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A literature database on the mating behavior of stylommatophoran land snails and slugs*

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Abstract: Stylommatophoran land snails and slugs generally mate by shell-mounting or face-to-face. Although phylogenetic evidence suggests that the mating position has remained more or less constant throughout the evolution of most lineages, other aspects of mating behavior and associated reproductive characters are highly variable. Along with other gastropods, therefore, stylommatophoran land snails and slugs could be particularly useful in trying to understand sex and sex allocation theory in hermaphrodites. It is often difficult, however, to compare mating behavior in different species because the literature is difficult to access or reports have not been formally published. Here we review studies on the mating behavior of snails and slugs, with the additional aim of creating a central access point and database for use as a resource by those interested in stylommatophoran mating behavior. As we maintain the database, updated versions will be made available at http://www.molluscs.org.

Key words: love darts, mollusc, sexual conflict, reciprocal mating, simultaneous hermaphrodite

The mating behavior of a wide variety of stylommatophoran land snails has been observed, but the descriptions are often within texts that are not easily accessible, or cannot be searched electronically. Many malacologists have also made their own informal observations of mating behavior, but do not publish them for lack of time, or because they are not perceived to be of sufficient worth on their own. Because there have been no recent reviews of the mating behavior of snails and slugs, we set out to collect as many observations together as possible, both formal and informal. Such an approach has already proved useful in trying to understand how so-called "love" darts evolved (Davison *et al.* 2005). Differences in mating behavior have also been used to understand the distribution of chiral variation (or asymmetry) among different taxonomic groups (Asami *et al.* 1998) and the evolution of external sperm exchange (Emberton 1994). The aim of this brief review, therefore, is to create a starting point for a compilation of data on the mating behavior of stylommatophoran snails and slugs.

Although there are some exceptions (*e.g.*, the elongated penes and external fertilization of *Limax maximus* Linnaeus, 1758), mating in the majority of land snails and slugs can be classified as either face-to-face or shell-mounting (Figure 1; Asami *et al.* 1998). The vast majority of species are also simultaneous hermaphrodites. In theory, therefore, four different modes of mating are possible because sex is also either simultaneous reciprocal (both individuals are male and female at the same time) or unilateral (each individual has a defined role as male or female during a single round of mating):

Face-to-face, simultaneous reciprocal;
Face-to-face, unilateral;
Shell-mounting, simultaneous reciprocal;
Shell-mounting, unilateral.

When two individuals mate unilaterally, they often switch roles after one round of mating—male becomes female and female becomes male. The frequency with which this occurs is difficult to assess because it requires extended observations, and also the frequency of mate switching depends upon the condition (or desire) of each snail (Koene and Ter Maat 2005). The problem is further complicated because often the most efficient means to make laboratory observations of mating behavior is to isolate individuals for some time before bringing them together. For a variety of possible reasons (*e.g.*, availability of seminal fluid), isolated individuals are more likely to switch mates after one round of mating (Koene and Ter Maat 2005).

Another concern is whether sperm or spermatophore transfer is always reciprocal if mating is reciprocal; from an evolutionary point of view, the reciprocal exchange of sperm is just as important. In some species of *Succinea* Draparnaud,

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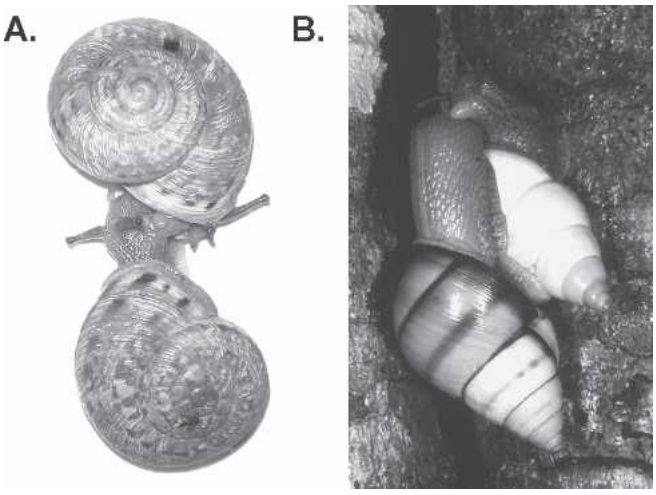

Figure 1. A, *Iberus marmoratus* Férussac, 1801 (Helicidae) mating face-to-face and simultaneous reciprocally. Horizontal field width approximately 6 cm. Photo by A. Davison, in the laboratory. B, *Liguus fasciatus* Pilsbry, 1912 (lower snail, acting as male) and *Orthalicus floridensis* Pilsbry, 1899 (upper snail, acting as female) (Orthalicidae) mating by shell-mounting. Specimens in hardwood hammock in the Redlands of southern Dade County, Florida. Image reproduced with the kind permission of the photographer, Phil Poland, ppoland1@tampabay.rr.com. Vertical field width approx. 7 cm.

1801 that mate reciprocally by shell-mounting, sperm transfer is sometimes unilateral (Jordaens *et al.* 2005), whereas other species such as *Arianta arbustorum* Linnaeus, 1758 have a high reciprocity (Baur 1998). In species that develop as males before becoming simultaneous hermaphrodites, such as *Lissachatina* (*Achatina*) *fulica* Bowdich, 1822, sperm transfer may frequently be unilateral (Tomiyama 1993).

We surveyed the formal literature on the mating behavior of land snails and slugs and then classified each species as to whether it mates face-to-face, by shell-mounting, simultaneous reciprocally, or unilaterally (Table 1). We also included informal observations, when available (mating position and, to a lesser extent, reciprocity can be scored from photographs), and tried to identify video recordings of mating behavior (Table 2). One striking, immediately apparent result is that face-to-face mating is exclusively associated with simultaneous reciprocal mating. Snails and slugs in three monophyletic groups mate face-to-face and simultaneous reciprocally: the Helicoidea, Limacoidea, and Philomycidae (Davison *et al.* 2005).

One other reason to study mating behavior is to understand the evolution of "love" darts. Despite the attention that greets each advance, little is known about the use of darts outside of *Cantareus aspersus* (*Helix aspersa* Müller, 1774) (Koene and Chase 1998a, 1998b, Landolfa *et al.* 2001, Rogers and Chase 2001, Rogers and Chase 2002, Koene and Schulenberg 2005, Chase 2006), except that there is considerable variation in the timing of the use of the dart, its morphology, and the number used in different species (Ashford 1883, Tompa 1980, Baminger *et al.* 2000, Koene and Schulenberg 2005). At the extreme of the spectrum, some species of *Euhadra* Pilsbry, 1890 repeatedly stab a dart (~3000 times) during "foreplay" prior to mating (J. Koene and S. Chiba, personal communication). Opinions also vary over what constitutes a dart. Although some might contend that an "amatorial" organ is a dart, we argue that while darts and amatorial organs may (or may not) have similar functions, they are clearly distinguishable because only the former is a "hard, calcified or chitinous organ that is used to pierce a partner during mating" (Davison *et al.* 2005).

There have been very few formal observations of dart use. The only photographs that we are aware of showing darts "in use" are of *C. aspersus* (Koene and Chase 1998a, 1998b, Landolfa *et al.* 2001, Rogers and Chase 2001, Rogers and Chase 2002, Koene and Schulenberg 2005), *Cepaea nemoralis* (Davison *et al.* 2005), and *Trichotoxon heynemanni* (Schilthuizen 2005). It would therefore be useful if creating a database also stimulated malacologists to record dart use and to publicize their efforts. We have recently used information in the database to show that dart-bearing species are confined to the same three monophyletic groups mentioned above (the Helicoidea, Limacoidea, and Philomycidae) and that they all mate face-to-face and simultaneous reciprocally. However, there is no evidence that the relationship is causal (Davison *et al.* 2005).

Although there are still some large clades of snails for which there have been few observations of mating behavior, an interesting dichotomy has emerged between invariant mating position and other highly variable reproductive characters. Some species have head warts (Binder 1977, Takeda 1982, Falkner 1993), penial stimulators (Reise 2004), or amatorial organs (Panha 1987), whereas individuals in other species bite off the penis of their partner (Leonard *et al.* 2002) or entwine their penes before exchanging sperm externally (Quick 1960). Although it has been known that some families tend to have the same shell shape (Cain 1977), the strong and (almost) invariant correlation between mating position and shell shape has mostly been overlooked (Asami *et al.* 1998, Davison *et al.* 2005).

Our attention is drawn to the exceptions. In the helicoid group, species of *Amphidromus* Albers, 1850 have high-spired shells but still mate reciprocally, even between chirally-reversed individuals (M. Schilthuizen, personal communication). As they also lack darts, it is tempting to speculate that the shell-shape change and lack of darts are in some way associated, but there is no firm evidence. Clausiild snails are interesting because some species mate unilaterally whereas others mate reciprocally; there is even within-species variation (Nordsieck 2005a, 2005b). Finally, *Oreohe-*

Table 1. An overview of the literature on the mating behavior of stylommatophoran land snails and slugs. Mating behaviour: FF, face-to-face; I, idiosyncratic; SM, shell-mounting; SR, simultaneous reciprocal; U, unilateral (includes sequential unilateral mating); ?, not known. Shell shape: H, high-spired; L, low-spired; S, slug or semi-slug. Darts: N, dart and art-sac absent; Y, dart or dart-sac present.

Family	Genus	Mating		Shell shape	Darts	References
Helicoidea						
Bradybaenidae	*Bradybaena* Beck, 1837	FF	SR	L	Y	Asami *et al.* 1998
	Euhadra Pilsbry, 1890	FF	SR	L	Y	Takeda and Tsuruoka 1979, Azuma 1995, Asami *et al.* 1998, S. Chiba, A. Davison, J. Koene, pers. obs.
Camaenidae	*Mandarina* Pilsbry, 1895	FF	SR	L	N	S. Chiba & A. Davison, pers. obs.
	Caracolus Montfort, 1810	FF	SR	L	N	Howell-Rivero 1950, Webb 1970b, 1974
	Polydontes Montfort, 1810	?	?	L	N	Webb 1970b, 1974
	Pleurodonte Fischer von Waldheim, 1807	FF	SR	L	N	Sánchez Muñoz 2005a
	Satsuma A. Adams, 1868	FF	SR	L	N	Abbott 1989, Azuma 1995
	Amphidromus Albers, 1850	FF	SR	H	N	Schilthuizen and Davison 2005, M. Schilthuizen, pers. comm.
	Zachrysia Pilsbry, 1894	FF	SR	L	N	Howell-Rivero 1946, Sánchez Muñoz 2005b
Helicidae	*Cepaea* Held, 1837	FF	SR	L	Y	Beaumont 1988
	Cantareus Risso, 1826	FF	SR	L	Y	Giusti and Lepri 1980-1981, Adamo and Chase 1988, Giusti and Andreini 1988
	Theba Risso, 1826	FF	SR	L	Y	Giusti and Andreini 1988
	Arianta Leach in Turton, 1831	FF	SR	L	Y	Hofmann 1923, Locher and Baur 2000
	Helix Linnaeus, 1758	FF	SR	L	Y	Meisenheimer 1907, Jeppesen 1976, Lind 1976, Giusti and Lepri 1980-1981, Chung 1987
	Tacheocampylaea Pfeiffer, 1877	FF	SR	L	Y	Giusti and Lepri 1980-1981
	Eobania P. Hesse, 1913	FF	SR	L	Y	Giusti and Lepri 1980-1981
	Iberus Montfort, 1810	FF	SR	L	Y	Rabaneda-Bueno *et al.* 2004, this paper
Helminthoglyptidae	*Cepolis* Montfort, 1810	FF	SR	L	Y	Webb 1942, 1952a
	Helminthoglypta Ancey, 1887	FF	SR	L	Y	Webb 1942, 1952a, van der Laan 1971, van der Laan 1980
	Humboldtiana Ihering, 1892	FF	SR	L	Y	Webb 1980b
	Monadenia Pilsbry, 1895	FF	SR	L	Y	Webb 1952b
	Sonorella Pilsbry, 1900	FF	SR	L		Webb 1980a, 1990
	Polymita Beck, 1837	FF	SR	L	Y	Moreno 1950, Tur *et al.* 2002
Hygromiidae	*Cochlicella* Férussac, 1820	FF	SR	H	Y	Schileyko and Menkhorst 1997, Asami *et al.* 1998
	Monacha Fitzinger, 1833	FF	SR	L	Y	Storey 2005
	Halolimnohelix Germain, 1913	FF	SR	L	Y	Block 1968a
Polygyridae[2]	*Allogona* Pilsbry, 1939	FF	SR	L	N	Webb 1948a, Emberton 1994, Atkinson 2005
	Ashmunella Pilsbry & Cockerell, 1899	FF	SR	L	N	Webb 1954a, Emberton 1994
	Cryptomastix Pilsbry, 1939	FF	SR	L	N	Webb 1970c, Emberton 1994
	Mesodon Rafinesque in Férussac, 1821	FF[1]	SR	L	N	Webb 1954b, Emberton 1991
	Neohelix Ihering, 1892	FF	SR	L	N	Webb 1952d, Emberton 1994
	Polygyra Say, 1818	FF[1]	SR	L	N	Archer 1933, Emberton 1994, Webb 1994a, 1994b

Table 1. Continued

Family	Genus	Mating		Shell shape	Darts	References
	Stenotrema Rafinesque, 1819	FF[1]	SR	L	N	Webb 1947, 1948b, Emberton 1994
	Trilobopsis Pilsbry, 1939	FF	SR	L	N	Webb 1965, Emberton 1994
	Triodopsis Rafinesque, 1819	FF	SR	L	N	Webb 1948a, 1959, Emberton 1994
	Vespericola Pilsbry, 1939	FF	SR	L	N	Webb 1970a, Emberton 1994
Limacoidea						
Agriolimacidae	*Deroceras* Rafinesque, 1820	FF	SR	S	N	Reise 1995, Reise 2004
Arionidae	*Arion* Férussac, 1819	FF	SR	S	N	Adams 1910, Quick 1946, Davis 1977
	Geomalacus Allman, 1842	FF	?	S	N	Platts and Speight 1988
	Ariolimax Mörch, 1859	FF	SR/U	S	N	Leonard *et al.* 2002
Ariophantidae	*Ariophanta* Desmoulins, 1829	FF	SR	L	Y	Dasen 1933
	Hemiplecta Albers, 1850	FF	SR	L	N	S. Panha, pers. comm.
	Macrochlamys (*Syama*) Godwin-Austen, 1908	FF	SR	L	N	S. Panha, pers. comm.
	Microparmarion Simroth, 1893	FF	?	S	N	Liew Thor Seng, pers. comm.
Gastrodontidae	*Oxychilus* Fitzinger, 1833	FF	SR	L	N	Rodriguez and Gomez 1999
Limacidae	*Limax* Linnaeus, 1758	I[1]	SR	S	N	Chase 1952, Quick 1960, Langlois 1965, Baur 1998
	Limacus Lehmann, 1864	FF	SR	S	N	Barker 1999
Milacidae	*Tandonia* (*Milax*) Lesson & Pollonera, 1882	FF	SR	S	N	Quick 1960
Trochomorphidae	*Bertia* Ancey, 1887	FF	SR?	L	N	Menno Schilthuizen, pers. comm.
Urocyclidae	*Trichotoxon* Simroth, 1889	FF	SR	S	Y	Bernard Verdcourt, pers. comm.
	Gymnarion Pilsbry, 1919	FF	SR	L	N	Binder 1977
	Sheldonia Ancey, 1887	FF	SR	L	N	Herbert and Kilburn 2004
	Elisolimax Cockerell, 1893	FF	SR	S	N	Herbert and Kilburn 2004
Vitrinidae	*Semilimax* Agassiz, 1845	FF	SR	S	Y	Künkel 1933
	Vitrinobrachium Kunkel, 1929	FF	SR	S	N	Künkel 1933
Zonitidae	*Mesomphix* Rafinesque, 1819	FF	SR	L	N	Webb 1952c
	Ventridens Binney & Bland, 1869	FF	SR	L	Y	Pilsbry 1946, Webb 1948c
Other						
Acavidae	*Helicophanta* Westerlund, 1886	SM	U	L	N	George Williams, pers. comm.
Achatinidae	*Achatina* Lamarck, 1799	SM	SR	H	N	Tomiyama 1994, 1996
	Archachatina Albers, 1850	SM	SR	H	N	Plummer 1975
Cerastidae	*Zebrinops* Thiele, 1931	FF	SR	H	N	Block 1968b
Ceriidae	*Cerion* Röding, 1798	?	U	H	N	Woodruff 1978
Chondrinidae	*Solatopupa* Pilsbry, 1917	?	U	H	N	Boato and Rasotto 1987
Clausiliidae	*Albinaria* Vest, 1867	SM	SR	H	N	Schilthuizen and Lombaerts 1995, Menno, Schilthuizen, pers. comm.
	Euphaedusa O. Boettger, 1877	SM	U	H	N	Asami *et al.* 1998
	Luchuphaedusa Pilsbry, 1901	SM	U	H	N	Asami *et al.* 1998
	Stereophaedusa O. Boettger, 1877	SM	U	H	N	Asami *et al.* 1998
(Alopilinae)	*Agathylla* H. & A. Adams, 1855	SM	SR	H	N	Nordsieck 1969, 2005a, 2005b
	Cochlodina Férussac, 1821	SM	U	H	N	Nordsieck 2005a, 2005b
	Delima Hartmann, 1842	SM	SR	H	N	Nordsieck 1969, 2005a, 2005b
	Herilla H. & A. Adams, 1855	SM	SR	H	N	Nordsieck 2005a, 2005b
	Medora H. & A. Adams, 1855	SM	SR	H	N	Nordsieck 2005a, 2005b
(Baleinae)	*Balea* Gray, 1824	SM	U	H	N	Nordsieck 2005a, 2005b
(Clausiliinae)	*Laciniaria* Hartmann, 1842	SM	U	H	N	Nordsieck 2005a, 2005b
	Macrogastra Hartmann, 1841	SM	U	H	N	Nordsieck 2005a, 2005b
	Clausilia Draparnaud, 1805	SM	U	H	N	Nordsieck 2005a, 2005b
	Ruthenica Lindholm, 1924	SM	U	H	N	Nordsieck 2005a, 2005b
	Neostyriaca A. Wagner, 1920	SM	U	H	N	Nordsieck 2005a, 2005b

Table 1. Continued

Family	Genus	Mating		Shell shape	Darts	References
Discidae	*Anguispira* Morse, 1864	SM[1]	SR	L	N	Webb 1968b
Enidae	*Mastus* Beck, 1837	SM	SR	H	N	Paramakelis and Mylonas 2002, Paramakelis, pers. comm.
Haplotrematidae	*Haplotrema* Ancey, 1881	SM	U	L	N	Webb 1943
Oreohelicidae	*Oreohelix* Pilsbry, 1904	SM	U	L	N	Webb 1951
Orthalicidae	*Liguus* Montfort, 1810	SM	U	H	N	Davidson 1965, Poland 2005
Partulidae	*Partula* Férussac, 1819	SM	U	H	N	Lipton and Murray 1979
Philomycidae	*Philomycus* Rafinesque, 1820	FF	SR	S	Y	Webb 1968a
Rhytididae	*Paryphanta* Albers, 1850	SM	U	L	N	Stringer *et al.* 2003
Spiraxidae	*Euglandina* Fischer & Crosse, 1870	SM	U	H	N	Cook 1985
Strophocheilidae	*Strophocheilus* Spix, 1827	SM	U	H	N	Wiswell and Browning 1967
Succineidae	*Catinella* Pease, 1870	SM[1]	SR	H	N	Webb 1977a
	Oxyloma Westerlund, 1885	SM	U/SR	H	N	Webb 1977a, 1977b, 1977c
	Succinea Draparnaud, 1801	SM	U/SR	H	N	Rieper 1912, Hecker 1965, Webb 1977a, Jackiewicz 1980, Villalobos *et al.* 1995, Jordaens *et al.* 2005
Valloniidae	*Vallonia* Risso, 1826	FF	SR?	L	N	Barker 1999
Vertiginidae	*Vertigo* Müller, 1774	SM	U?	H	N	Barker 1999

[1] External sperm exchange; sperm is deposited on the male's everted penis without intromission (see Emberton 1994)
[2] See Emberton (1994) for details of mating in other Polygyrid species (mostly papers by Webb).

Table 2. Species for which there are videos showing mating behavior.

Taxon	Mating behavior	Film-maker
Ariolimax dolichophallus Mead, 1943	Face-to-face	Brooke Miller, UC Santa Cruz (miller@biology.ucsc.edu) http://bio.research.ucsc.edu/grad/weaver/Pages/project.html
Cantareus aspersus Müller, 1774	Face-to-face	Joris Koene, Vrije Universiteit (joris.koene@falw.vu.nl) Ronald Chase, McGill University (ronald.chase@mcgill.ca)
Deroceras sp.	Face-to-face	Heike Reise, Staatliches Museum fur Naturkunde Gorlitz (Heike.Reise@smng.smwk.sachsen.de http://www.malacsoc.org.uk/Malacological%20Bulletin/BULL43/king2.htm#dive
Euhadra sandai Kobelt, 1879	Face-to-face	Nishi Hirotaka (movie archives of animal behaviour) http://zoo2.zool.kyoto-u.ac.jp/ethol/
Satsuma amanoi Kuroda, 1960	Face-to-face	Nishi Hirotaka (movie archives of animal behaviour) http://zoo2.zool.kyoto-u.ac.jp/ethol/
Mastus pupa Linnaeus, 1758	Shell-mounting	Aris Paramakelis, University of Crete (parmakel@nhmc.uoc.gr)

lix Pilsbry, 1904 is another intriguing genus because it mates by shell-mounting (Webb 1951). Although its phylogeny is unclear (Wade *et al.* 2006), we predict that it will either fall within the helicoid group or be basal to it.

We expect that observations of mating behavior will grow over the coming years and so will continue to update the database of mating behavior (updated versions at http://www.molluscs.org). We welcome any data that we have inadvertently excluded, including single photographs.

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