>	The sperm donor intromits its penis into the vagina of the sperm recipient and sperm is released inside the female reproductive system
<i>'Male' role</i>	The sperm donor
<i>Mating behaviour</i>	Any behavioural aspect related to mate-choice, courtship behaviour and the act of copulation
<i>Mating position</i>	The position in which individuals copulate. This can be either face-to-face or shell mounting
<i>Penis intromission</i>	During mating the penis is intromitted into the atrium and/or the female reproductive tract (see also <i>Penis entwining</i>)
<i>Penis entwining</i>	The penis is not inserted into the atrium and the female reproductive tract of the partner but both penises are exerted and entwine; sperm is then exchanged at the tips of the penises. In this kind of mating, the penis is also used to take up the allosperm (see also <i>Penis intromission</i>)
<i>Pre-copulatory behaviour</i>	See <i>Courtship behaviour</i>
<i>Reciprocal intromission</i>	Both individuals intromit their penises during a single copulation. Mostly this is performed simultaneously; very rarely, intromission appears to be alternated during the same copulation
<i>Reciprocal mating</i>	Both partners act in the 'male' and the 'female' role. This can be done in a single mating (= <i>Simultaneous mating</i>) or through subsequent copulations whereby individuals change sex roles (i.e. the 'male' becomes 'female' and <i>vice versa</i> ; = <i>Sex role alternation</i>)
<i>Reproductive behaviour</i>	Any behavioural aspect related to reproduction, including mating behaviour, egg-laying, parental care, intraspecific egg-cannibalism, etc.
<i>Sex change</i>	Individuals change their sex in the course of a reproductive season or between reproductive seasons. This can either be proterandric (first male, then female) or protogynic (first female, then male)
<i>Sex role</i>	The role an individual adopts during copulation. This can be either the 'male' role (i.e. sperm donor), the 'female' role (i.e. sperm receiver) or both (i.e. individual acts as 'male' and 'female')
<i>Sex role alternation</i>	Reciprocal matings where one individual acts in the 'male' role and the other in the 'female' role. After this copulation, both individuals change roles and mate again with each other
<i>Shell mounting</i>	Mating position whereby one individual climbs onto the shell of the other individual
<i>Simultaneous hermaphrodite</i>	An individual that produces sperm and ova at the same time
<i>Simultaneous reciprocal mating</i>	Both partners act in the 'male' and 'female' role during a single mating; sometimes referred to as 'two-way copulation'
<i>Two-way copulation</i>	See <i>Simultaneous reciprocal mating</i>
<i>Unilateral intromission</i>	Only one of the mating partners (i.e. the 'male') intromits its penis into the 'female' partner
<i>Unilateral mating</i>	Mating whereby one individual acts in the 'male' role (sperm donor) and the other in the 'female' role (sperm receiver). After mating, individuals separate and do not change sex roles

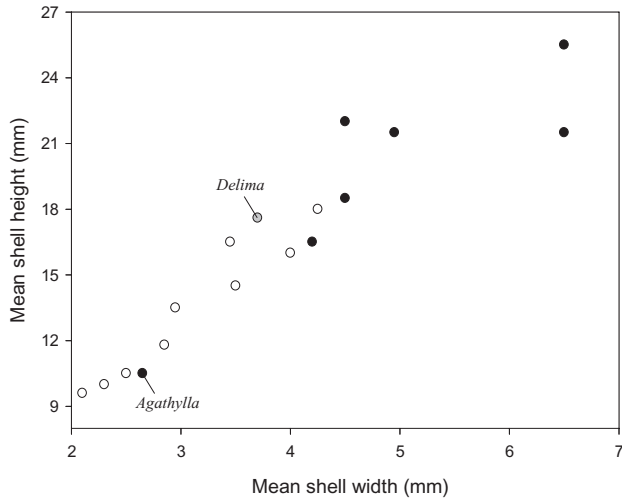


Figure 3. The relationship between body size and penis intromission in the family Clausiliidae.

Biomphalaria have low-spined shells, the shell is held vertically so that the partner has to climb the shells to achieve successful copulation (Duncan, 1975; Vianey-Liaud, 1998). Finally, the non-stylommatophoran eupulmonate genus *Melampus* comprises high-spined species that mate face-to-face (Apley, 1970).

RELATIONSHIP BETWEEN SHELL-SHAPE/MATING POSITION AND PENIS INTROMISSION/ENTWINING

The relationship between shell shape or mating position and penis intromission/entwining is even less clear (Fig. 2; see also Supporting information, Appendix S1). Among the high-spined species, this is best illustrated in species of the family Clausiliidae where mating is always achieved by shell mounting but penis intromission may be unilateral (nine genera), reciprocal (seven genera), or even both (one genus) (Fig. 3; see also Supporting information, Appendix S1). Interestingly, within the Clausiliidae, there appears to be a striking relationship between shell size and whether penis intromission is unilateral or reciprocal (Fig. 3) (i.e. smaller species appear to mate unilaterally, whereas mating is reciprocal in larger species; the only exception to this rule is *Agathylla*).

Besides several clausiliid genera, other shell-mounting high-spined taxa have reciprocal penis intromission, such as the Achatinidae (two genera studied) (Plummer, 1975; Tomiyama, 1994), Succineidae (all three genera studied) (Webb, 1977a, b, c; Jordaens, Pinceel & Bacheljau, 2005; Fig. 1D, E, Fig. 4), and *Euglandina* (Cook, 1985) (Fig. 2A).

Face-to-face mating is strongly related to reciprocal penis intromission/entwining (Fig. 2). Yet,

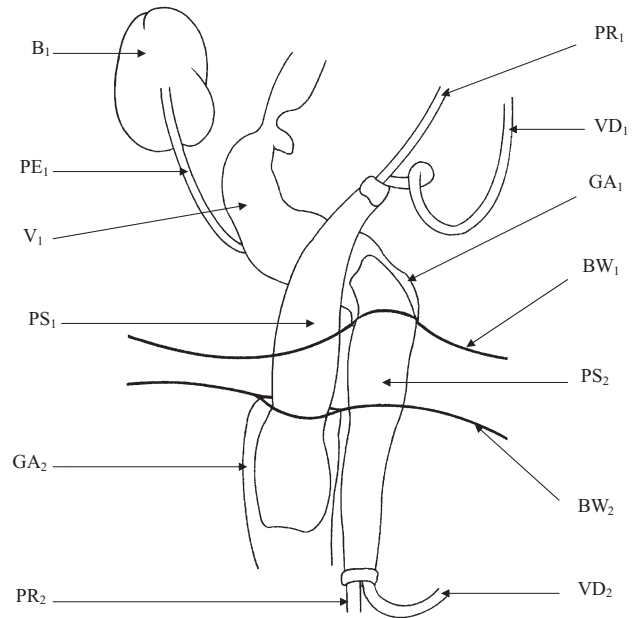


Figure 4. Camera lucida drawing of the proximal genitalia of copulating *Succinea putris* (family Succineidae) showing the reciprocally intromitted penises (modified after Hecker, 1965). B, bursa copulatrix; BW, body wall; GA, genital atrium; PS, penis sheath; PE, pedunculus of the bursa copulatrix; PR, penis retractor muscle; V, vagina; VD, vas deferens. The number in subscript refers to the individual to which the structure belongs.

penis intromission is both unilateral or reciprocal in the low-spined genera *Glyptostoma* (Webb, 1961), *Sonorella* (Webb, 1980b, 1990a), and *Helminthoglypta* (Webb, 1952b) that mate face-to-face and in the genus *Oreohelix* that mates by shell mounting (Roscoe, 1950; Webb, 1951) (Fig. 2B). In *Triodopsis vannostrandi*, three out of four pairs showed unilateral penis intromission. One of these matings was face-to-face, another by shell mounting and a third in which the snails had met at a 90° angle (Webb, 1959). Out of approximately 100 matings in *Mandarina*, one was unilateral instead of simultaneously reciprocal (Davison *et al.*, 2005b). Penis intromission is unilateral in the low-spined genus *Zonitoides* (Bartsch & Quick, 1926), but the mating position was not recorded. Finally, *Anguispira* and *Haplotrema* have low-spined shells and reciprocally intromit penises, but mate by shell mounting (Webb, 1943, 1968c) (Fig. 2A).

In general, in species with reciprocal penis intromission, both penises are intromitted reciprocally. However, in the clausiliid genera that mate reciprocally, the intromission is not simultaneous but alternated. The shell-mounter mounts the shell of the lower individual and puts the left front part of the

head-foot close to that of its mate. The lower partner then everts the atrium (and sometimes the vagina), which, in turn, stimulates the shell-mounter to introduce its penis. Thereafter, the lower individual will intromit its penis (Nordsieck, 2005). Alternated penis intromission has further been observed in the genera *Caracolus* (Webb, 1970c) and in some species of *Helminthoglypta* (Webb, 1942, 1952b). *Helminthoglypta californiensis*, *Helminthoglypta dupetithouarsi*, and *Helminthoglypta umbilicata* reciprocally intromit penises (Webb, 1942), whereas penis intromission is alternately reciprocal in *Helminthoglypta traski fieldi* (Webb, 1952b). In the latter species, mating starts unilaterally with the intromission of the penis of the male actor. Subsequently, the female acting individual also intromits its penis. Shortly thereafter, the 'male' retracts its penis so that mating becomes unilateral again but with partners switching roles (Webb, 1952b).

Some Succineidae, Polygyridae, and Helicodiscidae have external sperm exchange (see also Supporting information, Appendix S1). During copulation, spermatozoa are deposited on the mate's everted penis without intromission. Reciprocal eversion of penises is a necessity for a successful copulation because the penis is also needed for the uptake of sperm by the partner. Penis entwining therefore becomes per definition reciprocal.

All basommatophorans mate by shell-mounting and penis intromission is unilateral. However, penis intromission in *Biomphalaria glabrata* (Brumpt, 1941; Vernon & Taylor, 1996; Trigwell, Dussart & Vianey-Liaud, 1997; Vianey-Liaud, 1998), *Biomphalaria tenogophila* (Springer de Freitas, Pires Paula & Cariello, 1997), and *Helisoma trivolvis* (Duncan, 1975) is sometimes simultaneously reciprocal.

RELATIONSHIP BETWEEN SHELL-SHAPE/MATING POSITION, WHOLE-BODY ENANTIOMORPHY AND DART-SHOOTING

The Supporting information (Appendix S1) lists five taxa showing whole-body enantiomorphy (i.e. *Bradybaena*, *Amphidromus*, *Liguus*, *Partula*, and *Lymnaea*). *Bradybaena* has a globular shell shape, mates face-to-face, and has reciprocal penis intromission. *Liguus*, *Partula*, and *Lymnaea* have a high-spined shell, mate by shell mounting and (except for *Liguus* where the mode of penis intromission is not known) have unilateral penis intromission. *Amphidromus* has a high-spined shell, mate face-to-face (sometimes side-by-side) and has reciprocal penis intromission.

The mating behaviour of species of 19 genera that have a dart(-sac) is relatively well-known (see also Supporting information, Appendix S1). Species of all

these taxa, except for *Zonitoides* and *Cochlicella*, have a low-spined (or globular) shell-shape, mate face-to-face, and have reciprocal intromission of penises. *Zonitoides arboreus* has a low-spined shell but penis intromission is unilateral (Bartsch & Quick, 1926). The position in which individuals mate is unknown. *Cochlicella* has a high-spined shell and penis intromission is reciprocally, but individuals mate face-to-face.

DISCUSSION

The survey performed in the present study clearly illustrates that the presumed strong relationship between shell shape and mating behaviour in pulmonate gastropods (i.e. low-spined species mate face-to-face and reciprocally and high-spined species mate by shell mounting and unilaterally) is not straightforward and that many exceptions to this rule exist. Below, we illustrate and discuss how these new findings may affect our current ideas on evolutionary hot-topics in hermaphroditic gastropods (i.e. sexual selection and gender conflict, dart-shooting and whole-body enantiomorphy). Because dart-shooting is the best documented aspect of sexual selection (but see also Chase & Vaga, 2006), it will be considered separately.

SEXUAL SELECTION AND GENDER CONFLICT

There is considerable support for the idea that hermaphrodite mating systems are prone to develop gender conflicts (Anthes, Putz & Michiels, 2006), the evolutionary origin of, and potential adaptive responses to, such conflicts are still controversial; for a full discussion, see Anthes *et al.* (2006). Many of the complex reproductive characters and behaviours are assumed to have evolved in response to conflicts between the two sexual functions within a hermaphrodite. Sexual conflict could provoke co-evolutionary arms races in which the repeated origin of traits advantageous for one sexual function but disadvantageous to the other, is accommodated by counter-adaptations in the other sexual function (Koene & Schulenburg, 2005). Evidently, to elucidate the evolutionary trajectories of genital structures, it is essential to have a thorough understanding of not only the functional significance of the reproductive morphology, but also of the mating behaviour of species.

Our survey shows that, except for the land snail *Delima semirugata*, in pulmonates with unilateral penis intromission, the shell-mounter introduces its penis and adopts the male role, whereas the lower partner adopts the female role. Sex role alternation may be common in basommatophoran snails but has

not been observed in stylommatophoran snails, except for *Partula suturalis* and *Partula taeniata* (Lipton & Murray, 1979) and (together with reciprocal penis intromission) in *Polygyra* (Archer, 1933). *Helminthoglypta traski fieldi* appears to switch roles during a single mating (Webb, 1952b). Possible factors that affect sex role alternation have been studied in the basommatophoran snails *Lymnaea stagnalis* and *Physa acuta*. Koene & Ter Maat (2005) showed that, in *L. stagnalis*, sex role alternation occurred more often in pairs in which both individuals were isolated for some period than in pairs where only one, or none, of the partners was isolated. Moreover, partners that were isolated acted as male. This shows that sexual isolation increases the eagerness to mate and indicates that the occurrence of sex role alternation should not necessarily be interpreted as conditional reciprocity (Koene & Ter Maat, 2005). However, in pairs where both individuals were isolated, a sexual conflict may still exist since insemination avoidance behaviours were observed regularly. Facon, Ravigné & Goudet (2008) showed that sex role alternation in *Physa acuta* did not preferentially occur with the same partner, suggesting that each individual showed a preference for sex role alternation.

In most species that intromit penises reciprocally, or that show penis entwining, it is not known whether sperm transfer is also reciprocal. Sperm transfer when penises are simultaneously reciprocally intromitted is normally reciprocal in *Arianta arbustorum* (Baur, 1998), *Cornu aspersum* (Rogers & Chase, 2001; Chase & Vaga, 2006), *Euhadra subnimbosa* (Koene & Chiba, 2006) and *Polymita muscarum* (Reyes Tur & Koene, 2007). However, Jordaens *et al.* (2005) observed in *Succinea putris* that sperm transfer was not always reciprocal despite that penis intromission always was (i.e. 12 out of 87 pairings involved the unilateral transfer of sperm). No relationship was found with the activity role (shell-mounter or mounted individual) or the size (difference) of the partners.

Little variation in mating behaviour is observed in basommatophoran species because they all mate by shell mounting with the shell-mounter acting as the 'male' sperm donor and the mounted individual acting as the 'female' sperm receiver (irrespective of shell shape). Hence, sperm transfer in basommatophorans is unilateral. Nevertheless, reciprocal penis intromission has been observed in some species whereas others display sex role alternation. Hence, in these species, reciprocal sperm exchange may be achieved during a single or during alternated matings (although this need not be a conditional exchange of sperm; Koene & Ter Maat (2005). By contrast, many stylommatophoran species show intraspecific varia-

tion in mating behaviour and even closely related taxa may differ substantially in their mating behaviour (see also Supporting information, Appendix S1). Unfortunately, any effect of phylogenetic dependence cannot be investigated because the phylogenetic resolution for the Pulmonata remains poor (Wade *et al.*, 2006). Five clades (Fig. 5) show a relatively high resolution but in those groups data on the mating behaviour is either very restricted (for the 'achatinoïd' clade, Fig. 5A; the Limacoidea, Fig. 5D; and the Orthurethra, Fig. 5E) or there is little variation in shell shape, mating position, penis intromission and the presence/absence of darts (for the Clausillidae, Fig. 5B, and the Helicoidea, Fig. 5C).

DART SHOOTING

Love-darts are calcareous or chitinous structures that many snails and slugs use to pierce the skin of their partner during mating (Koene & Schulenburg, 2005). Calcareous darts are covered by mucus that contains allohormones (Koene & Ter Maat, 2001). A well-shot dart promotes the survival of sperm (Rogers & Chase, 2001) and by successfully darting its partner, a sperm donor increases its chances of paternity (Rogers & Chase, 2002; Chase & Blanchard, 2006). Darts have repeatedly been gained and lost during pulmonate evolution (Davison *et al.*, 2005b) and elucidating the evolutionary pattern of these gains and losses may provide insights in the strength of sexual selection in pulmonates (Koene & Schulenburg, 2005; Schilthuizen, 2005; but see also Chase & Vaga, 2006). This prompted Davison *et al.* (2005b) to compare the bimodality of mating behaviour against dart use across stylommatophorans. Three hypotheses are proposed to explain the evolution of darts in low-spined and the absence of darts in high-spined species. First, darts would only evolve in low-spined taxa because these species enforce simultaneous reciprocity during mating. Consistent with this hypothesis, Davison *et al.* (2005b) reported that darts only occur in low-spined species. These authors further speculated that high-spined species, which mate unilaterally by shell mounting, lack darts, probably because mating by shell mounting does not correlate with reciprocity and because it may be more difficult to successfully hit a partner with a dart during shell mounting. Finally, Davison *et al.* (2005b) proposed that part of the dart shooting behaviour could also be explained if high-spined species are more commonly found on vertical surfaces, and reciprocal mating would be more difficult in that position.

Two observations are not in agreement with the first hypothesis. First, several high-spined taxa mate simultaneously reciprocally although they do not have darts. Hence, the claim of Davison *et al.* (2005b)

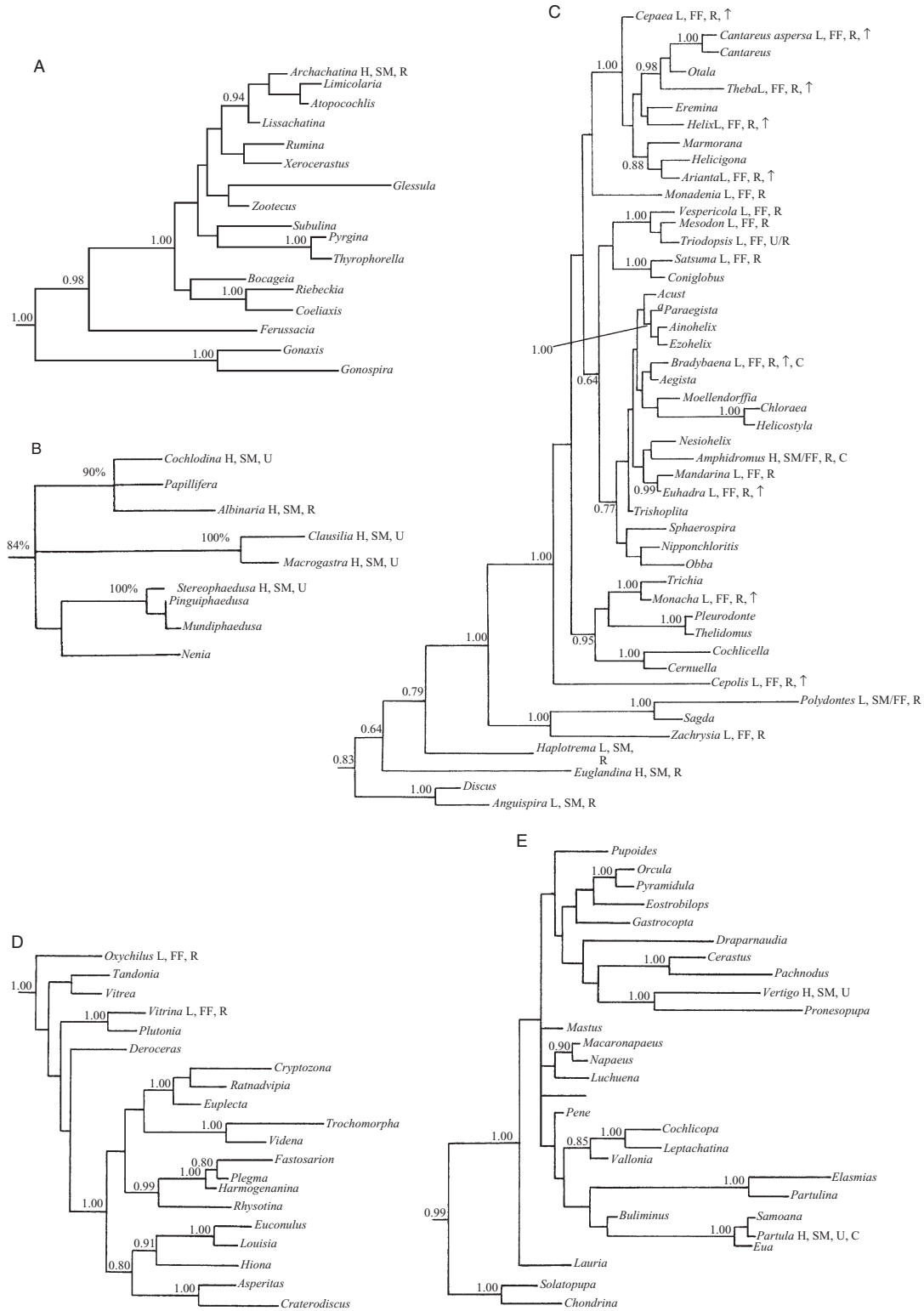


Figure 5. Phylogenetic tree for the five well-supported larger clades within the stylommatophoran pulmonates; modified *sensu* Wade *et al.* (2006). Bayesian posterior probabilities when >60% or relevant are indicated. Shell shape (L, low-spired; H, high-spired), mating position (SM, shell mounting; FF, face-to-face), dart(-sac) presence (↑), presence of whole-body enantiomorphy (C) and whether penis intromission is reciprocal (R) or unilateral (U) are plotted next to the genera. A, 'achatinoidei' clade. B, Clausilliidae. C, Helicoidea. D, Limacoidea. E, Orthurethra.

that it is more difficult to enforce reciprocity in high-spined species does not appear to be justified. Second, mating in *Z. arboreus* is unilateral even if the species has a dart (Bartsch & Quick, 1926). However, because the description of the mating behaviour and dart-use in *Zonitoides* was not very detailed (Bartsch & Quick, 1926), these observations need to be confirmed.

The second hypothesis could not be refuted, but is difficult to test because all taxa with darts mate face-to-face, even the high-spined *Cochlicella*. The observation that two low-spined taxa mate by shell mounting and reciprocally but lack darts (i.e. *Anguispira*, *Haplotrema*) may further strengthen the idea that it is neither shell-shape, nor reciprocity of penis intromission, but the mating position that is the more important factor in explaining the evolution of darts. Indeed, darts are never found in species that mate by shell mounting and only evolved in species that mate face-to-face.

If the third hypothesis would hold, then the relationship between mating position and substrate inclination appears to be weak because climbing during courtship has been observed in several low-spined, reciprocally mating taxa (Webb, 1952a, b, 1954b), and mating in *Succinea* and *Oxyloma*, which are high-spined and mate reciprocally, appears to be as easy on a vertical as on a horizontal surface (K. Jordaens, L. Dillen & T. Backeljau, pers. observ.).

WHOLE-BODY ENANTIOMORPHY

Whole-body enantiomorphy is the left-right polarity of whole-body asymmetry or of the primary asymmetry resulting in the co-occurrence of two chiral morphs (i.e. right-handed or dextral individuals and left-handed or sinistral individuals). Whole-body enantiomorphy has evolved repeatedly within the Gastropoda (Asami *et al.*, 1998; Schilthuisen & Davison, 2005). Within the Pulmonata, it has been recorded in at least 13 genera over eight superfamilies (Asami *et al.*, 1998). Interchiral mating is prevented or hindered in low-spined species that mate face-to-face because genitalia exposed by a sinistral on its left side cannot be joined with those exposed by a dextral on its right side. High-spined species, which mate unilaterally by shell mounting, appear to be able to circumvent this problem to some extent by small behavioural changes (Asami *et al.*, 1998; Schilthuisen & Davison, 2005; Sutcharit *et al.*, 2007), which may explain why whole-body enantiomorphy is only observed in high-spined species that mate unilaterally and by shell mounting (see Supporting information, Appendix S1; Asami, 1993; Asami *et al.*, 1998).

Still, it remains unknown which of these three factors (shell shape, mating by shell mounting or

unilateral sperm transfer) is the more important one in explaining the repeated evolution of whole-body enantiomorphy because shell shape, mating position, and the pattern of sperm transfer (unilateral or reciprocal) may have arisen due to shared ancestry (Davison *et al.*, 2005b; Wade *et al.*, 2006). Unfortunately, the mating behaviour has only been studied to some extent in few of the 13 genera that show whole-body enantiomorphy (see Supporting information, Appendix S1). Nevertheless, we speculate that mating position may be the most important one. Although snails of different chirality that mate face-to-face have to change their body orientation, snails that mate by shell mounting can align their genitalia by moving chiefly their heads and necks, whereas shell mounting takes place as usual (Asami, 1993) or partners may align side-by-side such as, for example, in *Amphidromus atricallosus* (Sutcharit *et al.*, 2007: fig. S3a; Fig. 1F). It appears that behavioural adjustments to allow interchiral matings is more easy to accomplish by species that mate by shell mounting. Even though species that mate face-to-face may have some behavioural adjustments, these never result in successful mating. An exception are some of the *Amphidromus* species that are able to mate reciprocally even when mating is face-to-face. The long epiphallial caecum of these species may be necessary for reciprocal interchiral copulation (Sutcharit *et al.*, 2007) (Fig. 1F).

If mating position is the most important factor in explaining the maintenance of long-term whole-body enantiomorphy, whole-body enantiomorphy should arise more easily in low-spined species that mate by shell mounting (e.g. *Anguispira*, *Haplotrema*, *Paryphanta*, *Helicophanta*). Yet, to date, whole-body enantiomorphy has not been recorded in these taxa. Interchiral mating may not depend on whether mating is simultaneously reciprocal or unilateral because interchiral matings are possible in both *Partula* and *Amphidromus*, which mate unilateral and simultaneously reciprocal, respectively.

CONCLUSIONS AND FUTURE DIRECTIVES

Several exceptions to the presumed dichotomy of shell shape and mating behaviour emerge from our data: (1) several low-spined species mate unilaterally; (2) several low-spined species mate by shell mounting; (3) several high-spined species mate face-to-face; and (4) several high-spined species mate reciprocally. Moreover, some other striking results should be highlighted from these data: (1) sex role alternation is more common in freshwater snails compared to land snails; (2) in unilateral matings, it is not always the shell-mounter that is the sperm donor; (3) reciprocal mating is not always simultaneous, but sometimes

alternated; and (4) reciprocal penis intromission not necessarily implies reciprocal sperm transfer.

However, studies on the evolutionary relationship between shell shape and reciprocity with, for example, dart-shooting and whole-body enantiomorphy, often make use of the presumed dichotomy of shell shape and mating behaviour. Therefore, the current view of the evolution of these phenomena should consider the lack of a straightforward relationship between shell shape and mating behaviour and need to be fine-tuned. Our findings, and the near absence of basic knowledge on the mating behaviour of many pulmonates, suggest that, currently, generalizations with respect to shell shape, mating behaviour, and the reciprocity of penis intromission, are difficult to make.

A major problem is that for most species, data on the reproductive behaviour are restricted to few observations (see Supporting information, Appendix S1). This makes it hard to discriminate among general patterns in reproductive behaviour and intraspecific variation in mating behaviour. Snail mating behaviour inherently varies even within individuals of the same species. Evidently, some of the intraspecific variation mentioned in this survey may have no adaptive value but are rather exceptions of an underlying general pattern. With very low sample sizes, it will be almost impossible to discriminate among relevant (i.e. adaptive) intraspecific variation (e.g. different strategies that are adopted) and non-adaptive variation. Such non-adaptive variation may weaken or even obscure general reproductive patterns within and among species and will hamper the examination of causality of trait evolution. Moreover, observations are often made on individuals with unknown mating history or relatedness, whereas it has been shown repeatedly that the mating history of an individual (Koene & Ter Maat, 2005; Dillen *et al.*, 2008) or the relatedness between partners (McCarthy & Sih, 2008) affect an individual's mating behaviour. Future studies should take these factors into account.

Nevertheless, if the lack of a straightforward relationship between shell shape and mating behaviour is further corroborated, then we may be able to accurately estimate the relative influence of shell shape, mating position and reciprocity of penis intromission on several evolutionary phenomena and trait evolution of pulmonates. Furthermore, even though the phylogenies of Davison *et al.* (2005b) and Wade *et al.* (2006) suggest that several well-supported clades either consist of low-spined species (e.g. Helicoidea and Limacoidea) or high-spined species (e.g. Orthurethra, Clausilioidea, and an 'achatinoïd' clade) (Fig. 5), several exceptions occur within these clades. These phylogenies also neatly illustrate the lack of knowledge on the mating behaviour of most of the genera of

several clades, especially of the Orthurethra, Limacoidea, and the 'achatinoïd' clade.

Based on our survey, which shows high intra- and interspecific variation in mating behaviour in pulmonate gastropods, and given the incomplete knowledge of the mating behaviour of most species, we propose several issues that deserve more attention because these may expand our current knowledge on snail reproductive behaviour and morphology, and the strength and mechanisms of sexual selection in pulmonate gastropods.

1. For most of the species, the description of the mating behaviour is based on single or few observations. Hence, it is unlikely that such few observations provide a representative and general picture. Observing more matings per species is needed to assess intraspecific variation in mating behaviour and to decide whether or not the curious variation that has been described for several species is exceptional. For example, in several species, unilateral and reciprocal penis intromissions have been observed, but the frequency of both is not known. Another curiosity is *Z. arboreus*, which may be the first example of a land snail that mates unilaterally, although it has a dart challenging the belief that dart shooting and reciprocal sperm transfer are tightly linked. Such studies should also focus on the pre-copulatory behaviour of species as the length and complexity of the pre-copulatory behaviour may be related to, for example, dart-shooting.
2. Part of the incomplete knowledge on the evolution of reproductive characters or reproductive behaviours may be due to ill-defined behaviours that cause confusion. In Table 1, we have defined some commonly used terminology of mating behaviour in hermaphroditic pulmonates that may help in reducing confusion.
3. Sperm transfer during reciprocal mating is normally reciprocal. Yet, in *S. putris*, 12 out of 87 matings involved unilateral sperm transfer despite reciprocal intromission (Jordaens *et al.*, 2005). Similarly, in the land slug *Deroceras rodnae* that exchanges sperm packages at the tips of entwined penises, sperm transfer was unilateral in three out of 15 apparently normal matings (Reise, 1995). Hence, reciprocal penis entwining or intromission does not necessarily involve reciprocal sperm transfer. To date, data for most taxa are lacking.
4. In stylommatophorans that mate by shell mounting, it is not always justified to appoint the 'male' role (sperm-donor) to the shell mounting individual and the 'female' role (sperm-receiver) to the inactive individual as: (1) several species that mate by shell mounting transfer sperm recipro-

cally (see Supporting information, Appendix S1); (2) in the genus *Delima* the shell-mounter is not always the sperm donor (Nordsieck, 2005); and (3) unilateral sperm transfer in *S. putris* was not related to the mating position of the individuals (Jordaens *et al.*, 2005). So far, in basommatophoran snails, the shell-mounter always acts as the sperm donor and the mounted individual as the sperm receiver (except for reciprocal intromission in *Biomphalaria*, where both partners may act as the sperm donor and receiver). Future studies that study the evolution of mating behaviours in pulmonates should keep in mind this intraspecific variation in behaviour.

5. There is still a lack of knowledge about the functional morphology of many pulmonate genital organs. For example, several species have a dart-sac, whereas other have a dart-organ which is not homologous (Barker, 2001). Some species have external sperm exchange (at the tips of entwined penises) that appears to have evolved several times independently (Barker, 2001). Even in species that mate by intromission, the intromitting organ is not necessarily the penis because, in several taxa, the vagina acts as the copulating organ. Moreover, the function of several structures (e.g. the ligula in the atrium, penis, or oviduct in many species) is unknown and poorly documented. Evidently, before general conclusions are drawn, the function of several reproductive characters need to be unraveled. Detailed morphological studies may even resolve enigmatic evolutionary questions, such as the maintenance of left-handed and right-handed individuals within single populations of the land snail genus *Amphidromus* (Schilthuizen *et al.*, 2007).
6. Finally, comparative studies only appear to be relevant when the molecular phylogeny of the study group is well-resolved. Currently, many important nodes within the stylommatophoran phylogeny are not supported which hampers comparative analysis (e.g. the use of independent contrasts). Also at the family level, well-resolved molecular phylogenies (together with basic ecological data) will prove invaluable to understand the evolution of mating behaviours in pulmonates. For example, there is no complete phylogeny of the family Clausiliidae so that the striking relationship between shell size and the reciprocity of penis intromission (Fig. 3) remains enigmatic.

EPILOGUE

The reproductive morphology and reproductive behaviours of pulmonates, and hermaphrodites in general, is very diverse. Still, we know very little

about the factors that shape this diversity. It is clear that there is scope for evolutionary arms races in pulmonates (Koene & Schulenburg, 2005; Michiels & Koene, 2006), which may result in adaptations that are at least as diverse as those seen in other groups of hermaphrodites or even gonochorists (Michiels, 1998). Above, we showed that generalizations with respect to the evolution of mating behaviour and related aspects should be made with much care. Even though some of the behavioural deviations from the typical pattern that are listed above may seem exceptional or rare, these observations may be of particular interest (e.g. unilateral transfer in otherwise reciprocally inseminating species, matings by shell mounting whereby the lower individual adopts the male role and the upper individual adopts the female role, reciprocal penis intromission in otherwise unilaterally mating species) (Michiels, 1998).

ACKNOWLEDGEMENTS

We thank Ronald Chase, Takahiro Asami, Gerhard Falkner, June Freitas, and Joris Koene for their information on snail mating behaviour and photographs and Harry Van Paesschen for the artwork. Ronald Chase, Takahiro Asami, and Joris Koene are also acknowledged for their critical comments and their stimulating discussions that shaped the various aspects of the manuscript. In addition, the comments of two referees improved the manuscript considerably. This work was financed by a BOF-NOI grant (FA070400/3/1040) from the University of Antwerp and a 'Krediet aan Navorsers' (1.5.066.06) of the Fund for Scientific Research – Flanders (F.W.O.) to K.J. K.J. is a Postdoctoral Fellow of the F.W.O.

REFERENCES

- Adamo SA, Chase R. 1988.** Courtship and copulation in the terrestrial snail *Helix aspersa*. *Canadian Journal of Zoology* **66**: 1446–1453.
- Anthes N, Putz A, Michiels NK. 2006.** Sex role preferences, gender conflict and sperm trading in simultaneous hermaphrodites: a new framework. *Animal Behaviour* **72**: 1–12.
- Apley ML. 1970.** Field studies on life cycle, gonadal cycle and reproductive periodicity in *Melampus bidentatus* (Pulmonata: Ellobiidae). *Malacologia* **10**: 381–397.
- Archer AF. 1933.** A study of *Polygyra inflecta* (Say). *Occasional Papers, Museum of Zoology, University of Michigan* **276**: 1–8.
- Asami T. 1993.** Genetic variation and evolution of coiling chirality in snails. *Forma* **8**: 263–276.
- Asami T, Cowie RH, Ohbayashi K. 1998.** Evolution of mirror images by sexually asymmetric mating behavior in hermaphroditic snails. *American Naturalist* **152**: 225–236.

- Baminger H, Locher R, Baur B. 2000.** Incidence of dart shooting, sperm delivery, and sperm storage in natural populations of the simultaneously hermaphroditic land snail *Arianta arbustorum*. *Canadian Journal of Zoology* **78**: 1767–1774.
- Barker GM. 2001.** Gastropods on land: Phylogeny, diversity and adaptive morphology. In: Barker GM, ed. *The biology of Terrestrial mollusca*. Wallingford: CABI Publishing, 1–146.
- Barraud EM. 1957.** The copulatory behaviour of the freshwater snail (*Limnaea stagnalis* L.). *British Journal of Animal Behaviour* **5**: 55–59.
- Bartsch P, Quick ME. 1926.** An anatomic study of *Zonitoides arboreus* Say. *Journal of Agricultural Research* **32**: 783–791.
- Baur B. 1998.** Sperm competition in molluscs. In: Birkhead TR, Möller AP, eds. *Sperm Competition and Sexual Selection*. San Diego, CA: Academic Press, 255–305.
- Beese K, Beier K, Baur B. 2006.** Coevolution of male and female reproductive traits in a simultaneously hermaphroditic land snail. *Journal of Evolutionary Biology* **19**: 410–418.
- Brumpt E. 1941.** Observations biologiques diverses concernant *Planorbis (Australorbis) glabratus* hôte intermédiaire de *Schistosoma mansoni*. *Annales de Parasitologie* **18**: 9–45.
- Cain AJ. 1977.** Variation in the spire index of some coiled gastropod shells, and its evolutionary significance. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **277**: 377–428.
- Chase R, Blanchard KC. 2006.** The snail's love-dart delivers mucus to increase paternity. *Proceedings of the Royal Society of London Series B, Biological Sciences* **273**: 1471–1475.
- Chase R, Vaga K. 2006.** Independence, not conflict, characterizes dart-shooting and sperm exchange in a hermaphroditic snail. *Behavioral Ecology and Sociobiology* **59**: 732–739.
- Cook A. 1985.** The courtship of *Euglandina rosea* Férussac. *Journal of Molluscan Studies* **51**: 211–214.
- Dasen DD. 1933.** Structure and function of the reproductive system in *Ariophanta*. *Proceedings of the Zoological Society of London* **134**: 97–118.
- Davison A, Chiba S, Barton NH, Clarke B. 2005a.** Speciation and gene flow between snails of opposite chirality. *PLoS Biology* **3**: e282.
- Davison A, Wade CM, Mordan PB, Chiba S. 2005b.** Sex and darts in slugs and snails (Mollusca: Gastropoda: Stylommatophora). *Journal of Zoology, London* **267**: 329–338.
- DeWitt RM. 1954.** Reproduction, embryonic development, and growth in the pond snail, *Physa gyrina* Say. *Transactions of the American Microscopical Society* **73**: 124–137.
- Dillen L, Jordaens K, Dieleman W, Backeljau T. 2008.** Effects of isolation and body size on the mating behaviour of the hermaphroditic land snail *Succinea putris*. *Animal Behaviour* **75**: 1401–1411.
- Duncan CJ. 1975.** Reproduction. In: Fretter V, Peake J, eds. *Pulmonates*, Vol. 1. London: Academic Press, 309–365.
- Facon B, Ravigné V, Goudet J. 2008.** Gender-role alternation in the simultaneously hermaphroditic freshwater snail *Physa acuta*: not with the same partner. *Behavioural Ecology and Sociobiology* **62**: 713–720.
- Férussac JBL. 1819.** *Histoire naturelle générale et particulière des mollusques terrestres et fluviatiles*. Paris: Fol.
- Giusti F, Andreini S. 1988.** Morphological and ethological aspects of mating in two species of the family Helicidae (Gastropoda Pulmonata): *Theba pisana* (Müller) and *Helix aperta* Born. *Monitore Zoologico Italiano* **22**: 331–363.
- Giusti F, Lepri A. 1980.** Aspetti morfologici ed etologici dell'accoppiamento in alcune specie della famiglia Helicidae (Gastropoda: Pulmonata). *Atti della Accademia dei Fisiocritici in Siena* 1–17.
- Hecker U. 1965.** Zur Kenntnis der mitteleuropäischen Bernsteinschnecken (Succineidae). I. *Archiv für Molluskenkunde* **94**: 1–45.
- Heller J. 1993.** Hermaphroditism in molluscs. *Biological Journal of the Linnean Society* **48**: 19–42.
- Herzberg F, Herzberg A. 1962.** Observations on reproduction in *Helix aspersa*. *American Midland Naturalist* **68**: 297–305.
- Howell-Rivero LH. 1946.** Notas sobre la cópula de *Zachrysis guanensis* y *Veronicella tenax*. *Revista de la Sociedad Malacológica 'Carlos De La Torre'* **4**: 75–84.
- Howell-Rivero LH. 1950.** Reproducción de *Caracolus sagemon* Beck. *Revista de la Sociedad Malacológica 'Carlos De La Torre'* **7**: 45–52.
- Jackiewicz M. 1980.** Some observations on biology of reproduction of *Succinea Draparnaud* (Gastropoda, Pulmonata). *Annales Zoologici* **35**: 65–73.
- Jordaens K, Pinceel J, Backeljau T. 2005.** Mate choice in the hermaphroditic land snail *Succinea putris* (Stylommatophora: Succineidae). *Animal Behaviour* **70**: 329–337.
- Koene JM, Chiba S. 2006.** The way of the samurai snail. *American Naturalist* **168**: 553–555.
- Koene JM, Schulenburg H. 2005.** Shooting darts: co-evolution and counter-adaptation in hermaphroditic snails. *BMC Evolutionary Biology* **5**: 25.
- Koene JM, Ter Maat A. 2001.** Allohormones: a class of bioactive substances favoured by sexual selection. *Journal of Comparative Physiology A* **187**: 323–326.
- Koene JM, Ter Maat A. 2005.** Sex role alternation in the simultaneously hermaphroditic pond snail *Limnaea stagnalis* is determined by the availability of seminal fluid. *Animal Behaviour* **69**: 845–850.
- Künkel K. 1933.** Vergleichende experimentelle Studie über *Vitrina elongata* Draparnaud und *Vitrina brevis* Férussac. *Zoologischer Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie der Tiere* **52**: 399–432.
- Leahy WM. 1983.** Comportamento e características anatómicas da reprodução em *Bradybaena similis* (Molusco pulmonado). *Ciência e Cultura, São Paulo* **36**: 1389–1392.
- Lipton CS, Murray J. 1979.** Courtship of land snails of the genus *Partula*. *Malacologia* **19**: 129–146.
- McCarthy TM, Sih A. 2008.** Relatedness of mates influences mating behaviour and reproductive success of the hermaphroditic freshwater snail *Physa gyrina*. *Evolutionary Ecology Research* **10**: 77–94.

- Maddison WP. 2000.** Testing character correlation using pairwise comparisons on a phylogeny. *Journal of Theoretical Biology* **202**: 195–204.
- Mead AR. 1950.** Comparative genital anatomy of some African Achatinidae (Pulmonata). *Bulletin of the Museum of Comparative Zoology at Harvard College* **105**: 219–291.
- Michiels NK. 1998.** Mating conflicts and sperm competition in simultaneous hermaphrodites. In: Birkhead TR, Möller AP, eds. *Sperm competition and sexual selection*. San Diego, CA: Academic Press, 219–253.
- Michiels NK, Koene JM. 2006.** Sexual selection favors harmful mating in hermaphrodites more than in gonochorists. *Integrative and Comparative Biology* **46**: 473–480.
- Nordsieck H. 2005.** Mating biology of Clausiliidae. *Mitteilungen der Deutschen Malakozoologischen Gesellschaft* **73/74**: 29–34.
- Plummer JM. 1975.** Observations on the reproduction, growth and longevity of a laboratory colony of *Archachatina (Calachatina) marginata* (Swainson) subspecies *ovum*. *Journal of Molluscan Studies* **41**: 395–413.
- Pokryszko B. 1990.** Life history and population dynamics of *Vertigo pusilla* O.F. Müller, 1774 (Gastropoda: Pulmonata: Vertiginidae), with some notes on shell and genital variability. *Annales Zoologici* **43**: 407–432.
- Purvis A, Rambaut A. 1995.** Comparative analysis by independent contrasts (CAIC) – an Apple Macintosh application for analyzing comparative data. *Computer Applications in the Biosciences* **11**: 247–251.
- Reise H. 1995.** Mating behaviour of *Deroceras rodnae* Grossu & Lupu, 1965 and *D. praecox* Wiktor, 1966 (Pulmonata: Agriolimacidae). *Journal of Molluscan Studies* **61**: 325–330.
- Rensch I. 1955.** On some Indian land snails. *Journal of the Bombay Natural History Society* **53**: 163–176.
- Reyes Tur B, Koene JM. 2007.** Use of the dart apparatus by the hermaphroditic land snail *Polymita muscarum*. *Animal Biology* **57**: 261–266.
- Reyes Tur B, Velázquez AF, Ortiz Cabrera Y. 2000.** Conducta de apareamiento y aspectos de la relación estructuración del sistema reproductor en *Polymita muscarum* Lea 1834, (Gastropoda: Pulmonata). *Revista de Biología* **14**: 161–166.
- Rodríguez AS, Gómez BJ. 1999.** Copulatory process in *Oxychilus (Drouetia) atlanticus* (Morelet & Drouët, 1857) (Pulmonata: Zonitidae). *Invertebrate Reproduction and Development* **36**: 1–3.
- Rogers DW, Chase R. 2001.** Dart receipt promotes sperm storage in the garden snail *Helix aspersa*. *Behavioral Ecology and Sociobiology* **50**: 122–127.
- Rogers DW, Chase R. 2002.** Determinants of paternity in the garden snail *Helix aspersa*. *Behavioral Ecology and Sociobiology* **52**: 289–295.
- Roscoe EJ. 1950.** Some observations on reproduction in *Oreohelix* in Utah. *Proceedings of the Utah Academy of Sciences* **25**: 166–167.
- Rudolph PH. 1979a.** The strategy of copulation of *Stagnicola elodes* (Say) (Basommatophora: Lymnaeidae). *Malacologia* **18**: 381–389.
- Rudolph PH. 1979b.** An analysis of copulation in *Bulinus (Physopsis) globosus* (Gastropoda: Planorbidae). *Malacologia* **19**: 147–155.
- Schilthuisen M. 2005.** The darting game in snails and slugs. *Trends in Ecology and Evolution* **20**: 581–584.
- Schilthuisen M, Craze PG, Cabanban AS, Davison A, Stone J, Gittenberger E, Scott BJ. 2007.** Sexual selection maintains whole-body chiral dimorphism in snails. *Journal of Evolutionary Biology* **20**: 1941–1949.
- Schilthuisen M, Davison A. 2005.** The convoluted evolution of snail chirality. *Naturwissenschaften* **92**: 504–515.
- Schilthuisen M, Lombaerts M. 1995.** Life on the edge: a hybrid zone in *Albinaria hippolyti* (Gastropoda: Clausiliidae) from Crete. *Biological Journal of the Linnean Society* **54**: 111–138.
- Springer de Freitas J, Pires Paula D, Cariello MO. 1997.** The influence of self-fertilization performance and copulation behaviour in reproduction by cross-fertilization in groups of *Biomphalaria tenagophila* (Mollusca, Planorbidae). *Memórias do Instituto Oswaldo Cruz* **92**: 739–743.
- Stringer IAN, Bassett SM, McLean MJ, McCartney J, Parrish GR. 2003.** Biology and conservation of the rare New Zealand land snail *Paryphanta busbyi watti* (Mollusca, Pulmonata). *Invertebrate Biology* **122**: 241–251.
- Sutcharit C, Asami T, Panha S. 2007.** Evolution of whole-body enantiomorphy in the tree snail genus *Amphidromus*. *Journal of Evolutionary Biology* **20**: 661–672.
- Tomiyama K. 1994.** Courtship behaviour of the giant African land snail *Achatina fulica* (Férussac) (Stylommatophora: Achatinidae) in the field. *Journal of Molluscan Studies* **60**: 47–54.
- Tomba AS. 1984.** Land snails (Stylommatophora). In: Tompa AS, Verdonk NH, van den Biggelaar JAM, eds. *The Mollusca*, Vol. 7. *Reproduction*. New York, NY: Academic Press, 47–140.
- Trigwell J, Dussart G, Vianey-Liaud M. 1997.** Mating strategies in the freshwater hermaphrodite snail *Biomphalaria glabrata* (Say, 1918). *Haliotis* **26**: 25–32.
- Van Duivenboden YA, Ter Maat A. 1985.** Masculinity and receptivity in the hermaphrodite pond snail, *Lymnaea stagnalis*. *Animal Behaviour* **33**: 885–891.
- Van Duivenboden YA, Ter Maat A. 1988.** Mating behaviour of *Lymnaea stagnalis*. *Malacologia* **28**: 53–64.
- Vernon J, Taylor J. 1996.** Patterns of sexual roles adopted by the schistosome-vector snail *Biomphalaria glabrata*. *Journal of Molluscan Studies* **62**: 235–241.
- Vianey-Liaud M. 1998.** La reproduction chez un mollusque hermaphrodite simultané, la planorbe *Biomphalaria glabrata* (Say, 1818) (Gastéropode, Pulmoné). *Haliotis* **27**: 67–114.
- Wade CM, Mordan PB, Naggs F. 2006.** Evolutionary relationships among the pulmonate land snails and slugs (Pulmonata, Stylommatophora). *Biological Journal of the Linnean Society* **87**: 593–610.
- Webb GR. 1942.** Comparative observations of the mating habits of three California landsnails. *Bulletin of the Southern California Academy of Sciences* **41**: 102–108.

- Webb GR. 1943.** The mating of the landsnail *Haplotrema concavum* (Say). *American Midland Naturalist* **30**: 341–345.
- Webb GR. 1947a.** Studies of the sex-organs of mating polygyrid landsnails. *Illinois Academy of Science Transactions* **40**: 218–227.
- Webb GR. 1947b.** The mating-anatomy technique as applied to polygyrid landsnails. *American Naturalist* **81**: 134–147.
- Webb GR. 1948a.** Comparative observations on the mating of certain Triodopsinae. *The Nautilus* **61**: 97–103.
- Webb GR. 1948b.** The mating of *Stenotrema fraternum* (Say). *The Nautilus* **62**: 8–12.
- Webb GR. 1948c.** Notes on the mating of some Zonitoides (Ventridentis) species of land snails. *The American Midland Naturalist* **40**: 453–461.
- Webb GR. 1950.** The sexology of *Polygyra septemvolva* Say, life-history notes, possible utility, and data on *Stenotrema* (Mollusca, Gastropoda, Pulmonata, Polygyridae). *Transactions of the American Microscopical Society* **69**: 387–393.
- Webb GR. 1951.** Sexological notes on the landsnail *Oreohelix*. *Natural History Miscellanea* **78**: 1–5.
- Webb GR. 1952a.** Pulmonata, Xanthonycidae: comparative sexological studies of the North American land-snail, *Monadenia fidelis* (Gray) – a seeming ally of Mexican helicoids. *Gastropodia* **1**: 1–3.
- Webb GR. 1952b.** Pulmonata, Helminthoglyptidae: Sexological data on the land-snails, *Cepolis maynardi* & *Helminthoglypta traski fieldi* and their evolutionary significance. *Gastropodia* **1**: 4–5.
- Webb GR. 1952c.** Pulmonata, Polygyridae: a sexological revision of some triodopsine land-snails, *Xolotrema*, *Neohelix*, & *Wilcoxorbis*. *Gastropodia* **1**: 7–8.
- Webb GR. 1952d.** Sexological notes on *Mesomphix cupreus* and *M. subplanum*. *Transactions of the American Microscopical Society* **71**: 408–411.
- Webb GR. 1954a.** The life-history and sexual anatomy data on *Ashmunella* with a revision of the triodopsine snails. *Gastropodia* **1**: 13–18.
- Webb GR. 1954b.** Pulmonata, Polygyridae, Polygyrinae: the sexology and taxonomy of seven species of land-snails of the genus *Mesodon*. *Gastropodia* **1**: 19–20.
- Webb GR. 1959.** Pulmonata, Polygyridae: notes on the sexology of *Triodopsis*, a new sub-genus, *Haroldorbis*, and a new section, *Shelfordorbis*. *Gastropodia* **1**: 23–25.
- Webb GR. 1961.** Studies on the sexology and development of the genitalia of *Glyptostoma gabriellense* Pilsbry. *Gastropodia* **1**: 29–30.
- Webb GR. 1965.** On the sexology of *Trilobopsis loricata sonomaensis* (Hemphill). *Gastropodia* **1**: 58–60.
- Webb GR. 1967a.** Erotology of three species of *Praticolella*, and of *Polygyra pustula*. *The Nautilus* **80**: 133–140.
- Webb GR. 1967b.** Erotology of three species of *Praticolella*, and of *Polygyra pustula*. *The Nautilus* **81**: 11–18.
- Webb GR. 1968a.** Notes on the sexology of the polygyrid land-snail, *Mesodon sargentianus* (Johnson & Pilsbry). *Gastropodia* **1**: 62–65.
- Webb GR. 1968b.** Sexological notes on *Mesodon (Ragsdaleorbis) christyi* (Bland). *Gastropodia* **1**: 66.
- Webb GR. 1968c.** Observations on the sexology of the endodontid land-snail, *Anguispira alternata* (Say). *Gastropodia* **1**: 66–67.
- Webb GR. 1968d.** Sexological notes on *Ventridentis elliotti*, *V. acerra*, *V. demissus brittsi*, and *V. ligera*. *Gastropodia* **1**: 67–70.
- Webb GR. 1968e.** Sexological notes on *Allogona*. *Gastropodia* **1**: 70–72.
- Webb GR. 1970a.** Fragmentary observations on sexology of *Cryptomastix hendersoni* Pilsbry and *C. magnidentata* Pilsbry and a new subgenus (Pulmonata, Polygyridae, Ashmunellinae). *Gastropodia* **1**: 77–78.
- Webb GR. 1970b.** Observations on the sexology of *Vespericola columbiana* (Lea) from Olympic Peninsula, Washington. *Gastropodia* **1**: 75–77.
- Webb GR. 1970c.** Pulmonata, Camaenidae: comparative sexology and genital development of *Caracolus caracolla* (L.), *C. marginella* (Gmelin), and *Polydotes lima* (Ferussac). *Gastropodia* **1**: 79–84.
- Webb GR. 1977a.** On the sexology of *Catinella (Mediappendix) avara* (Say) or *C. (M.) vermeta* (Say). *Gastropodia* **1**: 100–102.
- Webb GR. 1977b.** Some sexologic observations on *Oxyloma retusa* (Lea). *Gastropodia* **1**: 102–104.
- Webb GR. 1977c.** The comparative sexology of several Succineidae. *Gastropodia* **1**: 105–107.
- Webb GR. 1980a.** The sexology of a Texan *Humboldtiana* (Pulmonata). *Gastropodia* **2**: 2–7.
- Webb GR. 1980b.** Notes on the sexology of *Sonorella (Masculus) virilis* Pilsbry, Pulmonata, Xanthonycidae. *Gastropodia* **2**: 7–8.
- Webb GR. 1983.** On the sexology of *Mesodon kiowaensis* (Simpson) Pulmonata, Polygyridae, Polygyrinae. *Gastropodia* **2**: 19–20.
- Webb GR. 1990a.** Notes on the sexology of *Sonorella simonsi* Miller. *Gastropodia* **2**: 22–24.
- Webb GR. 1990b.** The sexology of five species of *Polygyra* (Polygyridae, Polygyrinae). *Gastropodia* **2**: 28.
- Webb GR. 1994.** Notes on mating-anatomies of *Helicella caperata* from near Bury St. Edmonds, England. *Gastropodia* **2**: 31–33.
- Wiswell O, Browning HC. 1967.** The mating of the giant South American snail *Strophocheilus oblongus*. *Anatomical Record* **157**: 409.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Association of shell shape [L, low-spined (i.e. globular or flat); H, high-spined (i.e. tall)], mating position (FF, face-to-face; SM, shell mounting; SS, side-by-side), penis usage during copulation [AR, alternate

reciprocal; R, reciprocal; U, unilateral; (S), sex role alternation may occur], sperm exchange (I, internal; E, external), the presence of a dart or dart-sac (Y, yes; N, no), and the occurrence of intraspecific whole-body enantiomorphy (Y, yes; N, no) in pulmonate land and freshwater snails. The first column gives an estimate of the number of matings on which the observations were based ('?', the number of mating observations was not mentioned; 'many', a high number of matings were studied (> 100) but that specific numbers were not reported).

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.