

Dedicated to GR Webb, the Alfred Kinsey of snail sex. Last updated 19th April 2006.

Family	Genus	(species)	1	2	3	4	Comments	References
Helicoidea:								
Bradybaenidae	<i>Bradybaena</i>	<i>similaris</i>	FF	SR	L	Y		[1]
	<i>Euhadra</i>	<i>congenita</i> <i>quaesita</i> <i>peplomphala</i>	FF	SR	L	Y		[1-3] S. Chiba, A. Davison, J. Koene, pers. obs.
	<i>Mandarina</i>	<i>ponderosa</i> <i>aureola</i>	FF	SR	L	N	Of ~100 matings, we recently observed one that was unilateral	S. Chiba & A. Davison, pers. obs.
Camaenidae	<i>Caracolus</i>	<i>sagemon</i> <i>caracolla</i> <i>marginella</i>	FF	SR	L	N		[4-7]
	<i>Polydontes</i>	<i>lima</i>	?	?	L	N		[4, 6]
	<i>Satsuma</i>		FF	SR	L	N		[2, 8]
	<i>Amphidromus</i>		FF	SR	H	N		M. Schilthuizen, pers. obs.; [9]
	<i>Zachrysia</i>	<i>guanensis</i>	FF	SR	L	N		[10]
Helicidae	<i>Cepaea</i>	<i>nemoralis</i> <i>hortensis</i>	FF	SR	L	Y		[11]
	<i>Cantareus</i>	<i>aspersus</i>	FF	SR	L	Y		[12-14]
	<i>Theba</i>		FF	SR	L	Y		[13]
	<i>Arianta</i>		FF	SR	L	Y		[15]
	<i>Helix</i>	<i>pomatia</i> <i>lucorum</i>	FF	SR	L	Y		[14, 16, 17]
	<i>Tacheocampylaea</i>	<i>tacheoides</i>	FF	SR	L	Y		[14]
	<i>Eobania</i>	<i>vermiculata</i>	FF	SR	L	Y		[14]
	<i>Iberus</i>	<i>gualtierianus</i> <i>marmoratus</i>	FF	SR	L	Y	Photo by myself	[18] A. Davison, pers. obs.
Helminthoglyptidae	<i>Cepolis</i>	<i>maynardi</i>	FF	SR	L	Y		[19, 20]
	<i>Helminthoglypta</i>	<i>arrosa</i> <i>californiensis</i> <i>dupeti</i> <i>traski</i> <i>umbilicata</i>	FF	SR	L	Y		[19-22]
	<i>Humboldtiana</i>		FF	SR	L	Y		[23]
	<i>Monadenia</i>	<i>fidelis</i>	FF	SR	L	Y		[24]
	<i>Sonorella</i>		FF	SR	L			[25, 26]
	<i>Polymita</i>	<i>muscarum</i>	FF	SR	L	Y	'in three of the experiments one of the partners tried unilateral intromision, always without success' (translated from Spanish)	[27, 28]
Hygromiidae	<i>Cochlicella</i>		FF	SR	H	Y	Most other genera of Hygromiidae are low-spired. Original source is?	[1, 29]
	<i>Monacha</i>	<i>cantiana</i>	FF	SR	L	Y		[30]
Polygyridae [#]	<i>Allogona</i>	<i>profunda</i>	FF	SR	L	N		[31-33]
	<i>Ashmunella</i>		FF	SR	L	N		[33, 34]
	<i>Cryptomastix</i>		FF	SR	L	N		[33, 35]
	<i>Mesodon</i>		FF*	SR	L	N	External sperm exchange	[36, 37]
	<i>Neohelix</i>		FF	SR	L	N		[33, 38]

	<i>Polygyra</i>		FF*	SR	L	N	External sperm exchange	[33, 39-41]
	<i>Stenotrema</i>	<i>fraternum</i>	FF*	SR	L	N	External sperm exchange	[33, 42, 43]
	<i>Trilobopsis</i>		FF	SR	L	N		[33, 44]
	<i>Triodopsis</i>		FF	SR	L	N		[32, 33, 45]
	<i>Vespericola</i>		FF	SR	L	N		[33, 46]
Limacoidea								
Agriolimacidae	<i>Deroceras</i>		FF	SR	S	N	See amazing videos at http://www.malacsoc.org.uk/Malacological%20Bulletin/BULL43/king2.htm#dive	[47]
Arionidae	<i>Arion</i>		FF	SR	S	N	www.naturereportfolio.com/inverts/gastropods_snails.php	[48-50]
	<i>Geomalacus</i>		FF		S	N		[51]
	<i>Ariolimax</i>	<i>californicus</i> <i>dolichophallus</i>	FF FF	SR U	S S	N N		[52]
Ariophantidae	<i>Ariophanta</i>	<i>ligulata</i>	FF	SR	L	Y		[53]
	<i>Hemiplecta</i>	<i>distincta</i>	FF	SR	L	N	Has 'amatorial organ' which is 'analogous to the dart'	[54]
	<i>Macrochlamys</i> (<i>Syama</i>)	<i>asamurai</i>	FF	SR	L	?	Amatorial organ but does it have a dart? Photo kindly provided by Somsak Panha	[54]
Gastrodontiidae	<i>Oxychilus</i>		FF	SR	L	N		[55]
Limacidae	<i>Limax</i>	<i>maximus</i> <i>cinereoniger</i> <i>flavus</i>	I*	SR	S	N	External sperm exchange	[56-59]
	<i>Limacus</i>		FF	SR	S	N		[60]
Milacidae	<i>Tandonia</i> (<i>Milax</i>)		FF	SR	S	N		[56]
Urocyclidae	<i>Trichotoxon</i>	<i>heynemanni</i>	FF	SR	S	Y		Bernard Verdcourt, pers. comm. + photo
	<i>Gymnariion</i>	<i>coronatus</i>	FF	SR	L	N	[61, pre mating photo on p344]. No dart according to Pilsbry, Bull. Am. Mus. Nat. Hist. 40:275. 1919. The so-called dart sac was always empty and is probably just an amatorial organ.	[62]
	<i>Sheldonia</i>	<i>cornea</i>	FF	SR	L	N	Herbert & Kilburn, 2004, imply that there is no dart, just a pointed sarcobellum	[63]
	<i>Elisolimax</i>	<i>flavescens</i>	FF	SR	S	N	'The specimens lie side by side ... and the bodies are twisted inwards to bring the genital openings closer together. At the same time, their mouths are brought to face each other and they appear to kiss (or bite) one another During copulation, the middle to anterior portion of the foot may be raised off the substratum, and the slugs remain hanging only by the hind part of the foot. Copulation is mutual, the penis of each individual penetrating the ...partner' No dart according to Van Goethem, Ann. Mus. Roy. Afr. Cent. Belg. 218. 1977	[63, p291-292]
Vitrinidae	<i>Semilimax</i>		FF	SR	S	Y		[64]
	<i>Vitrinobrachium</i>		FF	SR	S	N		[64]
Valloniidae	<i>Vallonia</i>	<i>excentrica</i>	FF	SR?	L	N		[60]
Zonitidae	<i>Mesomphix</i>		FF	SR	L	N		[65, 66]
	<i>Ventridens</i>		FF	SR	L	Y		[67]
Trochomorphidae	<i>Bertia</i>	<i>brookei</i>	FF	SR?	L	N		Menno Schilthuisen, pers. obs.
Other								
Philomycidae	<i>Philomycus</i>	<i>carolinianus</i>	FF	SR	S	Y		[68]
Achatinidae	<i>Achatina</i>	<i>fulica</i>	SM	SR	H	N	Protandrous – so sperm transfer must sometime be unilateral	[69]

stylommatophora							
	<i>Tropidophora</i>	<i>ligata</i>				N	[63, p94]
	<i>Physa</i>	<i>gyrina</i>		U	H	N	[95, 96]
	<i>Lymnaea</i>	<i>peregra stagnalis</i>		U	H	N	[97-99]
	<i>Stagnicola</i>	<i>elodes</i>		U	H	N	[100]
	<i>Bulinus</i>	<i>globosus</i>		U	H	N	[101]
	<i>Ellobium</i>	<i>chinense</i>		U	H	N	[102]
	<i>Heliosoma</i>			U		N	Switching may occur Jenny Bronson, pers. comm. (Asilomar)
Veronicellidae	<i>Veronicella</i>	<i>tenax</i>		U	S	N	'Dos individuos se ponen arqueados, uno sobre el lado izquierdo, dejando en alto el lado derecho donde esta el orificio genital femenino, y el otro, en un plano perpendicular y por encima, con la extremidad anterior hacia la convexidad del individuo inferior. Dispuestos en esta forma, el individuo que ocupa el plano superior, vierte el pene, sumamente distensible, en el orificio genital femenino del que ocupa el plano inferior, quedando largo rato en esta posicion.'

The citation is Davison, A, Wade, CM, Mordan, PB and Chiba, S (2005). Sex and darts in slugs and snails (Mollusca: Gastropoda: Stylommatophora). Journal of Zoology (London), 267: 329-338., and also Asami et al. (1998). On a similar vein, readers might like to read Koene and Schulenburg [103] and Schilthuizen [104].

I have attempted to bring together all of the information that is out there on stylommatophoran mating behaviour. Thanks to those pioneering people that thought to investigate snail mating behaviour, then publish their observations, as well as my collaborators, Chris Wade, Peter Mordan and Satoshi Chiba.

This table is not yet complete (especially the references section). If you have any further information, or can point me to any publications on snail mating behaviour that I have missed (or images – even better), then I would be delighted to hear from you (angus.davison@nott.ac.uk). For some of the species, there have been multiple observations on their mating behaviour (e.g. *Cepaea*), and it is not possible to list them all.

Incidentally, if you are looking for *Helix aspersa* but can't see it, that's because it is now called *Cantareus aspersus*.

* indicates external sperm exchange, by which sperm is deposited on the mate's everted penis without intromission [see 33]

See [33] for links to details of mating in other Polygyrids (mostly by Webb).

Key: 1. SM, shell-mounting; FF, face-to-face.; I, idiosyncratic 2. U, unilateral (includes sequential unilateral mating); SR, simultaneous reciprocal. 3. L, low-spined; H, high-spined; S, slug or semi-slug. 4. Dart or dart-sac. For further details see Davison et al. or Asami et al. 1998.

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